THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 14. THE ALGAE OF PICO DEL OESTE [1]

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PUERTO RICO is the most easterly and the smallest of the Greater Antilles. The Sierra de Luquillo highlands are located in the northeastern interior. The study site, described in ecological detail by Howard (1968), called Pico del Oeste, is located in these highlands. This peak, 1050 meters above mean sea level, has a vegetational veneer referred to as an elfin forest (Howard, 1968). Gleason and Cook (1927) have also termed this area of windswept ridges above the 700 meter elevation the mossy or elfin forest. Pico del Oeste extending above the 700 meter line into the clouds is exposed to the constant effects of the northeast trade winds which carry moisture-laden clouds up the easterly slopes of the Sierra and keep the forest constantly humid (Liboy & Sabio, 1966; Baynton, 1968, 1969). This high moisture content, coupled to an annual temperature range of 10°C. to 32°C. (average 21°C.) provides conditions adequate for the growth of the regional flora. Baynton (1969) has described the rainfall pattern on the peak as a function of convective, orographic, and synoptic scale weather conditions. He further stated that due to extensive cloud cover the solar radiation is reduced 40 percent. In the two papers by Baynton (1968, 1969) the weather conditions and influences within the study area have been adequately described.

Puerto Rico is an island where numerous phycological studies have been completed. Such workers as Möbius (1888), Wille (1915), Gardner (1927, 1932), Tiffany (1936), Tiffany and Britton (1944), Almodovar (1963), and Halicki (1964) have compiled information concerning freshwater and terrestrial species from the lowland and rain-forest regions of the island. Almodovar (1963) presented a well-documented analysis of the taxonomic history of the Cyanophyta on the island. The remaining algal Divisions have been treated only slightly. As for the algal investigations of the elfin forest, only Liboy and Sabio (1966) have reported on the algal epiphytes. Their work consisted mainly of investigating gelatinous growths on tree trunks, and their casual observations correlate well with this study.

Algae in the tropics have had limited study from an ecological stand-

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point. A study of the algal flora of elevated elfin-like forest regions from around the world, as well as in the Caribbean area, has not been made. Most tropical investigations are carried out at lower elevations and are usually concerned with the aquatic habitat. Other Caribbean islands have been studied taxonomically by West and West (1894, 1899) and Drouet (1942). Taylor (1935) studied the alpine regions of Colombia, but his investigations concerned various lakes which were far above the elevation of the elfin habitat and away from the influence of the north-east trades. Fritsch (1907) noted the extensive subaërial algal flora in the tropics. He reported that Cyanophyta predominate, and Chlorophyta are reduced in numbers, with the green alga *Trentepohlia* being the most successful of the group. No reference was made to subaërial diatoms or flagellates.

The investigation reported here contributes to our knowledge of algae from a tropical area. After completing identification of a series of samples it was noted that the algal flora of the region was not uniformly distributed, but divided into intergrading phyco-synusia. Data are presented to show the epiphytic algal taxa of several habitats including four endemic vascular species, vascular and non-vascular epiphytes, and various ground locations. Further, data are offered to demonstrate gross ecological influences on spatial distribution.

METHODS

Terrestrial algal epiphytes were collected during the months of February, March, April, May, and August 1966, and during February 1968 from the elfin forest on Pico del Oeste, Sierra de Luquillo, Puerto Rico. Each sample was preserved for later analyses and unpreserved co-samples were used to prepare cultures. Specimens were identified and cross referenced, utilizing the present, most up-to-date and available monographic works. The nomenclature adopted is as follows: for the Cyanophyta, Desikachary (1959); for Bacillariophyta, Patrick and Reimer (1966); for the Chlorophyta, Prescott (1962), Randhawa (1959), Saxena (1962), and Islam (1963); for the Chrysophyta, Pyrrophyta, and Euglenophyta, Prescott (1962). Some of the other works employed included Tilden (1910), Drouet and Daily (1956), Van Huerck (1896), Tiffany and Britton (1952), and many other short papers on individual species and genera. Vascular plants were identified by Dr. R. A. Howard of the Arnold Arboretum, Harvard University.

Analyses were made of the probability that numbers of species collected from each location may exhibit preference of substrate, and/or of microclimate. Analysis of variance (ANOVA) was applied to the difference in numbers of algal species found on the various plants and to the difference in number found on the vascular stem at various heights above the ground. Linear regression was further employed to test the height-species number variation and relationship. These gross ecological parameters were chosen as representative of multiple factors, such as light, moisture, nutrients, etc., which this portion of the study was not equipped to measure directly.

RESULTS AND DISCUSSION

One of the principal realizations conveyed by the data is that species of subaërial algal epiphytes are not uniformly distributed but are segregated into various intergrading phyco-synusia. In this study microhabitation is to be analyzed and related to the physical aspects of vascular host differentiation, height above the ground, and meteorological conditions only. Lyford (1969) has reported that in an area-to-area comparison the trunks of the trees are covered with organic material in an amount that approximates that on the surface of the soil. This would then indicate a somewhat uniform substrate throughout the study site. If this is true, then light, moisture, and temperature become more important limiting factors.

In all samplings the effect of moisture both as wetness and as a light shield appears to be a significant limiting factor. Due to the island's geographical location the seasonal differences in solar radiation are small and only the thickness of the cloud cover would significantly influence the levels of incident light intensity. When the sun is most direct the atmospheric moisture content is greatest, and when its zenith is lowest for the year the atmospheric moisture content is less. The action of moisture as a filter for the light tends to maintain relatively constant light quantities. In fact Baynton (1968) shows monthly mean light intensity to vary from a low of 212 Langleys per square centimeter to a high of 322 Langleys per square centimeter over the year 1966. Though Baynton (1968) has also shown light attenuation to be 40 percent, Szeicz (1966) has reported no loss of spectral components by the light passing through fog.

TABLE 6 is a compilation of the species identified from the February-March 1966 collections. These are related to the vascular host and to their position on the host. Note the high proportion of Cyanophyta which dominate the microhabitats studied. Diatoms were also present.

Lund (1945) and Fritsch (1922) reported diatoms in the terrestrial habitat. They further stated that the amount of moisture appears to be a limiting factor. Liquid moisture in the elfin forest seems to be adequate for diatom growth. Further, the presence of flagellates in the samples was noted. A film of moisture was present in the area where they were found. Baynton (1969) reports that 21.4 percent of the rain falling on the forest canopy flows down the trunks of the vascular hosts. A build-up of moisture near the base of the trunk would then increase the probability of occurrence of species such as diatoms and flagellates which are more susceptible to desiccation than many of the other algae reported. Therefore, the moisture laden winds become extremely important in maintaining an appropriately moist habitat. They also are probably important in providing some of the algal colonizers.

Schlichting (1960, 1961, 1964), along with many others cited by him, has shown that air currents and birds can transport diatoms and flagellates, as well as species from all algal classes. Therefore, in the situation under study the existence of these species in a vegetative state is a distinct possibility as the northeast trade winds carry their moisture-laden air up the mountain slopes. Here the adiabatic cooling condenses the water vapor producing precipitation in the form of rain, clouds, dew, mist, and fog, establishing an environment suitable for algal epiphytes. The precipitation would deposit any of the airborne algae which were trapped as nuclei of condensation during evaporation at lower levels. Further, the migration of temperate zone birds and the wanderings of native bird and other animal species must not be ruled out as a possible source of algal introduction.

TABLE 1 depicts the principle phyco-synusia encountered in the February-March, 1966, collections relating them to the vascular host and

TABLE 1. **Subaërial Epiphytic Phyco-synusia of Four Vascular Species Sampled during February-March, 1966**

VASCULAR HOST	APPEARANCE	MAJOR PHYCO-SYNUSIA	DISTANCE ABOVE GROUND (METERS) 0–1	1–2
Cyathea pubescens	white globular mass	a diatom-filamentous bluegreen association in an extensive Ascomycete fungal mat	X	
Miconia pachyphylla	always moist gelatinous flat mass, greenish-gray	*Stigonema-Lyngbya-Hapalosiphon* (chiefly *Stigonema informe*)		X
Ocotea spathulata	green material on dead leaves	almost pure association of *Hapalosiphon luteolus*	X	
	white, globular gelatinous mass	*Mougeotia caimani* chief species	X	
	green, gelatinous growth	*Hapalosiphon-Trentepohlia*		X
Tabebuia rigida	flat-green gelatinous	*Stigonema-Hapalosiphon-Oedogonium* (*Stigonema* is principle)	X	
	solid mass	*Stigonema-Hapalosiphon-Scytonema* (*Stigonema panniforme* principle)	X	
	flat mass	*Chroococcus-Cylindrocystis-Synechococcus*	X	
	flat mass	*Synechococcus-Cylindrocystis-Frustulia*	X	
	gelatinous, white colony	*Chroococcus-Hapalosiphon-Trentepohlia*		X

their relative height above the ground. It is interesting to note that dominant species change with height on the tree. Particularly, this is noted on *Tabebuia rigida* as the dominance shifts from a *Stigonema* association to a *Trentepohlia* association (a shift from a blue-green to a green algal synusium). The reason for the shift in association dominance, and the diminishing number of species present undoubtedly rests in the microhabitat itself. It is not the purpose of this paper to analyze these various limiting factors, but to point out the composition of the subaërial algal epiphytic flora on the principle vascular plant hosts, and to note the intricacies of the spatial distribution of component species. What causes the variation is still uncertain but physical data indicate that moisture as wetness or as a light shield may be a principal factor. Grubb and Whitmore (1966) report that fog is an important limiting factor in tropical montane forests. For the algae this suggests not only a high atmospheric moisture content, but also light attenuation.

TABLE 2 is a representation of the mean climatic conditions of the sample site for February-March, 1966. The mean temperature is moderate, solar

TABLE 2. **Mean Climatic Data for the February-March Period of Sampling** *

MEASUREMENT	MEAN READING
Temperature	18.3°C.
Minimum Relative Humidity	80.6%
Langleys (gram calories/cm.^{2})	283.45 (above canopy)
Daily Precipitation	
above canopy	12.7 mm.
below canopy	9.7 mm.
Percent of Time Humidity less than 100% above canopy	28.4%
Humidity at ground level below canopy	100%

* Means computed from data supplied by Dr. R. A. Howard.

energy is available, precipitation is adequate, and the relative humidity seldom drops below 100 per cent above the forest canopy and appears to remain saturated beneath the forest canopy at ground level.

As previously noted (TABLES 1 and 6) fewer species are found in the February-March samples taken higher up the trunk of the vascular host. Analysis of variance (ANOVA) was applied to test the variation between the samples collected 1 meter above the ground and 2 meters above the ground on *Tabebuia rigida* and *Ocotea spathulata*. A second ANOVA tested the variation between the vascular hosts *Miconia pachyphylla*, *T. rigida* and *O. spathulata*. A third ANOVA tested the variation between *T. rigida*, *O. spathulata* and *Cyathea pubescens*. The hypothesis tested was that there is no difference between mean numbers of species in the samples (H: $\mu_l = \mu_k$). All results demonstrated that the populations varied significantly and the hypothesis was rejected at the 99 per cent level of confidence. A definite variation appears to exist between the samples.

However, it must be pointed out that, while samples were randomly collected, the number of samples on which the statistics are based is of necessity small. The ideas of microhabitat are introduced to demonstrate that the algal flora of the cloud forest is not a superficial veneer, but, as in an aquatic habitat, is distributed in relation to the stress of the microclimate in which it exists. Varying the microclimate may in some instances accentuate or retard various species and thus shift the community structure both quantitatively and qualitatively.

A regression analysis was performed on the height above the ground where samples were collected (X) and the relation of this height to the number of species found (Y). Samples 9 and 10 (see TABLE 6) are not used in this computation because they are isolated growths not found on the trunks of the trees. Though the data are limited, a definite relationship appears to exist and is presented here to demonstrate the possibility of microhabitat existence. The regression equation ($\hat{Y} = 45.5 - 18.2X$) was computed to test the height factor hypothesis, and the line derived (FIGURE 1) showed that as samples were taken higher on the tree trunks the number of species diminished. This is an indirect relationship further qualified by the correlation coefficient ($r = -.757$), a high negative correlation.

Other samplings reported here were made during April-May, 1966, August, 1966, and February, 1968. TABLE 3 is a listing of the algal species from five habitats not previously described. Specimens from a flowing stream (1), from bryophytic ground-covering adjacent to the access road (2), from cement drains at the experimental site on the access road (3), from bryophytic ground-covering receiving some ground water run-off (4), and from a horizontal trunk of *Tabebuia rigida* (5). Again the results of the qualitative survey indicate the existence of microhabitats. The major phyco-synusia are listed in TABLE 4.

It is interesting to note that the diatom *Frustulia rhomboides* var. *capitata* is the most prevalent species in the habitats listed for April-May, 1966. Further, it is thought that this species exhibited polymorphism in the samples investigated. In all samples studied a small number of *F. rhomboides* var. *viridula* were found, a larger number of *F. rhomboides* var. *saxonica,* and an extremely large number of *F. rhomboides* var. *capitata*. In light of Stoermer's recent report (1967) on polymorphism in *Mastogloia*, the probability exists that these three varieties are growth forms, each variety being reduced in size by approximately half in the following order: var. *viridula*, var. *saxonica*, var. *capitata*. Culturing *Frustulia* was not successful, and therefore only field observations can be offered as evidence.

The April-May, 1966, collections were composed mainly of diatoms (1, 2,3,4). The habitats from which the samplings were made were on the ground and bathed in moisture. Specimens from *Tabebuia rigida* were dominated by the blue-green alga *Hapalosiphon*, with many lesser impor-

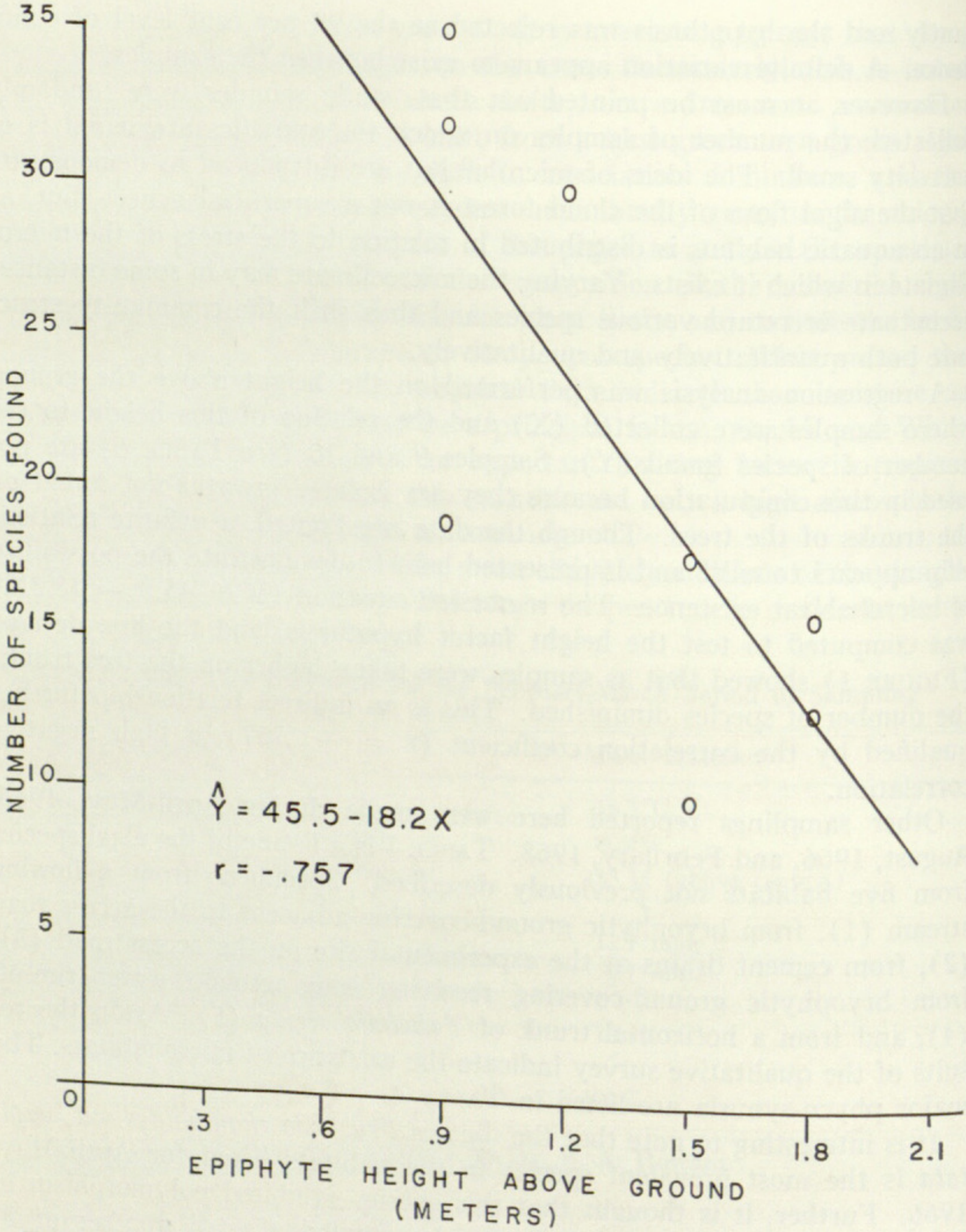

FIGURE 1. Relationship of the height of collection on the vascular host to the number of species from the February-March, 1966 sampling.

tant diatom species. The horizontal trunk of *T. rigida* was approximately one-half meter above the ground under the canopy where light and moisture conditions appear different from the other four sample points.

During August, 1966, approximately the same collection sites that were sampled during February-March were resampled. TABLE 7 is a listing of the species found in relation to the vascular hosts. TABLE 5 is a comparison of major organisms in the various synusia, number of species, and height of collection. A shift from an association dominated by Cyanophyta to one with increased dominance of the Bacillariophyta is indi-

TABLE 3. **Species Found in Five Samples Collected during April-May, 1966**

SPECIES	HABITAT *
CYANOPHYTA	
Nostocales	
Anabaena sp.	(3) (4)
Aulosira fritschii Bharadw.	(3) (4)
A. prolifica Bharadw.	(4)
Oscillatoria foreaui Frémy	(2)
Stigonematales	
Hapalosiphon welwitschii W. & G. West	(5)
CHLOROPHYTA	
Ulotrichales	
Stichococcus subtilis (Kütz.) Klercker	(1) (2)
Ulothrix variabilis Kütz.	(1) (2)
Zygnematales	
Euastrum sp.	(1) (2)
Cosmarium sp.	(1) (2)
CHRYSOPHYTA	
Rhizochrysidales	
Chrysidiastrum catenatum Lauterb.	(1) (2)
BACILLARIOPHYTA	
Centrales	
Biddulphia favus (Ehrenb.) Van Heurck	(1) (2) (3) (4) (5)
Cyclotella glomerata Bachm.	(5)
Melosira varians C. Ag.	(1) (2)
Pennales	
Achanthes hauckiana Grun.	(5)
A. microcephala (Kütz.) Grun.	(1) (2)
Diatoma vulgare Bory	(1) (2) (5)
Eunotia naegelii Migula	(4)
E. praerupta Ehrenb.	(1)
E. tenella (Grun.) Hust.	(1) (4?) (5)
E. sp.	(4)
Frustulia rhomboides var. *capitata* (A. Mayer) Patr.	(1) (2) (3) (4) (5)
F. rhomboides var. *saxonica* (Rabenh.) DeToni	(1) (2) (3) (4) (5)
F. rhomboides var. *viridula* (Bréb.) Cl.	(1) (2) (3) (4)
Navicula tenelloides Hust.	(1) (2) (4) (5)
N. sp.	(4)
Nitzschia biacrula (?) Hohn & Hellerman	(1) (2)
N. hantzschiana Rabenh.	(5)
Pinnularia sudetica Hilse	(1) (2)
P. viridis var. *minor* Cleve	(4)
Rhopalodia gibberula (Ehrenb.) Mueller	(1) (2) (5)
R. ventricosa (Kütz.) Mueller	(2)

* Sample numbers correspond to the following:
(1) Specimens found growing one inch deep in the water of a flowing stream.
(2) From bryophytic growth covering ground adjacent to access road.
(3) From cement drains along access road.
(4) From bryophytic ground-covering kept wet by rain and clouds, as well as some water flow.
(5) From a growth on a horizontal trunk of *Tabebuia rigida* (two feet off ground).

TABLE 4. **Phyco-synusia of Samples from April-May, 1966**

HABITAT *	SYNUSIA	TOTAL NO. SPECIES
1. In small flowing stream	*Ulothrix-Frustulia*	18
2. On bryophytes near road	*Oscillatoria-Frustulia*	18
3. From cement drains	*Aulosira-Frustulia*	6
4. On bryophytes receiving water run-off	*Aulosira-Frustulia*	13
5. On horizontal trunk of *Tabebuia rigida*	*Hapalosiphon-Frustulia-Trentepohlia*	11

* See also footnote to Table 3.

TABLE 5. **Phyco-synusia of Samples from August, 1966**

HABITAT (vascular host)	SYNUSIA	DISTANCE ABOVE GROUND (METERS) 0–1	1–2	NUMBER OF SPECIES
Tabebuia rigida	*Stigonema-Chroococcus*	X		14
T. rigida	*Aulosira-Zygnemopsis*	X		8
Ocotea spathulata	*Hapalosiphon-Phormidium*	X		13
O. spathulata	*Stigonema-Frustulia*	X		8
Miconia pachyphylla	*Stigonema-Chroococcus*		X	14
Cyathea pubescens	*Navicula-Frustulia*	X		3
T. rigida	*Phormidium-Frustulia*	X		8
T. rigida	*Stigonema-Frustulia*		X	15
O. spathulata	*Aulosira-Frustulia*		X	14

cated. The samplings for February-March, 1966, were made during a period of less rainfall and less cloud cover, and the samplings of August, 1966, were taken during a higher moisture period (Baynton 1968). Baynton (1968) reports longer periods of cloud cover during the month of August. This is the greatest overall comparative meteorological fluctuation on the peak between the two samplings.

A regression analysis was again performed to test the same relationship as discussed for the February-March samples. The line derived (FIGURE 2) by the regression equation ($\hat{Y} = 6.30 + 4.55X$) showed that a positive relationship now exists. This is further qualified by the positive correlation coefficient ($r = .548$). As the samples were taken higher the number of species increased. Since the samples were collected from the same site, and since only a slight change in precipitation, humidity, and temperature was reported (Baynton 1968), it would appear that cloud cover may be an important limiting factor. Though solar radiation has increased, so has the clouding, a factor not as prevalent in the February-March samplings.

TABLE 6. Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966

Species	1	2	6 *Tabebuia rigida*	7	8	3	4 *Ocotea spathulata*	9	5 *Miconia pachyphylla*	10 *Cyathea pubescens*
CYANOPHYTA										
Chroococcales										
Aphanocapsa										
biformis A. Br.					X					
roeseana DeBary	X									
Aphanothece										
clathrata W. & G. West							X			
microscopica Näg.						X				
saxicola Näg.									X	
Chroococcus										
dispersus (Keissler) Lemm.		X		X	X					
dispersus var. *minor* G. M. Sm.	X			X			X			
giganteus W. West			X							
limneticus Lemm.	X									
minor (Kütz.) Näg.				X	X		X			
minutus (Kütz.) Näg.		X	X	X				X		
pallidus Näg.		X		X						
turgidus (Kütz.) Näg.		X	X		X				X	X
varius A. Br.				X					X	
Dactylococcopsis										
smithii R. & F. Chodat							X			
Gloeocapsa										
aeruginosa (Carm.) Kütz.				X						
polydermatica Kütz.								X		
Gloeothece										
linearis var. *composita* G. M. Sm.		X								
Merismopedia										
aeruginea Bréb. ex Kütz.		X								
elegans A. Br. ex Kütz.				X						
glauca (Ehrenb.) Näg.		X		X						
punctata Meyen			X	X						
tenuissima Lemm.				X						
Microcystis										
elabens (Bréb.) Kütz.			X							
incerta Lemm.								X		
Pelogloea										
bacillifera Lauterborn				X						
Rhabdoderma sp.							X			
Synechococcus										
aeruginosus Näg.		X		X	X			X		
Chamaesiphonales										
Chamaesiphon										
confervicola A. Br.		X								
rostafinskii Hansg.										

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	6 *Tabebuia rigida*	7	8	3	4 *Ocotea spathulata*	9	5 *Miconia pachyphylla*	10 *Cyathea pubescens*
Nostocales										
Anabaena										
anomala Fritsch										X
laxa (Rabenh.) A. Br.					X					
oscillarioides Bory ex Born. & Flah.										X
oryzae Fritsch						X				
sp.	X	X								
Calothrix										
epiphytica W. & G. West	X									
weberi Schmidle								X		
Coelosphaerium										
dubium Grun.			X							
Gloeotrichia										
echinulata (J. E. Sm.) Richter							X			
longiarticulata G. S. West							X			
Lyngbya										
limnetica Lemm.		X			X					
Microchaete										
uberrima Carter									X	
Oscillatoria										
agardhii Gom.		X								
annae van Goor					X					
limnetica Lemm.				X						
sp.					X		X			
Phormidium										
tenue (Menegh.) Gom.				X					X	
Pseudanabaena										
catenata Lauterb.					X					
constricta (Szafer) Lauterb.		X		X						
Schizothrix										
ericetorum Lemm.		X								
Scytonema										
amplum W. & G. West			X							
burmanicum Skuja						X				
hofmannii C. Ag. ex Born. & Flah.	X									
stuposum (Kütz.) Born. ex Born. & Flah.								X		
tolypothricoides Kütz. ex Born. & Flah.								X		
Scytonematopsis										
kashyapii (Bharadw.) Geitler					X					
Spirulina										
subtilissima Kütz.		X								

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	6 *Tabebuia rigida*	7	8	3	4 *Ocotea spathulata*	9	5 *Miconia pachyphylla*	10 *Cyathea pubescens*
Tolypothrix										
distorta Kütz. ex Born. & Flah.							X			
Pleurocapsales										
Xenococcus										
kerneri Hansg.		X								
Stigonematales										
Camptylonema										
indicum Schmidle						X				
Hapalosiphon										
fontinalis (Ag.) Born.		X								
hibernicus W. & G. West	X									
intricatus W. & G. West	X	X								X
luteolus W. & G. West		X	X		X					
stuhlmannii Hieron.					X					
welwitschii W. & G. West					X				X	
Nostochopsis										
lobatus Wood em. Geitler								X		
Plectonema										
indica Dixit					X					
Stigonema										
aerugineum Tilden					X					
hormoides (Kütz.) Born. & Flah.			X	X	X	X		X		
informe Kütz.									X	
mesentericum Geitler	X	X			X			X		
panniforme Harv. ex Born. & Flah.			X	X						
Stigonema										
turfaceum (Berk.) Cooke ex Born. & Flah.	X									
CHLOROPHYTA										
Chaetophorales										
Protococcus										
viridis C. Ag.		X								
Trentepohlia										
aurea (L.) Martius	X							X		
iolithus (L.) Wallroth					X					
umbrina (Kütz.) Born.						X				
Chlorococcales										
Ankistodesmus										
falcatus (Corda) Ralfs		X								
Characium										
stipitatum (Bachm.) Wille							X			

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	6 *Tabebuia rigida*	7	8	3	4 *Ocotea spathulata*	9	5 *Miconia pachyphylla*	10 *Cyathea pubescens*
Chlorella										
vulgaris Beyerinck		X	X				X			
Chlorococcum										
humicola (Näg.) Rabenh.		X		X	X			X		
Oocystis										
borgei Snow				X						X
pyriformis Prescott					X					X
submarina Lagerheim									X	
Pediastrum										
muticum var. *crenulatum* Prescott		X				X				
Quadrigula										
chodatii (Tanner-Füllemann) G. M. Sm.									X	
lacustris (Chod.) G. M. Sm.									X	
Scenedesmus										
arcuatus var. *platydisca* G. M. Sm.							X			
Tetraedron										
tumidulum (Reinsch) Hansg.						X				
Cylindrocapsales										
Cylindrocapsa										
conferta W. West	X						X			
geminella Wolle									X	
Oedogoniales										
Oedogonium sp.		X								
Sphaeropleales										
Sphaeroplea										
annulina (Roth) C. Ag.								X		
Tetrasporales										
Gloeocystis										
major Gerneck								X	X	
vesiculosa Näg.						X				
Sphaerocystis										
schroeteri (?) Chodat			X						X	X
Tribonematales										
Tribonema										
utriculosum (Kütz.) Hazen		X					X			
Ulotrichales										
Stichococcus										
subtilis (Kütz.) Klercker							X			
Ulothrix										
aequalis Kütz.					X					

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

SPECIES	1	2	*Tabebuia rigida* 6	7	8	3	*Ocotea spathulata* 4	9	*Miconia pachyphylla* 5	*Cyathea pubescens* 10
Zygnematales										
Cosmarium										
dentatum Wolle					X					
Cylindrocystis										
brebissonii var. *minor* W. & G. West			X	X	X				X	
Hyalotheca										
undulata Nordst.		X		X						
Mougeotia										
caimani Transeau					X		X			
floridana Transeau			X							
Netrium										
digitus (Ehrenb.) Itzigos. & Rothe				X			X			
Zygnemopsis										
desmidioides (W. & G. West) Transeau			X	X	X					
CHRYSOPHYTA										
Heterococcales										
Peroniella										
planctonica G. M. Sm.				X						
Pleurogaster										
lunaris Pascher				X						
Tetragoniella										
gigas Pascher				X						X
Rhyzochrysidales										
Lagynion										
reductum Prescott		X								
BACILLARIOPHYTA										
Centrales										
Melosira										
crenulata (Ehrenb.) Kütz.				X						
Triceratium										
semicirculare Brightw.										X
undulatum Ehrenb.			X	X			X	X		
Pennales										
Anomoeoneis										
costata (?) (Kütz.) Hust.				X						
Denticula sp.									X	
Diatoma										
hiemale (Roth) Heib.					X					
Diatomella										
balfouriana Grev.	X			X						
Diploneis										
oculata (Breb.) Cl.										X

TABLE 6. **Subaërial Epiphytic Algal Species and Their Vascular Hosts from Pico del Oeste, February-March, 1966** (*continued*)

	Tabebuia rigida					*Ocotea spathulata*			*Miconia pachyphylla*	*Cyathea pubescens*
SPECIES	1	2	6	7	8	3	4	9	5	10
Eunotia										
tenella (Grun.) Hust.				X						X
Fragilaria										
lapponica Grun.		X								
Frustulia										
rhomboides var. *capitata* (A. Mayer) Patr.		X	X		X				X	
rhomboides var. *viridula* (Bréb.) Cl.					X					
Nitzschia										
dissipata (Kütz.) Grun.										X
ignorata Krasske				X		X				X
Stauroneis										
ignorata (?) Hust.			X	X						
EUGLENOPHYTA										
Euglenales										
Euglena										
elastica (?) Prescott								X		
polymorpha Dangeard					X					
Glenodinium										
kulczynskii (?) (Wolosz.) Schiller										X
Trachelomonas										
charkowiensis (?) Swirenko							X			
TOTAL NUMBER OF SPECIES	13	31	18	35	30	10	19	16	17	14

KEY TO NUMBERS
1 — gelatinous white colony on *Tabebuia rigida*
2 — gelatinous green colony on *T. rigida*
3 — green gelatinous mass on *Ocotea spathulata*
4 — white gelatinous mass on *O. spathulata*
5 — always wet gelatinous mass on *Miconia pachyphylla*
6 — solid mass on *T. rigida*
7 — gelatinous mass on *T. rigida*
8 — another gelatinous mass on *T. rigida*
9 — green material on dead leaves of *O. spathulata* (on ground)
10 — hard mass growing on dead stump of *Cyathea pubescens*

TABLE 7 qualitatively reflects the major synusia as distributed more randomly. It would appear that moisture, light, and seasonal succession during the wetter months combine to reduce the height effect.

During August, 1966, water from a vascular epiphyte and from the bryophytic tree epiphytes was also sampled. The water from the bromeliad *Vriesea sintenisii* and liquid obtained from squeezing the epiphytic bryophyte sheath on tree trunks was analyzed. In TABLE 8 the species

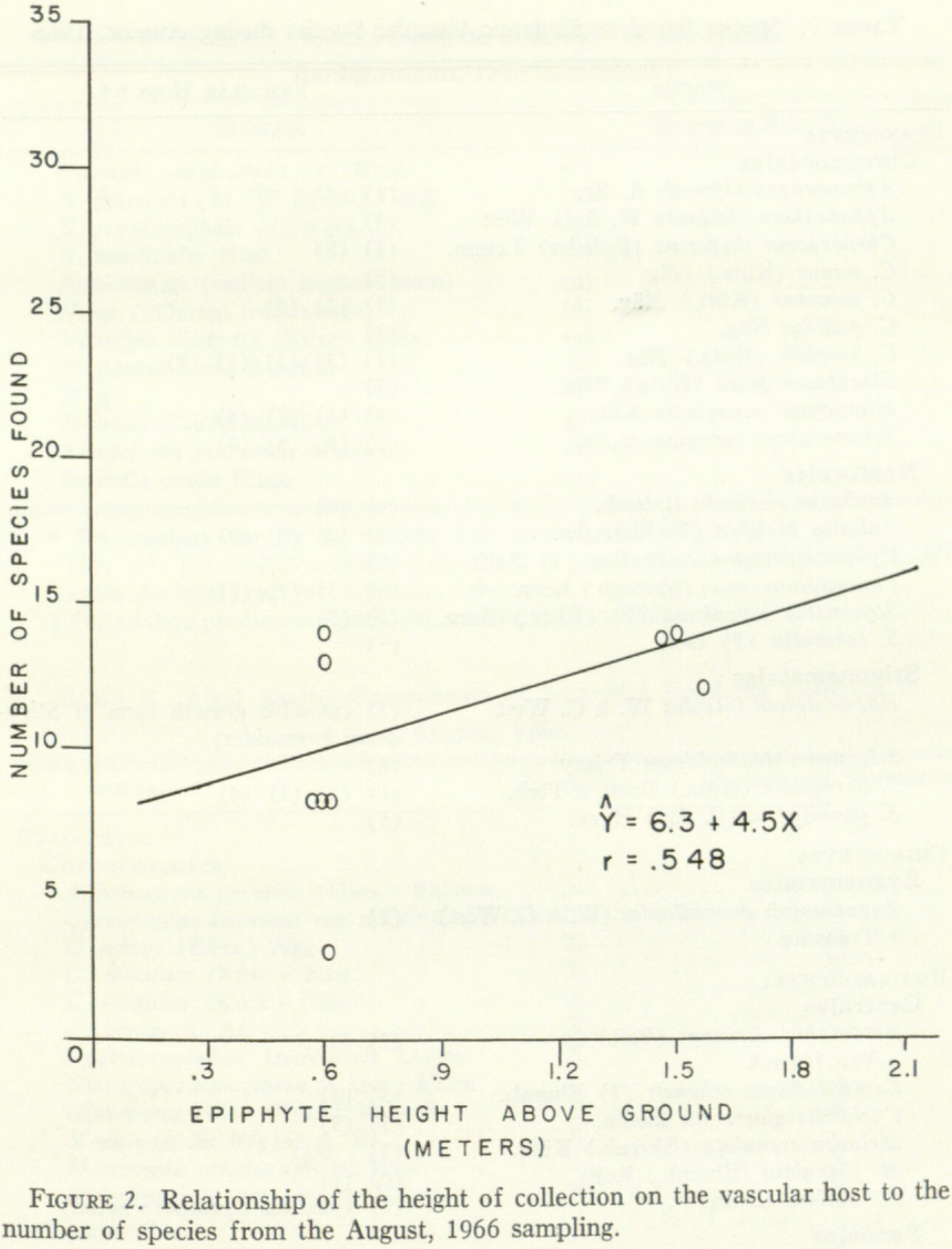

FIGURE 2. Relationship of the height of collection on the vascular host to the number of species from the August, 1966 sampling.

are listed from each sampling. The dominant organisms forming the phyco-synusium in *V. sintenisii* were *Diatoma-Stigeonema-Pithophora*, and the diatom *Diatoma vulgare* was the most prevalent species. The leaves of these epiphytic bromeliads overlap forming a natural catch basin for moisture. The species found in this basin are more predominantly aquatic in nature than species previously reported.

The bryophytic squeezings revealed a synusium dominated by *Diatoma-Eunotia-Chroococcus*. *Diatoma vulgare* was again the dominant species; diatoms were generally more prevalent. The dominance of the

TABLE 7. **Species found on Endemic Vascular Species during August, 1966**

SPECIES	VASCULAR HOST * †
CYANOPHYTA	
Chroococcales	
Aphanocapsa biformis A. Br.	(1) (2)
Aphanothece clathrata W. & G. West	(3)
Chroococcus dispersus (Keissler) Lemm.	(1) (8)
C. minor (Kütz.) Näg.	(5)
C. minutus (Kütz.) Näg.	(1) (3) (5)
C. pallidus Näg.	(3)
C. turgidis (Kütz.) Näg.	(1) (3) (5) (8) (9)
Gloeothece palea (Kütz.) Näg.	(5)
Microcystis aeruginosa Kütz.	(1) (3) (5) (8)
Synecococcus aeruginosus Näg.	(1) (3) (5) (8)
Nostocales	
Anabaena circinalis Rabenh.	(1) (8)
Aulosira prolifica (?) Bharadw.	(1) (2) (5) (9)
Cylindrospermum catenatum (?) Ralfs	(8)
Phormidium tenue (Menegh.) Gom.	(3) (5) (7) (8)
Scytonema javanicum (?) (Kütz.) Born.	(2) (5)
S. schmidtii (?) Gom.	(5)
Stigonematales	
Hapalosiphon luteolus W. & G. West	(3) (possible growth form of *Stigonema hormoides*)
Stigonema dendroideum Frémy	(8)
S. hormoides (Kütz.) Born. & Flah.	(1) (2) (3) (4)
S. panniforme (C. Ag.) Harv.	(5)
CHLOROPHYTA	
Zygnematales	
Zygnemopsis desmidioides (W. & G. West) Transeau	(2)
BACILLARIOPHYTA	
Centrales	
Biddulphia alternans (Bail.) Van Huerck	(2) (4)
Campylodiscus echeneis (?) Ehrenb.	(3) (5)
Cyclotella glomerata Bachn.	(7) (9)
Melosira crenulata (Ehrenb.) Kütz.	(1)
M. granulata (Ehrenb.) Ralfs	(6) (9)
M. varians C. Ag.	(3) (possible auxospore noted)
Pennales	
Cymbella ventricosa Kütz.	(7) (9)
Eunotia exigua (?) (Bréb) Rabenh.	(3) (4) (8)
E. naegelii Mig.	(7) (9)
E. perpusilla (?) Grun.	(4)
E. praerupta Ehrenb.	(3) (9)
E. tenella (Grun.) Hust.	(7) (9)
Frustulia rhomboides var. *capitata* (Mayer) Patr.	(1) (2) (4) (5) (6) (7) (8) (9)
F. rhomboides var. *saxonica* (Rabenh.) DeToni	(2) (4) (9)
F. rhomboides var. *viridula* (Bréb.) Cl.	(8)
Isthmia enervis Ehrenb.	(9)

TABLE 7. **Species found on Endemic Vascular Species during August, 1966** (*continued*)

SPECIES	VASCULAR HOST * †
Navicula carniolensis (?) Hust.	(7)
N. crucicula (?) (W. Smith) Donk	(9)
N. cryptocephala (?) Kütz.	(8)
N. tenelloides Hust.	(4) (6)
Navicula sp. (radiate, capitate form)	(8)
N. sp. (different from above)	(9)
Nitzschia dissipata (Kütz.) Grun.	(4)
N. hantzschiana Rabenh.	(8)
N. sp.	(1) (5)
Pinnularia sudetica Hilse	(7)
Rhopalodia gibberula Mueller	(1) (8) (9)
Surirella ovata Kütz.	(1)

* The numbers identify the vascular host species as follows: (1), (2), (7), (8), *Tabebuia rigida*; (3), (4), (9), *Ocotea spathulata*; (5), *Miconia pachyphylla*; (6), *Cyathea pubescens*.

† For relative position of sample on vascular host see Table 5.

TABLE 8. **Algal Species Components of Non-algal Epiphytes Collected in August, 1966**

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
CYANOPHYTA		
Chroococcales		
Aphanocapsa grevillei (Hass.) Rabenh.	X	
Chroococcus dispersus var. *minor* G. M. Sm.	X	
C. minor (Kütz.) Näg.	X	X
C. minutus (Kütz.) Näg.	X	X
C. turgidus (Kütz.) Näg.	X	X
C. varius A. Br.	X	
Dactylococcopsis fascicularis Lemm.	X	
Gloeocapsa aeruginosa (Carm.) Kütz.		X
Gloeothece palea (Kütz.) Rabenh.		X
Merismopedia elegans A. Br.	X	
Microcystis orissica (?) W. West		X
Synechococcus aeruginosus Näg.	X	X
Nostocales		
Aulosira prolifica Bharadw.		X
Nostoc muscorum C. Ag.	X	
Oscillatoria geitleriana Elenkin		X
O. subbrevis Schmidle		X
Pleurocapsales		
Myxosarcina spectabilis Geitler	X	
Stigonematales		
Hapalosiphon delicatulus W. & G. West	X	
H. welwitschia W. & G. West		X
Stigonema aerugineum Tilden	X	
S. hormoides (Kütz.) Born. & Flah.	X	X
S. minutum (C. Ag.) Hass.		X

TABLE 8. **Algal Species Components of Non-algal Epiphytes Collected in August, 1966** (*continued*)

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
CHLOROPHYTA		
Chaetophorales		
Cephaleuros virescens Kunze		X
Protococcus viridis C. Ag.	X	X
Stigeoclonium polymorphum (?) (Franke) Heering	X	
Trentepohlia aurea var. *tenuior* Brühl & Biswas	X	
T. aurea (L.) Martius	X	
T. torulosa De Wildeman	X	
Chlorococcales		
Characium obtusum (?) Braun	X	
Chlorella ellipsoidea Gern.	X	
Crucigenia quadrata Morren	X	
Pediastrum muticum Kütz.	X	
Trochiscia granulata (Reinsch) Hansg.	X	
Cylindrocapsales		
Cylindrocapsa conferta W. West	X	
Oedogoniales		
Pithophora oedogonia (Mont.) Wittr.	X	
Tribonematales		
Tribonema utriculosum (Kütz.) Hazen	X	
Ulotrichales		
Geminella interrupta Turpin	X	
Zygnematales		
Micrasterias denticulata (?) Bréb.	X	
Mougeotia globulispora Jao		X
Temnogametum transeaui Prescott	X	
Zygogonium ericetorum Kütz.		X
BACILLARIOPHYTA		
Centrales		
Coccinodiscus lacustris (?) Grun.		X
Cyclotella bodanica (?) Eulenst.	X	
Melosira crenulata (Ehrenb.) Kütz.	X	
M. granulata (Ehrenb.) Ralfs	X	
Triceratium semicirculare Brightw.	X	X
Pennales		
Amphora ovalis Kütz.		X
Diatoma hiemale (Roth) Heib.	X	X
D. hiemale var. *mesodon* (Ehrenb.) Grun.	X	
Diatoma tenue var. *elongatum* Lyngb.	X	
D. vulgare Bory	X	X
Eunotia pectinalis f. *elongata* Van Huerck	X	
E. pectinalis var. *minor* (Kütz.) Rabenh.		X
E. soleirolii (Kütz.) Rabenh.		X
E. tenella (?) (Grun.) Hust.		X
Fragilaria brevistriata Grun.		X

TABLE 8. **Algal Species Components of Non-algal Epiphytes Collected in August, 1966** (*continued*)

SPECIES	BROMELIAD	BRYOPHYTE SQUEEZINGS
Frustulia rhomboides var. *capitata* (Mayer) Patr.		X
Hantzschia amphioxys (Ehrenb.) Grun.	X	X
Navicula sp.	X	X
Nitzschia tryblionella Hantzsch.		X
Surirella ovata Kütz.		X
Tropidoneis sp.		X
PYRROPHYTA		
Dinococcales		
Cystodinum cornifax (Schilling) Klebs	X	
TOTAL NUMBER OF SPECIES	42	32

diatoms plus the fact that the trunks of the vascular hosts transmit to the ground 21.4 per cent of the rainfall reaching the forest canopy may be one of the principal factors in determining the presence of this diatom-dominant association.

During February of 1968, mucilaginous material from around aërial roots of *Hedyosmum arborescens* was analyzed for algal components. One sample was fluid, containing a large amount of water, while the second sample was highly consolidated and, in comparison to the other sample, low in water. TABLE 9 compares the algal species found in the two samples differing in moisture content. The sample containing the most moisture (1) has the highest number of species. Species such as *Trentepohlia aurea*, *Melosira varians*, and *Frustulia rhomboides* var. *capitata* are represented in both samples. Throughout the entire study these species have exhibited eurybiont characteristics. The green alga *T. aurea* was the major component in both samples, while none of the other species appeared more than occasionally.

As a gross ecological parameter the height above the ground seems to become a limiting factor to many diatoms and blue-green algae. Height would include the above mentioned factors of light, moisture, and temperature as well as many others. A general shift from a Bacillariophyta-dominated to a Cyanophyta-dominated to a Chlorophyta-dominated algal synusium is noted as samples are taken from points higher above the ground.

In concluding, it is important to compare the regression and correlation analyses of the February-March, 1966, to August, 1966, samples. A shift in environmental utilization is evident. This could be called a seasonal response and it may be a reaction to light attenuation caused by increased cloudiness during August. It is possible that the algal species are re-distributing to a higher portion of the vascular stem in response to a more favorable light condition. Only samples taken at higher levels

TABLE 9. **Algal Species Found among Mucilaginous aërial root secretions of Hedyosmum arborescens**

SPECIES	SAMPLE NUMBER*	
CYANOPHYTA		
Chroococcales		
Chroococcus dispersus (Keissler) Lemm.	1	
C. turgidis (Kütz.) Näg.		2
Microcystis ramosa Bharadw.	1	
Nostocales		
Anabaena circinalis (?) Rabenh.	1	
Aulosira prolifica (?) Bharadw.	1	
Oscillatoria foreaui (?) Frémy		2
Stigonematales		
Stigonema hormoides (Kütz.) Born. & Flah.	1	
CHLOROPHYTA		
Chaetophorales		
Protococcus viridis C. Ag.	1	
Trentepohlia aurea var. *tenuior* Brühl & Biswas	1	2
Chlorococcales		
Chlorella-like	1	
BACILLARIOPHYTA		
Centrales		
Biddulphia alternans (J. W. Bailey) Van Heurck	1	
Melosira varians C. Ag.	1	2
Pennales		
Eunotia fallax Cleve-Euler	1	
Frustulia rhomboides var. *capitata* (Mayer) Patr.	1	2
Navicula cincta (Grun.) Cl.	1	
N. contenta Grun.	1	
Nitzschia parvula Lewis		2
TOTAL NUMBER OF SPECIES	14	6

* Sample (1) refers to a very watery mucoid material, and Sample (2) refers to a very thick and highly viscous mucoid material.

on these stems would help resolve this apparent successional shift. What is important to note is that a shift occurs and that it appears to be related more to light attenuation than to other factors.

In further comparison of FIGURES 1 and 2 it is evident that the number of species has declined. This is reinforced by the number of species reported in TABLES 6 and 7. It would appear that during February-March 1966, a more favorable set of environmental conditions existed than in August when reduction in numbers of species was evident.

Finally, it is important to report other observations concerning distribution of diatoms and green algae. Diatoms have certain water requirements (Lund, 1945). Their distribution on the vascular hosts when samples from February-March, 1966, are compared to August, 1966, may not directly reflect a "wetness" requirement but may be related to the amount and duration of light, which is affected by moisture in the form of clouds and fog. Further, Fritsch (1922) reported *Trentepohlia* to be very resistant to fluctuating moisture. Therefore, *Trentepohlia* dominance higher on the vascular trunk may be related not only to a tolerance for changing moisture but also to a higher light tolerance (or requirement).

In all the investigations of nearly aquatic ground samples and highly moist aërial roots there is a high incidence of diatoms, while samples from drier habitats shift to non-diatom dominant forms. It is reasonable to conclude on the basis of the samples investigated that the large number of algal epiphyte species studied have become successfully established and exist in distinct microhabitats. The algae exhibit seasonal variation in possible response to meteorological conditions. The gross ecological parameter of height above the ground appears to be a proper method of assessing environmental influences in a vertical direction.

SUMMARY

The cloud forest can be likened to a large natural culture unit having uniformly constant meteorological conditions, and, judging from the relatively large number of species found, adequate nutrients. Though all would appear uniform at the first casual investigation, careful analysis indicates that the subaërial algal epiphytes are not uniformly distributed, but are segregated into phyco-synusia. These seem to be microhabitats related to height above the ground and type of host material. The data depict an apparent random horizontal distribution but a less random vertical pattern of distribution. This vertical distribution and apparent seasonal succession pattern appears related to slight changes in meteorological conditions. Samples taken higher on a tree trunk during drier months contain fewer species than those collected closer to the ground. The probability exists that epiphytes located higher above the ground are subjected to greater fluctuations in temperature, moisture, and light. However, the lower parts of a tree trunk are older and perhaps more stable chemically. Further, during wetter months the species-count on the host appears to be rearranged and seasonal species variation appears. During this period increased cloud cover and fog reduce light penetration which may be instrumental in this change.

Subaërial epiphytic algal growth in all samples studied, and especially on the four principle vascular host species in the Luquillo elfin forest on Pico del Oeste, appears not as a uniformly distributed algal veneer, but rather as associations of species representing various intergrading microhabitats.

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