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DISTRIBUTION PATTERNS OF FIVE BROMELIACEAE GENERA IN ATLANTIC RAINFOREST, RIO DE JANEIRO STATE, BRAZIL

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ABSTRACT. The epiphytic flora of Brazilian tropical rainforest is poorly known. The aims of this study are to list the bromeliad genera that occur in high altitude rainforest in the Macaé de Cima region and to study their distribution on phorophytes. The frequency of bromeliads on phorophytes within 20 sample plots was determined using the observation from distance method recording: 1) clumps, 2) height above ground, and 3) location. Bromeliad genera height, percent of epiphytism/diameter at breast height (DBH), size, class and percent of epiphytism of all individuals were determined. Univariate and multivariate analyses were used to determine significance, correlations and epiphytic-vegetational gradient on host trees. A total of 122 phorophytes representing 20 families and 46 species supported epiphytes. Five genera of Bromeliaceae were found: *Vriesea, Nidularium, Billbergia, Tillandsia* and *Quesnelia.* Concerning vertical distribution, two levels were found. The establishment of bromeliads apparently depended on phorophyte species. DBH was not correlated with bromeliad frequency, and multivariate analysis showed three-way attachment of bromeliads on the phorophytes. The genera could be classified as selective, preferential, indifferent and accidental.

Vascular epiphytes are abundant in many wet forests of the tropical regions. According to Gentry and Dodson (1987), peak diversity is reached at lower elevations in the northern Andes and Central America. However, due to the lack of knowledge concerning epiphytes in the rainforests of Brazil, this statement may be questioned. Brazil has large areas covered by tropical rainforests which are the preferred habitat of vascular epiphytes (Richards 1952). Hertel (1940) was the first researcher in Brazil to examine the physical, chemical, and biological characteristics of their substrate. Coutinho (1963, 1965, 1969) studied CO_2 fixation and Waechter (1980) studied the phytosociology of Orchidaceae in a rainforest in the state of Rio Grande do Sul. Most of the information on the occurrence of epiphytes is contained in floristic studies of rainforest remnants (Araujo & Oliveira 1988; Barros et al. 1988, 1990; Gavilanes et al. 1990; Leme 1983, 1986; Pereira *et al.* 1990). The substrate of each species is usually not mentioned.

Bromeliads have developed mechanisms which enable them to become independent of the soil and to tolerate a discontinuous supply of nutrients (Benzing & Renfrow 1974). Studies on attachment preferences of epiphytes in Brazil are few, and are concentrated in southern Brazil where Veloso (1952, 1953), Veloso and Klein (1957) and Aragão (1967) studied the biogeography of bromeliads and the relationship of these plants to malaria epidemics. Smith and Downs (1974) briefly discussed the stratification of these species on one individual tree.

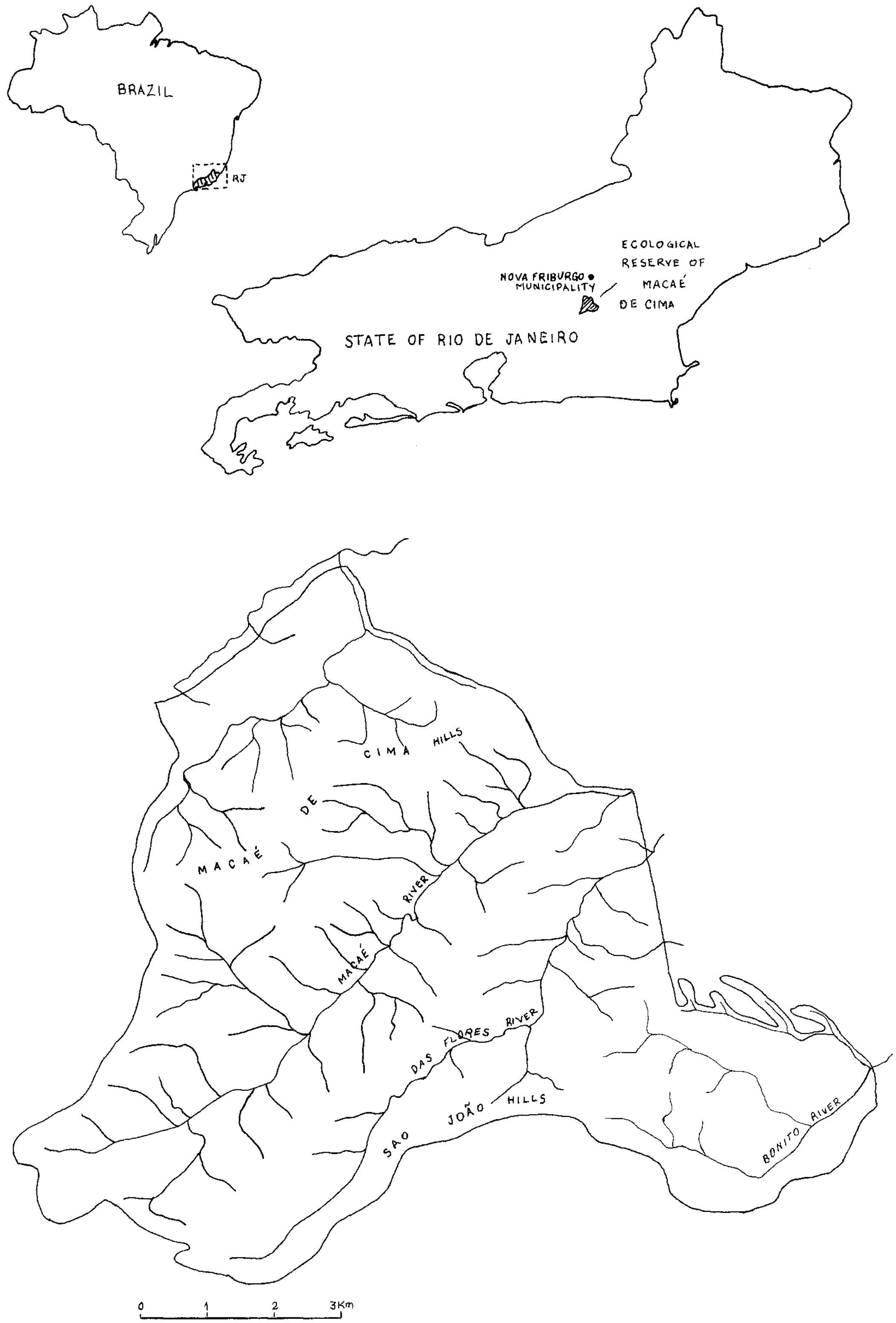
The present study was carried out in the Rio de Janeiro Botanical Garden's Atlantic Rainforest Research Program in the Macaé de Cima region, Nova Friburgo Municipality, State of Rio de Janeiro, Brazil. The aims of this study were to list the bromeliad genera which occur in a high-altitude rainforest sample plot (sensu Hueck 1972), and to study their distribution patterns on phorophytes.

METHODS

The study area was located in Nova Friburgo Municipality, in an area known as Macaé de Cima (22° 27′ 30″S 42° 32′W), near the headwaters of the Macaé de Cima and Flores River, Brazil. The altitudinal average was 1100 m (FIGURE 1). Twenty plots (10 × 10m) were sampled (total of 0.2 ha) along a gradient stretching from the banks of a small stream up the slope for a distance of 100 m. Trees with a diameter at breast height (DBH) ≥ 2.5 cm were sampled and complete results were presented in the Atlantic Rainforest Program Final Report (G. Martinelli 1990). All fertile specimens collected were deposited in the Rio de Janeiro Botanical Garden herbarium (RB).

Frequency of bromeliads on all phorophytes within the sample plots was determined using the "distance method" (Johansson 1974); only adult bromeliads were recorded. Because just a few bromeliads were flowering during the field survey, they were identified at the genus level. The following data were recorded:
a) Class: single plant (1), clump of 2–5 plants (2), clump of 6 or more plants (3); b) height on host; c) location: stem, main branch, and terminal branch.

Due to the difficulty of observing epiphytes on


BRAZIL
RJ
ECOLOGICAL RESERVE OF MACAÉ DE CIMA
NOVA FRIBURGO MUNICIPALITY
STATE OF RIO DE JANEIRO
CIMA HILLS
MACAÉ DE
MACAÉ RIVER
DAS FLORES RIVER
SÃO JOÃO HILLS
BONITO RIVER
0 1 2 3Km

hemi-epiphytes (lianas), these phorophytes were not used in the statistical treatment of the data.

Associations of bromeliad genera, stratification, percent epiphytism per DBH size class and percent epiphytism per family were determined.

By theoretical definition the Chi-Square test (χ^2) can be used only: a) when the sample size is larger than 20; b) if the sample size is larger than 10 but smaller than 40, all the expected frequencies have to be greater than 5; c) if all the expected frequencies assume a >1 value (Vieira 1981). Since not all trees had the same number of epiphytes, χ^2 was used at the family level, assuming that all host families could be an anchorage place with equal probabilities to epiphytism. This test was used for significance between number of hosts and non-hosts using the families of host trees. None of the data required transformation.

Simple linear regression was used to verify the correlation between bromeliad frequency and DBH size for all host trees. Bromeliad frequency was also correlated separately by DBH within families which had number of hosts $\geq$ 6 individuals.

Principal components analysis (an ordination technique) "attempts to place each stand in relation to one or more axes in such a way that a statement of its position relative to the axes conveys the maximum information about its composition" (Greig-Smith 1983). Cluster analysis (a classification procedure) "involves arranging stands into classes the members of other classes" (Greig-Smith 1983). These two techniques were based on bromeliad genera by host species data matrix, with an entry in the matrix representing the frequency of each bromeliad genus on each host species. A correlation matrix was obtained from the data matrix, by calculating the Pearson product-moment correlation coefficient (Sneath & Sokal 1973) between each pair of characters. Dendrograms were obtained with the unweighted pair group method using arithmetic averages (UPGMA; Sneath & Sokal 1973).

The association indices of Dice and Jaccard (Ludwig & Reynolds 1988) were used to measure the intergeneric associations. These indices measure how often the genera co-occurred on trees.

RESULTS

The sample area contained 686 individuals in 17 families and 106 species. The most important phytosociological parameters (Mueller-Dumbois & Ellemberg 1974) are described as follows: maximum diameter was 84.2 and total volume of wood was 189.5 cm^3. *Alchornea triplinervia* (Spreng.) M. Arg. had the highest importance value index (31.92) and *Leandra breviflora* Cogn., had the largest number of individuals (71). The Myrtaceae with 117 individuals presented the highest family importance value index (36.4). The next highest belonged to Euphorbiaceae with 19 individuals.

The liane species *Pfaffia pulverulenta* (Amaranthaceae), *Tournefortia breviflora* (Boraginaceae), *Fuchsia regia* (Onagraceae), *Serjania psicatoria* (Sapindaceae) and one species of Vitaceae (*Cissus* sp1) were hosts of bromeliads. A total of 122 individuals (17% of sampled trees) in 20 families and 45 species supported epiphytes (TABLE 1). Frequency distribution of the phorophytes within plant families is in FIGURE 2. Myrtaceae, Rubiaceae, Melastomataceae and Monimiaceae represented the highest percentages of phorophytes supporting epiphytes (5.1%, 2.3%, 1.7% respectively); Leguminosae, Chloranthaceae, Solanaceae and Vochysiaceae were the lowest (all 0.1%). Only 29.9% of individuals of the Myrtaceae, 17.8% of the Rubiaceae, 11.8% of the Melastomataceae and 25.5% of the Monimiaceae supported epiphytes (TABLE 2). Most of the phorophytes were represented within the diameter class > 15 cm (FIGURE 3); there were only a small number of phorophytes within the DBH <5cm class.

The χ^2 test on fourteen families (TABLE 3) resulted in a statistically significant result (χ^2=45.4; $p<0.01$). The populations with and without bromeliads are different depending upon the tree family and probably the distribution of bromeliads is not random on trees.

Five genera of Bromeliaceae were found in the study area: *Vriesea, Tillandsia, Billbergia, Nidularium,* and *Quesnelia.* The maximum number of genera found on any phorophyte was four, represented by the *Vriesea-Tillandsia-Nidularium-Quesnelia* group (group VTNQ) on *Coussapoa microcarpa* (Schott.) Rizz., and the group *Vriesea-Tillandsia-Billbergia-Nidularium* (VTBN) on *Alchornea triplinervia* (FIGURE 4). Clumps of *Vriesea* and *Vriesea-Nidularium* were found on 33 of the 45 tree species with epiphytes. Groups of individuals of *Nidularium* plus other combinations of bromeliad genera were present on only a small portion of the phorophytes.

Bromeliad frequency decreased on phorophytes in the following order: *Vriesea, Nidular-*

←

FIGURE 1. Map of study area. The sample plot is located in the Biological Reserve of Macaé de Cima between the headwaters of Macaé and Flores rivers.

TABLE 1. General distribution among phorophytes of five selected bromeliad genera. (') = Phorophytes with liane species: (*) = no recorded data. (Class = class of bromeliads; Loc = location on phorophyte: S = stem, M = main ramification, T = terminal ramification, Miss = missing values.)

		Vriesea								
		Class			Height			Loc		
Families/species	No. phor.	1	2	3	Min	Med	Max	S	M	T
Icacinaceae										
Citronella panicullatta	2	4			6	8.5	10			
'Boraginaceae										
Cordia ecalyculata	2	5			3	5.3	8	5		
Celastraceae										
Maytenus communis	2		3		4	5.3	6			3
Chloranthaceae										
Hedyosmum brasiliense	1	1			3	3	3	1		
Dichapetalaceae										
Stephanopodium organense	1	1			2.5	2.5	2.5		Miss.	
Flacourtiaceae										
Casearia decandra	2		2		6	8	10	1		1
Euphorbiaceae										
Alchornea triplinervia	9	17	26	2	2.5	7.6	13	15	14	16
Lauraceae										
Beilschmiedia rigida	1	1	2		8	10.7	14	1	1	1
Lauraceae sp. 2	1		2		10	10	10	1		1
Cinnamomum estrellense	1		1		4	4	4	1		
Ocotea divaricata	1	4	1		2	4.5	7		2	3
O. elegans	1	1			1.6	1.6	1.6		1	
Persea pyrifolia	1	1	1		7	7.5	8	2		
Nectandra aff. *leucantha*	1	1	1		6	7	8		1	1
Leguminosae										
Inga sessilis	1	2	1		1.6	7.5	11	1	2	
Melastomataceae										
Leandra breviflora	6	4			2	3.9	6	1	3	
Meriania robusta	4	5			1.6	2.6	6	2	2	1
Tibouchina fissinervia	1	5	3		6	8.9	14	1	2	5
T. arborea	1		1		8	8	8	1		
Meliaceae										
Cabralea canjerana	4	7	5		2.5	7	11	1	3	8
Monimiaceae										
Mollinedia gilgiana	8	7	9		2	4.8	9	2	7	
M. salicifolia	2	2	4		5	8.3	12	3		7
M. micrantha	2									3
Moraceae										
Coussapoa microcarpa	1	3	3		5	8.8	11		3	3
Sorocea bomplandii	2	2	2		2.5	4.1	7		1	3
Myrtaceae										
Calyptranthes aff. *lucida*	2	1	1		5	5	5		1	
Eugenia cuprea	5	5	3		5	6.7	10		7	1
E. martinellii	3	4	6		2.5	5.6	8		8	3
E. subavenia	1	2			5	5.2	5.5	2		
Gomidesia aff. *lindeniana*	1	1			2	2	2			1
G. warmingiana	1	2			6	8	10			2
Marlierea suaveolens	5	7			1.8	4.9	7.5	5	2	
Myrcia plusiantha	5	5	4		1.8	5.6	9	4	2	

TABLE 1. Extended.

Tillandsia									Billbergia					
Class			Height			Loc			Class			Height		
1	2	3	Min	Med	Max	S	M	T	1	2	3	Min	Med	Max
										2		1.8	2.1	2.5
2			6.5	7	7.5	2					2	2	2.2	5
1			11	11	11			1						
										1		1.6	1.6	1.6

TABLE 1. Extended.

	Billbergia			Nidularium					
	Loc			Class			Height		
	S	M	T	1	2	3	Min	Med	Max
Icacinaceae									
Citronella panicullatta					1		2	2	2
'Boraginaceae									
Cordia ecalyculata	2			2	3	1	0.5	1.9	2
Celastraceae									
Maytenus communis				2	2		1.7	1.9	2
Chloranthaceae									
Hedyosmum brasiliense					2		0.5	1.2	2
Dichapetalaceae									
Stephanopodium organense									
Flacourtiaceae									
Casearia decandra					1		2	2	2
Euphorbiaceae									
Alchornea triplinervia	1	1		5	7		0.5	3	8
Lauraceae									
Beilschmiedia rigida					2		0.5	4.7	9
Lauraceae sp. 2				1			2	2	2
Cinnamomum estrellense									
Ocotea divaricata				1			1.5	1.5	1.5
O. elegans				2			0.5	1	1.6
Persea pyrifolia					1		1.6	1.6	1.6
Neotandra aff. *leucantha*									
Leguminosae									
Inga sessilis									
Melastomataceae									
Leandra breviflora				2	3		0.5	1.4	3
Meriania robusta				4	1		1.5	3	5.5
Tibouchina fissinervia				1			2	2	2
T. arborea									
Meliaceae									
Cabralea canjerana				2	3		1.6	3	6.5
Monimiaceae									
Mollinedia gilgiana				2	8		1	2.6	5
M. salicifolia				2			2	2.1	2.3
M. micrantha				4	3		0.5	1.8	3
Moraceae									
Coussapoa microcarpa				3			2	2.7	3
Sorocea bomplandii					1		2	2	2
Myrtaceae									
Calyptranthes aff. *lucida*					1		1.8	1.8	1.8
Eugenia cuprea				5	1		0.5	1.9	3
E. martinellii				5	5		0.5	2	2.5
E. subavenia									
Gomidesia aff. *lindeniana*					1	1	0.5	0.6	0.7
G. warmingiana				1			2.5	2.5	2.5
Marlierea suaveolens				2	1		1.8	3.1	5
Myrcia plusiantha				6	1		2	5.1	6.8
M. pubipetala				5	4		2.5	4.8	7
Psidium sp.					1		1.5	1.5	1.5
Siphoneugena kiaerskoviana					1		2	2	2

TABLE 1. Extended.

Nidularium				Quesnelia								
Loc			No. phor.	Class			Height			Loc		
S	M	T		1	2	3	Min	Med	Max	S	M	T
	1		2	1			5.5	5.5	5.5	1		
6			2									
	4		2									
2			1									
			1									
1			2									
7	4	1	9									
1	1		1									
1			1									
			1									
	1		1									
1			1									
1			1		1		7	7	7			
			1							1		
			1									
			4		6							
			2		4							
		1			1							
1	3				1							
5			4									
5	5		8		1		3	3	3	1		
2			2									
	7		2									
3	1		1		2		3.5	4.2	5	1	1	
	1		2									
1			2									
4	2		5									
5	5		3		1		4	4	4	1		
			1									
2			1									
	1		1									
3			5									
7			6			2	4	4.5	5	1		
6	3		7									
1			3									
1			1									

TABLE 1. Continued.

		Vriesea								
		Class			Height			Loc		
Families/species	No. phor.	1	2	3	Min	Med	Max	S	M	T
M. pubipetala	8	14	7		2.5	8.1	16	10	2	9
Psidium sp. 1	3	7	2		3	6.1	10	1	6	
Siphoneugena kiaerskoviana	1	2	2		3	5.7	7	1	1	2
Palmae										
Euterpe edulis	5	4	2		3	5.1	8	6		
Rubiaceae										
Bathysa meridionalis	9	8	5	1	1.6	6.7	13	6	4	4
Psychotria suterella	5	3			2	2.5	3	2	1	
Psychotria velloziana	2	2	1		6	7.3	9	2	1	
'Sapindaceae										
Allophylus edulis	1	1			2.5	2.5	2.5	1		
Cupania oblongifolia	4	3	7	2	5	9.5	14	8	3	1
C. zanthoxyloides	1		2		4.5	4.7	5	2		
Solanaceae										
Solanum argenteum	1		2		2	3	4	1		1
Vochysiaceae										
Vochysia saldanhana	1	1			8	8	8	1		

ium, *Quesnelia, Billbergia* and *Tillandsia. Vriesea* was clearly the predominant genus on the majority of hosts; it was present on 42 of 45 phorophytes. In general, frequency classes of this genus were also higher on all phorophytes: class 1 = 146 individuals; class 2 = 116; class 3 = 9. For *Nidularium,* 70, 63 and 4 clumps belonged to classes 1, 2 and 3 respectively, distributed mainly on the lower part of the trunk in strongly shaded conditions.

Vertical distribution of the bromeliads on the phorophytes is given in FIGURE 5. Most individuals of *Nidularium, Billbergia* and *Quesnelia* are found below an average of 4.5 m. The tillandsioid genera occupied a second "band" around 5–10 m.

Simple linear regression among all diameter at breast height and bromeliad frequencies indicated that DBH was not generally correlated with bromeliad frequency ($r = 0.0001$; $Y = 0.0093X + 17.5568$). When this parameter is broken down

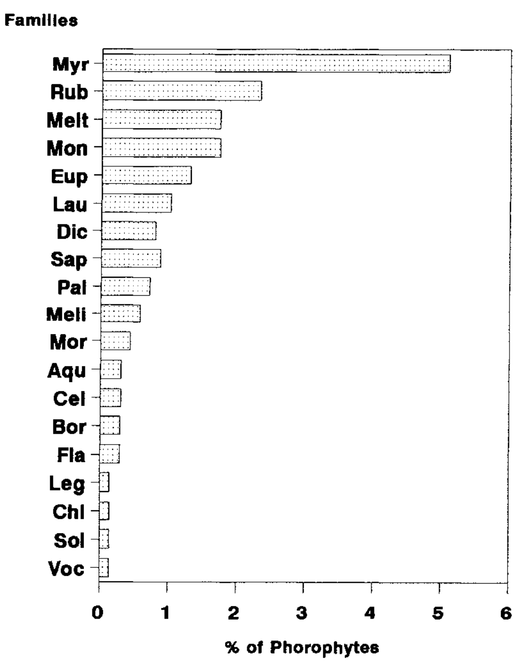


FIGURE 2. Frequency distribution of phorophytes among plant families. Plant families are represented by symbols using the first three letters of each name, except for the following: Melastomataceae (MELT) and Meliaceae (MELI). The other families are represented as follows: Aquifoliaceae (AQU), Boraginaceae (BOR), ←

Celastraceae (CEL), Chloranthaceae (CHL), Dichapetalaceae (DIC), Flacourtiaceae (FLA), Euphorbiaceae (EUP), Icacinaceae (ICA), Lauraceae (LAU), Leguminosae (LEG), Monimiaceae (MON), Moraceae (MOR), Myrtaceae (MYR), Palmae (PAL), Rubiaceae (RUB), Sapindaceae (SAP), Solanaceae (SOL), Vochysiaceae (VOC).

TABLE 1. Extended. Continued.

Tillandsia									Billbergia					
Class			Height			Loc			Class			Height		
1	2	3	Min	Med	Max	S	M	T	1	2	3	Min	Med	Max
										2		1.8	2.1	2.5
2			6.5	7	7.5	2					2	2	2.2	5
1			11	11	11			1						
										1		1.6	1.6	1.6

by family, Sapindaceae (r = 0.8448; Y = 0.4417X − 0.3807) and Euphorbiaceae (r = 0.9375; Y = 04829X − 6.4378) are the only families whose DBH was correlated with bromeliad frequency.

The results of Principal Components Analysis (FIGURE 6) showed that the 11 species with lower loadings on the first Principal Component (PC I) are those which have only one individual of *Vriesea* attached to them. All phorophytes which tended to support higher numbers of individuals of this genus presented higher loadings on the PC I. *Alchornea triplinervia* contained the highest numbers of *Vriesea* and was the only tree species with *Billbergia* attached to it. For higher values of PC II, we can see the hosts with non-*Tillandsia-Billbergia* epiphytic clusters.

The results of Cluster Analysis were analyzed at the similarity level of 0.9 (FIGURE 7). At this level, eight phorophyte species at the lower part of the dendrogram showed higher numbers of *Nidularium*; the species positioned in the middle part of the dendrogram showed more *Vriesea*; and finally, the 16 phorophytes in the upper part of the dendrogram hosted almost exclusively *Vriesea*.

Association among bromeliad genera as shown by the Dice and Jaccard indices were higher between *Vriesea-Nidularium*, decreasing between *Tillandsia-Billbergia* and *Nidularium-Quesnelia* (TABLE 4). It remains unclear why these genera

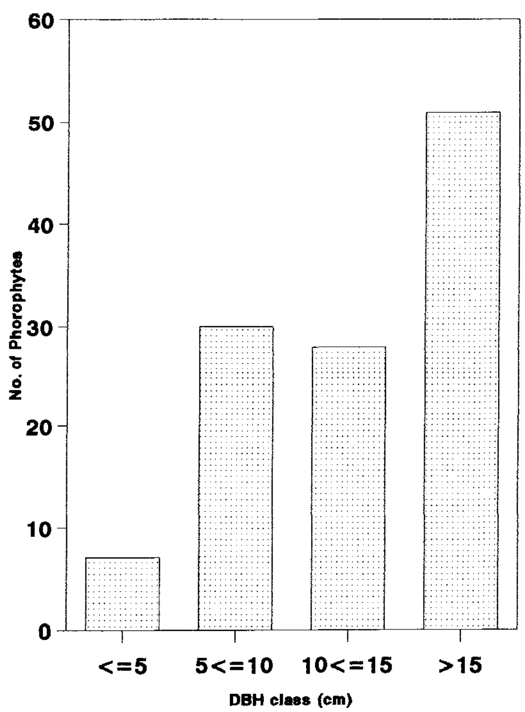


FIGURE 3. Distribution of epiphytes among DBH classes.

TABLE 1. Extended. Continued.

	Billbergia			Nidularium					
	Loc			Class			Height		
	S	M	T	1	2	3	Min	Med	Max
Palmae									
Euterpe edulis				4	1		1.5	1.6	2.5
Rubiaceae									
Bathysa meridionalis				6	3		0.5	2.8	6
Psychotria suterella				1	4		1.8	2.2	2.7
Psychotria velloziana									
'Sapindaceae									
Allophylus edulis									
Cupania oblongifolia				2	1	1	0.5	2.9	5
C. zanthoxyloides									
Solanaceae									
Solanum argenteum									
Vochysiaceae									
Vochysia saldanhana									

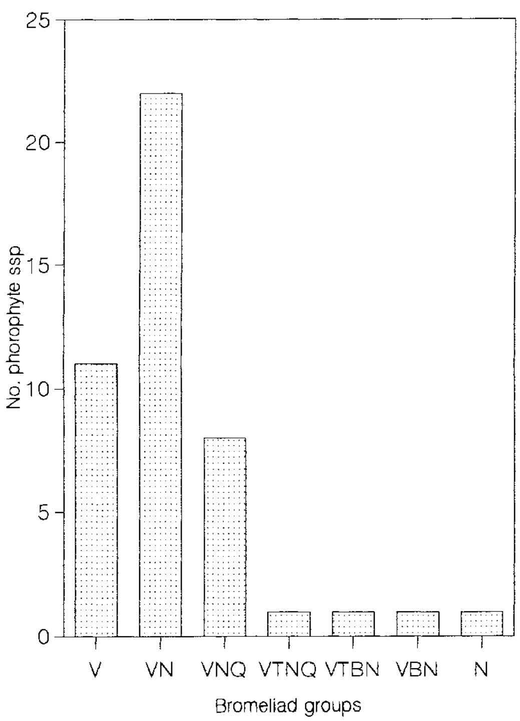


FIGURE 4. Bromeliad groupings. Group V = *Vriesea;* VN = *Vriesea-Nidularium*; VNQ = *Vriesea-Nidularium-Quesnelia*; VTNQ= *Vriesea-Tillandsia-Billbergia-Nidularium*; VBN = *Vriesea-Billbergia-Nidularium*; N = *Nidularium.*

presented these results (the first association value was very high) but it is hypothesized that these plants require almost the same conditions for establishment.

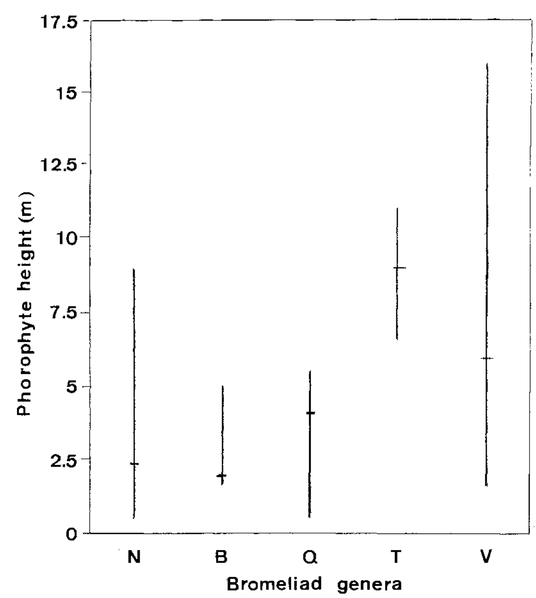


FIGURE 5. Vertical distribution of epiphytes in host trees. Horizontal lines represent mean height. Bromeliad heights (minimum, medium, maximum) were extracted from Table 1.

TABLE 1. Extended. Continued.

Nidularium				Quesnelia								
Loc			No.	Class			Height			Loc		
S	M	T	phor.	1	2	3	Min	Med	Max	S	M	T
5			5									
6	3		9									
1	2	2	5									
			2									
			1									
3	1		4		1		0.5	0.5	0.5	1		
			1									
			1									
			1									

DISCUSSION

Sudgen & Robbins (1979) suggest that the density of epiphytes is often underestimated because it is difficult to examine each clump on phorophytes. The difficulty of identifying epiphytes in the higher tree limbs was reduced in this study, since in most cases it was possible to identify bromeliads to the genus level. Other genera which might be confused with the ones cited here (e.g. *Aechmea*) are not found in the sample area.

The use of methodological sampling in plots helped to quantify epiphyte distribution and will enable future comparisons to other study areas using the same method. It also allows precise

TABLE 2. Distribution of phorophytes in relation to the total number of trees sampled in each family.

Families	Number of hosts	Total individuals	%
Vochysiaceae	1	1	100
Celastraceae	2	3	66.6
Aquifoliaceae	2	4	50
Dichapetalaceae	1	2	50
Moraceae	3	6	50
Flacourtiaceae	2	4	50
Euphorbiaceae	9	19	47.4
Meliaceae	4	13	30.8
Myrtaceae	35	117	29.9
Monimiaceae	12	47	25.5
Lauraceae	7	29	24.1
Sapindaceae	6	29	20.7
Boraginaceae	2	10	20
Rubiaceae	16	90	17.8
Chloranthaceae	1	6	16.6
Melastomataceae	12	102	11.8
Leguminosae	1	9	11.1
Solanaceae	1	13	7.7
Palmae	5	109	4.6

TABLE 3. Chi-square test results of occurrence of epiphytes on host families. The families with expected frequencies lower than "1" were eliminated.

Families	Obs. freq.	Exp. freq.
Boraginaceae	2	1.903
Cloranthaceae	1	1.141
Euphorbiaceae	9	3.616
Lauraceae	7	5.519
Leguminosae	1	1.712
Melastomataceae	12	19.412
Meliaceae	4	2.474
Monimiaceae	12	8.944
Moraceae	3	1.141
Myrtaceae	35	22.267
Palmae	5	20.744
Rubiaceae	16	17.128
Sapindaceae	6	5.519
Solanaceae	1	2.474

```
X: min=    0.24394 max=    25.98064 mean=    3.0362 var=  18.1102
Y: min=   -0.02991 max=     6.05359 mean=    0.9723 var=   1.5282
```

```
Line
01  PC II
02     |
03     |
04  7.1-
05     |
06     |
07     |        Mypl <7,8,12,0,0>
08     |        *
09     |
10     |
11     |
12     |
13     |
14     |
15     |
16  4.7-
17     |
18     |
19     |                    Mogi
20     |                    *
21     |       Coec   Euma
22     |       *      *
23     |
24     |
25     |                   Cuob
26     |                   *
27  2.3-       Comi   Bame Mypu<28,12,0,0,0>
28     |       *         * *
29     | Momi*   Caca*
30     |      *Pssu                                         Altr
31     |Goli* 2                                               *
32     |   *Pepy <3,2,2,0,0>                         <79,19,0,2,12>
33     |      **  *
34     |   ****
35     |
36     |  ***2 2
37-----|- 2 * *---------|---------------|---------------|----------|
38     | 344           8.0            16.0            24.0     32.0
   -0.1-                                                        PC I
       |
       |
       |
       |
       |
     -2.5-
```

quantification of the phorophytes which contain the epiphytes, without which the basic structure of the vegetation could not be described.

The results suggest that bromeliad distribution is influenced by factors other than total number of host individuals. The Rubiaceae, with 90 individuals, has the second largest number of phorophytes. The Melastomataceae and Monimiaceae have the same percentage of phorophytes, yet the total number of individuals in each family differs considerably (Melastomataceae = 102; Monimiaceae = 47). These results plus those of hosted individuals per family corroborate the Chi-Square results which show that bromeliad establishment depends at least in part on phorophyte species. It is obvious that *Euterpe edulis* does not present adequate conditions for bromeliad colonization (only 5 in 109 individuals were hosts). However, the presence of even a few bromeliads on this species corroborates the work by Waechter (1980), who reports that the occurrence of epiphytes on phorophytes with smooth trunks shows that good environmental conditions are present.

Bromeliad genera may be classified by preference according to Waechter (1980): *Billbergia* is "selective;" it occurs almost exclusively on *Alchornea triplinervia*; *Quesnelia* is "preferential" on *Myrcia plusiantha*; *Vriesea* and *Nidularium* are "indifferent" and occur on almost all the phorophytes; *Tillandsia* is "accidental," with rare occurrence in the sample area and low frequencies on the host plants. The distribution pattern of this genus is easily discernible since it occurred almost exclusively on the subplots nearest the river (showing a possible humidity dependence) or occupying only the upper part of the trunk and terminal branches of the host, showing need for most light. Bromelioideae genera are more selective than those in Tillandsioideae. It could be hypothesized that better developed root systems of Bromelioideae genera and the almost non-rooting in Tillandsioideae may determine their specificity on host trees, but I think this is not the most important reason. Instead, the seed dispersal of Bromelioideae by animals may also play an important role.

TABLE 4. Association indices among bromeliad genera. Right upper shows Dice index; lower left Jaccard index: (V) = *Vriesea*; (N) = *Nidularium*; (Q) = *Quesnelia*; (T) = *Tillandsia*; (B) = *Billbergia*.

	V	N	Q	T	B
V	0	0.846	0.34	0.087	0.087
N	0.733	0	0.419	0.111	0.111
Q	0.205	0.265	0	0.182	0.000
T	0.045	0.059	0.100	0	0.5
B	0.045	0.059	0.000	0.333	0

The low correlation between total DBH and number of epiphytes is very similar to the results of Bennett (1986). However, in certain families of trees, the available surface area (represented by DBH) may be an important factor.

Both association indices showed the same trend: *Nidularium* and *Vriesea* have the highest association indices, i.e. these genera are strongly associated with the phorophytes which are more suitable. There is a gradual decrease in association in other genera pairs: *Tillandsia-Billbergia* and *Nidularium-Quesnelia.* More studies are necessary to reveal reasons for the high degree of association among *Nidularium* and *Vriesea.*

Multivariate analysis was useful to show how phorophytes are occupied by bromeliads. There were three patterns of distribution: a) those with more *Nidularium*; b) those with almost exclusively *Vriesea*; c) those with both, but more *Vriesea.* The advantage of these methods is that they do not give excessive weight to number differences and species diversity of phorophytes, which are often cited as being a problem in the qualification or establishment of patterns (Johansson 1974; Madison 1979). At the same time, the existing gradient as well as the pattern of epiphytism in the area is revealed.

←

FIGURE 6. Principal Components Analysis (PCA). Some bromeliad frequencies are signed in "=*="; the sequence followed is: *Vriesea, Nidularium, Quesnelia, Tillandsia, Billbergia.* Species names are represented by first two letters of generic and specific names and some could not be represented on graphic:

line 33: Maco, Eued, Eucu
line 34: Hebr, Cipa, Beri
line 36: Ocel, Calu, Cade (Sobo, Siki) (Mosa, Mysc)4
line 37: (Cies, Gowa), Ocdi, Tifi ⟨2,1,0,0,0⟩ <2,1,0,0,0><6,1,0,0,0><9,1,0,0,0>
line 38: (Stor, Vosa, Aled) Myrh, Nele, Soar, Tiar) (Lasp2, Cuza, Inse, Psve)

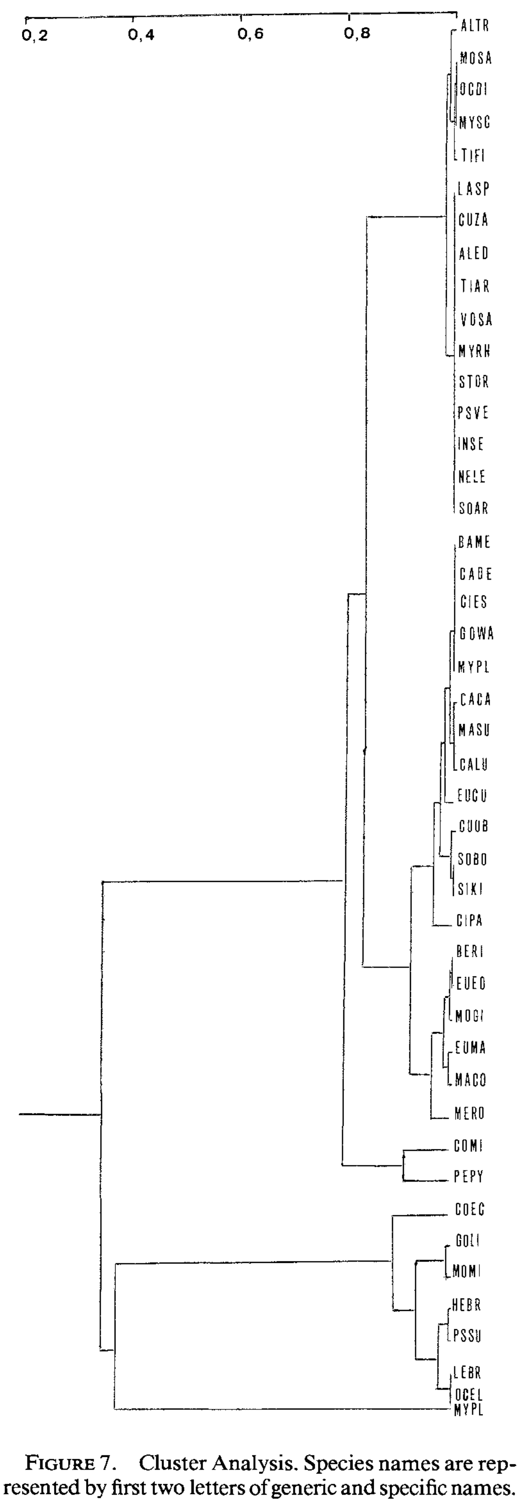


FIGURE 7. Cluster Analysis. Species names are represented by first two letters of generic and specific names. The main groups were assumed at 0.9 level.

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