Vegetation change along an altitudinal gradient, Santa Cruz Islands, Galapagos. Volume 7, Number 3 1975

[Washington, D.C.?]: Association for Tropical Biology, 1975

https://digital.library.wisc.edu/1711.dl/SRRNKNT434SX28O

Vegetation Change Along an Altitudinal Gradient, Santa Cruz Island, Galapagos

William G. Reeder and **Susan E. Riechert**[1]

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

Vegetation Change Along an Altitudinal Gradient, Santa Cruz Island, Galapagos

William G. Reeder and **Susan E. Riechert**[1]
Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

ABSTRACT

Quantitative study of the vegetation along a limited altitudinal gradient (183 m rise in 12,900 traverse) on Santa Cruz Island, Galapagos, demonstrates the presence above the coastal mangrove zone of three distinctive zones, the *Cryptocarpus,* arid, and protean (transition) zones. The *Cryptocarpus* (immediate coastline) and arid zones differ only in species composition, while the protean zone vegetation differs from that of the lower altitudes in both species representation and stand organization. The two lower zones are dominated by one or two species; the protean zone contains a larger number of more equitably represented species. Much of the variability of the vegetation is continuous and associated with altitude (39.8%, first canonical variate). Deviation from the altitudinal trend is evidenced in the arid zone vegetation where local patchiness is characteristic. Factors contributing to the continuity include precipitation, evaporation, and substrate, but all associated with altitude. Cover provided by the tree canopy also increases with altitude. Discrete breaks in continuity were observed between zones. This disjunction might result from the effect of steep slopes on the physical environment; it is evidenced wherever a 10-meter rise in altitude occurs in a relatively short distance when compared with the remainder of the gradient. At this scale, few associations were observed among plant species; individual species presumably appear and disappear according to their range of tolerances.

"El Cambio de la Vegetacion a lo Largo del Declive Altitudinal," Isla de Santa Cruz, Galapagos[2]

COMPENDIO

Un estudio cuantitativo de la vegetación a lo largo de un declive altitudinal delimitado (183M aumento altitudinal en un travesero de 12,900M) en la Isla de Santa Cruz, Galápagos comprueba la presencia de tres zonas distintas superiores a la zona litoral de manglares: la zona *Cryptocarpus,* la zona Árida y la zona de Transición. La zona *Cryptocarpus* (contingua al litoral) y la zona Árida se diferencian unicamente en la composición de las especies mientras que la vegetación de la zona de Transición se diferencia de ésa de las altitudes inferiores tanto en las especies representadas como en organización de la comunidad (*Stand*). Las dos zonas inferiores están dominadas por una o dos especies, la zona de Transición incluye mayor cantidad de especies con representación más equitativa. La zonación manifestada por este recuesto está ampliamente relacionada con la casi equitativa representación proporcional y la riqueza de las especies de árboles.

Mucha de la variabilidad de la vegetación es continua y asociada con la altitud [39.8% en la primera variación canónica (canonical variate)]. Desviación de la tendencia altitudinal se manifiesta en la vegetación de la zona Árida, caracterizada por sus manchones locales. Factores que contribuyen a esta continuidad incluyen la precipitación, la evaporación y el porcentaje de pedregal (todos asociados con la altitud). La cubierta formada por el baldaquín de los árboles también aumenta con la altitud. Discretas brechas de continuidad se observaron entre las zonas. Dichas brechas se reflejan más en el carácter total de la comunidad (*Stand*) que en un cambio súbito en la composición de las especies. Este descoyuntamiento aparece donde ocurre un aumento altitudinal repentino dentro de una distancia relativamente corta en comparación con el resto del declive. Sobre este recuesto, las disyunciones no fueron causadas por la exclusión competitiva que pueda suceder en la distancia horizontal limitada, caracterizada por los recuestos precipituosos, sino que fueron causadas por el alto nivel de densidad de los árboles jóvenes ubicados en los recuestos escarpados, en comparación con la disposición clasificada por altura a lo largo del resto del declive. Este aspecto estructural permitióel discernimiento de brechas discretas que de otra manera se hubiera creido que la vegetación cambia continuamente con la altitud. Usando la escala de obtener datos descrita en este informe, pocas asociaciones se observaron entre las especies de plantas; los datos implican que las especies individuales aparecen y desaparecen según su límite de tolerancia.

THE UNIQUENESS OF THE VEGETATION of the Galapagos Islands has been known since the initial reports of Darwin (1840) and the description of endemic plants by J. D. Hooker (1847a,b) and others. Sporadic but occasionally intensive botanical exploration (e.g., Voyage of the H.M.S. Sulphur, 1844-46; California Academy of Sciences Expeditions, 1905-1906; Astor Expedition, 1930; and Galapagos Scientific Project, 1964) has resulted in a satisfactory inventory of species for most of the more accessible islands. The recent publication of the *Flora of the Galapagos Islands* (Wiggins and Porter 1971) has stimulated interest in further study of the island flora (Simkin, Reeder, and MacFarland 1974).

Plant species associations, communities, and zones of similarity have been described for various islands (Steward 1911, 1915; Svenson 1930a, b, 1935; Bowman 1961; Wiggins and Porter 1971). These quali-

---

[1] Present address: Department of Zoology, University of Tennessee, Knoxville, Tennessee 37916, U.S.A.

[2] The government of Ecuador now requires that all papers published on the Galapagos Islands have a Spanish summary.

tative descriptions allow comparison with vegetation elsewhere and permit the Galapagos fauna, vertebrates in particular (*e.g.,* Bowman 1961), to be placed in a vegetative context. There have been few attempts at quantitative description of the Galapagos vegetation, though Itow (1965) related species distributions on the southern slopes of Isla Santa Cruz to altitude and percentage of ground surface covered by lava.

The present study reports on the presence, density, and cover of herbs, shrubs, and trees along a 200 m altitudinal range frequented by the Galapagos tortoise, *Geochelone elephantopus porteri,* on the southern slope of Isla Santa Cruz (fig. 1). This transect runs through the arid and transition zones (of Bowman 1961) to the lowermost *Scalesia* forest. The sea-level mangrove forest, dominated by *Rhizophora* and *Laguncularia,* and the *Scalesia* forest above 183 m altitude were not sampled.

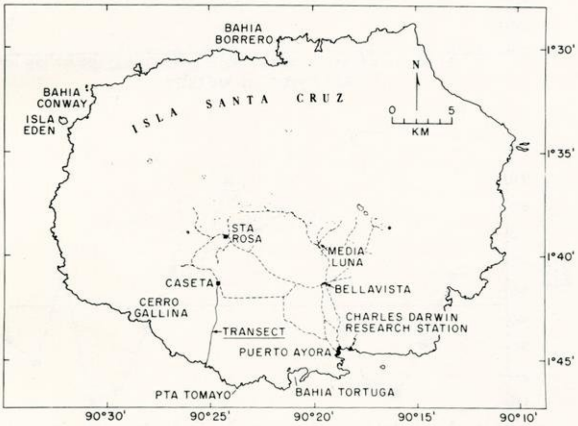


FIGURE 1. Map of Isla Santa Cruz, Galapagos, showing location of caseta-coast transect.

Our interest was in evaluating the usefulness of both field techniques and methods of analysis in describing the character of the Galapagos vegetation (species composition and structure, as measured by presence, size, dominance, and diversity). In addition we wanted to examine changes of vegetation with altitude on this gentle south-facing slope (183 m rise in 12,900 m horizontal distance; mean slope $= 0°48'$) to test whether a continuum (Gleason 1926, 1939), a series of discrete zones (Clements 1905), or a combination of both (Whittaker 1951, 1956; Beals 1969) best characterizes this vegetation. It is intended that this sampling be continued on other slope exposures of Santa Cruz and additional selected islands of the archipelago.

FIELD METHODS

Sampling sites were established at approximately 10 m intervals of altitude along the transect (see fig. 2). At each site, five linearly arranged contiguous 10 x 10 m quadrats were set up to the east of the transect and, so far as possible, along the contour. Within each quadrat all trees and shrubs (>1 m in height) were tallied as to species and height. Overlying trees and shrubs (>1 m tall) were recorded in each 0.5 m interval of a line intercept through the middle of the quadrats and plants (<1 m tall) in each 2 cm interval of the central 2 m. The substrate of 2 cm intervals was classified as being predominantly a) lava rock, b) bare soil, c) litter, or d) fallen wood. Where more than one type was present in a given interval, only the predominant type was tallied. A single oblique photograph of the sample locality was taken from outside the southwest corner of each quadrat, while at each of eight stations (the four corners of each quadrat and four sites chosen by random numbers within each of four 5 x 5 m quarter-quadrats) a vertical photograph of the overhead vegetation was taken with the camera positioned at a standard height of 180 cm.

This sampling sequence was followed for each of the five successive quadrats along the 50 m line at each altitude. The combined data from the five quadrats at each site constituted an altitudinal sample.

RESULTS AND DISCUSSION

NATURE OF SPECIES GROUPINGS: Different views exist as to what information is valuable in characterizing vegetation (Shimwell 1972; Whittaker 1973). In the present study, dominance (importance) values were determined for individual tree species. Dominance is considered here to be the average of relative density, height class, and cover. Relative values were obtained by dividing individual frequencies or densities by the sum of the frequencies or densities of all species in the sample. Figure 2 depicts the change in dominance of species with increasing altitude along the transect. Species exhibiting a dominance value between 0.10 and 0.20 are arbitrarily designated as subdominants while those with values greater than 0.20 are considered dominants. It is apparent from changes in the composition of the dominance ranking that the species representation is highly variable over the altitudinal gradient studied. The coefficient of dissimilarity ($1-2w(a+b)$; Curtis 1956; Beals 1969) was used to measure the degree of change occurring between adjacent altitudes (fig. 3A, B, C). The mean dissimilarity value

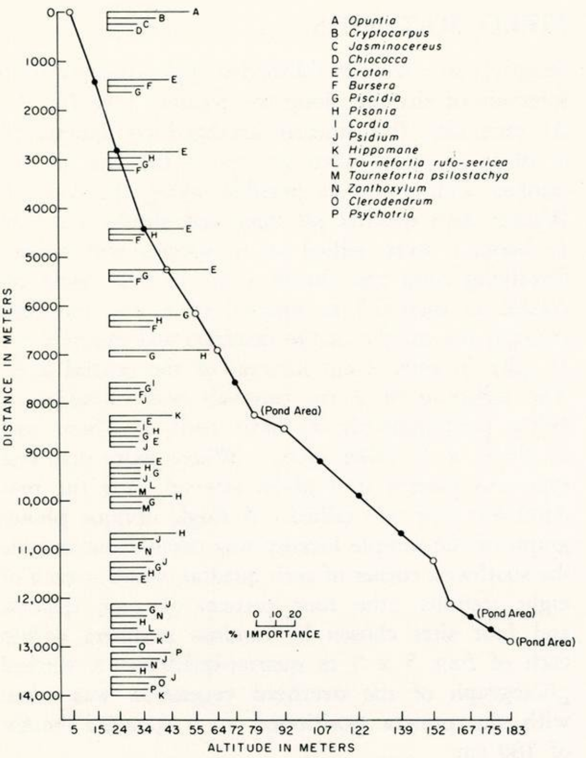


FIGURE 2. An altitudinal representation of species complexes imposed on a plot of sample location (altitude) against linear distance. Relative lengths of the horizontal lines signify species dominance scores. Open-circle locations are those for which exact linear distance measurements are available. Positions of other points along the trail are estimates.

ranged from 0.39-0.58 on a scale of 0-1 in the different samples.

Just inland of the immediate coastline, *Croton scouleri* Hook.f. appears to dominate the lower altitudes (15-43 m) with the taller but less numerous tree species *Pisonia floribunda* Hook.f., *Piscidia carthagenesis* Jacqu. and *Bursera graveolens* (HBK). Trian & Planc. acting as subdominants and changing in relative dominance from one altitude to the next (fig. 2). The coastline vegetation and *Croton*-dominated stands occur within the altitudinal limits (5-40 m) of the arid, coastal-zone vegetation described by earlier authors (Stewart 1911; Bowman 1961; Itow 1965, 1966). Based primarily on collections and observations, Itow (1965) characterized the arid, coastal-zone vegetation as dominated by *Opuntia echios* Howell and *Bursera,* while Bowman (1961) had considered *Opuntia* and *Jasminocereus thouarsii* (Weber) Backg. to be dominant, with *Bursera* and *Maytenus octogona* (L'Her.) DC. forming a continuous understory. Our quantitative assessment indicates that *Opuntia* dominates stand character only along the coast in conjunction with the coastal shrub *Cryptocarpus pyriformis* HBK (fig. 2). Although *Opuntia* does form a low, open forest of arborescent cacti on the coastal plain, its distribution is limited to a relatively narrow zone, most of which was missed in our sampling, since it occurred within the interval between altitudinal samples at 15 and 24 m. It is shown here that the entire zone is best characterized as a dense tangle of *Croton,* which forms an almost continuous low canopy (mean height

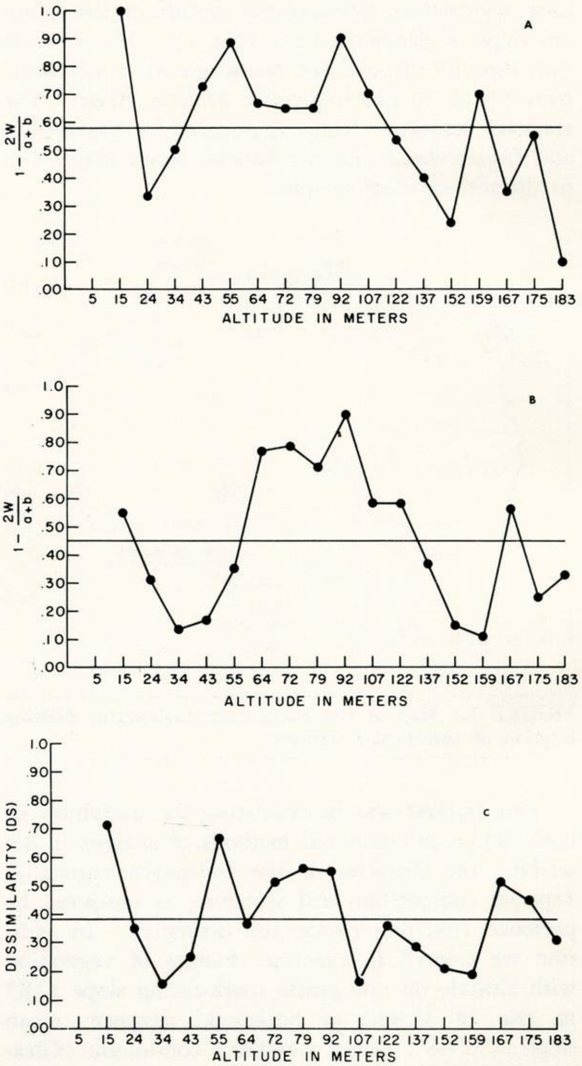


FIGURE 3. Dissimilarity [1-2w(a+b)] of adjacent segments of the altitudinal gradient along the caseta-coast trail based on A) herb cover, B) tree and shrub cover, and C) dominance values. High values signify rapid changes in vegetation, low values signify slower changes. Mean dissimilarity is represented by the horizontal line.

class = 1.5±.53) throughout the area. It is this species which effects the quality of the local environment encountered in the zone.

The remainder of the altitudinal gradient studied on this island differs markedly from the arid zone in organization. Unlike the one to three species representation of the arid zone, throughout the 72-183 m range of altitude, vegetation character is influenced by a number of species (fig. 2); in many transects no one species exerts a dominant influence (≧0.20), but rather a number of subdominants are present. Because of the variability exhibited in the composition of species complexes in this altitudinal range (fig. 3A-C), this area has been termed a transition zone (Stewart 1911, 1915; Bowman 1961). By definition a transition zone is "the population of taxa observable along a gradient between two unlike phytocoenoses" (Kuchler 1973). It implies a directed change from one distinct group of taxa to another. Admittedly, a great deal of change is occurring in species complexes here. The question though is whether this change represents a "phase-out" of the arid, coastal-zone taxa and the introduction of the *Scalesia* forest taxa (edge mixture), or rather represents a synusia of species that merely blends into the other zones at its boundaries. We feel the latter alternative best describes this range of the gradient in which individual species rapidly gain and lose prominence (figs. 2 and 4A-C). For some species this situation denotes a rather sudden appearance, gain in prominence, and disappearance, as seen for example in the shrub *Cordia lutea* Lam. which appears at 64 m, is dominant at 72 m, subdominant at 79 m, and is absent from our transect samples above 92 m (figs. 2 and 4B). Other species may be present throughout most of the transect length, but they exhibit peaks in density and dominance over but a short interval. *Psychotria rufipes* Hook.f. is first encountered at 92 m (fig. 4C), but is dominant only at 175 m (figs. 2 and 4C). Other species show less pattern and occur sporadically along the gradient, because their environmental requirements are not primarily altitudinal. For example, *Hippomane mancinella* L. is present in pond areas (79, 167, and 183 m; figs. 2, 4A) and where clearings were maintained by tortoise and goat activity. In our opinion the term transition zone, while used in the interpretation of Galapagos vegetation for a very long time, is inappropriate and might well be superseded by a term such as protean.

CONTINUITY OF CHANGE: On the basis of structure and composition, the vegetation characterizing the lower altitudes (arid coastal area) seems to differ from that at higher altitudes (protean). We wished to determine whether the vegetation is continuous

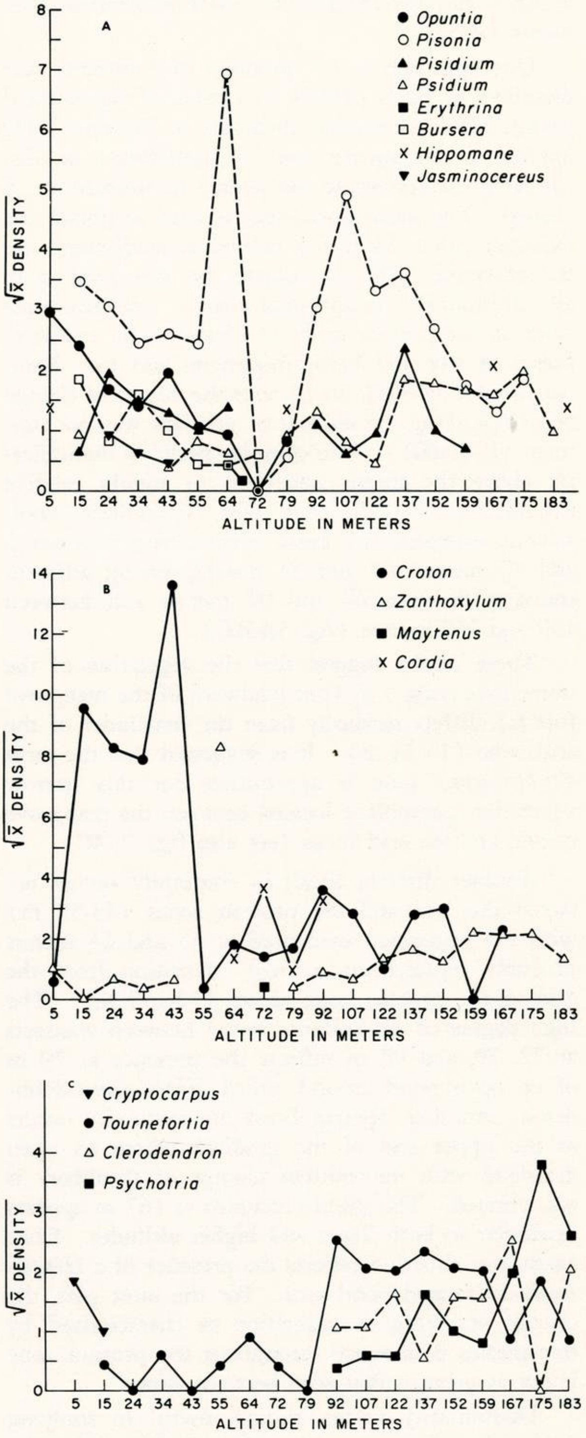


FIGURE 4. Distribution of canopy layer species along the caseta-coast altitudinal gradient. A) trees, B) tree-shrubs, and C) shrubs.

(Gleason 1926, 1939) or whether breaks in vegetational change along the altitudinal gradient occur, which would warrant defining zonal boundaries (Clements 1905).

One approach to the problem of continuity was described by Beals (1969) in a study of vegetational change along altitudinal gradients in Ethiopia. He applied a chi square test to coefficients of dissimilarity to determine the degree of uniformity of change. The mean coefficient is used to obtain the expected value, while the individual coefficients are the observed. The chi square test was applied to all altitudinal, sample-dissimilarity measurements made in the present study [$1-2w/(a+b)$ measurements of tree and herb frequencies and tree dominance value results]. In all cases the degree of change occurring along the altitudinal gradient was not uniform ($P<0.001$). We consider peaks in dissimilarity above the mean coefficient to signify relative disjunction. For the most part, dissimilarity coefficients exceeded the mean dissimilarity between 5 and 15 meters, 43 and 55 meters, among adjacent transects between 64 and 92 meters and between 159 and 167 meters (fig. 3A,B,C).

These results suggest that the vegetation of the immediate coast 5 m (but landward of the mangrove forests) differs markedly from the remainder of the arid zone (15-34 m). It is suggested that the term *Cryptocarpus* zone is appropriate for this narrow vegetation assemblage located between the mangrove coastal and the arid zones (see also figs. 2, 4C).

Another discrete break in continuity occurs between the arid and the protean zones (43-55 m) with the vegetation evidenced at 55 and 64 meters probably representing a "real" transition from the arid to the protean zone above (72-159 m). The high degree of dissimilarity noted between transects at 72, 79, and 92 m reflects the presence at 79 m of an open pond around which *Hippomane* dominates. Another discrete break in continuity occurs at the upper end of the gradient where an open grassland with intermittent clumps of shrubbery is encountered. The species complex at 167 m appears dissimilar to both lower and higher altitudes. Once again, this situation reflects the presence of a *Hippomane*-dominated pond area. For the most part, the change occurring in vegetation as characterized by tree-species dominance throughout the protean zone is not as great as that seen between zones.

Dissimilarity values, though useful in studying uniformity of change, are somewhat biased in that the stands are ordered on the basis of altitude and only adjacent stands are compared. A more powerful test of the influence of altitude on vegetation character is one that assumes no prior ordering and rather arranges stands on the basis of measurements of interstand distances or similarities using a number of different variables. Such methods of analysis are the multivariate methods: canonical analysis, ordination, and association analysis. Canonical analysis (Seal 1964) separates similar transects from less-similar transects by making maximum the between-transect variance while taking into account the pooled within-transect variances of a number of variates (*e.g.*, tree and herb species frequencies, tree density, and mean height class). It considers all weighted averages as linear combinations of the original variates and finds the ordering that makes maximum the spread of the mean of the transects on the real line, measured in units of the within-transect standard deviation. $Y = a'x = a_1x_1 + a_2x_2 + \dots + a_px_p$, where the a_i ($i = 1 \dots, p$) are the coefficients of the linear combination (Seal 1964).

When more than two samples are involved in the analysis, N-1 canonical variates are possible where N equals the number of samples. A restriction is placed on subsequent canonical variates such that sample correlation between the variates is zero. Thus the various canonical variates are defined as statistically independent of one another and contain different information; the first canonical variate offers more information than the second, and each subsequent variate accounts for less variance until all of the significant variability is explained. The variates used in the present study for canonical analysis are ranked in table 1 on the basis of their individual usefulness in discriminating among samples (a ratio of among-sample variance to within-sample variance). Figure 5 depicts the results of the best linear combination of the weighted variates (first canonical variate) plotted against altitude. This first canonical variate accounts for 39.8 percent of the total between-sample variance. Differences in stand representation based on this first canonical variate are clearly related to the altitudinal gradient with discrete breaks occurring between 5 and 15, 43 and 55, and 167 and 175 meters. The range between 55 and 167 meters shows a remarkable continuity in change from one altitude to the next. However, the open-pond area represented at 79 meters is separated from the other species complexes in the protean zone, and greater irregularity occurs at the bottom of this zone than at higher altitudes. These results closely coincide with those observed from the dissimilarity measures. The arid-zone group of samples (15-43 m) shows the greatest deviation from the trend of increased canonical score with rise in altitude. We attribute this deviation to local patchiness noted throughout the arid region.

TABLE 1. *Initial canonical characters ranked according to usefulness in discriminating among species complexes. Significance levels represent results of univariate F test.*

	Character	F	Probability
1	Total Tree and Shrub Density	30.82	< 0.000
2	Total Herb Cover	30.23	< 0.000
3	Density *Croton scouleri*	26.42	< 0.000
4	Frequency *Justicia galapagana*	23.16	< 0.000
5	Frequency Lava	20.04	< 0.000
6	Frequency Litter	14.57	< 0.000
7	Frequency *Scleria pterota*	14.35	< 0.000
8	Height *Croton scouleri*	10.19	< 0.000
9	Density *Psychotria rufipes*	7.93	< 0.000
10	Density *Opuntia echios*	7.52	< 0.000
11	Density *Pisonia floribunda*	6.68	< 0.000
12	Height *Pisonia floribunda*	6.41	< 0.000
13	Height *Opuntia echios*	6.21	< 0.000
14	Height *Clerodendrum molle*	6.16	< 0.000
15	Density *Tournefortia rufo-sericea*	6.10	< 0.000
16	Density *Galactia tenuiflora*	5.94	< 0.000
17	Height *Psidium galapageium*	5.62	< 0.000
18	Height *Galactia tenuiflora*	5.51	< 0.000
19	Height *Psychotria rufipes*	5.36	< 0.000
20	Height *Bursera graveolens*	5.33	< 0.000
21	Height *Hippomane mancinella*	5.31	< 0.000
22	Density *Cryptocarpus pyriformis*	5.16	< 0.000
23	Frequency Bare Ground	4.59	< 0.000
24	Frequency *Salvia occidentalis*	4.57	< 0.000
25	Density *Zanthoxylum fagara*	4.29	< 0.000
26	Height *Cryptocarpus pyriformis*	4.25	< 0.000
27	Density *Hippomane mancinella*	4.21	< 0.000
28	Density *Bursera graveolens*	4.14	< 0.000
29	Frequency *Psychotria rufipes*	3.73	< 0.000
30	Height *Ipomoea nil*	3.43	< 0.000
31	Height *Jasminocereus thouarsii*	3.38	< 0.000
32	Height *Piscidia carthagenesis*	3.17	< 0.000
33	Height *Tournefortia rufo-sericea*	3.06	< 0.000
34	Frequency *Stenotaphrum secundatum*	2.87	< 0.000
35	Density *Ipomoea nil*	2.86	< 0.001
36	Density *Psidium galapageium*	2.62	< 0.002
37	Total Canopy Cover	2.47	< 0.004
38	Frequency *Cissus sicyoides ?*	2.45	< 0.004
39	Density *Jasminocereus thouarsii*	2.17	< 0.012
40	Frequency *Blechum brownei*	1.96	< 0.026
41	Density *Clerodendrum molle*	1.85	< 0.038
42	Height *Zanthoxylum fagara*	1.56	< 0.098
43	Density *Piscidia carthagenensis*	1.28	< 0.232
44	Frequency Wood	1.07	< 0.399
45	Density *Maytenus octogona*	1.00	< 0.469
46	Frequency *Portulaca oliacea*	1.00	< 0.490
47	Density *Erythrina velutina*	0.94	< 0.531

FACTORS CONTRIBUTING TO CHANGE: Canonical results demonstrate a fairly continuous variation in vegetation which is highly correlated with an altitudinal gradient (fig. 5); this and other measures indicate that discrete breaks occur in this continuity at specific altitudes. Diverse factors might account for the observed patterns of change in vegetation along the caseta-coast transect. The altitudinal gradient, accounting for much of the among-transect-sample variability (39.8%), could reflect the gradual change of number of parameters of the physical environment; differences may exist in climatic factors, *i.e.*, rainfall, temperature, wind velocity, solar radiation, or in topography or substrate. One or a combination of these factors might limit plant-species distributions. The pattern of change might also reflect plant-species competition along the gradient, competitive exclusion (Gause and Witt 1935; Hutchinson 1953; Beals 1969).

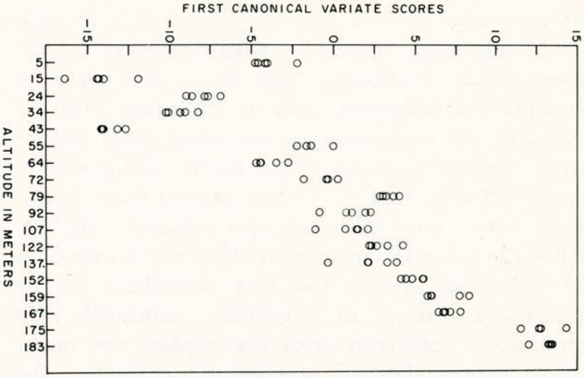


FIGURE 5. First canonical variate scores for individual quadrat samples plotted against altitude.

In a previous study, Itow (1965) found that the distribution of several plant species was correlated with the percentage of lava substrate present. The range of percent lava over which the various species occurred was broad in most cases (spread of between 20 and 70 percentage points). It is difficult to determine from those data whether plant distributions were directly related to the available substrate or to some other factor whose properties changed with altitude as well. One method of discerning the factors which influence plant-species distribution is to determine the dependence of plant-species associations on physical factors by systematic removal of the significance contributed to the associations by single factors (Beals 1965; Riechert and Reeder 1973). Beals (1965) found that chi square associations due to common or different preferences of a factor could be eliminated, if samples were grouped according to the presence or absence of the particular factor, and if the expected values for joint occurrences were determined for the individual groups. The chi square value for the 2 X C table would then result from the summation of individual values for all groups. Chi square tests demonstrated 16 significant associations between plant species (table 3). Three of these associations were attributed to altitude (probably a combination of factors associated with change in altitude), and only one to substrate, the negative association ($P<0.001$) noted between *Croton* and *Bursera*. *Bursera* was limited in its distribution to altitudes below 79 meters, the point at which a discrete break in an otherwise continuous decrease in percentage of lava substrate occurs with increase in altitude (figs. 4A and 5) whereas *Croton* was far more widely distributed (fig. 4B). The break in continuity of substrate cover at 79 meters (fig. 6) disclosed the correlation of two other plant species with substrate character. The shrubs *Clerodendrum* and *Psychotria* (fig. 4C) were present only at altitudes where litter was the major substrate (fig. 6). Although substrate appears to affect the distribution of individual species and may contribute to the continuous change in vegetation associated with altitude, it apparently does not explain the major discontinuities observed in vegetation character. An exception is the discontinuity observed at 79 meters which is related to the predominance of bare ground in the pond area (fig. 6).

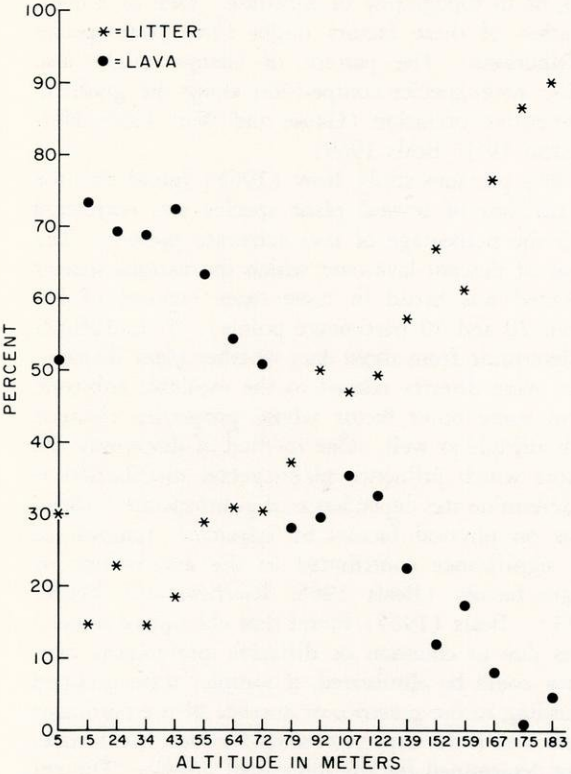


FIGURE 6. Variation of substrate types with altitude. Only the two dominant substrates, lava and litter, are included here. Values represent percentage of cover.

The three plant-species associations related to altitude included positive correlations ($P < 0.001$) between *Cryptocarpus* and *Opuntia* and between *Psychotria* and *Scleria* and a negative association between *Clerodendrum* and *Psychotria.* The entire population of *Cryptocarpus* was found within the limits of the distribution of *Opuntia* (fig. 4A and C), while *Psychotria* and *Scleria* were both limited to higher altitudes (figs. 4C and 6; table 2). *Clerodendrum* and *Psychotria* were negatively associated even though both were present from 92-183 m, because where one was very dense, the other was sparse (fig. 4C). The performance of these two species in association with one another is indicative of interspecific competition as discussed by Skellam (1951). They are able to coexist in an equilibrium that depends on such factors as their patterns of distribution and densities. By eliminating the altitude factor, the variability in their densities was removed, and their negative association was no longer significant. Associations of this type might account for some of the continuous change observed; they do not explain the discontinuities.

According to Alpert (1962) "the areal distribution of the (Galapagos) vegetation reflects the area rainfall distribution." As with substrate, precipitation and evaporation were found to vary continuously along the altitudinal gradient. From weather stations maintained along the caseta-coast trail (data from C. MacFarland) and from measurements recorded at the Charles Darwin Research Station, precipitation increased with altitude (ann. diff. betw. 0 & 200 m = 230.2 mm), while evaporation decreased (ann. diff. betw. 55 & 200 mm = 815.2 ml). We were unable to discern specific breaks in continuity along these moisture gradients at the level of measurement. We, thus, assume that climatic factors and substrate, although undoubtedly influential in effecting the gradual vegetation change from one altitude to the next, are not responsible for the breaks in continuity observed between the arid and the protean zone nor between the protean zone and the meadow area bordering the *Scalesia* forest zone.

The results of the second canonical variate suggest the cause of the observed discontinuities (fig. 7). The second variate, accounting for 17.5 percent of the total variance, separates 34-, 43-, 92-, 15-, 175-, and 183-meter samples from the remainder of the altitudinal gradient. These samples (excepting 152 m) represent altitudes at which greatest discontinuity is observed (figs. 3, 4, 5), and all (except 152 m) exhibit a 10-meter rise in altitude over a relatively short distance when compared with altitudinal samples along the remainder of transect (fig. 2). The discontinuities between 43 and 55 m and between 167 and 175 m, therefore, appear to represent slope effects. The physical environment by the steep slopes clearly differs from the more gentle slopes in terms of water runoff and soil deposition. The plant species themselves (Beals 1969) may impose disjunctions on a steep slope; increased competition

TABLE 2. *Altitudinal change in herb species frequency (percent). (Individual expected values for removal of the factor "altitude" were computed within the quadrat samples (altitude). Those for substrate were determined from groups of quadrat samples demonstrating similar substrate composition,* i.e., *predominantly litter, lava, or bare ground.)*

	5	15	24	34	43	55	64	72	79	92	107	122	137	152	159	167	175	183
Acacia rorudiana								5.2										
Alternanthera halimifolia						.4	.4	.8	.6		1.2	7.4	6.2	1.8	5.6	2.8	9.6	
Bastardia viscosa					1	1.8	.8	1										
Blechum brownei															5.0	21.4	22.6	1.0
Boerhaavia erecta		4.2	7	2.8														
Castela galapageia	.6																	
Cissus sicyoides								1.8	1.4	1	.4							
Clerodendrum molle												.2		1	13.6	10.6		7.8
Croton scouleri				1.4	4.8													
Desmodium canum										.6		1	.6	.8		2.4	1	5.4
Desmodium procumbens															.2	.2		.2
Fleury aestuans									.6			6.8			6.4	3		
Galactia tenuiflora								.4		1	10.6	17.2	8	.6	13.8	.6	4.2	
Ipomoea nil						4.4		.6		.4	.6	2.2	.6	.6	4.6		.6	12.4
Ipomoea triloba						1.6				2.8								
Justicia galapagana													.2	9.6	16.6	16.6	100	47.8
Momordica charantia		1.4				.8							1.6	1	4.6	4.2	1.6	2
Oplismenus setarius						.8	1.6		1		.2		2	1.8	6.2	.6	.8	
Opuntia echios						.4												
Phyllanthus caroliniensis												.2		.6				
Pisonia floribunda							1			.4	.6	.8						
Psychotria rufipes														.4		8.2	10.8	10.8
Salvia occidentalis												6	1.6					
Scleria pterota																		84.4
Solarum nodiflorum															.2	1	.4	.2
Stenotaphrum secundatum									1.4									
Tournefortia psilostachya												1.6						
Tournefortia rufo-sericea															4.8		2.8	
Zanthoxylum fagara									.6									

might occur where little marginal habitat is offered for mutual invasion by similar species. At least the former of these possibilities seems to be operating in the present study, since differences in the structure of the species complexes can be seen between the steep-slope samples and the remainder of the gradient. Semilog plots of percent of stand representation of tree-height classes show a much higher representation of small-height-class individuals on steep slopes than on other parts of the gradient (fig. 8A, B, C). With greater runoff of water one would expect less growth on these slopes and therefore smaller trees. In addition, steep slopes tend to be more open than gentle slopes and thus might exhibit greater seedling production (Beals, personal communication). The operation of physical-slope effects on vegetation character does not necessarily exclude disjunction due to plant-species competition. Both factors might influence the discontinuity observed on these steep slopes.

TRENDS: Analysis of the vegetation of this altitudinal gradient has disclosed several generalities or trends in vegetation character. A striking feature of the vegetation as a whole is the apparent paucity of associations among plant species. Of the 72 species encountered in the samples, only 16 significant associations were found to exist (table 3). This situation might well be expected along an altitudinal gradient where individual species appear and disappear according to their ranges of tolerance. It is probably indicative of the variability in physiological capabilities of plants at the species level and is one expression of their distributional individuality according to Gleason's principle (Gleason 1926, 1929).

Some general observations can be made concerning plant-species diversity along the gradient as well. Various diversity measures were performed on the vegetation samples. These included (table 4): the

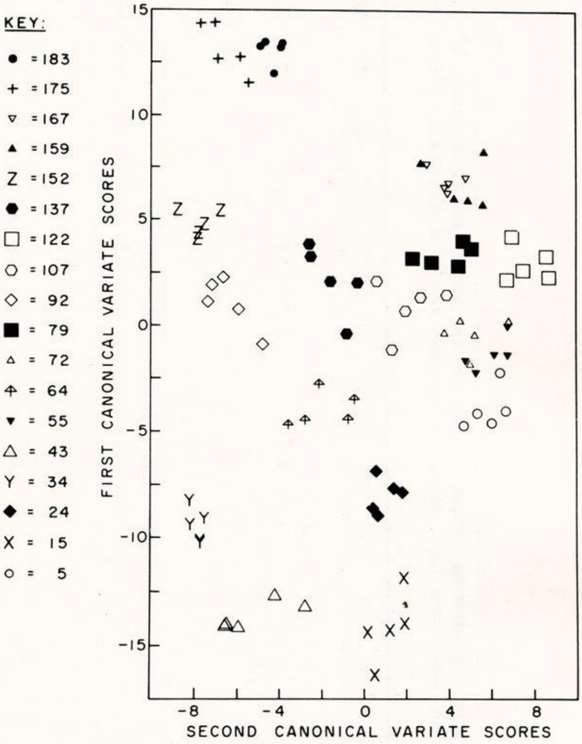
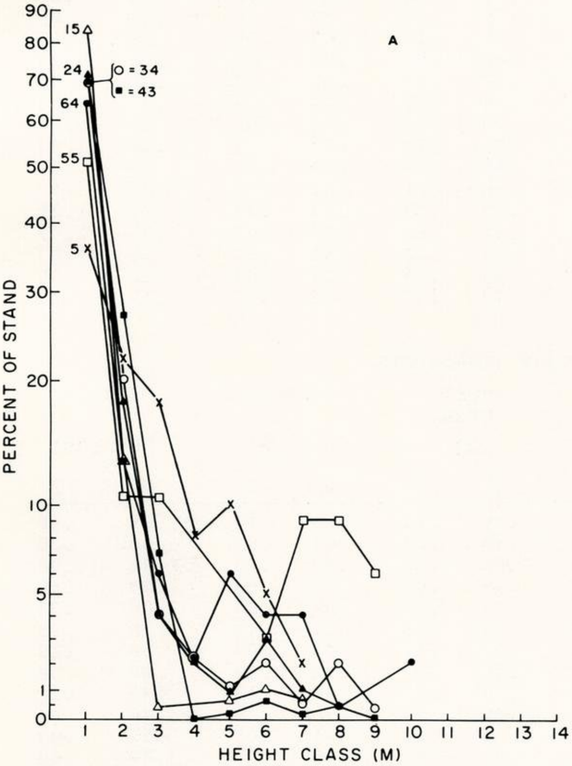


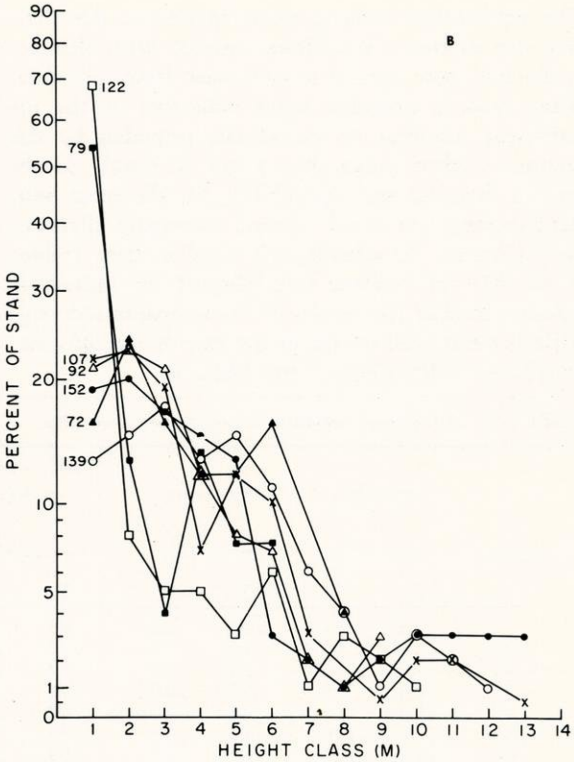
FIGURE 7. Second canonical variate scores plotted against those of the first. Symbols indicate altitudinal samples.

TABLE 3. *Plant species associations before and after factor removal.*

Species associations	Chi square probability	After factor removal	
		Altitude	Substrate
Blechum - Hippomane	− P < 0.001	P < 0.001	P < 0.001
Blechum - Zanthoxylum	+ P < 0.001	P < 0.001	P < 0.001
Bursera - Croton	− P < 0.001	P < 0.001	NS
Clerodendrum - Justicia	− P < 0.001	P < 0.001	P < 0.001
Clerodendrum - Psychotria	− P < 0.001	NS	P < 0.001
Clerodendrum - Zanthoxylum	+ P < 0.001	P < 0.001	P < 0.001
Croton - Pisonia	− P < 0.001	P < 0.001	P < 0.001
Cryptocarpus - Opuntia	+ P < 0.001	NS	P < 0.001
Erythrina - Pisonia	+ P < 0.001	P < 0.001	P < 0.001
Hippomane - Cissus	− P < 0.001	P < 0.001	P < 0.001
Justicia - Psychotria	+ P < 0.001	P < 0.001	P < 0.001
Justicia - Scleria	− P < 0.001	P < 0.001	P < 0.001
Justicia - Tournefortia rufo-sericea	− P < 0.001	P < 0.001	P < 0.001
Psidium - Psychotria	+ P < 0.001	P < 0.001	P < 0.001
Psychotria - Scleria	+ P < 0.001	NS	P < 0.001

diversity indices combining species richness and equitability devised by Simpson (1949), McIntosh (1967), and the Hbar of Shannon and Weaver (1949); a measure of equitability (Evar) proposed by Peet (1971); and two measurements devised by Hurlbert (1971) to estimate 1) the probability of intraspecific encounter (Delta 2) and 2) a ratio of the probability of interspecific to intraspecific encounter (Delta 4). These measures were applied to individual and combined herb- and tree-frequency values and tree-density counts from the quadrat samples. A trend test (Cox and Stuart 1955) computed on sample values ranked according to altitude in all cases indicated a significant increase in tree-species diversity and the probability of interspecific encounter over intraspecific encounter of the species with increase in altitude (table 4). By its nature the trend test compares the upper half of the gradient to the lower (in this case the protean zone to the arid and *Cryptocarpus* zones). In actuality, the results reflect the difference in diversity existing between the upper and lower zones rather than necessarily asserting a trend of increased diversity with increasing altitude.





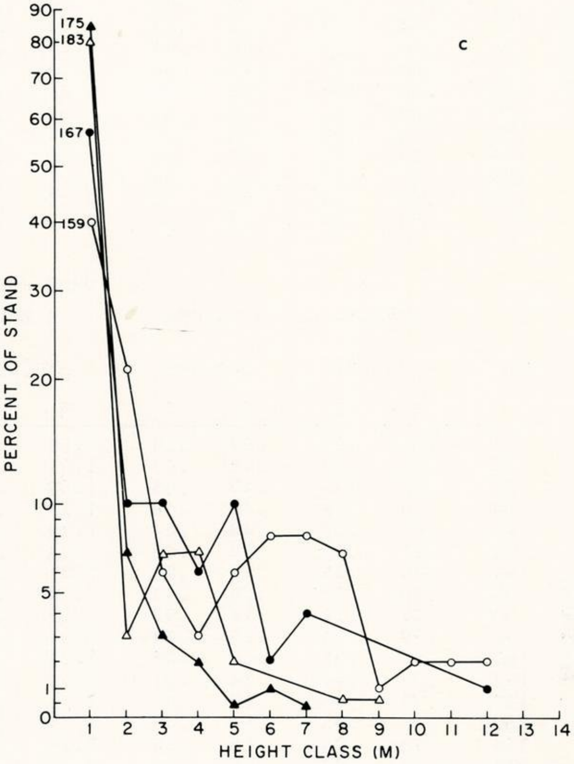


FIGURE 8. Semilog plot of percentage of stand representation versus tree-height class. A) 5–64 meters altitude, B) 72–152 meters altitude, and C) 159–183 meters altitude.

The equitability measure when applied to tree density also showed a significant increase with altitude. It did not show a trend to exist with frequency data. This result is probably more indicative of the insufficient numbers of individuals provided by the transect method rather than a lack of trend. Herb-species diversity and equitability, for the most part, demonstrated no trend toward increasing diversity with altitude. In actuality the trend is there (tables 2 and 4); the extreme variability of the individual samples masked the results of the nonparametric significance test used except in the case of the information-based index (Hbar) and Delta 4.

The observed increase in species richness and equitability from the arid zone to the protean zone is reasonable when one considers that available moisture increases with altitude and, therefore, more mesic conditions are approached in the protean zone. The extremes of any moisture gradient, in general, are more restrictive (Curtis 1956), and one would expect to find fewer species inhabiting the arid zone than as one approaches the more mesic conditions in the protean zone. Greater equitability in vegetation was also observed in the protean zone than in the arid zone (table 4). It is possible that competition in this area of species complexity is involved in

TABLE 4. ***Altitudinal variation in vegetation diversity.***

ALL TRANSECT VEGETATION

ALTITUDE	SIMPSON		MCINTOSH		H BAR		PEET EVAR		DELTA 2		DELTA 4	
Sign.	p<0.001		p<0.001		p<0.001		p<0.1		p<0.001		p<0.001	
	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±
5	.47	.11	.47	.12	.02	.28	.83	.10	.43	.11	.17	.31
15	.76	.02	.76	.02	.07	.12	.91	.02	.73	.02	.29	.39
24	.68	.02	.68	.02	.82	.07	.78	.04	.66	.02	.20	.27
34	.65	.08	.65	.08	.71	.28	.77	.10	.63	.08	.49	.81
43	.72	.06	.72	.06	.07	.23	.79	.08	.70	.06	.04	.61
55	.68	.06	.68	.06	.95	.21	.67	.10	.68	.05	.58	.67
64	.63	.07	.63	.07	.80	.25	.66	.08	.60	.07	.06	.43
72	.67	.02	.67	.02	.59	.06	.79	.07	.65	.04	.06	.18
79	.54	.14	.54	.14	.30	.43	.64	.19	.47	.13	.02	.72
92	.86	.01	.86	.01	.89	.18	.90	.02	.84	.01	.52	.88
107	.84	.02	.80	.06	.79	.22	.91	.02	.82	.03	.12	1.44
122	.82	.02	.64	.03	.82	.13	.88	.03	.82	.02	.32	1.01
137	.85	.01	.68	.01	.07	.08	.88	.01	.84	.01	.99	.43
152	.74	.07	.55	.07	.54	.27	.77	.09	.73	.07	.02	1.21
159	.88	.02	.70	.03	.35	.18	.91	.02	.87	.02	.88	1.49
164	.85	.03	.66	.04	.25	.23	.87	.04	.84	.03	.70	1.42
175	.67	.04	.45	.03	2.30	.12	.69	.05	.66	.04	.12	.32
183	.73	.06	.53	.06	2.60	.24	.77	.07	.73	.06	.49	.83

TREE FREQUENCY (TRANSECTS)

ALTITUDE	SIMPSON		MCINTOSH		H BAR		PEET EVAR		DELTA 2		DELTA 4	
Sign.	p<0.001		p<0.001		p<0.001		NS		p<0.001		p<0.001	
	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±
5	.31	.13	.24	.10	.66	.27	.78	.14	.28	.12	.68	.30
15	.64	.04	.48	.03	1.51	.17	.88	.03	.61	.05	1.90	.30
24	.55	.05	.40	.05	1.37	.18	.69	.08	.53	.05	1.41	.38
34	.54	.09	.40	.08	1.27	.28	.79	.08	.52	.08	1.59	.59
43	.65	.05	.48	.04	1.72	.13	.75	.08	.64	.05	2.06	.33
55	.11	.11	.08	.08	.24	.24	.94	.06	.11	.11	.25	.25
64	.45	.05	.31	.04	1.05	.12	.54	.11	.43	.05	.88	.19
72	.35	.14	.26	.11	.74	.31	.90	.07	.32	.13	.86	.38
79	.21	.12	.14	.08	.53	.31	.70	.17	.20	.12	.35	.21
92	.78	.04	.63	.04	2.26	.24	.88	.03	.75	.05	4.20	.71
107	.76	.05	.59	.06	2.22	.26	.88	.03	.74	.05	3.92	.93
122	.72	.04	.54	.04	2.03	.14	.81	.07	.70	.04	2.87	.60
137	.70	.05	.52	.05	2.01	.22	.75	.07	.68	.06	2.70	.61
152	.72	.05	.53	.05	2.14	.16	.79	.07	.70	.05	2.97	.60
159	.75	.06	.58	.06	2.26	.22	.82	.08	.73	.06	3.70	.87
164	.72	.07	.56	.06	2.11	.24	.78	.12	.70	.07	3.23	.71
175	.74	.02	.56	.02	1.99	.10	.85	.02	.71	.02	2.85	.28
183	.55	.14	.41	.10	1.38	.36	.88	.05	.53	.13	1.81	.53

equalizing species numbers.

In addition to trends in moisture, productivity, and amount of litter accumulation, there was an increase in percentage of canopy cover with increasing altitude. Figure 9 is a graphic representation of the two measures of cover used in the study, line intercept and photographic. The line-intercept method suggests that tree cover is high at most altitudes, excepting the more open areas associated with steep slopes or ponds (figs. 2 and 9). This method portrays cover as the presence of some part of a tree within an interval (50 cm). It does not provide information as to the quality of the cover and in addition overestimates the existing cover when compared with the results of the photographic method (fig. 9). The line-transect-cover measure only partially reflects canopy cover in that it appears to yield high values whether sampling dense canopy or high individual numbers, factors which are not biologically equivalent.

On the other hand the pattern of change in canopy cover with altitude using the photographic

TABLE 4. (Cont'd.)

HERB FREQUENCY (TRANSECTS)

ALTITUDE	SIMPSON		MCINTOSH		H BAR		PEET EVAR		DELTA 2		DELTA 4	
sign.	$p<0.05$		$p<0.1$		$p<0.001$		NS		$p<0.001$		$p<0.05$	
	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±
5	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
15	.48	.04	.37	.03	.89	.05	.77	.10	.43	.03	.95	.12
24	.11	.11	.09	.09	.20	.20	.99	.01	.10	.10	.27	.27
34	.19	.13	.14	.09	.40	.23	.52	.29	.17	.11	.31	.23
43	.40	.13	.31	.11	.70	.24	.74	.25	.34	.12	.68	.28
55	.77	.02	.64	.03	1.85	.09	.78	.06	.70	.02	3.40	.30
64	.70	.06	.60	.06	1.48	.20	.87	.05	.61	.06	2.76	.62
72	.44	.23	.36	.19	1.24	.64	.98	.01	.38	.20	1.42	.87
79	.54	.18	.47	.16	1.04	.44	.98	.03	.44	.16	2.06	.86
92	.80	.06	.71	.08	1.56	.28	.71	.19	.61	.05	3.29	.63
107	.48	.14	.38	.11	1.17	.36	.75	.10	.45	.13	1.65	.81
122	.67	.05	.49	.05	1.80	.18	.78	.04	.65	.04	2.28	.48
137	.70	.05	.53	.05	2.06	.24	.72	.06	.67	.04	2.85	.96
152	.51	.11	.39	.10	1.27	.29	.32	.17	.45	.10	1.44	.48
159	.78	.04	.59	.05	2.55	.19	.85	.06	.77	.04	4.14	.78
164	.76	.05	.56	.05	2.55	.23	.80	.06	.75	.05	3.93	.98
175	.54	.05	.35	.04	1.72	.10	.58	.07	.54	.05	1.28	.27
183	.66	.08	.46	.07	2.14	.26	.71	.09	.66	.08	2.55	.67

TREE DENSITY (QUADRATS)

ALTITUDE	SIMPSON		MCINTOSH		H BAR		PEET EVAR		DELTA 2		DELTA 4	
Sign.	$p<0.001$		$p<0.001$		$p<0.001$		$p<0.001$		$p<0.001$		$p<0.001$	
	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±	$\bar{X}$	±
5	.54	.05	.41	.05	1.21	.16	.71	.08	.50	.04	1.31	.28
15	.20	.04	.12	.05	.32	.20	.19	.05	.20	.04	.27	.06
24	.41	.10	.27	.07	1.20	.26	.43	.10	.41	.09	.90	.31
34	.34	.08	.21	.05	1.06	.24	.30	.09	.33	.08	.61	.19
43	.14	.04	.08	.03	.49	.11	.21	.08	.14	.04	.18	.06
55	.69	.11	.60	.14	1.35	.17	.40	.17	.53	.06	2.48	1.65
64	.30	.07	.19	.05	.98	.21	.22	.08	.30	.07	.50	.15
72	.83	.06	.75	.08	1.97	.15	.39	.18	.70	.04	5.22	2.97
79	.66	.09	.62	.02	2.50	.09	.46	.15	.57	[illegible]	2.52	.75
92	.79	.02	.55	.10	1.48	.20	.81	.02	.77	.02	3.94	.37
107	.65	.07	.48	.07	2.01	.20	.65	.11	.64	.07	2.42	.65
122	.74	.06	.59	.07	2.21	.24	.74	.09	.71	.06	3.77	1.06
137	.82	.04	.65	.05	2.80	.19	.83	.04	.80	.03	5.53	1.48
152	.81	.05	.66	.06	2.63	.23	.81	.07	.79	.05	5.72	1.53
159	.81	.02	.66	.03	2.33	.11	.81	.05	.77	.02	4.31	.46
164	.71	.08	.55	.08	2.07	.36	.80	.05	.68	.08	3.45	.98
175	.67	.04	.50	.04	1.73	.17	.78	.03	.65	.04	2.21	.42
183	.65	.10	.52	.10	1.78	.27	.62	.13	.61	.09	2.79	.90

* Significance levels represent results of Cox and Stuart (1955) Trend Test computed on individual sample values. Only sample means are presented here.

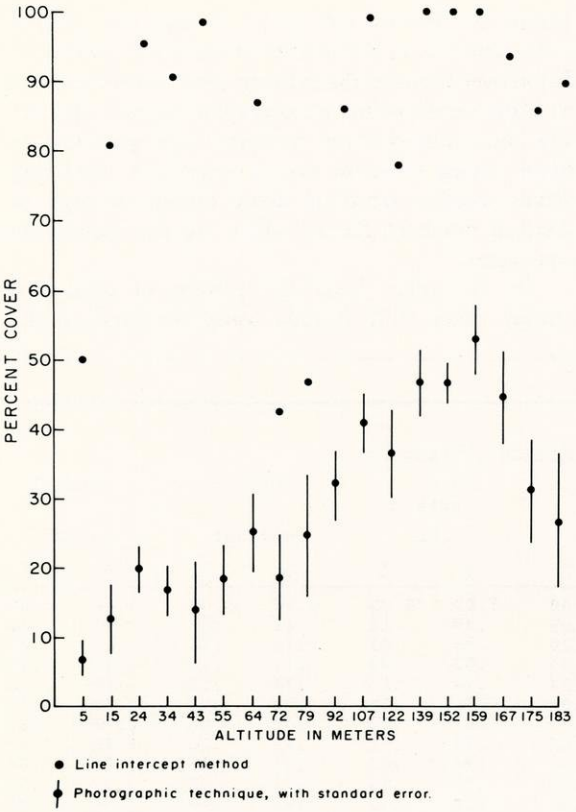


FIGURE 9. Graph of canopy cover plotted against altitude using two measures, line intercept (mean value) and photographic scanning.

method demonstrates finer discrimination than the line-intercept method. The scanning unit consisting of a KGM 113T camera (KGM Vidraids, Ltd), a Tektronix R4501 scan converter (Tektronix, Inc.), and a Data Craft 6024/5 computer, used to analyze the cover photographs, placed all sampled densities in a given photograph on a relative voltage scale of 1 to 10. Percentage of cover was evaluated by determining the percentage of 135,000 sampling points belonging to each of the 10 density levels. The photographic-cover percentage represents an actual value of the mosaic of cover (usefully allowing evaluation of light penetration through the canopy) as opposed to those methods which estimate total cover by presence or absence within a limited number of line segments. The photographic-cover measure suggests a trend toward increased percentage of cover with increasing altitude through the arid and protean zones (fig. 9). The high standard error exhibited in percentage of cover in the relatively open areas (79, 175, 183 m) signifies a dense cover provided by the sparsely distributed *Hippomane*. This trend in cover signifies the change from species exhibiting protective mechanisms against desiccation including smaller leaves and drought deciduousness. In the more mesic situations, existing at higher altitudes on this transect, species exhibiting larger leaves would be favored, since desiccation is increasingly less a problem.

CONCLUSIONS

In our study of vegetation change on the south slope of Santa Cruz Island, we have found structural features rather than species representation to contribute much of the variability exhibited in this vegetation. In fact, the zonation evidenced on this slope is largely related to tree-species equitability and richness: the protean zone is separated from the lower zones by its greater number of equally dominant plant species. Breaks in the continuity of vegetation change likewise are reflected more in the total character of the stand than in a sudden change in species composition. We found steep slopes to impose disjunctions on the continuity of vegetation change similar to those observed by Beals (1969) along an altitudinal gradient in Ethiopia. However, in our study, the disjunctions were not caused by competitive exclusion occurring in the limited horizontal distance afforded by steep slopes (Beals 1969), but rather by the unusually large number of young trees present on steep slopes when compared with the height-class distributions along the remainder of the gradient. This structural feature allowed discrimination of discrete breaks in what otherwise might have been considered continuous vegetational change with altitude.

ACKNOWLEDGEMENTS

We acknowledge gratefully the support of the National Science Foundation (Grant GB-12256) and the National Geographic Society for the field work, initiated as a part of an ecological study of the Giant Galapagos Tortoise (*Geochelone*). The University of Wisconsin Graduate School and Department of Zoology covered the costs incurred in the analysis of the data. For their strenuous efforts in field sampling, we thank Frank and Margaret Iwen and Jeffrey Reeder. Logistical assistance was provided in the field by the Charles Darwin Research Station under the directorships of Roger Perry and Dr. Peter Kramer. We thank Dr. Robert Kowal, Mr. Wilfred Post III, and Mr. Daniel P. Smith for computer assistance. Dr. Duncan Porter aided in the identification or verification of voucher plant specimens, and he and Dr. E. W. Beals critically reviewed the manuscript. Lastly to Craig MacFarland we give highest appreciation for his energetic assistance in the field and careful reading of the manuscript.

LITERATURE CITED

ALPERT, L. 1962. The climate of the Galapagos Islands. Occ. Pap. Calif. Acad. Sci. 44: 21–44.

BEALS, E. W. 1965. Species patterns in a Lebanese poterietum. Vegetatio 13: 69–87.

———. 1969. Vegetational change along altitudinal gradients. Science, N.Y. 165: 981–985.

BOWMAN, R. I. 1961. Morphological differentiation and adaptation in the Galapagos finches. Univ. Calif. Publs. Zool. 58: 1–302.

CLEMENTS, F. E. 1905. Research Methods in Ecology. Univ. Publ. Co., Lincoln-Woodruff.

COX, D. R., AND A. STUART. 1955. Some quick tests for trend in location and dispersion. Biometrika 42: 80–95.

CURTIS, J. T. 1956. The Vegetation of Wisconsin. Univ. of Wis. Press, Madison.

DARWIN, C. 1840. Voyage of the Beagle. London.

GAUSE, F. G., AND A. A. WITT. 1935. Behavior of mixed populations and the problem of natural selection. Am. Nat. 69: 596–609.

GLEASON, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey bot. Club. 53: 7–26.

———. 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21: 92–110.

HOOKER, J. D. 1857a. An enumeration of the plants of the Galapagos Archipelago: with descriptions of those which are new. Trans. Linn. Soc. Lond. 20: 163–233.

———. 1847b. On the vegetation of the Galapagos Archipelago, as compared with that of some other tropical islands and of the continent of America. Trans. Linn. Soc. Lond. 20: 235–262.

HURLBERT, H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 377–386.

HUTCHINSON, G. E. 1953. The concept of pattern in ecology. Proc. Acad. nat. Sci. Philad. 105: 1–12.

ITOW, S. 1965. Preliminary note on the vegetation of the Galapagos Islands, Ecuador. Hikobia, 4: 318–324.

———. 1966. Ecological approaches to the vegetation of the Galapagos—future needs. Noticias de Galapagos, N. 7/8: 10–12.

KUCHLER, A. W. 1973. Problems in classifying and mapping vegetation for ecological regionalization. Ecology 54: 512–523.

MCINTOSH, R. P. 1967. An index of diversity and the relation of certain concepts of diversity. Ecology 48: 392–404.

PEET, R. 1971. The definition and measurement of diversity: a discussion of indices. Ms. thesis. Univ. Wis.

RIECHERT, S. E. AND W. G. REEDER. 1973. Effects of fire on spider distribution in southwestern Wisconsin Prairies. Proc. Second Midwest Prairie Conf. (1970): 1–27.

SEAL, H. 1964. Multivariate Statistical Analysis for Biology. Methuen, London.

SHANNON, E. C., AND W. WEAVER. 1949. The Mathematical Theory of Communication. Univ. Ill. Press, Urbana.

SHIMWELL, D. W. 1972. The Description and Classification of Vegetation. Univ. of Wash. Press, Seattle, 322 pp.

SIMKING, T., REEDER, W. G., AND C. MACFARLAND (Eds.). 1974. Galapagos science: 1972 status and needs. Galapagos Sci. Conf. Report, Wash. D.C. pp. 1–87.

SIMPSON, E. H. 1949. Measurement of diversity. Nature, Lond. 163–688.

SKELLAM, J. G. 1951. Random dispersal in theoretical populations. Biometrika. 38: 196–218.

STEWART, A. 1911. A botanical survey of the Galapagos Islands. Proc. Calif. Acad. Sci. (4) 1: 7–288.

———. 1915. Some observations concerning the botanical conditions on the Galapagos Islands. Trans. Wis. Acad. Sci. Arts Lett. 18: 272–340.

SVENSON, H. K. 1930a. Report on a botanical exploration trip to the Galapagos Islands. Brooklyn bot. Gdn. Rec. 19 (6): 269–284.

———. 1930b. The vegetation of Indefatigable Island. Bull. N.Y. zool. Soc. 33 (4): 163–170.

———. 1935. Plants of the Astor Expeditions, 1930 (Galapagos and Coastal Islands). Am. J. Bot. 22: 208–277.

WHITTAKER, R. H. 1951. A criticism of the plant association and climatic climax concepts. NW. Sci. 25: 17–31.

———. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1–69.

———. 1973. Handbook of Vegetation Science. V. Ordination and Classification of Vegetation. Junk B. V. The Hague.

WIGGINS, I. L., AND D. M. PORTER. 1971. Flora of the Galapagos Islands. Stanford Univ. Press, California.