The Determination of Plant Communities Along a Complex Environmental Gradient at Hilaan Beach, Guam[1]

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Abstract—A belt transect 5 m × 290 m was established at Hilaan Beach. The transect extended from the beach, through a fresh water cenote and terminated at the base of the cliff which rises to the plateau of northern Guam. All vascular plants within each 5 m^2 subplot were identified and measured. From these data a profile diagram was drawn and species importance values computed, graphed and analyzed by statistical clustering. Six distinct vegetational communities were distinguished and named according to computed dominance: *Scaevola/Messerschmidia, Cocos, Aglaia/Guamia, Pandanus dubius/* Marsh Ferns, and *Merrilliodendron.* Each community was described by species composition and physiognomy. Soil samples were mechanically and chemically analyzed. A correlation exists between the number of species present and exchangeable soil potassium, sodium and calcium.

Introduction

Long before the discovery of Guam by Magellan in 1521, the indigenous Chamorro people of Guam commonly used plants and their products for food, medicine, and material culture. Stone (1970) has reviewed the various botanical expeditions which studied the flora of Guam. Additional significant floristic studies on Guam have been made by Safford (1905), Merrill (1914, 1919), Wagner and Grether (1948), Walker and Rodin (1949) and Stone (1970). In 1960, Fosberg described the vegetation of Guam. Moore (1973) studied the composition of vegetation along a transect at Pagat Point in the northeastern, windward, part of the Island.

Fosberg (1959) states that most forests presently on Guam are of second growth. The original forest that occurred on limestone was of large trees with a thick canopy. A long history of disturbance has left very little original primary forest. These remanants are in scattered patches on the northern plateau, on cliffs and relatively inaccessible terraces around the steep coasts.

The primary purpose of this study is to determine and describe the several plant communities apparent along a complex environmental gradient at Hilaan Beach on the leeward, western, side of Guam, 1.2 km northeast of Naval Communications Station Beach (Figure 1). The environmental gradient is complex because of a substratum cline extending from beach deposits to pitted limestone, an exposure cline away from the seacoast and an especially unique moisture cline involving the

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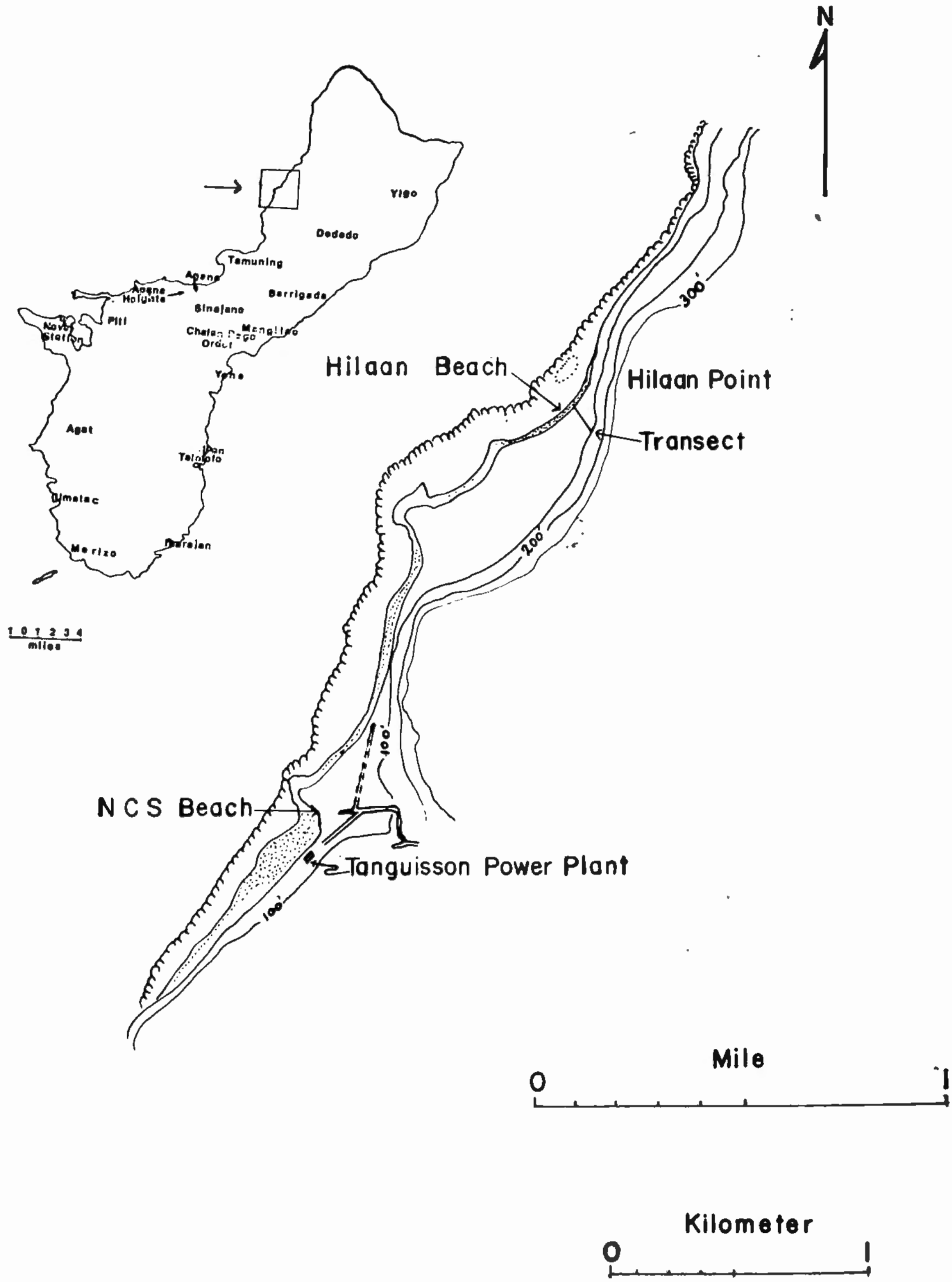

Fig. 1. Map of Guam with an enlarged detail indicating the location of the Hilaan Beach transect. The transect is approximately 1.2 km north of Naval Communications Station Beach. Detailed map is after USGS, 1968. A major reef-flat hole is indicated by a dotted oval.

presence of Guam's only true fresh water cenote. Associated plant communities affect considerable change over relatively short distances, are basically undisturbed, well developed, and include rare and localized species. In addition to its scientific value the entire area between NCS Beach and Hilaan Point is of great scenic beauty and it is hoped that this study may somehow contribute to its preservation.

Methods

FIELD METHODS

The belt transect is useful for the study of gradient changes in vegetation as in profile studies or the analysis of transition zones between communities (Braun-Blanquet, 1932; Oosting, 1956; Kuchler, 1967; Shimwell, 1972). Becking (1957) asserts that subjective selection of sample plots is a major advantage as compared with objective sampling, making it possible to select the most typical sites. These suggestions were utilized in this study.

A belt transect 5 m wide and 290 m long was established perpendicular to the shore at Hilaan Beach. The entire transect was consecutively divided into 5 m^2 subplots and numbers were assigned to each. The first subplot was adjacent to the level of mean high tide and the last was at the base of the cliff which rises to the plateau of northern Guam. There were 58 contiguous subplots. To include the greatest possible number and diversity of plant communities the transect was aligned to bisect a nearly circular, 34 m diameter, cenote. Subplots 41 through 49 are within this fresh water filled limestone sink-hole.

All vascular plants rooted within the transect were identified and measured one subplot at a time. Height was determined with the aid of an extendible 9.9 m measuring pole. Trunk diameters at breast height (DBH) were taken most often with a diameter tape. Crown diameter and the position of each plant was noted. These measurements plus additional notes and sketches were eventually used to draw a profile diagram which was repeatedly checked and modified in the field. Diameter at breast height and crown diameter were converted to area at breast height and area of crown. All measurements were then summed for species. Species data were then divided by subplot sums to obtain relative figures. For each subplot relative density, relative height, relative area at breast height, and relative crown area were computed for each species. These figures were summed for each species in each subplot to obtain species importance values. These composite values were used to reflect the distribution of species along the transect.

Species importance values were also used in a Fortran IV computer program to explore Sørensen's formula for the coefficient of community. Sørensen (1948) gives the similarily coefficient as $K=2C/(a+b)$. Where C is the number of species which two subplots have in common. The number of species in each of the two subplots is represented by a and b. This was used to find the similarity coefficient of all possible pairings within the 54 subplots with rooted vegetation. The resultant data were eventually used to compile a cluster diagram.

The relative humidity of the air near the cenote and at the beach was measured with a Bacharach sling psychrometer. This was performed at about noon during each visit. Air and water temperature at the cenote and at the seashore were determined with a Weston mercury-in-glass thermometer. Thermographs, Bacharach Case Model 14-7030 with a seven day movement, were occasionally used to record temperatures near the cenote and near the beach.

Visits to the study site for the purpose of collecting data commenced on May 24, 1975 and continued until March 27, 1976. About 41 days were spent in the field. Numerous herbarium specimens were collected and phenological observations recorded. Vouchers were deposited in the University of Guam Herbarium.

Plant identifications were achieved mainly by reference to The Flora of Guam (Stone, 1970). Additional aid was obtained by comparisons with herbarium specimens and with the help of local authorities.

SOIL LABORATORY METHODS

In each terrestrial subplot 5 soil samples were collected from a depth of 2 to 20 cm. These samples were pooled in the laboratory, air dried with the aid of an electric fan, and crushed with a wooden mallet. Portions passing through a 0.825 mm sieve were used in the determination of pH, salt concentration, and soil texture. Subsequent portions which passed through a 0.5 mm sieve were used to determine organic matter and the major cations. A Beckman pHASAR–I digital pH meter utilizing a 1: 1 ratio of soil to water was used to measure pH. Texture, particle size distribution, was performed by the hydrometer method of Bouyoucos (1951). Salt concentration was determined through electrical conductance expressed in micromhos per cm using a 1: 1 soil: water extract and a Beckman solu-bridge. Measurements of organic matter made use of the Walkley-Black method (Jackson, 1958).

The major cations sodium, potassium, calcium, and magnesium were extracted using a normal ammonium acetate pH 7$\pm$05 solution. A 1: 10 soil to ammonium acetate ratio was used. For calcium and magnesium determinations, a portion of the extracts were diluted to volume with a 1560 ppm lanthanum oxide solution to control interferences. Levels of the major cations were determined using a Perkin Elmer Model 305B atomic absorption spectrophotometer.

Results and Discussions

Figure 2 is an illustration of the profile of plants 1 m or taller occurring within the entire 5 m$\times$290 m transect. This type of figure was developed by Richards (1952). Such a diagram can be used as a laboratory tool in determining plant communities along a transect. It can further be used to explore the exact nature of community boundaries and the presence of ecotones. It is also helpful in examining community physiognomy, i. e., trunk and crown character, stratification and species arrangement. Many of these observations are difficult to conclude while in the field. One can only stand and inspect one small part of the forest at a time and it is

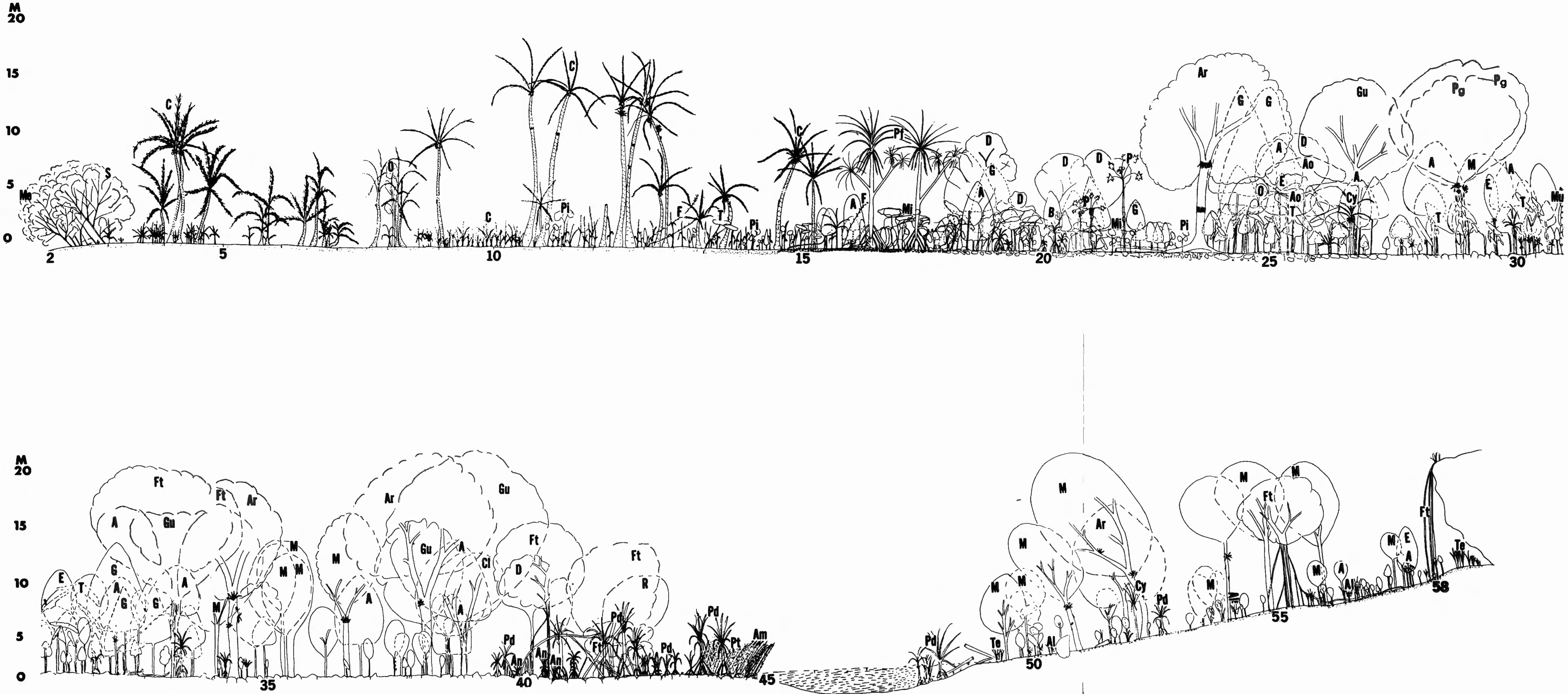

Fig. 2. Profile diagram of the 5 m × 290 m transect. Height scale and subplot numbers are indicated. The lower strip of the diagram is a continuation of the upper strip. Arrows and numbers indicate the several communities. All individual plants taller than 1 m are included. See Table 1 for key to species abbreviations.

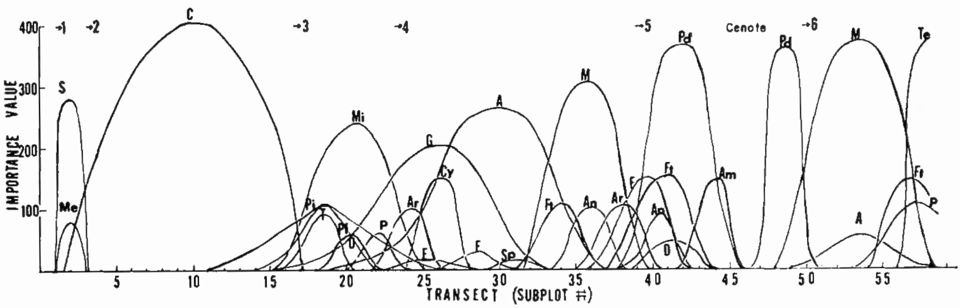

Fig. 3. Distribution of species along the transect. Importance values for species in each subplot are plotted for the entire transect and these points have been connected by smoothed lines. The several communities are indicated by arrows and numbers. Letters refer to species as indicated in Table 1.

Table 1. Relative importance percent (RIP), growth-form, Raunkier life-form, and origin of on-transect plant species greater than 1 m tall. Species abbreviations as used in Figures 2, 3, and 4

Plant species	Abbr.	R.I.P.	Growth-Form[1]	Life-Form[2]	Origin[3]
Cocos nucifera L.	C	23.90	Rt	P	Intro/not nat
Merrilliodendron megacarpum (Hemsley) Sleumer	M	14.20	Blet	P	Indig
Aglaia mariannensis Merrill	A	10.18	Blet	P	En
Pandanus dubius Sprengel	Pd	5.96	Rt	P	Indig
Mikania scandens (L.) Willd.	Mi	4.78	V	P	Intro/nat
Guamia mariannae (Safford) Merrill	G	4.16	Blet	P	En
Triphasia trifolia (Burm. f.) P. Wils.	T	3.90	Blets	P	Intro/nat
Flagellaria indica L.	F	3.21	V	P	Indig
Ficus prolixa G. Forster	Ft	3.16	Blest	P	Indig
Asplenium nidus L.	An	2.81	E/t	E	Indig
Piper guahamense DC.	Pi	2.46	Bles	P	Indig
Artocarpus mariannensis Trécul	Ar	2.28	Blet	P	Indig
Tectaria crenata Cavanilles	Te	2.08	F	H	Indig
Pteris tripartita Swartz	Pt	1.93	E/t	E	Indig
Cycas circinalis L.	Cy	1.54	Rt	P	Indig
Dendrocnide latifolia (Gaud.) W. L. Chew	D	1.37	Blet	P	Indig
Scaevola taccada (Gaertner) Roxburgh	S	1.36	Blet	P	Indig
Acrostichum aureum L.	Am	1.22	F	G	Indig
Guettarda speciosa L.	Gu	1.09	Blet	P	Indig
Pisonia grandis R. Brown	Pg	1.03	Blet	P	Indig
Carica papaya L.	P	0.95	Rt	P	Intro/nat
Pandanus fragrans Gaud.	Pf	0.90	Blet	P	Indig
Eugenia reinwardtiana DC.	E	0.79	Blet	P	Intro/nat
Claoxylon marianum Mueller-Argoviensis	Cl	0.76	Blet	P	En
Ochrosia oppositifolia (Lamarck) K. Schumann	O	0.57	Blet	P	Indig
Annona squamosa L.	Ao	0.51	Blet	P	Intro/not nat

Table 1. (continued)

Plant species	Abbr.	R.I.P.	Growth-Form[1]	Life-Form[2]	Origin[3]
Randia cochinchinensis (Lour.) Merrill	R	0.50	Blet	P	Indig
Messerschmida argentea (L. f.) Johnston	Me	0.41	Blet	P	Indig
Alocasia macrorrhiza (L.) Schott	Al	0.41	Fo	H	Intro/not nat
Thelypteris interrupta (Willd.) Iwatsuki	Th	0.24	E/t	E	Indig
Morinda citrifolia L.		0.21	Blet	P	Indig
Merremia tuberosa (L.) Reudle		0.17	V	P	Intro/not nat
Discocalyx megacarpa Merrill		0.13	Blet	P	En
Streblus pendulinus (Endlicher) F. Von Mueller	Sp	0.13	Blet	P	Indig
Melanolepis multiglandulosa (Reinwardt) Reichb. f. & zoll.		0.13	Blet	P	Indig
Procris pedunculata (J. R. & G. Forster) Weddel.		0.13	Fo	Ch	Indig
Planchonella obovata (R. Brown) Pierre		0.11	Blet	P	Indig
Clerodendrum inerme (L.) Gaertner		0.09	V	P	Indig
Momordica charantia L.		0.09	V	P	Intro/nat
Nephrolepis hirsutula (Forster) Presl	N	0.06	E	E	Indig
Bikkia tetrandra (Forst. f.) A. Rich	B	0.04	Blet	P	Indig
Pachyrrhizus erosus (L.) Urban		0.03	V	P	Intro/not nat
Mucuna gigantea (Willd.) DC	Mu	0.02	V	P	Indig

[1] Growth-Form
Bles—Broad leaved evergreen shrub
Blest—Broad leaved evergreen strangling tree
Blets—Broad leaved evergreen thorn shrub
Blet—Broad leaved evergreen tree
Rt—Rosette tree
E/t—Epiphyte/terrestrial V–Vine
F—Fern
Fo—Forb
Gr—Graminoid
To—Terrestrial orchid

[2] Life-Form
E—Epiphyte
Ch—Chamaeophyte
G—Geophyte
P—Phanerophyte

[3] Origin
En—Endemic
Intro/nat—Introduced and naturalized
Indig—Indigenous
Intro/not nat—Introduced and not naturalized

quite difficult, even for the experienced field botanist, to analyze a complex forest or transect without the aid of such a figure or model.

Figure 3 shows the distribution of species along the transect and is patterned after illustrations by Whittaker (1967). It was constructed by plotting the importance value (sum of relative density, relative area at breast height, relative height and relative crown area) of a species in each subplot in which it occurs and connecting these points with a curved line. This was repeated for the 22 species with greatest transect species importance values (Table 1). The area under each curve is relative to the proportion of available spatial niche occupied by each species. Species are generally independently distributed along the transect, and discrete communities with

Table 2. Transect density, growth-form, life-form, and origin of on-transect species less than 1 m tall. Abbreviations are as used in Table 1, see Table 1 for footnotes.

Plant species	Abbr.	Density	Growth-Form[1]	Life-Form[2]	Origin[3]
Allophylus timorensis (DC) Blume		1	Blet	P	Indig
Barringtonia asiatica (L.) Kurz	Ba	4	Blet	P	Indig
Davallia solida (Forster fil.) Swartz		3	E	E	Indig
Elatostema calcareum Merrill	El	26	Fo	Ch	Indig
Hedyotis foetida (Forster) J. E. Smith	Hf	118	V	P	Indig
Hernandia nymphaeifolia (Presl) Kubitzki	H	4	Blet	P	Indig
Jasminum marianum DC		16	Bles	P	Indig
Lepturus repens (G. Forster) R. Brown			Gr	Ch	Indig
Nervilia aragoana Gaud.	Na	16	To	G	Indig
Peperomia mariannensis C. DC	Pm	10	Fo	Ch	Indig
Phymatodes scolopendria (Burmann) Ching	Ps	115	E	E	Indig
Premna obtusifolia R. Brown		5	Blet	P	Indig

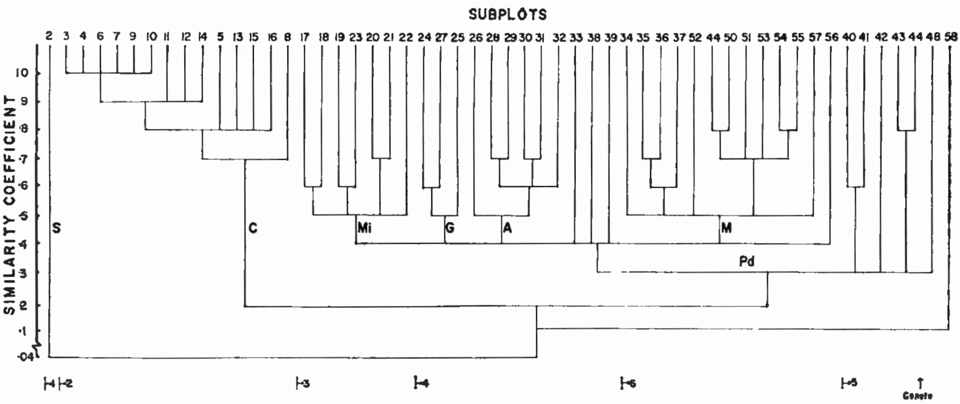

Fig. 4. Cluster analysis of subplots. The similarity coefficients are expressed by horizontal lines. A value of 1.0 indicates that those subplots share all species. The several communities are emphasized by arrows and numbers. Letters refer to species as indicated in Table 1.

definite composition and sharp boundaries are not common. Species less than 1 m tall (Table 2) were not included in the above mentioned computations.

The coefficient of similarity (Figure 4) was used as a basis for cluster analysis. A set of subplots is joined into a cluster on the basis of species shared. The highest values in the similarity matrix are located to identify subplots that form the nucleus of the first cluster. The similarity level is then decreased by 0.1 and a search is made for new clusters. By 'single-linkage' additional subplots are then admitted to the first cluster. The process is repeated until all clusters have finally merged into a single cluster containing all of the subplots. Cluster analysis establishes internally homogeneous groups. Subplots within each group are relatively similar in their species composition.

COMMUNITIES

By integrating the information gleaned from Figure 2, 3 and 4, six plant communities were identified along the transect. They are:

1) *Scaevola/Messerschmidia*,
2) *Cocos*,
3) *Mikania*,
4) *Aglaia/Guamia*,
5) *Pandanus dubius*/Marsh Ferns, and
6) *Merrilliodendron*.

In naming communities generic names are used for monospecific species. See Table 3 for an indication of the subplots occupied by each community and a complete list of vascular plants occurring in each community. Also included are corresponding species importance values and relative importance values as computed on a community basis for individuals 1 m or taller. Additional species represented only by individuals less than 1 m tall are also listed. A discussion of each community follows.

1) *Scaevola/Messerschmidia* Community

These two tree species form a discrete strand community slightly above the wave splash zone. It forms a continuous belt along adjacent sandy beaches but is replaced by *Pemphis acidula* on rocky cliffs and headlands. Although rooted only in subplot 2, the crowns of individuals extend well into subplots 1 and 3. Both species tend to branch low so that their crowns actually begin at ground level and extend to a height of about 7 m. A rather dense hedge-like barrier is thus formed. This community does not share species with the remainder of the transect and statistically joins the transect with a very low (0.04) similarity coefficient.

2) *Cocos* Community

This community is a near consociation as *Cocos* obtains a relative importance value within this zone of about 92%. This community is actually an abandoned coconut plantation which was originally planted and probably maintained until World War II. The oldest trees are quite regularly spaced and now act as seed trees. Piles of germinating and rotting nuts have accumulated beneath their crowns. Although frequent gaps occur, probably from wind-throw and old age death, the crowns of mature trees form a nearly continuous canopy between 9 and 20 m in height. The taller individuals generally occur further from the sea. The crowns of subadults form an open stratum between 4 and 10 m. Juveniles and seedlings develop an often dense stratum less than 3 m tall. Twenty-two adults, 37 subadults and 299 juveniles, and seedlings were counted on subplots within this community. Statistically, four subcommunities are evident. Most are dependent upon the appearance of secondary species. Many coconut trunks are laden with epiphytic ferns including: *Asplenium nidus, Nephrolepis hirsutula, Phymatodes scolopendria, Davallia solida, Pyrrosia adnascens* and *Vittaria elongata*.

Table 3. Composition of communities along transect. Species importance values (SIV) are given. Relative importance percents (RIP) are in reference to each community. Species without values are less than 1 m tall. See Tables 1 and 2 for a list of complete scientific names.

Species	S. I. V.	R. I. P.
1. *Scaevola/Messerschmidia*	Subplot 2	
Scaevola taccada	293.96	73.49
Messerschmidia argentea	88.53	22.14
Cocos nucifera	17.51	4.37
Barringtonia asiatica		
2. *Cocos*	Subplots 3–16	
Cocos nucifera	5139.82	91.80
Piper guahamense	116.58	2.10
Ochrosia oppositifolia	81.38	1.50
Asplenium nidus	56.53	1.00
Guamia mariannae	46.93	0.80
Mikania scandens	34.72	0.60
Triphasia trifolia	27.76	0.50
Aglaia mariannensis	27.34	0.50
Flagellaria indica	23.91	0.40
Claoxylon marianum	17.00	0.30
Nephrolepis hirsutula	13.05	0.20
Cycas circinalis	11.34	0.20
Pachyrrhizus erosus	3.65	0.10
Davallia solida		
Hernandia peltata		
Lepturus repens		
Premna obtusifolia		
Phymatodes scolopendria		
3. *Mikania*	Subplots 17–23	
Mikania scandens	989.79	35.30
Piper guahamense	371.74	13.30
Triphasia trifolia	277.39	9.90
Aglaia mariannensis	227.47	8.10
Guamia mariannae	187.32	6.70
Pandanus fragrans	169.46	6.10
Flagellaria indica	150.32	5.40
Artocarpus mariannensis	121.18	4.30
Dendrocnide latifolia	100.94	3.60
Carica papaya	76.17	2.70
Asplenium nidus	37.08	1.30
Merremia tuberosa	35.65	1.30
Melanolepis multiglandulosa	27.99	1.00
Momordica charantia	9.15	0.30
Bikkia tetrandra	6.70	0.20
Morinda citrifolia	4.81	0.20
Ochrosia oppositifolia	4.30	0.20
Pachyrrhizus erosus	2.81	0.10
Hedyotic feotida		

Table 3. (continued)

	Species	S. I. V.	R. I. P.
4.	*Aglaia/Guamia*	Subplots 24–39	
	Aglaia mariannensis	1639.21	25.50
	Merrilliodendron megacarpum	890.13	14.00
	Guamia mariannae	653.08	10.30
	Triphasia trifolia	456.99	7.20
	Flagellaria indica	453.20	7.10
	Asplenium nidus	333.47	5.20
	Artocarpus mariannensis	297.76	4.70
	Cycas circinalis	260.66	4.10
	Guettarda speciosa	235.95	3.70
	Pisonia grandis	222.90	3.50
	Eugenia reinwardtiana	150.86	2.40
	Claoxylon marianum	133.82	2.10
	Pandanus dubius	124.78	2.00
	Ficus prolixa	119.42	1.90
	Dendrocnide latifolia	114.66	1.80
	Annona squamosa	110.87	1.70
	Ochrosia oppositifolia	37.01	0.60
	Streblus pendulinus	28.73	0.50
	Planchonella obovata	24.13	0.40
	Pandanus fragrans	19.18	0.30
	Morinda citrifolia	18.97	0.30
	Discocalyx megacarpa	17.50	0.30
	Piper guahamense	13.88	0.20
	Mikania scandens	7.95	0.10
	Mucuna gigantea	4.05	0.10
	Allophylus timorensis		
	Davallia solida		
	Elatostema calcareum		
	Jasminum marianum		
	Nervilia aragoana		
	Peperomia mariannensis		
	Planchonella obtusifolia		
5.	*Pandanus dubius*/Marsh Ferns (45–47 no vegetation)	Subplots 40–48	
	Pandanus dubius	1162.63	48.40
	Ficus prolixa	356.30	14.80
	Acrostichum aureum	263.46	11.00
	Pteris tripartita	263.46	11.00
	Asplenium nidus	149.82	6.20
	Randia cochinchinensis	90.51	3.80
	Dendrocnide latifolia	59.24	2.50
	Alocasia macrorrhiza	21.93	0.90
	Clerodendrum inerme	19.01	0.80
	Flagellaria indica	13.64	0.60
6.	*Merrilliodendron*	Subplots 49–58	
	Merrilliodendron megacarpum	2165.89	54.30

Table 3. (continued)

Species	S. I. V.	R. I. P.
Tectaria crenata	448.09	11.20
Aglaia mariannensis	313.80	7.90
Ficus prolixa	174.84	4.40
Pteris tripartita	153.07	3.80
Carica papaya	128.08	3.20
Triphasia trifolia	79.94	2.00
Artocarpus mariannensis	74.39	1.90
Alocasia macrorrhiza	67.57	1.70
Cycas circinalis	60.43	1.50
Thelypteris interrupta	50.84	1.30
Flagellaria indica	49.05	1.20
Asplenium nidus	28.52	0.70
Pandanus dubius	28.18	0.70
Procris pedunculata	27.09	0.70
Piper guahamense	27.09	0.70
Dendrocnide latifolia	22.41	0.60
Morinda citrifolia	21.67	0.50
Eugenia reinwardtiana	19.17	0.50
Randia cochinchinensis	15.97	0.40
Claoxylon marianum	13.05	0.30
Discocalyx megacarpa	11.05	0.30
Momordica charantia	9.54	0.20
Elatostema calcareum		
Peperomia mariannensis		

3) *Mikania* Community

This very weedy and viny zone includes subplots 17 through 23. It begins quite abruptly with the discontinuation of *Cocos* and terminates gradually as it blends into a taller forest. It extends laterally in this same relative position and suggests being an ecotone. *Mikania* and four other species of vines densely wrap all trees and shrubs into a tangle which is very difficult to traverse. An even canopy of stratified tree crowns is absent. This results in a very irregular, lumpy appearance. Similarity coefficients identify four subdivisions within this zone. It is interesting to note that old Chamorro artifacts, especially pot sherds, are common on these subplots. Latte sites are found in this community slightly south of the transect (Reinman, 1968).

4) *Aglaia*/*Guamia* Community

Subplots 24 through 39 are occupied by a well developed forest of small to large trees with few low branches and little undergrowth. It presents minor problems when traversing on foot. Both *Aglaia* and *Guamia* are relatively small trees (averaging 2.3 cm and 2.7 cm DBH; 5 m and 6.6 m height, respectively) but their high density results in large relative importance values within the community. An important intrusion of *Merrilliodendron* occurs in subplots 34 through 38; this species forms a consociation later in the transect.

The largest trees of the transect *Artocarpus mariannensis*, *Guettarda speciosa*, *Pisonia grandis* and *Ficus prolixa* occur in this community but because of their sparse density they rank low in importance value. Because of their height they act as emergent trees which jutt above the surrounding vegetation. They form a nearly continuous overstory canopy between 7 and 22 m. A second stratum of tree crowns composed of *Aglaia*, *Guamia*, *Dendrocnide latifolia*, *Eugenia reinwardtiana*, and *Annona squamosa* is apparent between 5 and 15 m. It again is basically continuous but tends to be depressed when beneath the crowns of overstory species. A third stratum of mostly small trees occurs below 5 m. Members of this stratum are mostly new species not seen in the upper strata, e. g., *Pandanus dubius*, *Triphasia trifolia*, *Cycas circinalis*, *P. fragrans*, *Streblus pendulinus*, and *Planchonella obovata* but some are juvenile individuals of species normally found in the uppermost and intermediate strata.

Six subcommunities are apparent. Subplots 34 through 38, because of the presence of *Merrilliodendron*, are removed in the cluster analysis to combine with community number 6. The remaining five subcommunities are determined by *Aglaia/Guamia*, *Ficus prolixa*, *Artocarpus mariannensis* and *Claoxylon marianum*.

Numerous large clumps of the epiphytic fern *Asplenium nidus* are a characteristic feature of this community. Vines are not especially noticeable and other than *Flagellaria indica* and *Mucuna gigantea* they are lacking. This community terminates as it grades into the *Pandanus dubius* dominated zone at the edge of the cenote.

5) *Pandanus dubius/Marsh* Ferns Community

Subplots 40 through 44 on the near side of the cenote and subplot 48 on the far side, contain this community. It begins as *P. dubius* replaces the trees of the previous community. This occurs about 20 m from the flooded edge of the cenote. Because of the low branching, trunkless character and stilt roots of *P. dubius* this zone is very difficult to penetrate. Individual plants reach a height approaching 8 m. The belt of *Pandanus* trees extends into the water and to inspect them one must climb through their roots and branches while wading in soft ooze. At a point where the water is about 0.5 m deep *Pteris tripartita* grows intermingled within the *Pandanus*. At a depth of about 1 m both species terminate. A band of *Acrostichum aureum*, about 3 m wide, then extends to a water depth of about 1 m. The remainder of the pool, subplots 45 through 47, is open water reaching 2.3 m in depth and is free of major vegetation. The bands formed by *Pandanus* and the marsh ferns tend to encircle the majority of the cenote but are lacking on the generally rocky northwestern side. *Ficus prolixa* falsely obtains a large importance value within this community because of the presence of several displaced individuals. Where the transect leaves the far side of the cenote the marsh ferns are lacking and only a narrow band of rather small *Pandanus* are present.

6) *Merrilliodendron* Community

Merrilliodendron forms a near consociation within subplots 49 through 58, plus its earlier insertion into subplots 34 through 38. Mature trees form a nearly continuous canopy between 8 to 18 m in height. Those individuals nearest the cenote tend to lean to take advantage of the open space it presents. An intermediate stratum of subadults occupies the 5 to 14 m height. Numerous juveniles less than 5 m tall form a third stratum. The ground is often nearly carpeted with seedlings, the vast majority of which will not survive. As in the *Aglaia/Guamia* community there are numerous, often large, clumps of epiphytic ferns. This forest is quite free of shrubs and low branches and is comparatively easy to walk through. The community ends abruptly as one encounters the boulders which are strewn at the base of the cliff.

Fosberg (1959) describes the *Artocarpus* forest of the northern plateau of Guam as a discontinuous overstory of *Artocarpus* and *Ficus*. Beneath this is a continuous second story of lesser trees and an understory which is not sharply separated. This study was conducted at the base of the plateau within an area sheltered by the cliff. In such locations the overstory trees are often closer together and form the nearly continuous canopy reported in this study.

Moore (1973) studied a limestone forest on the windward coast of Guam. He found *Mammea* and *Eugenia* to be dominant. In the present study on the leeward side of the island *Mammea* was absent and *Eugenia* occurred only in small numbers.

Three tree strata are typical of highly developed tropical rain forests (Richards, 1952). The strata described in this study are of short stature when compared with the tropical rain forests of Africa, South America and Southeast Asia. This may be a reflection of evolutionary selection under typhoon pressure. Hence Stone (1971) suggests the name, "typhoon forests".

SPECIES ANALYSES

Fifty-five species of vascular plants were identified within the 5 m × 290 m belt transect. Even though *Streblus pendulinus* and *Merrilliodendron megacarpum* are mentioned by Stone (1970) as being rare on Guam and *Dendrocnide latifolia* and *Nervilia aragoana* are called not common, all four species were common to very abundant in or around the study area.

The number of species recorded for each subplot in the transect is shown in Figure 5. There is a general dearth of species in subplots near the sea and a maximum of twenty species appears in subplot 32. The area of highest species numbers occurs within the *Aglaia/Guamia* community

The species area curve from the transect (Figure 6) begins to level as an area of 0.15 hectare is approached. This is the type of curve which generally appears within a homogenous vegetation and it is quite surprising that it develops along the heterogenous belt transect of this study.

Relative importance percent for the forty-three species of plants represented by individuals greater than 1 m in height and for which density, height, DBH and crown coverage data were obtained are plotted on species sequence in Figure 7. The resultant sigmoid curve reflects a log-normal distribution of niche hypervolume (Whittaker 1965, 1967). This is the normal situation in tropical forest and suggests that

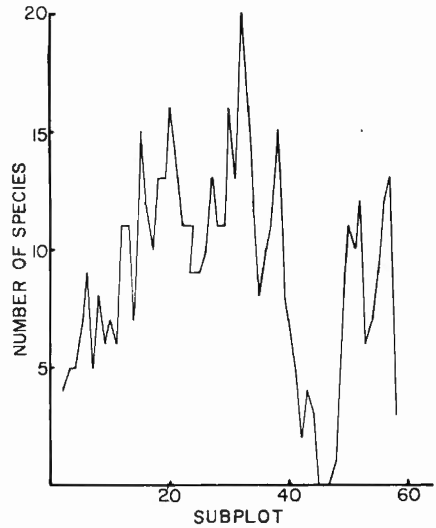

Fig. 5. Number of species of vascular plants occurring in each subplot along the transect. A maximum of 20 species is achieved in subplot 32. The cenote is centered in subplot 46.

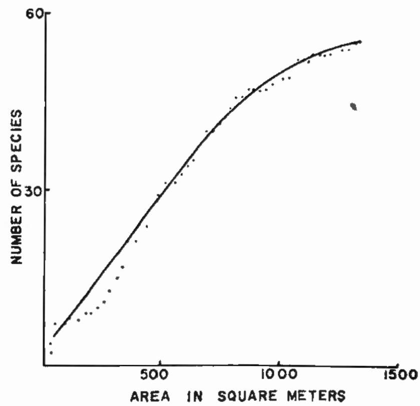

Fig. 6. Species/area curve. The cumulative total of va scular plant species is plotted on area in square meters. Area is summed as one traverses the transect.

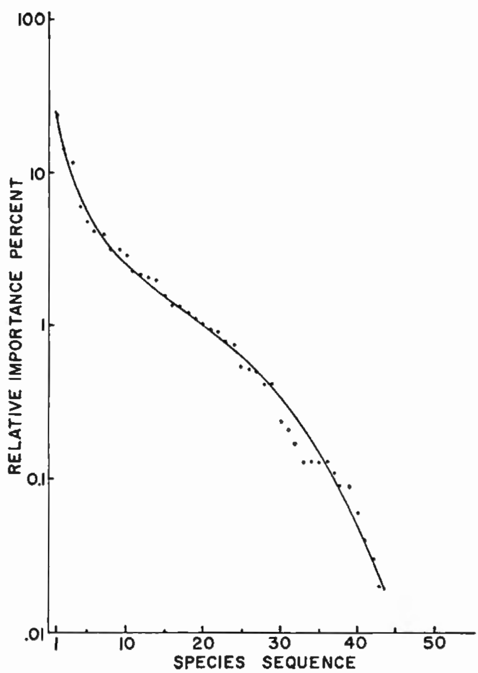

Fig. 7. Relative importance percent plotted on species sequence. The resultant sigmoid curve on semilogarithmic coordinates indicates a log-normal distribution.

the majority of niche space is nearly equally shared by numerous species and that relatively few species occupy both a large and a small amount of available space. This type of analysis has normally been applied only to homogenous vegetation and it is again surprising that typical results were obtained from the data obtained in this study.

The tabulation of growth-form (Whittaker, 1975) of the 55 species of vascular plants in the transect reveals: 44% to be broad leaved evergreen trees; 14% vines; 10% epiphytes; 9% rosette trees; 7% forbs; 4% broad leaved evergreen shrubs; 4% terrestrial/aquatic ferns; and 2% each of broad leaved evergreen strangling trees, broad leaved evergreen thorn shrubs, graminoids and terrestrial orchids. See Table 1 for a growth-form determination of each species. The three dominant categories are those growth-forms which typify tropical forests (Richards, 1952).

A retabulation according to Raunkier's life-forms (Whittaker, 1975) indicates: 75% phanerophytes (perennating bud high in air); 11% epiphytes (entire plant removed from the ground); 7% chamaephytes (bud near the ground); and 4% each of hemicryptophytes (bud on surface of ground) and geophytes (bud well buried). This tabulation also reflects typical tropical forests, perennating buds removed from the protection of the ground. See Table 1 for a life-form determination of each species. Similar percentages were found by Richards (1952) in New South Wales, Australia and by Whittaker (1975) in India.

If the same species are tabulated by origin (Stone, 1970) it is seen that: 7% are endemic to Guam or the Mariana Islands; 75% are indigenous (occurring in Guam prior to human habitation); 9% are introduced and naturalized; and 9% are introduced and not naturalized. See Table 1 for the origin of each species. The introduced species are contained in the *Cocos* community, *Mikania* community and *Aglaia/Guamia* community. It was also noted that all of the endemic species were found in the *Aglaia/Guamia* community.

Plank buttressing of the lower trunk, though weakly developed, is apparent in *Artocarpus mariannensis*. Both species of *Pandanus* exhibit stilt (=prop) roots. *Ficus prolixa* is a typical strangler with aerial roots. These several features are commonly found among tropical trees.

Species taller than 1 m and present within the transect were statistically examined by the variance/mean ratio method (Whittaker, 1975) to determine their type of horizontal distribution. Ninety-eight percent were resolved to be of the clumped type of distribution and two percent (*Davallia solida*) were of the regularly spaced type. None were randomly distributed.

Phenological observations were made during visits to the study site. It was generally noted that there are two flowering seasons. The primary flowering period is in June but there is a secondary period in November. The later period involves the reflowering of many of those species which flowered earlier.

ENVIRONMENTAL AND EDAPHIC FACTORS

Water temperature of the cenote ($\bar{x}$=26.4°C, range 21.5–29.4°C) was consistantly lower than reef flat sea temperature. It was also observed that cenote water temperature was always cooler than adjacent ambient air, while sea temperature was warmer than adjacent ambient air. Further, water and air temperature at the cenote were cooler and fluctuated less than corresponding temperature at the sea.

In July thermographs were kept for a week near the cenote and near the beach. Daily air temperature fluctuation at the cenote averaged 23.3–26.7°C while at the beach it was 25.6–30°C.

Relative humidity near the cenote was consistantly higher than on the open beach. Midday values were generally 90% and 80%, respectively. During rainy days relative humidity was generally uniform at both locations.

The general character of the substratum along the transect is: deep sand (mostly coral fragments) from subplot 1 through 15; gravelly limestone from subplot 16 through 24; deeply pitted coralline limestone with small pockets of soil occurring throughout the remainder of the transect. The cenote is within the latter zone but is edged and lined with soft ooze.

Soil texture analysis (Figure 8) reveals that all of the soils are highly sandy but the proportion of sand gradually decreases along the transect. Silt and clay show a reverse trend. The percent of organic matter increases to reach a high several subplots before the cenote.

Calcium obtains the highest value of the major cations. It is followed by potassium, sodium and magnesium (Figure 9). The first three ions increase in quantity along the transect to reach peaks several subplots before the cenote. Magnesium remains quite low and constant throughout the transect. Readings of ions within the water of the cenote are included in Figure 9.

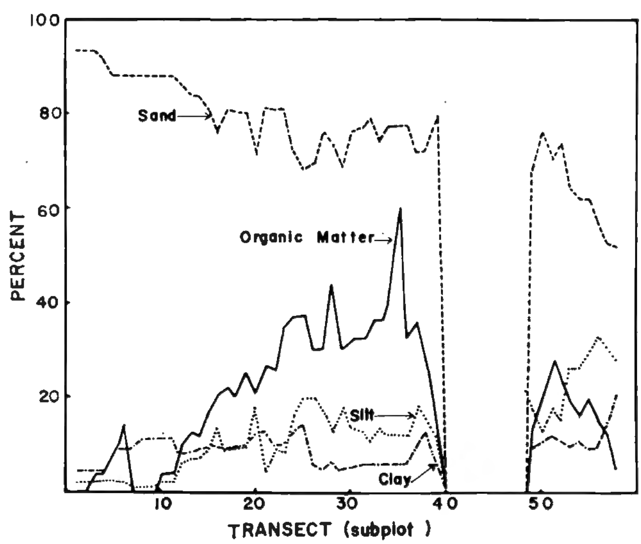

Fig. 8. Mechanical analysis and organic matter content of soil within the transect. Percent sand, silt, clay and organic matter were determined for each subplot. The gap indicates the location of the cenote.

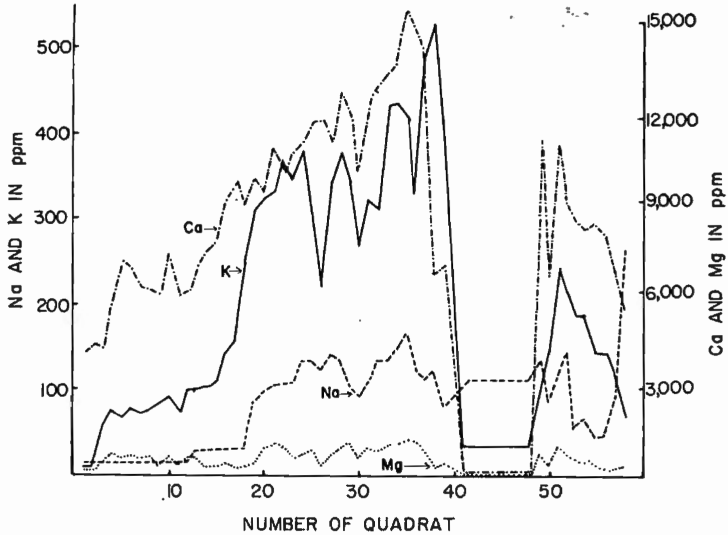

Fig. 9. Sodium, potassium, magnesium and calcium concentrations within the transect. All, except calcium, generally increase as one moves away from the beach.

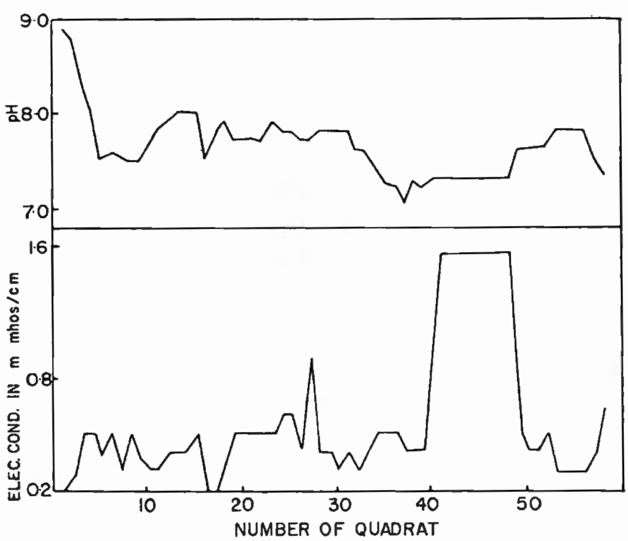

Fig. 10. Soil pH and electrical conductance of water extracts within the transect. Both determinations are relatively constant and lack distinct trends. A high salt concentration is evident within the water of the cenote.

Soil pH is shown in Figure 10. The first three subplots gave values higher than the pH of sea water (8.03). The remainder of the transect produced readings near pH 8. This is undoubtedly because of the alkaline nature of the limestone substratum. Water from the cenote had a pH of 7.28.

Table 4. Regression values of species on soil factors. Correlation coefficients (r) and levels of probability for the number of species occurring in a subplot in relationship to area and 10 different soil factors.

Factor	'r' Value	Levels of Probability
Area	.974	<.01
Organic matter	.490	<.01
Sodium	.492	<.01
Potassium	.527	<.01
Calcium	.490	<.01
Silt	.297	<.05
Sand	−.356	<.05
Salt	.042	>.05
pH	−.240	>.05
Magnesium	.223	>.05
Clay	−.010	>.05

Electrical conductance of water extracts (Figure 10) along the transect is quite constant. Water from the cenote gave high readings.

The species/area curve (Figure 6) and the species on subplots (Figure 7) showed the number of species to generally increase along the transect. The number of species occurring in each subplot was also statistically examined by correlation analysis to determine their relationship with 10 different soil factors. Resultant correlation coefficients (r) are given in Table 4. Six factors showed significant relationships. Four did not. Similar results are seen in the literature. Wikum and Wali (1974) resolved from a study in North Dakota that there was a high correlation between the number of species present, and potassium and calcium in the soil. Richmond and Mueller-Dombois (1972) did not observe significant correlation between species and salt concentration and pH in a study conducted in Oahu, Hawaii.

Conclusions

Quantitative investigations utilizing three major analytical devices, i. e., the profile diagram, plotted species importance values and statistical clustering, resulted in the determination of six vegetation communities. The communities named for dominant or codominant species as determined by computed species importance values are: 1) *Scaevola/Messerschmidia*; 2) *Cocos*; 3) *Mikania*; 4) *Aglaia/Guamia*; 5) *Pandanus dubius*/Marsh Ferns; and 6) *Merrilliodendron*.

Though individual species are independently distributed along the gradient the several communities are recognizable by species composition and physiognomy. Boundaries between the first two communities are quite discrete while boundaries between the remaining communities are indistinct. Ecotones are narrow or non-existent.

A total of fifty-five species of vascular plants were identified within the transect.

The major growth-form is broad leaved evergreen tree, 44%. The most complex community *Aglaia/Guamia* contained 32 species and a vertical structure of three nearly continuous tree strata. The simplest community, *Scaevola/Messerschmidia*, contained only three species and formed a narrow hedge-like band just above the beach.

Pandanus dubius dominates the marsh community which occurs at the edge of the cenote which is bisected by the transect. A second less mesic environment is occupied by a consociation of a tree rare on Guam, but locally abundant, *Merrilliodendron megacarpum*.

Strong statistical correlations exist between the number of species occurring within a subplot or community and increased amounts of soil potassium, sodium, and calcium.

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