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A MATHEMATICAL APPROACH TO DEFINING SPATIALLY RECURRING SPECIES GROUPS IN A MONTANE RAIN FOREST ON MAUNA LOA, HAWAII

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PREFACE

This report gives the results of one of two graduate student projects in plant ecology dealing with the structure of our major IBP site, an 80 hectare sample stand in an insular montane tropical rain forest. The montane tropical rain forest biome is one of the best preserved natural vegetation types in the mountainous Hawaiian Islands. The report is an abbreviated version of a Master of Science Thesis in Botanical Sciences carried out under the direction of D. Mueller-Dombois. The study was supported by NSF Grant No. GB 23230 of the Island Ecosystems IRP under the US/International Biological Program and a grant provided by the Bishop Estate Corporation.

ABSTRACT

This project was undertaken to determine whether spatial arrangements could be detected and species groups defined mathematically in a montane rain forest ecosystem, which is located on the island of Hawaii on the east side of Mauna Loa in the Kilauea Forest Reserve.

The vegetation was divided into four height layers, each of which contained species of similar life-form. A mathematical approach was used to determine if the vegetation could be further stratified on the ground. The data collected consisted of species quantities, such as cover or counts, in quadrats along transects. Plots, consisting of several of the smaller quadrats, were compared by ordination for the similarity of their composition. Species were compared by ordination for their similarity in occurrence by quadrats. The spatial arrangement within each life-form layer was determined by a new approach, called the heterogeneity test, utilizing random samples, the sum-of-squares clustering of the species and the comparison of the resultant dendrograms by statistical tests. Species groups within a heterogeneous layer were isolated by the sum-of-squares clustering.

The ordination of plots in general revealed some variation, but no different species assemblages were detected within any of the layers. The ordinations of species of the three understory layers indicated a gradually changing arrangement of common species with rare species interspersed randomly or in a homogeneous arrangement at the scales tested. The heterogeneity tests of the same layers indicated an arrangement which was not heterogeneous. The species ordination and the

heterogeneity test of the overstory layer indicated a heterogeneous arrangement of recurring species groups. Three species groups of overstory species were isolated by the clustering method.

The presence of recurring groups of overstory species is interpreted as resulting in part from recurring site conditions by the presence of fallen logs. Seedlings and sprouts on logs are more likely to succeed than seedlings on the ground which are vulnerable to the feral pigs which feed on, uproot, and trample the ground vegetation.

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INTRODUCTION

Vegetation ecology in general

A number of viewpoints concerning spatial patterns of species exist among ecologists.

According to Daubenmire (1968), a superficial examination of natural landscapes can reveal that plant species are inclined to group in distinct combinations forming communities. The individuals of each species are not randomly scattered but are arranged in a pattern over the landscape. Communities are formed through these spatial patterns of groups of species. The patterns are the result of species adaptations to spatial and temporal variations in environment and interactions among the species themselves.

Poore (1964) considers structural integration to be one of the most important features of the community. He believes that communities with an integrated structure are more resistant to environmental change in time or space. He quotes as examples the sharp discontinuities between structurally different communities along gradients of apparently continuously changing environments and the persistence of relict whole communities in areas which have climatically changed.

According to West (1966), recurring combinations of species may be used as indicators of certain site conditions and as such they are usually more reliable than single species. This can be explained by individual physiological amplitudes being modified by the influences of other plants.

These above authors (and many others) stress the concept of definite and integrated communities which Whittaker (1956, 1962) has called the "community-unit theory." According to Whittaker (1967), a person studying vegetation seeks to construct systems of abstraction by which relationships in the complex cover of vegetation may be comprehended. This traditional approach is through classification of plant communities into community types.

A conflicting concept must be pointed out which was first stated by Gleason (1926) and is called the "individualistic concept." He contended that no two species have the same spatial distribution, therefore vegetation varies continuously, so that recognition of types is strictly an arbitrary practice. Whittaker's studies (1951, 1956) supported Gleason's ideas. He saw vegetation as primarily a complex continuum of populations rather than a mosaic of discontinuous units. His was a direct approach of gradient analysis. Other results by Curtis and McIntosh (1951) and Brown and Curtis (1952) also demonstrated community continuity. Brown and Curtis (1952) compared communities to the spectrum of colors which blend from one into another.

Statement of the problem

This project was undertaken to study the spatial variation of the vegetation in a montane rain forest ecosystem. The original objective involved determining whether spatial arrangements could be detected and species groups defined mathematically within a forest which appears superficially homogeneous. With this goal in mind different methods of analyses were considered and a field survey was undertaken to obtain the data.

An attempt was made to determine the spatial arrangement of species in each of the vertical layers and/or life-form groups (Raunkiaer 1934) at various scales using ordination and classification techniques. Two possible horizontal spatial arrangements are considered to exist within these layers: (1) homogeneous (random, having no specific pattern); and (2) heterogeneous (non-random). Two types of heterogeneous arrangements were recognized as possible, a mosaic of recurring groups and a continuum (gradual change). If the species arrangements were determined to be heterogeneous at some scale as suspected, then it may be justified to identify the natural species groups which bring about the heterogeneity.

In the first phase of the work, data was collected and the literature was surveyed. Then the data for each plot was subjected to a simple Bray and Curtis (1957) ordination of plots for each layer. The ordination produced scatter diagrams on which gross patterns of similarity relations among plots were visually inspected. When several clumps were in evidence, heterogeneity (among plots) could be indicated. Concerning the species' ground arrangement, the data for each species was subjected to still another ordination based on the Newsome and Dix (1968) modification of the Bray and Curtis method.

The commonly used methods of pattern analysis are designed to handle only a single species at a time. I attempted to devise another method to test the species' arrangements jointly, rather than individually, at certain quadrat sizes associated with different ground scales. This method begins with sum of squares clustering (Orlóci 1967) of species from random samples. It incorporates a Chi-square test of the hypothesis that the same hierarchical relationship reappears consistently for the

same species in repeated random samples. Where such hierarchical relationships consistently reappear, the existence of distinct species groups is indicated. Then an analysis of the species groups by clustering using data from all the quadrats is appropriate.

Physical setting

The montane rain forest ecosystem studied is located on the island of Hawaii on the east side of the Mauna Loa massif. The study site is in the Kilauea Forest Reserve, shown in Fig. 1, on Transect 2, segment 11 from Mueller-Dombois (1966) at an elevation of 1590 to 1650 m. This belt of vegetation was called by the Hawaiians the "wao-maukele" (= rain-forest [Pukui & Elbert 1965]) or the region where the large trees grow (Malo 1971). The forest was classified as a mixed Acacia koa-Metrosideros collina forest with arborescent shrubs and Cibotium spp. (tree ferns).

Most of the following description is extracted from Mueller-Dombois (1966). This forest type represents a transition form between the typical Acacia koa (koa) forest (without Cibotium), which occurs above this zone (1520 to 1830 m), and the Metrosideros (ohia-lehua) rain forest which occurs below this zone (1370 m, downward). It occurs on "relatively deep, well weathered soil" with outcropping rocks. The upper tree canopy is dominated by tall (20-30 m) Acacia koa trees with large trunks (75-175 cm diameter). Metrosideros is generally not as tall or quite as large (the observed maximum was 147 cm diameter). A second tree layer is dominated by tree ferns (Cibotium spp.), but contains a number of other trees, such as Cheirodendron trigynum

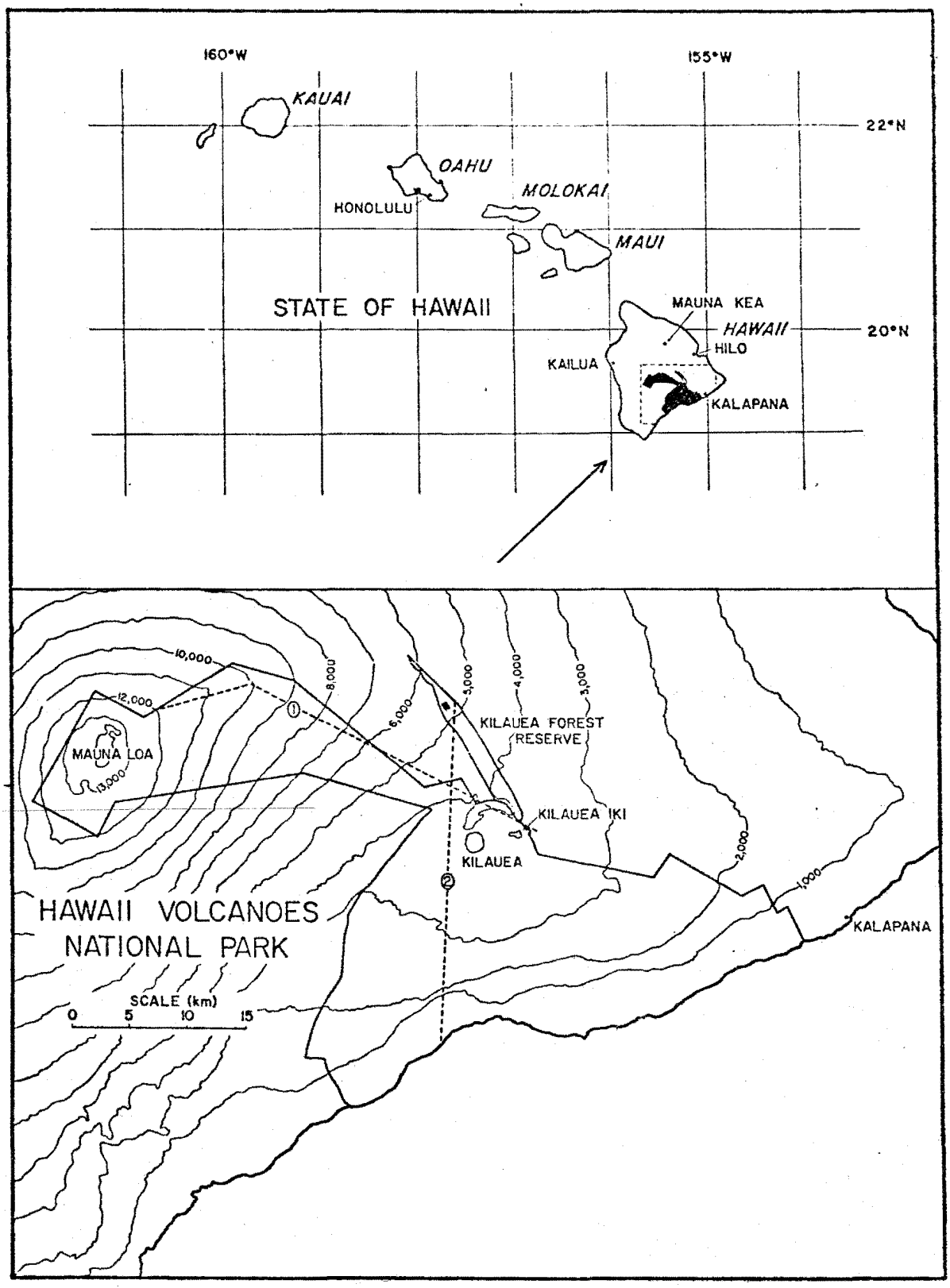

FIG. 1. Map showing location of Kilauea Forest Reserve and Hawaii Volcanoes National Park and the study site on Mauna Loa (at the north end of the dotted line, Transect 2).

('olapa), Ilex anomala (kawa'u) and Myoporum sandwicense (naio). Occasional openings in the tree canopy are occupied by sedges and other herbaceous plants.

The climate of the forest is represented in the climatograms in Fig. 2. As can be seen from this representation, the area receives a large amount of rainfall (mean annual = 2100 mm), especially in the winter months.

Compared to rain forests in other tropical regions this forest in Hawaii has a rather low species diversity. In the Kilauea Forest study site 22 woody plant species and 43 herbaceous plant species were found.

The overall impression of the study site and the surrounding forest is one of homogeneity from an aerial viewpoint. The most recent (1964) 1:6080 aerial photograph shows the Acacia koa trees as more or less randomly scattered individuals of the upper canopy. The impression upon first walking through this forest is also one of homogeneity.

Upon closer examination within the forest the vegetation appears to be more heterogeneous. For example, an aggregation of Metrosideros collina subcanopy trees was observed at one location, whereas elsewhere Metrosideros trees seemed to be more randomly distributed. The tree ferns, which for the most part form a closed canopy with their fronds (2-5 m above the ground), are conspicuously absent in certain places. At least one obvious species grouping was observed in the forest where several wet depressions are present and the tree canopy is open. In some of these depressions sedges and other herbaceous species of plants are grouped together in greater abundance than elsewhere in the forest.

Since a departure from randomness in the distribution of the above

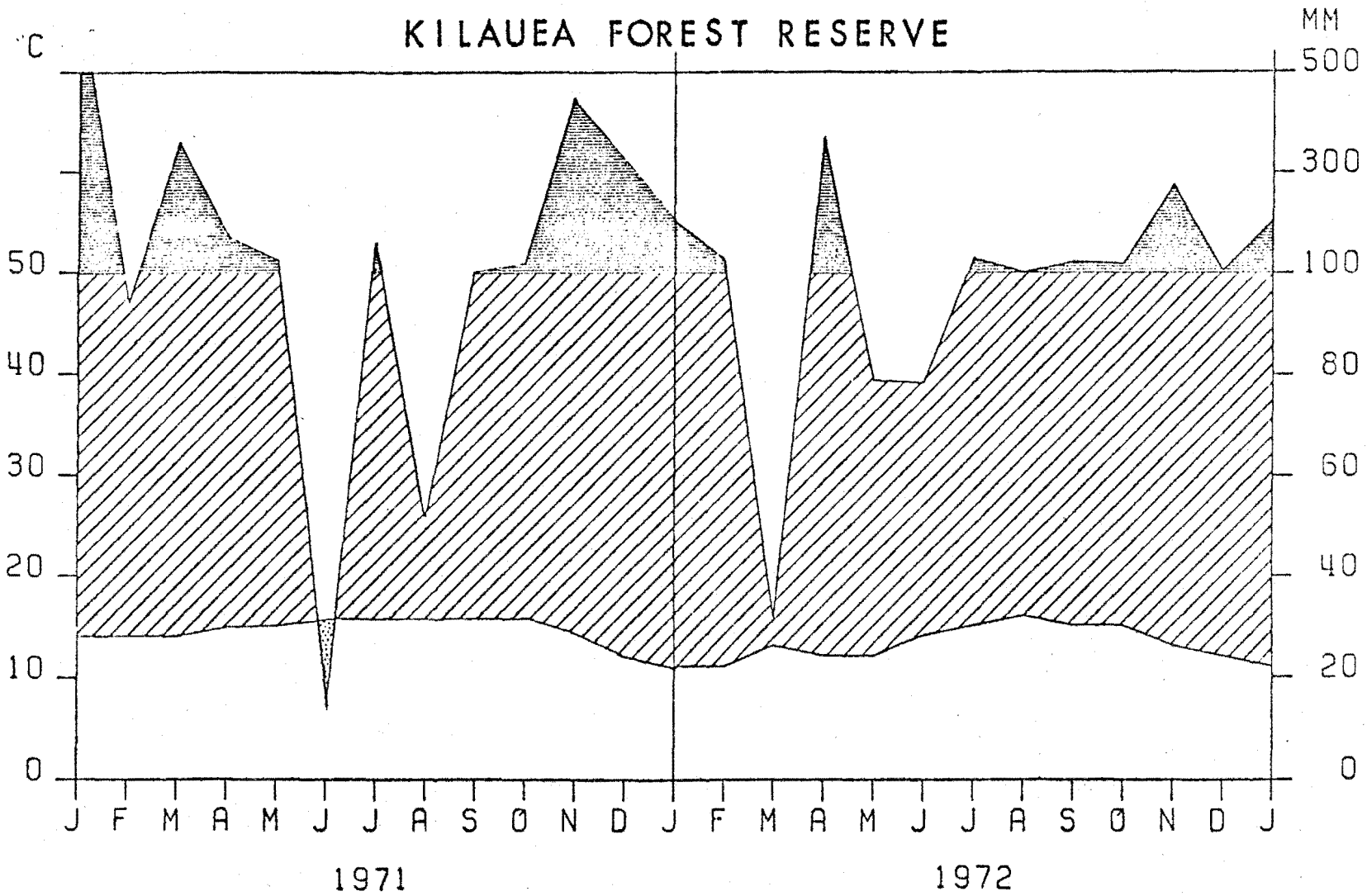

FIG. 2. Climatograms of rainfall (upper curve) and temperature (lower curve) for the Kilauea Forest Reserve for 1971 and 1972. The graph is prepared by the method described by Walter (1964, 1971). (For data see Bridges and Carey 1973).

mentioned species was observed, the question can be raised as to whether or not this departure is statistically significant, and if so, then what species are associated in groups which are repeated throughout the forest? The answer to this question depends on which subdivision of the vegetation is considered.

Subdivision of the vegetation according to functional-morphological groups is important, though there is no universally acceptable way. Daubenmire (1968) explains that groups exist with distinct environmental requirements: utilizing water at different levels in the soil; having different light requirements; depending on different agents of pollination or dissemination; and making demands on the habitats at different seasons. Superficially these groups inhabit the same general environment, but actually they live in well-defined sectors (i.e. niches) of it, separated by time, space, or both (Daubenmire 1968).

Oosting (1956) explains the stratification as resulting from competition among several species. A tall-growing species outgrows a potentially short one under the same conditions. The latter may survive if it can tolerate the shade from the first. Thus one species occupies a higher level than the other species and forms an overstory. In this way natural vertical stratification develops where the upper stratum includes species, called dominants, which may control and characterize the community.

The herbs and shrubs beneath the trees indirectly may compete with the dominant trees. If the seedlings of the tree species cannot meet the competition of lesser species, such trees eventually will disappear from the community. Thus permanent dominance depends on the ability to

compete successfully in all the strata of the community (Oosting 1956).

Since distinct environmental requirements of these species are unknown, for the purpose of this analysis some known structural groups (e.g. trees, shrubs, and woody climbers of the same height class) were combined into layers, one consisting of herbaceous plants, one of shrubs, small trees, and tree ferns, and one of upper canopy and emergent trees. Also included were the epiphytes which do not actually form a layer but which, for simplicity, will be referred to as such in the discussion. The herbaceous plant layer was given the life-form designation of chamaephytes; the shrub or tree fern layer includes two life-forms, the nanophanerophytes (0.5-2 m) and the microphanerophytes (2-5 m), the data of which were combined, and was given the designation of microphanerophytes; the tallest tree layer was given the designation of mesophanerophytes (5-50 m) (following the definitions of Ellenberg and Mueller-Dombois 1967).

METHODS

Test area

The study site is located on the Hawaii topographical sheet in the Kulani section as shown in Fig. 3. As indicated in the figure a climatic station (Stevenson screen shelter, operative since August 1, 1970) was at approximately the northwest corner of the 80 hm^2 (hm = hectometer*) study site. The exact corner was about 20 m northwest of the station, in the middle of the logging road which gave access to the area.

For convenience in sampling the layout was arranged, systematically with predetermined sample plot locations. The dense vegetation with many large logs obstructing the view and the passage, the slippery mud on the ground, and the moss covered logs and rocks--all would have made randomly located plots very difficult to reach.

The azimuth of the 800 m long base line was 55°. From this base line four transects ran at 145° (perpendicular to the base line). The twenty original plots began on the transect at a distance of 100 m from the base line. Each plot was 100 m long and was separated from the next plot by 100 m. The ten primary plots, in which all layers were sampled, were plots 1-5 on transect 1 and plots 16-20 on transect 4. The transects ran parallel to each other and were separated by 200 m.

The transects were marked by plastic tape tied to tree stems or branches. At the beginning of a plot, marked with orange and blue tapes,

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*1 hm = 100 m; 1 hm^2 = 10,000 m^2 = 1 hectare.

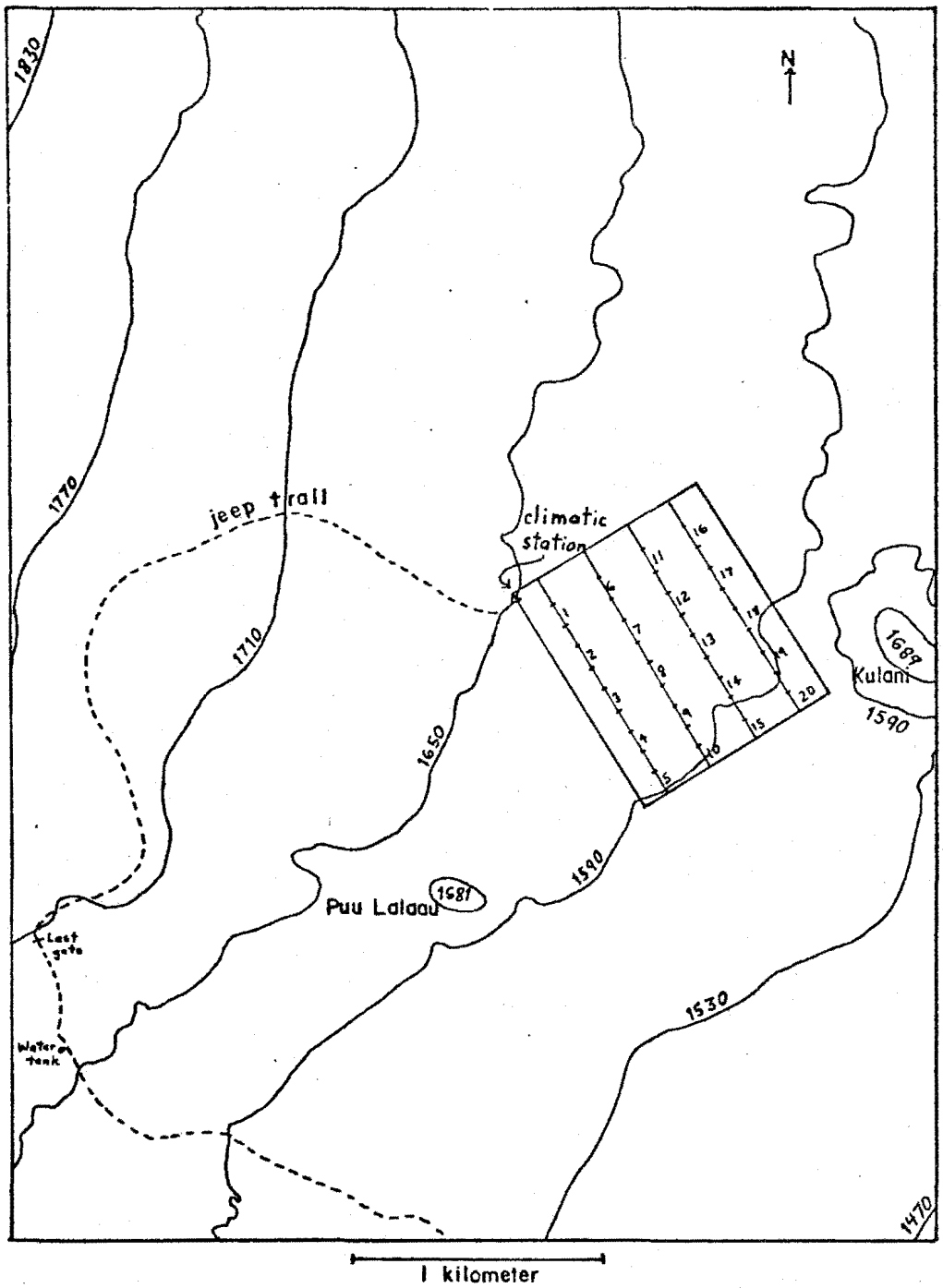

FIG. 3. Map of 80 hm^2 study site (section of Kulani, Hawaii Topographic sheet). The climatic station near the corner of the site is at $19^{o}31'N$ and $155^{o}19'W$. Elevation is given in meters.

a smaller, rectangular sampling unit referred to as a quadrat was located to the right of the transect 3 m in width and 5 m long (15 m^2). A second quadrat of the same size and adjacent to the first was located to the left of the transect. Fourteen more contiguous quadrats were located along the transect on either side as shown in Fig. 4. Within each plot, orange tapes were placed at 5 m intervals along the transect line.

In each of these quadrats the species present in each of the plant layers were noted. Estimates, measurements, and notes concerning the individual plants were taken. This basic procedure was repeated for all sixteen 15 m^2 quadrats. From here to the end of the plot only information concerning the highest layers (microphanerophytes and mesophanerophytes) was recorded from quadrats twice the size of the previous ones, 3 m in each direction perpendicular to the transect and 5 m along it (30 m^2). The end of the plot was marked by orange and blue tapes. Along the transect between plots blue tapes were used to mark the 5 m intervals. The area between plots was also divided into 30 m^2 quadrats like those shown in Fig. 4 for the assessment of the tallest trees.

A set of plant specimens were collected at critical stages in development (with flowers and fruits where possible) to help indicate which plants were recorded. These are presented as voucher specimens and are retained in the University of Hawaii herbarium in the Department of Botany.

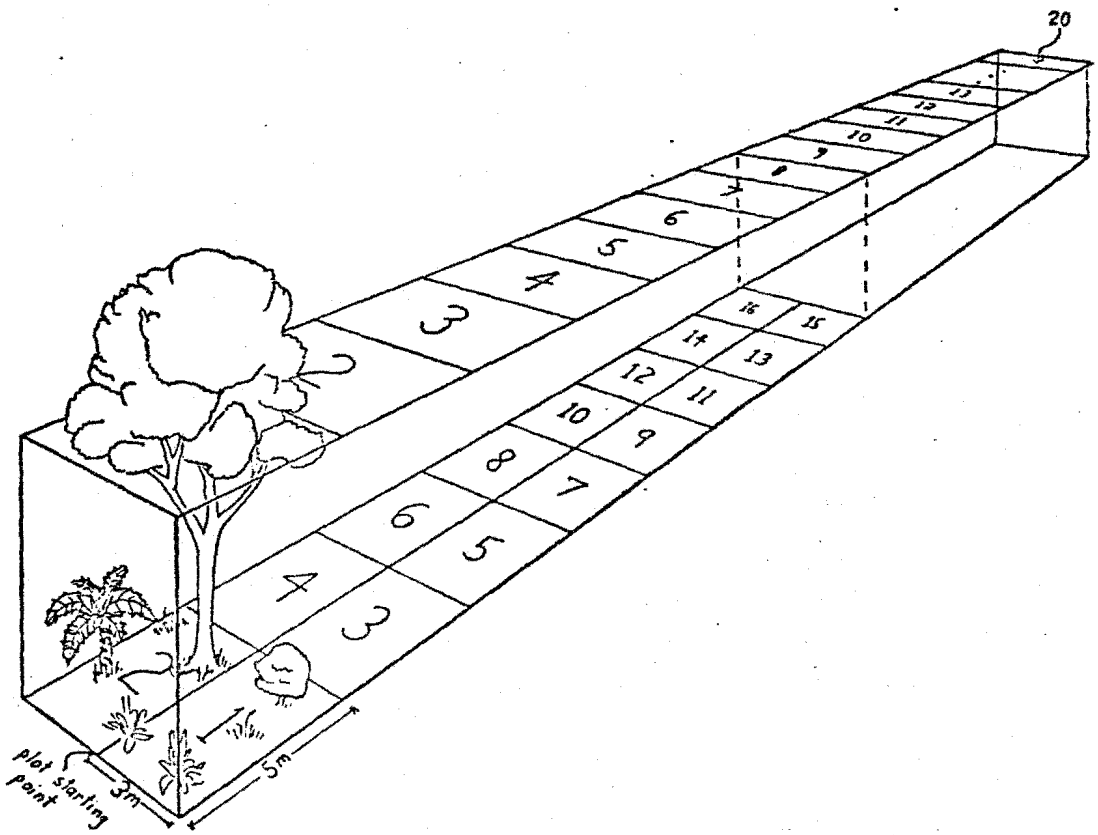

FIG. 4. Sampling layout for each plot (derived from Mueller-Dombois 1970). The diagram shows: the sixteen 15 m^2 quadrats used to record chamaephytes, epiphytes, and ground cover in each of ten primary plots; and above them the twenty 30 m^2 quadrats used to record microphanerophytes in each primary plot and mesophanerophytes in all the plots and the area between plots on all four transects. The sixteen 15 m^2 quadrats are contained within eight 30 m^2 quadrats (which are superimposed on them).

Sampling techniques

The vegetation was divided into four layers each of which contained species of similar life-forms; each will be described in more detail later. Various techniques were used to measure different parameters of each of these layers and of the physical environment; these techniques will be described along with special procedures which departed from the general plan already mentioned.

The bryophyte layer, which was recognized and originally considered for study, was found to be too difficult to evaluate in the field due to problems of identification. Samples of those species present were taken for identification in case the information might be desired at some later time.

The first layer studied was the understory of ferns and other herbaceous plants and seedlings all referred to as chamaephytes (Ch) according to the life-form classification of Ellenberg and Mueller-Dombois (1967). These plants have a mature shoot system that remains perennially within 25-50 cm above the ground surface. Woody plant seedlings were also included with the chamaephytes since, although not perennially this size, they are at least for a certain time of their life cycle in the same size range and have similar requirements and compete at the same level with these other plants.

For evaluating the chamaephytes sixteen quadrats of 15 m^2 (see Fig. 4) in each of ten primary plots on transects 1 and 4 were sampled. Since the understory consisted of small individuals it was believed that two transects (each having 5 plots) would already yield a sample representative of the area. Transects 1 and 4 were chosen since they

were farthest apart and therefore would be likely to show the greatest variation. If the data analysis had revealed the transects to be very dissimilar then plans would have been made to also sample the understory in transects 2 and 3.

The data collected were estimates of per cent ground cover of each of the species in this layer. The technique for estimating was that of Braun-Blanquet as described by Poore (1955). Each of the species present was given an index of cover-abundance. The index used is as follows:

5 = covering 75-100% of the area (average = 87.5%)
4 = 50-75% cover (67.5%)
3 = 25-50% cover (37.5%)
2 = 5-25% cover (15%)
1 = 1-5% cover (3%)
+ = scattered (0.1%)
r = only one individual (0.0%)

In this scale the larger figures relate to cover, the smaller to abundance. By this method two problems are avoided, that of assessing the cover of numerous small individuals, and that of defining an individual in vegetatively reproducing plants of high cover. The method stresses the value of cover for indicating the relative importance of the various species within the community (Poore 1955). These data were converted to quantitative average values for computer analysis (as shown above in parentheses).

The second layer studied consisted of shrubs, tree ferns and small trees (0.5-5 m). This actually was comprised of two life-forms, the nanophanerophytes and the microphanerophytes, but they were combined to provide a sample with a sufficient number of individuals and were studied as one layer called the microphanerophytes (MiP). The

individuals were chosen by height, and in the case of tree ferns, Cibotium spp., also by stem length, measured to the shoot apex. The fronds of the tree ferns usually extended beyond their shoot apex and also many of the plants were leaning or were even horizontal, therefore requiring this specific interpretation of height.

In each of the ten primary plots on transects 1 and 4, microphanerophytes were sampled in sixteen 15 m^2 quadrats plus twelve 30 m^2 quadrats (or a total area equal to twenty 30 m^2 quadrats). This was a total of 6000 m^2 (20 X 30 m^2) for each of ten plots. Fig. 4 shows the sampling layout. The larger plants of this layer were usually more widely spaced; this means that they were less abundant than the chamaephytes in the smallest 15 m^2 quadrats size. A greater number of quadrats was therefore used to study the microphanerophytes. (This reasoning was also applied to the larger plants, the mesophanerophytes, which were studied in more than ten plots.)

The number of individuals of each species in each quadrat was recorded. The average cover for each plot was measured by the line interception method as described by Canfield (1941). This method is based on the measurement of the vertical projection of the crown or shoot of plants (by species) that intercept a transect line. Along the transect within each plot the distance which was covered by the species' crowns was recorded. All of the distances for each species were summed and the per cent of the total plot length was calculated. This per cent value was recorded as the crown cover for plants of this layer.

The epiphyte "layer" was, unlike the previous layers, defined not by height but rather by position on other plants. An epiphyte (E) is

defined by Ellenberg and Mueller-Dombois (1967) as a plant which germinates and grows on other plants. The presence of all those vascular epiphytes on other plants, living or dead, at least 0.5 m from the ground, up to 5 m, was recorded in each quadrat of 15 m^2 (as shown in Fig. 4).

The tall trees (5-50 m), called mesophanerophytes (MesP), were assessed by recording the number of individuals present in each 30 m^2 quadrat in the 20 plots (shown in Fig. 3) plus the 20 areas along the transects which were in between the plots (see Fig. 7). The basic unit for mesophanerophyte analysis was 30 m^2 (6 X 5 m), the same as for the microphanerophyte layer. But, because the tall trees were generally more widely spaced than the shrubs and smaller trees more plots (and therefore more quadrats) were sampled for this layer to get an adequate numerical sample. Quadrats along the full length of all four transects or 24000 m^2 (6 m wide X 1000 m/transect X 4 transects) were sampled.

Trunk diameters (at 1.5 m = breast height) were measured for all trees and crown diameters of a number of subcanopy individuals (20-70) of each species were measured until the regression of crown diameter on trunk diameter was established for each species. To measure crown diameter a meter tape was stretched from one edge of the vertical projection of the crown onto the ground to the other edge. Two readings were taken at 90° to each other to allow somewhat for non-circular crowns. The average was considered to be the crown diameter, from which the circular area of cover was calculated. This crown diameter measurement was made only on subcanopy trees whose crowns were low and not obscured from view; upper canopy and emergent tree crowns were not

measured. In the case of trees that had grown on logs (i.e. beginning as epiphytes) the diameter at breast height (dbh) was taken at 1.5 m from the tree base irrespective of how high it was off the ground. The substrate on which a tree originally germinated (i.e. mineral soil or tree trunk) was also noted.

The distance between large mesophanerophytes or upper canopy and emergent trees, defined as those greater than 33 cm in diameter, was measured by the point-centered quarter method (Cottam and Curtis 1956). The measurement of the actual spacing of the trees in the field can lead to an estimate of the mean area and the density. In the point-centered quarter method each sampling point is considered to be the center of four quarters (quadrants). The sampling points were chosen systematically on the transect line at the beginning, middle (50 m point) and end of each of the ten primary plots. The transect line and a line 90° to it (determined by a compass) through the point formed the quarters. At each point one emergent tree closest to the point in each of the four quarters was chosen. Distances were measured from the point to each of the four trees and their species and trunk diameter (dbh) were recorded. The substrate on which the trees originally germinated was also recorded. The 33 cm diameter limit was chosen arbitrarily with the purpose of only measuring the upper canopy and emergent trees, particularly the dominant Acacia koa.

The percentage crown cover of the Acacia koa for the transects was assessed by using the 1964 aerial photograph (EKL-4CC-155) of the study site and by employing the point interception method described by Levy and Madden (1933). A dot grid (#45025, Forestry Suppliers, Inc.) was

placed over the site and each time a dot intercepted a koa crown (which was light in color) it was recorded. The number of interceptions was expressed in per cent of the total number of dots and is equal to the percentage of the area which was covered by Acacia koa crowns.

The soil depth was determined by a steel probe at every 5 m point along the entire length of each transect. This was one physical factor which was thought to be correlated with the presence of some species and it was easily measured. Other factors such as shade conditions could have also been measured, but with much more difficulty. Another researcher has subsequently studied disturbances by pigs which might also be correlated with some species arrangements.

Another factor, forest floor components, was estimated in per cent of the total ground surface area in each quadrat which was covered by: (1) rotting wood and lying logs; (2) humus and mineral soil; (3) rocks; and (4) bryophytes and herbaceous plants. The sum of the individual values of the first three categories equals 100%. A total of sixteen 15 m^2 quadrats (in the lower part of Fig. 4) were measured in each of the ten primary plots.

Methods of analysis

A clear pattern of horizontal variation could not be ascertained by mere observation of the raw data. For this reason a mathematical approach was used to determine if horizontal strata could be established. On a large scale, plots (600 m^2) were compared on the basis of their composition. On smaller scales species were compared on the basis of their occurrence in quadrats of various sizes.

Ordination is suitable to perform both of the above comparisons: of plots and of species. The ordinations produced were based on the method of Bray and Curtis (1957).

To determine the spatial arrangement within each vertical layer the use of a number of methods were theoretically possible. Other methods such as association analysis, factor analysis, and pattern analysis were considered, but these did not seem appropriate for this problem. A new approach was attempted which utilizes random samples, the sum-of-squares clustering of the species and comparison of the resultant dendrograms (topologies) by statistical tests. The basis of this approach was the sum-of-squares clustering by Orlóci (1967) with further consultation with Orlóci for modification to fit these specific goals.

The detailed descriptions of methods of analysis are incorporated in the Results section which follows. Each type of analysis is under an appropriate subheading.

RESULTS

Plot ordinations

The data collected in the field consisted of species quantities for each 3 X 5 m quadrat. The raw data from each quadrat were reduced to frequency values (number of quadrats in which a species occurred out of the total number), count totals, density values (trees per hm^2), average cover values, or basal area values of tree trunks (calculated from trunk diameters) for each plot. (The data for each layer are shown in Tables 9-13, Appendix B.) The sampling unit for assessing forest floor components, epiphytes, and chamaephytes was a 6 X 40 m = 240 m^2 portion of a plot; for microphanerophytes and mesophanerophytes the sampling unit was 6 X 100 m = 600 m^2 (the entire length of a plot--see Fig. 4).

The data were stored in the form of p X n matrices (i.e. tables); the p rows represent attributes and the n columns correspond to individuals. For the plot ordinations the attributes (in the rows) were the species and the individuals (in the columns) were the ten plots. (In other types of ordinations the rows and columns are reversed.)

These plot data were processed by the basic ordination method of Bray and Curtis (1957). A computer program was written by the author in FORTRAN IV* utilizing the equation of Beals (1960, 1965) for calculating the coordinates. Since the plots appeared very similar qualitatively, a quantitative coefficient (by Spatz 1970) was utilized to maximize the differences between plots. Spatz's (1970) coefficient (IS) calculated between two individuals (in this case plots), 1 and 2,

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*The program is available at the Department of Botany, University of Hawaii.

is as follows:

$$IS_{1,2} = [(Mw/Mg)/(a+b+c)][Mc/(Ma+Mb+Mc)][100],$$

where a = the number of attributes (in this case, species) confined to the first individual (plot) under comparison

b = the number of attributes (species) confined to the second individual (plot)

c = the number of attributes (species) common to both

Ma = the sum of the quantitative values of the attributes (species) unique to the first individual (plot)

Mb = the sum of the quantitative values of the attributes (species) unique to the second individual (plot)

Mc = the sum common to both

Mw = the smaller quantity of the attributes (species) common to both individuals (plots)

Mg = the greater quantity of the attributes (species) common to both individuals (plots)

The index has a theoretical range of 0-100. A zero coefficient indicates individuals with no attributes in common, and a coefficient of 100 indicates absolute similarity between two individuals in terms of the quantities of the attributes. 100 minus IS gives the dissimilarity or distance between individuals. An example showing how this coefficient is calculated using quadrats and also species as the individuals is in Appendix E.

The soil depth values for each plot were superimposed on the plot ordination graphs for all the layers to see if any trend (i.e. increase in depth in one direction) could be recognized (see Appendix F for this procedure). Where there was a trend in soil depths the individual species quantities for each were also superimposed on the plot ordination graph. Where species had trends increasing in the same

direction as the soil depths, the correlation coefficient (r) was calculated and tested for significance.

The ordination graphs for each layer are shown in Figs. 5, 6 and 8. The proximity of points representing plots in the ordination is directly proportional to the compositional similarity of the plots. This is based on three compositional elements: (a) forest floor components; (b) species presence and absence; and (c) quantitative variation in species.

Forest floor components (Fig. 5a)

Fig. 5a shows the graph of the forest floor, the components of which were percentage cover of rocks, bare soil, logs, and bryophytes and herbaceous plants. All of the plots of both transects appear to be very similar because all the points are close together. Hardly any separation is shown by the y-axis.

Species presence and absence (Fig. 5b-f)

The species of each layer are listed in Table 1. The epiphyte graph (Fig. 5b) shows that plots of transect 1 (plots 1 to 5) are separated (i.e. different) from those of transect 4 (plots 16 to 20) as indicated by the dashed line. The plots of transect 1, however, are relatively dissimilar to one another and plot 2, for example, is closer to plot 17 of transect 4 than to plots 1, 3, or 4 of its own transect 1. No distinct clusters of points are evident and therefore no group of plots is so dissimilar to the rest as to indicate another epiphyte flora or another discrete community.

The chamaephyte graph resembles the epiphyte graph in that the transects are also separate, as indicated by the dashed line, but not distinctly different.

FIG. 5. Ordination graphs for forest floor cover, for each of the four layers and for all layers combined (total species). In Figs. 5 and 6 numbers in the graphs refer to plot numbers (1-5 on transect 1 and 16-20 on transect 4). In all the ordination graphs the axes indicate dissimilarity, which in b-f of this figure is based on presence and absence (frequency) values. In Figs. 5 and 6 the dashed lines indicate separation between the two transects.

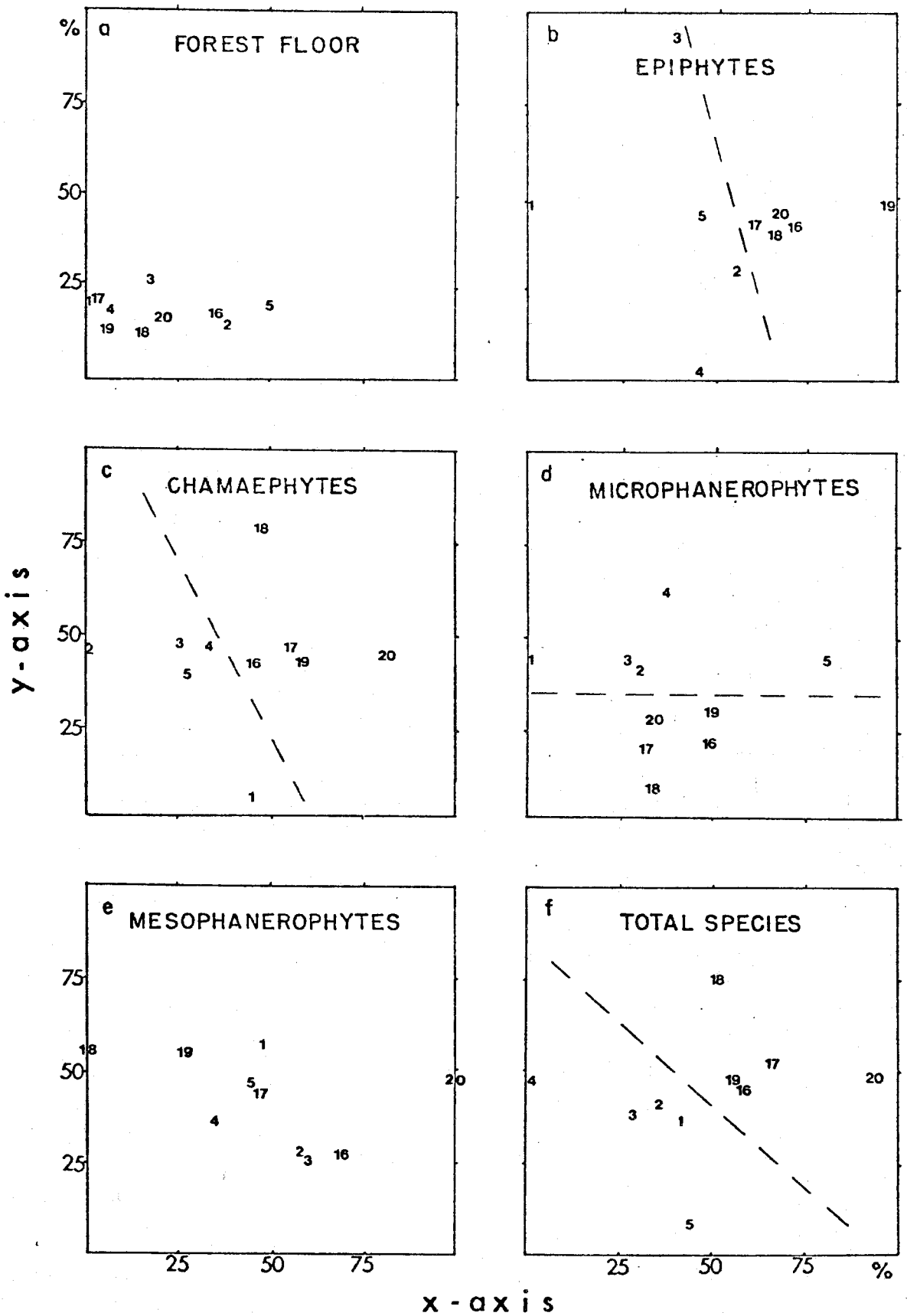

a
FOREST FLOOR
%
75
50
25
b
EPIPHYTES
c
CHAMAEPHYTES
d
MICROPHANEROPHYTES
e
MESOPHANEROPHYTES
f
TOTAL SPECIES
y-axis
x-axis
25
50
75
%

TABLE 1. List of species in each layer.

Epiphytes	Chamaephytes
1 Acacia koa PE	1 Acacia koa
2 Adenophorus tripinnatifidus ChE	2 Adenophorus tripinnatifidus
3 Alyxia olivaeformis PE	3 Alyxia olivaeformis
4 Asplenium contiguum ChE	5 Asplenium contiguum
5 Asplenium lobulatum ChE	6 Asplenium lobulatum
6 Asplenium normale ChE	7 Asplenium normale
7 Asplenium schizophyllum ChE	9 Astelia menziesiana
8 Astelia menziesiana ChE	10 Athyrium microphyllum
9 Athyrium microphyllum ChE	11 Athyrium sandwichianum
10 Athyrium sandwichianum ChE	12 Broussaisia pellucida
11 Broussaisia pellucida PE	13 Carex alligata
12 Carex alligata ChE	14 Carex macloviana
13 Carex macloviana ChE	15 Cheirodendron trigynum
14 Cheirodendron trigynum PE	16 Cibotium chamissoi
15 Cibotium chamissoi PE	17 Cibotium glaucum
16 Cibotium glaucum PE	18 Coprosma rhyncocarpa
17 Coniogramme pilosa ChE	19 Ctenitis rubiginosa
47 Coprosma ochracea PE	20 Cyanea sp.
18 Coprosma rhyncocarpa PE	21 Cyrtandra lysiosepala
19 Ctenitis rubiginosa ChE	25 Dicranopteris emarginata
20 Cyanea sp. PE	22 Dryopteris glabra
21 Dryopteris glabra ChE	23 Dryopteris paleacea
22 Dryopteris paleacea ChE	24 Dryopteris sp.
24 Elaphoglossum hirtum ChE	27 Elaphoglossum hirtum
23 Elaphoglossum wawrae ChE	26 Elaphoglossum wawrae
25 Gouldia sp. PE	28 Epilobium oligodontum
26 Grammitis hookeri ChE	29 Erechtites valerianifolia
27 Ilex anomala PE	4 Gnaphalium sp.
29 Lycopodium serratum ChE	30 Gouldia sp.
30 Marratia douglasii ChE	31 Grammitis hookeri
31 Metrosideros collina PE	32 Holcus sp.
32 Myoporum sandwicense PE	33 Hydrocotyle sibthorpiodes
33 Myrsine lessertiana PE	34 Hypericum japonicum
34 Nertera depressa ChE	35 Ilex anomala
35 Pelea clusiaefolia PE	63 Juncus planifolius
36 Peperomia leptostachya ChE	36 Ludwigia sp.
37 Pipturus hawaiiensis PE	37 Lycopodium cernuum
38 Pleopeltis thunbergiana ChE	38 Lycopodium serratum
39 Polypodium pellucidum ChE	39 Marattia douglasii
40 Rubus hawaiiensis PE	40 Metrosideros collina
41 Sadleria pallida ChE	41 Myoporum sandwicense
42 Sphaerocionium obtusum ChE	42 Myrsine lessertiana
43 Stenogyne calaminthoides ChE	43 Nertera depressa
44 Vaccinium calycinum PE	44 Pelea clusiaefolia
45 Vandenboschia davallioides ChE	45 Pelea (?) volcanica
46 Xiphopteris saffordii ChE	46 Peperomia leptostachya
	47 Pipturus hawaiiensis
	48 Pleopeltis thunbergiana

TABLE 1. (Continued) List of species in each layer.

Chamaephytes (cont.)	Mesophanerophytes
49 Polypodium pellucidum	1 Acacia koa
50 Pteridium aquilinum	11 Alyxia olivaeformis PL
51 Rubus hawaiiensis	2 Cheirodendron trigynum
52 Rubus rosaefolius	3 Coprosma rhyncocarpa
53 Sadleria pallida	4 Ilex anomala
54 Sphaerocionium obtusum	5 Metrosideros collina
55 Sphenomeris chusana	6 Myoporum sandwicense
56 Stenogyne calaminthoides	7 Myrsine lessertiana
58 Vaccinium calycinum	8 Pelea clusiaefolia
59 Vandenboschia davallioides	9 Pelea (?) volcanica
60 Veronica plebeia	10 Rubus hawaiiensis*
61 Veronica serphyllifolia	
62 Xiphopteris saffordii	

Microphanerophytes
1 Acacia koa
2 Alyxia olivaeformis PL
3 Broussaisia pellucida
4 Cheirodendron trigynum
5 Cibotium chamissoi
6 Cibotium glaucum
7 Clermontia hawaiiensis
8 Coprosma rhyncocarpa
9 Cyrtandra lysiosepala
10 Gouldia sp.
11 Ilex anomala
12 Metrosideros collina
13 Myoporum sandwicense
14 Myrsine lessertiana
16 Pelea clusiaefolia
17 Pelea (?) volcanica
18 Rubus hawaiiensis
19 Rubus rosaefolius
20 Vaccinium calycinum

ChE = Chamaephytic epiphyte
PE = Phanerophytic epiphyte
PL = Phanerophytic liana

*Note that Rubus is not a tree, but was included in this layer because of the height of its stem.

The microphanerophyte graph also resembles the other two graphs in its separation of transects, as indicated by the dashed line.

The mesophanerophyte graph, however, shows the floristic similarities (represented by plots) apparently randomly arranged. No dashed line is drawn in Fig. 5c since no separation of transects is shown.

The total species graph shows a slight separation between the two transects, much like the epiphyte and chamaephyte graphs.

Quantitative variation in species (cover and density, Figs. 6 and 8)

The chamaephyte graph (in reference to Fig. 6) shows an intermixing of plots which indicates that the two transects are compositionally similar with respect to the area covered by chamaephyte species. Thus when species quantities, in this case cover, are considered in addition to mere presence of species, the difference between transects disappears. This means in effect that the species with greater cover are also more evenly distributed throughout the forest and the species with smaller cover do not affect the result in Fig. 6 as much.

The microphanerophyte graphs (in Fig. 6) also show an intermixing of plots. The graph based on density can be separated into transects by a bent line as indicated, which is somewhat similar to the continuous change in the Fig. 5d graph, where only species presence and absence was considered.

Fig. 8 is the graph of mesophanerophytes based on density data from the entire length of all four transects, divided into ten plots (6 X 100 m in size) per transect. The layout of the forty plots is shown in Fig. 7. This graph shows a separation (indicated by the

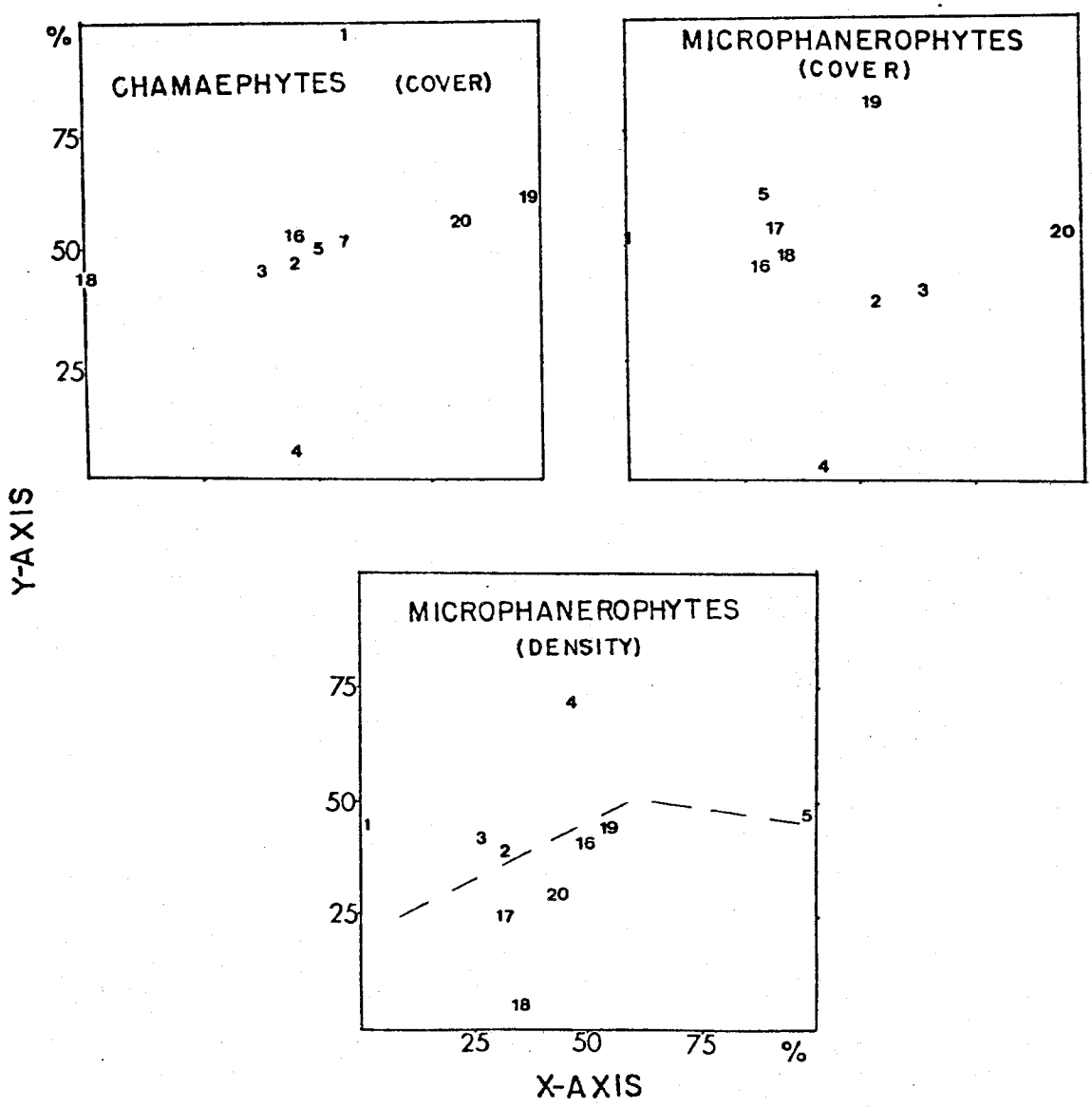


FIG. 6. Ordination graphs of two layers. Dissimilarity is based on cover or density values.

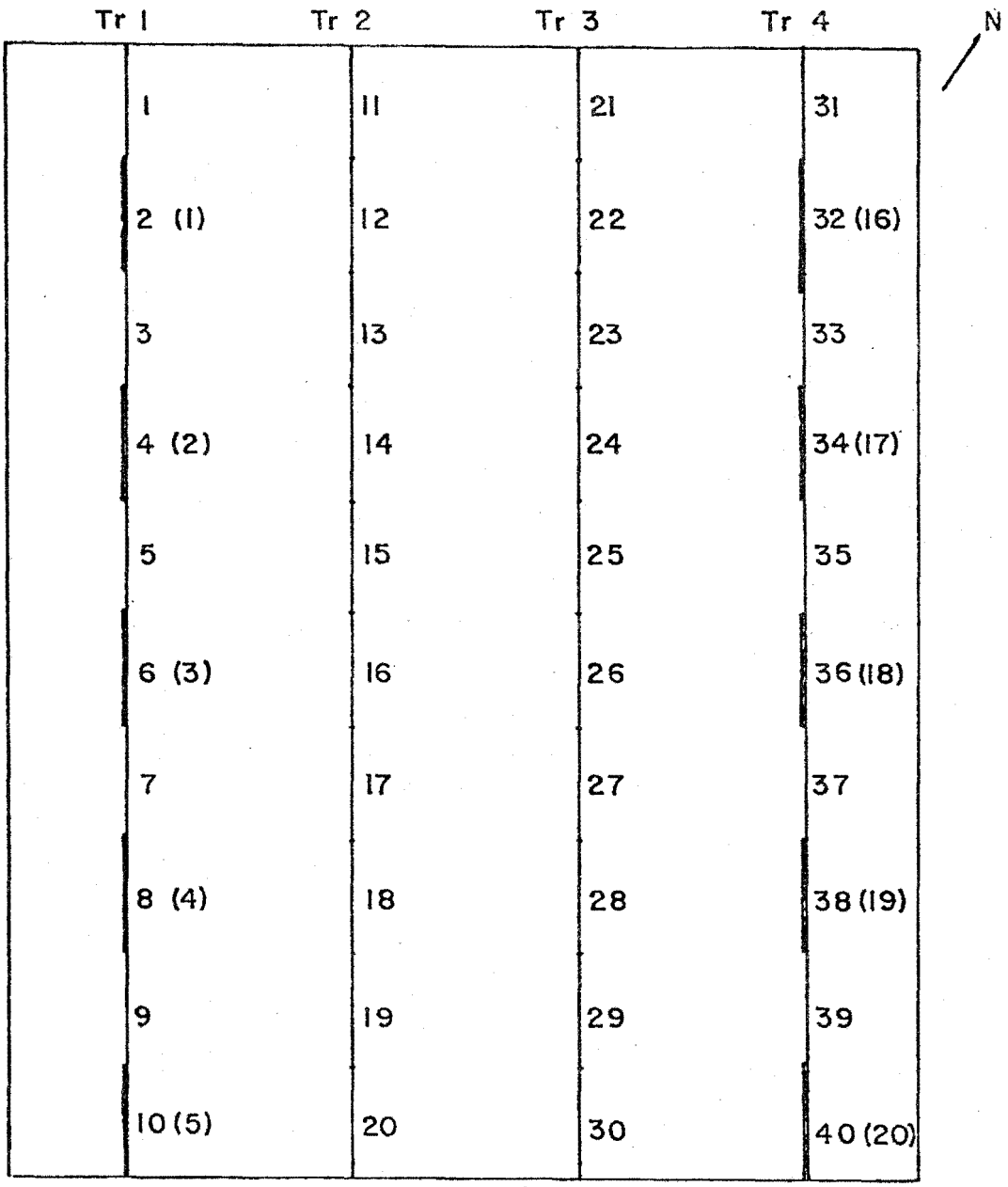


FIG. 7. Layout of the 40 plots in which mesophanerophytes were sampled. The numbers of the ten primary plots in which other layers were sampled are shown in parentheses.

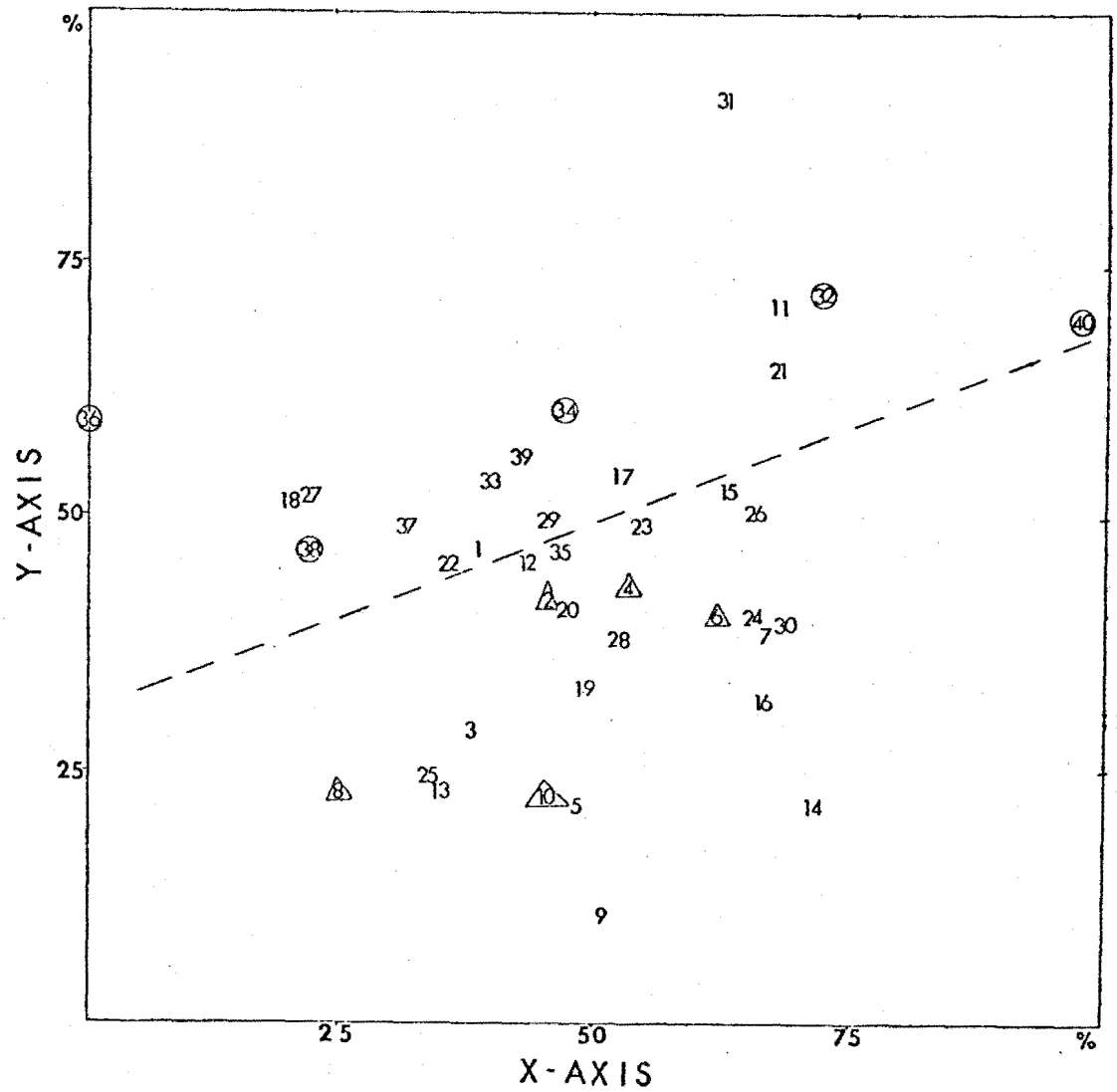


FIG. 8. Ordination graph of mesophanerophytes in 40 plots. Numbers in the graph refer to plot numbers on four transects (ten plots on each). Dissimilarity is based on density values. The plots are numbered consecutively along each transect. (Primary plots considered in other analyses on transect 1 are labeled here as 2, 4, 6, 8, and 10 and are in triangles and those on transect 4 are labeled 32, 34, 36, 38, and 40 and are in circles. The dashed line indicates their separation. See also FIG. 7.)

dashed line) of the primary plots of transects 1 and 4, indicated by the triangles and circles, respectively. The plots of transects 2 and 3 are intermingled among the plots on 1 and 4. Overall, this graph shows that there are no groups of plots which are distinct from the rest, but there is a continuous change from transect 1 to transect 4 with some overlap in between.

Synthesis of compositional elements

The ordinations of plots in general reveal that there is a compositional change across the width of the study site. This change is reflected in each layer by either species presence or quantities. This change does not coincide with the elevational trend in the forest (see Fig. 3).

Since no plot groups are evident and no individual plots stand out consistently from the rest at this resolution all plots were included for further analyses. A finer level of resolution was anticipated to bring out any possible differences within the study site.

Correlation of soil depths with ordinations (Fig. 9)

Table 2 lists the average soil depth values for the ten primary plots which were ordinated. These values were placed over the position of the respective plot numbers on the ordination graphs. If an increasing trend was exhibited in any direction isolines were drawn to emphasize this change. The results of soil depths superimposed on two of the ordinations are shown here in Fig. 9. Soil depths on other ordinations did not show trends.

Fig. 9a shows the soil depth values for each of the plots in the same position as in the chamaephyte ordination. The depth is greatest

TABLE 2. Average soil depths (cm) for ten primary plots.

	Plots	Depth	Standard deviation
Transect 1			
	1	30.0	14.1
	2	29.6	15.1
	3	41.4	15.8
	4	50.4	28.9
	5	60.8	23.3
Transect 4			
	16	51.4	14.5
	17	40.6	11.9
	18	47.0	15.8
	19	39.4	15.2
	20	33.2	7.7

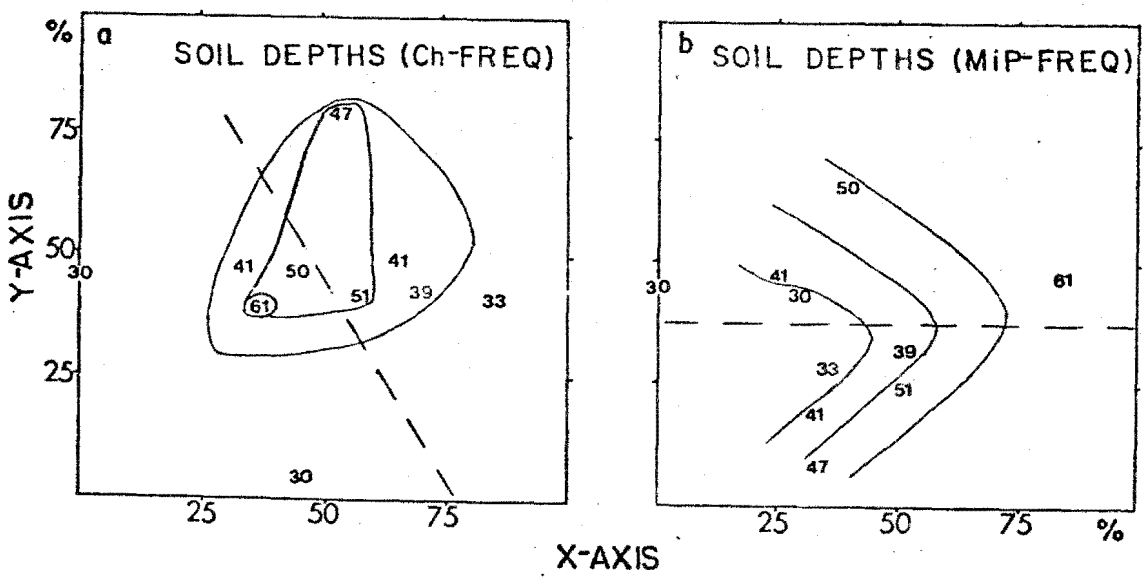


FIG. 9. Soil depth values (cm) for each plot substituted in the position of the plot numbers from the two plot ordination graphs. The isolines indicate an observed gradient. a is from the chamaephyte graph (FIG. 5c) and b is from the microphanerophyte graph (FIG. 5d). The dashed lines, from the ordination graphs, indicate separation between transects 1 and 4.

(61 cm) in plot 5 (see Fig. 5c) and decreases in the surrounding plots. The shallowest soil is in plots 1 and 2, which are at the periphery of the graph. Isolines were drawn which emphasize the greater depths in the center of the graph decreasing outward, or conversely, with an increasing trend inward.

Fig. 9b shows the soil depth values for each plot as in the microphanerophyte ordination. The depths increase from left to right (from plot 1 to plot 5) (see Fig. 5d), as indicated by isolines.

The trends in soil depth related to plot ordinations of these two layers indicate a relationship between the presence of species and the soil depth. Where the soil depths are similar the plots are also floristically similar, showing the same presence (or absence) of chamaephyte and microphanerophyte species.

Species distribution trends as related to plot ordinations (Tables 3-4 and Fig. 10)

Species frequency values (see Appendix B, Tables 9-13 for all the values) were placed over the position of the respective plot numbers on the ordination graphs of different layers. If a trend was revealed it was recorded in Table 3. Those species unique to one transect are listed in Table 4.

Those chamaephyte species which show a trend similar (or opposite) to the compositional change revealed in the plot ordination of chamaephytes (i.e. from left to right) are Sadleria pallida (R-L), Veronica plebeia (R-L) and Vandenboschia davallioides (L-R) (see Table 3). These three species may be responsible in part for the compositional change between transects 1 and 4 in Fig. 5c.

TABLE 3. Summary of visible trends of individual species values corresponding to the positions of the plots on the ordination of their respective layers.

Species	Increasing quantity
Epiphyte ordination graph (Fig. 5b)	
Astelia menziesiana	bottom to top
Cibotium glaucum	bottom to top
Broussaisia pellucida	right to left
Ilex anomala	left to upper right
Chamaephyte ordination graph (Fig. 5c)	
Athyrium microphyllum	lower right to upper left
Athyrium sandwichianum	lower right to upper left
Carex alligata	lower right to upper left
Dicranopteris emarginata	lower right to upper left
Veronica serphyllifolia	lower right to upper left
Dryopteris glabra	top to bottom
Polypodium pellucidum	top to bottom
Elaphoglossum hirtum	periphery to center (plot 4)
Grammitis hookeri	upper left to lower right
Sadleria pallida	right to left
Veronica plebeia	right to left
Vandenboschia davallioides	left to right
Microphanerophyte ordination graph (Fig. 5d)	
Cyrtandra lysiosepala	right to left
Myoporum sandwicense	right to left
Pelea clusiaefolia	upper right to lower left
Pelea sandwichiana	left to right

TABLE 4. Species unique to one transect.

Transect 1	Transect 4
Asplenium schizophyllum ChE*	Asplenium normale ChE
Stenogyne calaminthoides Ch*	Coniogramme pilosa ChE*
Hydrocotyle sibthorpiodes Ch	Coprosma ochracea PE*
Elaphoglossum wawrae Ch	Ctenitis rubiginosa ChE*
Myoporum sandwicense Ch	Cyanea sp. PE
Marattia douglasii Ch	Gouldia sp. PE*
Cibotium chamissoi Ch	Nertera depressa ChE
Gnaphalium sp. Ch*	Vandenboschia davallioides ChE
Hypericum japonicum Ch	Xiphopteris saffordii ChE
Ludwigia sp. Ch	Cyanea sp. Ch
Myoporum sandwicense Ch	Epilobium oligodontum Ch
Pelea volcanica Ch	Erechtites valerianifolia Ch
Pipturus hawaiiensis Ch*	Gouldia sp. Ch*
Pteridium aquilinum Ch	Holcus sp. Ch*
Sphaerocionium obtusum Ch	Juncus planifolius Ch
Acacia koa MiP	Xiphopteris saffordii Ch
Clermontia hawaiiensis MiP	Gouldia sp. MiP
Cyrtandra lysiosepala MiP	Rubus rosaefolius MiP
Myoporum sandwicense MesP	Pelea clusiaefolia MesP
Pelea volcanica MesP	

ChE = Chamaephytic epiphyte
Ch = Chamaephyte
PE = Phanerophytic epiphyte
MiP = Microphanerophyte
MesP = Mesophanerophyte

*These species were encountered only once.

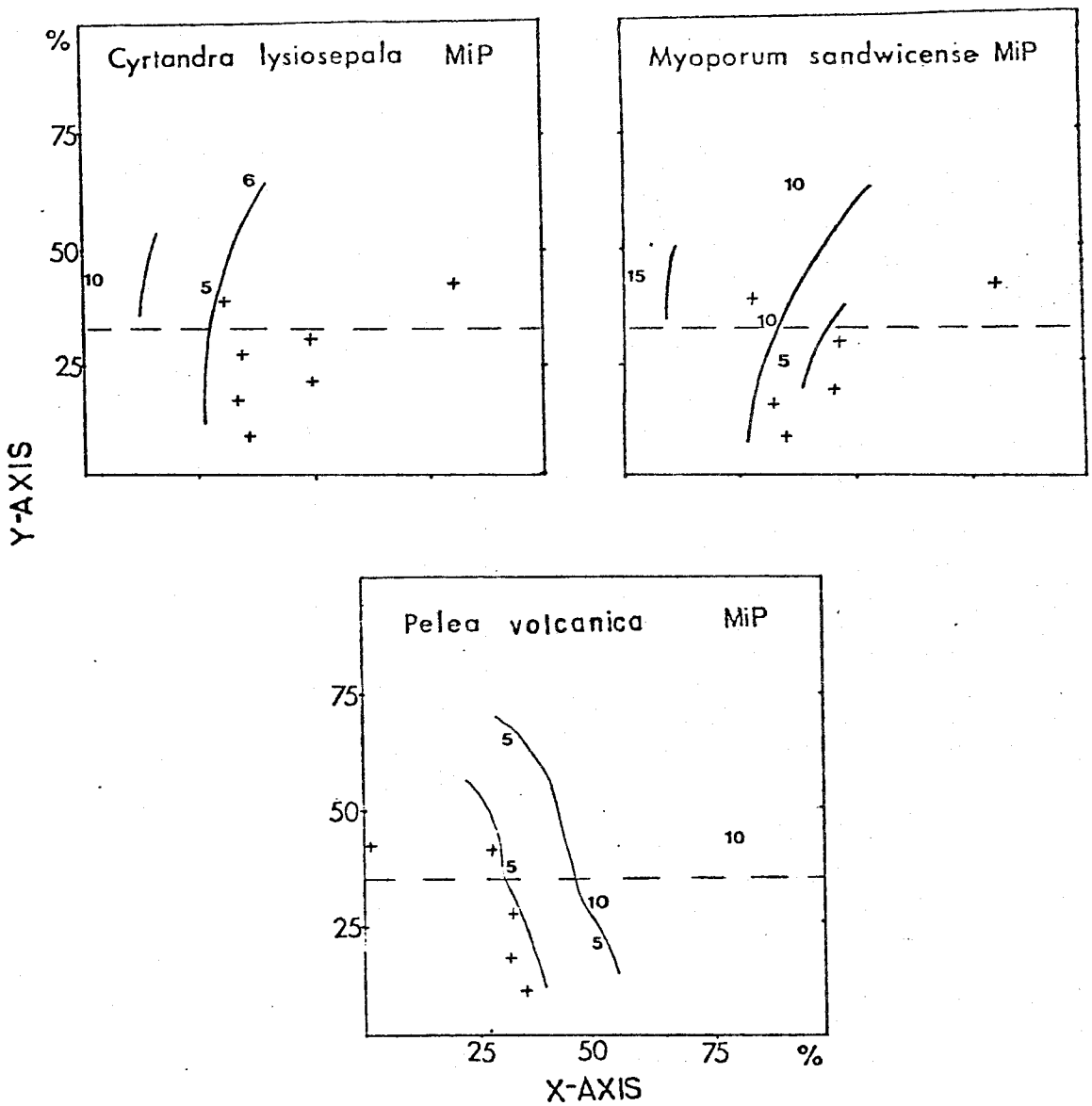


FIG. 10. Spatial arrangement of three selected microphanerophyte species within their plot ordination. Values are in per cent frequency. Plots from which the species are absent are shown by plus marks. Isolines give an indication of a gradient in species frequency values. The dashed lines refer to the separation between transect 1 and 4 as was indicated in FIG. 5d.

Other chamaephyte species which do not show trends in frequency values but which are unique to one transect also contribute to the difference in composition between the two transects. These are listed in Table 4.

The microphanerophyte species which show a trend similar (or opposite) to the soil depth trend (shown in Fig. 9b) (i.e. from left to right) are Cyrtandra lysiosepala (R-L), Myoporum sandwicense (R-L), and Pelea volcanica (L-R). These species values are shown in Fig. 10 on the ordination graph for (positive or negative) correlative comparison with the soil depth trend (Fig. 9b). The similar tendencies may indicate some correlation between the phytosociological behavior of the species and the soil depths, however the correlation coefficients (r) calculated for these three species and the soil depths are not statistically significant. This non-significance may be due to the small number of individuals. There appears to be no relationship between the presence of Myoporum and Pelea and the difference between the two transects (which was shown in Fig. 5d), since the species occur in both transects. Cyrtandra lysiosepala however is unique to transect 1.

Microphanerophyte species which do not show trends in frequency values in the direction of the compositional change revealed in the plot ordination graph (from top to bottom), but which are unique to one transect contribute to the differences between transects 1 and 4. These are listed in Table 4.

The density values of two mesophanerophyte species Metrosideros collina and Myoporum sandwicense are statistically correlated with soil depth averages for the forty plots (see Fig. 7). The r values are

0.552 and 0.495, respectively, with 38 degrees of freedom (d.f.). Both are highly significant (i.e. at the 0.01 level). As depth increases the density in a plot increases. Deeper soil may be able to support more trees of these two species in an area than the shallower soil. On the average in a plot there may be more favorable (deeper) habitats for these two species. Mesophanerophyte species which are unique to one transect contribute to the differences between transects 1 and 4 (revealed in Fig. 8). These species are listed in Table 4.

Differential species between transects 1 and 4

The species listed in Table 4 which occur in the sample more than once and other species from the total which have greater frequencies on one transect and only chance occurrences on the other were put into a differential table (Table 5). This table shows the species which indicate or differentiate each side of the study site. In Table 5 six chamaephytes species are predominantly found along transect 1 as opposed to only two species along transect 4. This suggests a greater diversity of chamaephyte species on transect 1. Perhaps this means that along transect 4 they are more widely spaced and sampled less frequently. From visual inspection of the data (see Table 10, Appendix B) this seems not to be the case, except for the species Metrosideros collina Ch which occurs throughout the forest but with apparently greater frequency in transect 1. As another comparison Table 4 lists thirteen species unique to transect 1, but also seven species unique to transect 4. The difference in diversity then is perhaps not too great.

From the data, however, there does appear to be a change in epiphyte diversity increasing towards transect 4. Table 5 shows several epiphyte species peculiar to transect 4 (and none to transect 1).

TABLE 5. Differential species between the two transects, 1 and 4. They were chosen by visual inspection of the frequency* data of all species of all layers in the ten primary plots.

Species	Plots: Transect 1					Transect 14				
	2	3	4	5	1	16	18	19	17	20
Acacia koa MesP	10.0	5.0	15.0	15.0	0.0	0.0	0.0	0.0	5.0	0.0
Veronica plebeia Ch	31.3	18.8	12.5	6.3	0.0	6.3	0.0	0.0	0.0	0.0
Polypodium pellucidum Ch	6.3	0.0	6.3	6.3	18.8	12.5	0.0	0.0	0.0	0.0
Hydrocotyle sibthorpiodes Ch	6.3	18.8	31.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Elaphoglossum wawrae Ch	6.3	18.8	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0
Cyrtandra lysiosepala MiP	0.0	5.0	5.0	0.0	10.0	0.0	0.0	0.0	0.0	0.0
Myoporum sandwicense Ch	0.0	6.3	6.3	0.0	12.5	0.0	0.0	0.0	0.0	0.0
Marattia douglasii Ch	6.3	0.0	0.0	6.3	6.3	0.0	0.0	0.0	0.0	0.0
Astelia menziesiana Ch	0.0	0.0	0.0	6.3	0.0	6.3	18.8	12.5	25.0	37.5
Broussaisia pellucida PE	12.5	0.0	0.0	0.0	0.0	6.3	12.5	6.3	18.8	12.5
Pelea clusiaefolia PE	6.3	0.0	0.0	0.0	0.0	18.8	25.0	6.3	12.5	43.8
Xiphopteris saffordii ChE	0.0	0.0	0.0	0.0	0.0	43.8	18.8	12.5	31.3	0.0
Cyanea spp. PE	0.0	0.0	0.0	0.0	0.0	12.5	6.3	0.0	43.8	6.3
Vandenboschia davallioides ChE	0.0	0.0	0.0	0.0	0.0	6.3	0.0	6.3	12.6	12.5
Nertera depressa ChE	0.0	0.0	0.0	0.0	0.0	6.3	12.5	18.8	0.0	0.0
Xiphopteris saffordii Ch	0.0	0.0	0.0	0.0	0.0	6.3	6.3	6.3	0.0	0.0
Gouldia sp. MiP	0.0	0.0	0.0	0.0	0.0	5.0	20.0	0.0	0.0	5.0

*Number of quadrats in which a species is present out of the total number. In the case of trees, if the trunk was within the quadrat the individual was considered present.

This greater diversity might be due to a greater number of shrubs and trees (on which the epiphytes grow) or a greater age of the trees (since as a tree gets older it acquires more epiphytes).

An inspection of the plot data shows that several microphanerophyte species have a much greater mean density (and therefore a greater number of individuals) in transect 4 than in transect 1: Broussaisia pellucida (ratio of transect 1 to transect 4 = 60/117), Cibotium glaucum (2293/2670), Pelea clusiaefolia (47/193), Coprosma rhyncocarpa (13/50), Ilex anomala (223/337) and Rubus hawaiiensis (37/83). Only Myoporum sandwicense has a much greater density in transect 1 (40/3). The mesophanerophytes, however, have more individuals in transect 1 than in transect 4 (626 = total in transect 1 and 603 in transect 4). The greater number of microphanerophytes in transect 4 may contribute to the greater epiphyte diversity there, especially the very abundant tree fern, Cibotium glaucum, which supports many epiphytes.

The presence of Acacia koa MesP in the list of differential species may give a false idea about this tree. It looks essentially absent from transect 4, in the primary plots (16-20), at least. In a case such as this with a species consisting of larger and therefore fewer individuals, ten plots were really not sufficient to give an adequate picture of the distribution of this species. The results of this method, concerning Acacia koa, must be evaluated in the light of other methods on the following pages.

Distribution of Acacia koa

Mean distances.--The mean distances (obtained from the point-centered quarter method) of Acacia koa for each sampling point are

recorded in Table 6. Three distance values are listed for each plot since three points within a plot (at the beginning, middle, and end) were sampled. As shown in Table 6 the mean distance to koa trees on transect 1 is 19.8 m and on transect 4 is 29.2 m. A comparison by the use of ranks (White 1952) for these two samples was made. They were found to be significantly different at the 0.01 level. This indicates that individuals of Acacia koa are farther apart on transect 4 than on transect 1. This does not support the previous suggestion that epiphyte diversity is greater on transect 4 due to a greater number of trees, at least Acacia koa trees. This also indicates that koa may be more clumped on transect 1 and is heterogeneously arranged within the study site rather than homogeneously (randomly) as previously assumed in the original choice of the site.

Cover.--Comparing the crown cover values (derived from the 1964 aerial photograph) of Acacia koa MesP between transect 1 (70%) and transect 4 (65%) revealed no significant difference (by the rank test). Other transects were drawn through the study site to compare the percentage cover in different parts of it. Two transects were run the width of the site in separate halves of it. The results were 67% and 68% cover values which are not significantly different. Transects running east and west were used to compare the north and south portions of the site and resulted in cover values of 73% and 70% which are not significantly different. Transects running north and south were used to compare the east and west portions and resulted in cover values of 67% and 78%, respectively, which are significantly different at the 0.01 level. This increase in cover coincides closely to

TABLE 6. Mean distances for Acacia koa from the sampling points in each of ten primary plots. Three points with four trees each were sampled per plot.

	Plot	Mean distance (m)	
Transect 1	1	9.8	
		28.0	
		8.8	
	2	20.8	
		33.2	
		13.8	
	3	18.9	Mean of Transect 1
		16.6	= 19.8
		17.7	
	4	22.3	standard deviation
		12.6	= 6.9
		28.1	
	5	20.4	
		24.1	
		21.9	
Transect 4	16	32.5	
		28.6	
		31.2	
	17	24.4	
		31.5	
		36.0	
	18	33.5	Mean of Transect 4
		20.8	= 29.2
		24.2	
	19	28.1	standard deviation
		27.2	= 9.8
		11.6	
	20	15.6	
		43.3	
		50.2	

increasing elevation (from 1590 m to 1650 m). No suggestion is made as to what effect elevation might have, but previously it was observed (Mueller-Dombois 1966) that the koa tends to become more dominant at higher elevations on Mauna Loa. This observation agrees with the crown cover results.

Comparison of methods.--The mean distances of Acacia koa MesP (from Table 6) indicate that the individuals are farther apart on transect 4 than on transect 1. This agrees with the plot frequency data of Acacia koa as shown in Table 5, where koa was not present in the primary plots (16-20) on transect 4. The crown cover data does not indicate any difference between transects 1 and 4. This may mean that though the trees are farther apart on transect 4, they may be larger individuals with larger crowns, the general effect of which is to cover the same area as those on transect 1.

Species ordinations

In this type of ordination species pairs were compared with regard to their distribution among the quadrats. Here species are the individuals to be ordinated and the quadrats are their attributes.

The basic quadrat size (3 X 5 m = 15 m^2) was doubled (to 30 m^2) by combining the data from the two contiguous quadrats. In cases where the size of the largest possible species group was estimated to be larger, this quadrat size was doubled a second or third time (to 60 m^2 or 120 m^2).

The species' presence values in each quadrat (the size of which varied according to the layer) were used to ordinate the species within

each layer in relation to one another. Since it was assumed that the differences between individual species' occurrences were generally very great, further differentiation by quantities was not necessary. A simpler, qualitative coefficient was used to comapre species pairs.

The simple matching coefficient (SM) (Sokal and Sneath 1963) can be used to compare two individuals (in this case, species), 1 and 2:

$$SM_{1,2} = [(a + d)/n][100]$$

where a = the sum of attributes (in this case, quadrats) which both individuals (species) have in common

d = the sum of those which neither has

n = the total number of attributes (quadrats sampled)

The coefficient has a theoretical range from 0-100. 100 minus SM gives the dissimilarity or distance between individuals (species). (See Appendix E for the application of this coefficient.)

The basic ordination program was modified by the additional criteria of Newsome and Dix (1968), as described in Part I. The number of individuals (species) in this exercise is great so that the more rigid criteria are suitable to prevent extremely different species from being chosen as reference points. A third axis or dimension was also added to this representation in order to separate species within any apparent clusters.

Epiphytes

Fig. 11 shows the graphs of epiphyte species related to three axes where a gradual change is revealed along the diagonal between them. Looking from left to right the first species points are not clustered and they represent epiphytes which are common (found in at least 30% of the quadrats). At the upper right end of the diagonals several

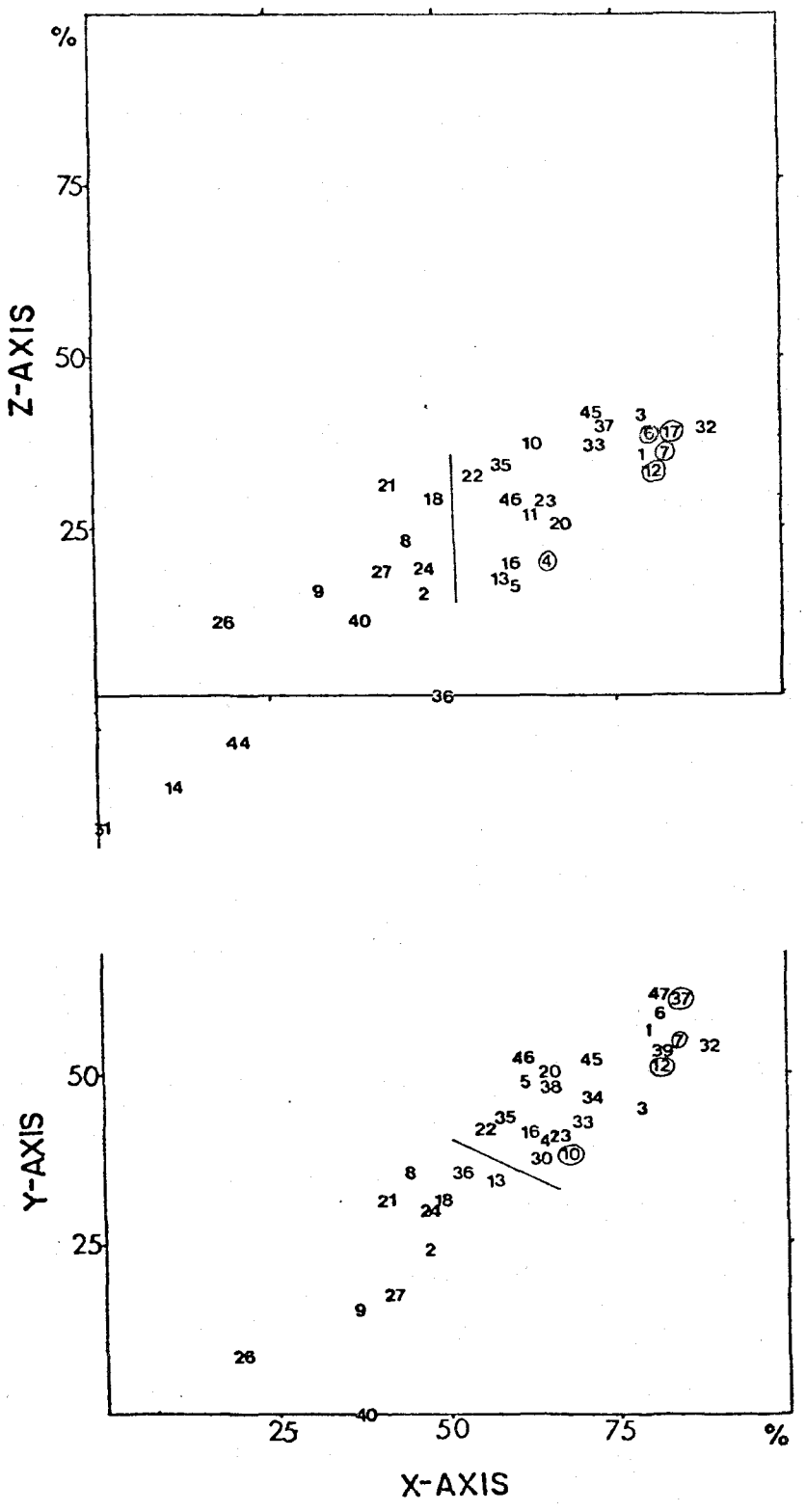


FIG. 11. Ordination of 46 epiphyte species from 40 quadrats of 60 m^2 each. In FIG's. 11-13 the simple matching coefficient was used together with the modification of Newsome and Dix of the Bray and Curtis method. Numbers in the graph refer to species or to groups of species (circled) in the (lower) xy plane: 7, 17, 19, 25, 29, 30, 43; 10, 11; 12, 15, 41; 37, 42; and the (upper) xz plane: 4, 38; 6, 15, 41; 7, 19, 29, 42; 12, 39; 17, 25, 30, 37, 43, 47. The names of those species are all listed in Table 1. In FIG's. 11-13 the lines indicate the approximate separation between "common" and "rarer" species.

clusters of species occur. These are the rarer species which are clustered only because of their mutual dissimilarity to the other more common species, especially to no. 31 (Metrosideros collina). They are not automatically also similar in their distribution since they for the most part do not occur in the same quadrats.

As stated earlier, variations in the study site may appear as a mosaic or as a gradual change of vegetational characteristics across the extent of a zone. In Fig. 11 a gradual change in relation to their presence in quadrats occurs among the more common species of epiphytes. This change is reflected in the earlier plot ordination (Fig. 5b) where the composition gradually changes from transect 1 to transect 4.

With further environmental data or experience with the species it might be possible to explain what the axes in Fig. 11 represent. The points in position along the diagonals are interpreted as being due to a gradual change in composition which may be related in some way to some environmental factors, physical or biological.

Clusters occur among the rarer species of epiphytes. This is interpreted as a more random (homogeneous) spatial arrangement at this scale (60 m^2). This ordination did not reveal dissimilarities in distribution of these species among the quadrats. By checking rare species close together in the ordination and comparing the quadrats in which they occur (Table 9, Appendix B), it is shown that generally they do not occur together at all.

To conclude, there is no evidence for markedly different distributions of groups of epiphytes at this scale (60 m^2). An ordination using quadrats of 30 m^2 also produced similar relationships.

Chamaephytes

The chamaephyte graph in Fig. 12 shows a diagonal line of species between the three axes with a distinct cluster at the upper right end. Starting from the lower left the first species are the most common chamaephytes found in at least 24% of the quadrats. These diagonal lines represent a gradual change in relation to these species' presence in quadrats. This change is also reflected in the plot ordination (Fig. 5c) of chamaephytes by frequency values where the composition changes slightly from transect 1 to transect 4.

The cluster of points at the upper right end of the diagonal consists of rarer species. They are clustered due to their great spatial dissimilarity to the common species, but not because of similarity among themselves. The cluster is interpreted as resulting from a random (homogeneous) arrangement of the rarer species at this scale (30 m^2). This ordination then gives no evidence of distinct species groupings among the commoner species, but shows a gradual change (continuum) in their spatial arrangement.

Microphanerophytes

Fig. 13 shows the ordination of microphanerophyte species revealing a gradual change along a diagonal between the x and z axes, perpendicular to the y-axis. The y-axis does not separate the species very much. All these ten species scattered along the diagonal occur in at least 24% of the quadrats.

The cluster of points together at the (upper right) end of the diagonal represents rarer species which are mutually dissimilar to the more common species, especially to no. 6 (Cibotium glaucum). No other

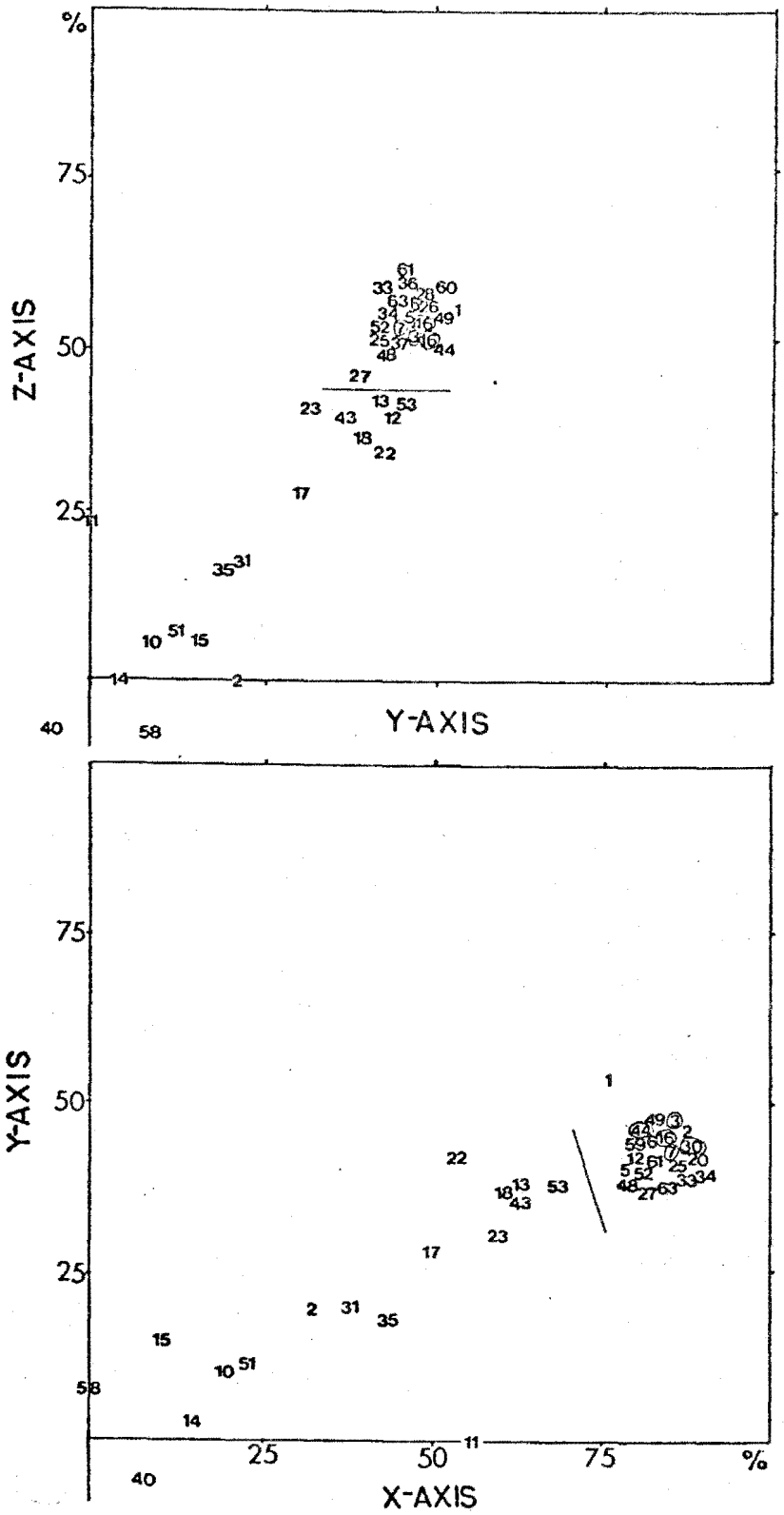


FIG. 12. Ordination of 61 chamaephyte species from 80 quadrats of 30 m^2 each. Numbers in the graph refer to species or to groups of species (circled) in the (lower) xy plane: 7, 9, 19, 24, 28, 26, 36, 37, 46, 50, 62; 3, 21, 29, 32, 39, 47, 54, 56; 16, 42; 30, 38, 41, 45, 55, 57; 44, 60; and the (upper) yz plane: 46, 47, 54; 7, 9, 19, 20, 26, 30, 38, 41, 45, 55, 57; 3, 59; 16, 42, 50; 6, 21, 24, 29, 32, 56. The names of these species are listed in Table 1.

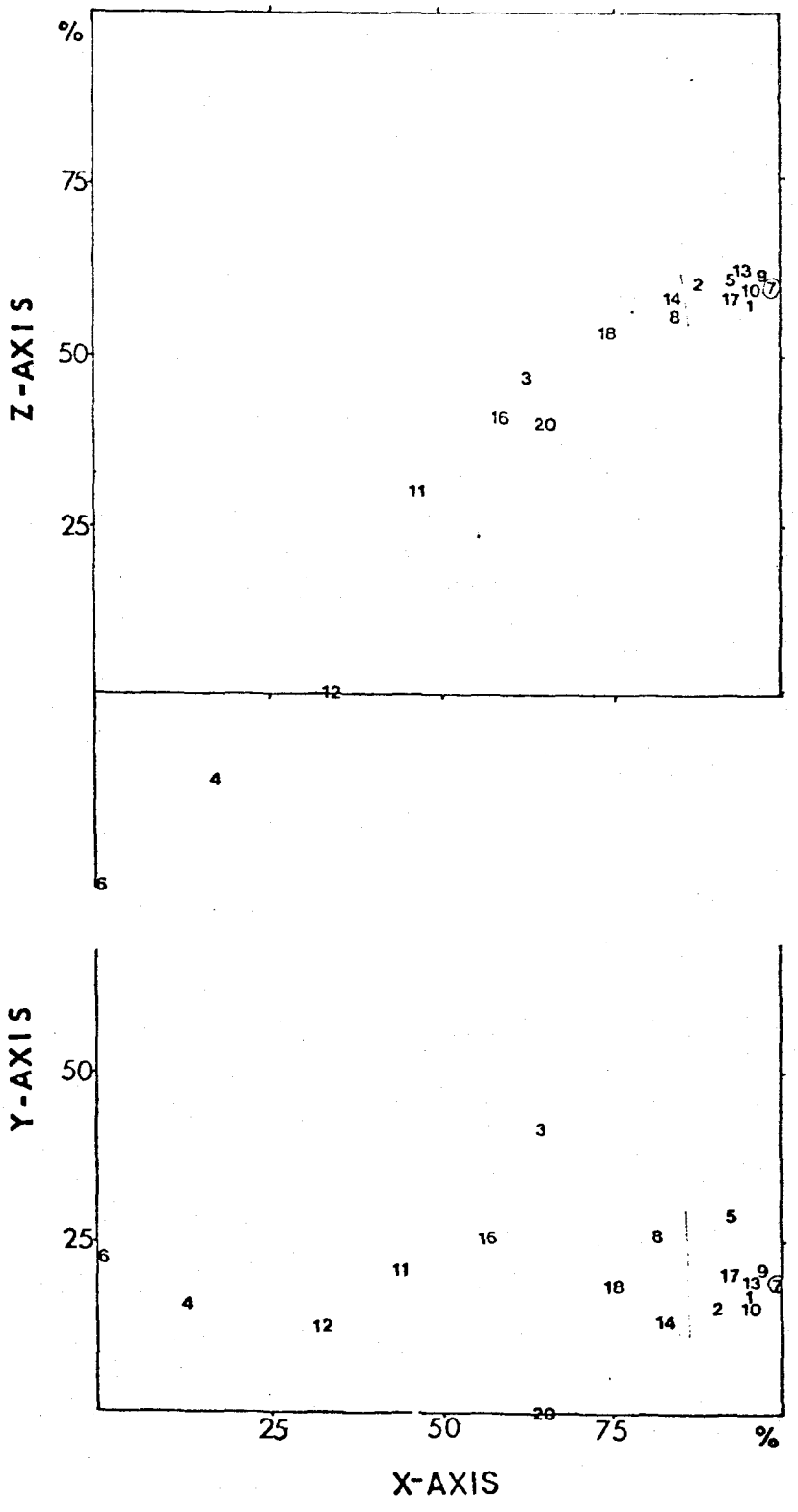


FIG. 13. Ordination of 19 microphanerophyte species from 100 quadrats of 60 m^2 each. Numbers in the graph refer to species (the names of which are listed in Table 1). In the case of species 7 and 19, both have the same coordinates and so are indicated by the number 7 (circled).

discrete clusters are present. Thus, there is no evidence for species groups markedly different in distribution from the other species.

The spatial arrangement of the common species is interpreted as a continuum or gradual change. The rarer species have a random (homogeneous) arrangement at this scale (60 m^2). An ordination using quadrats of 30 m^2 also produced similar relationships.

The possibility was considered that the ordinations might be biased by data from contiguous quadrats. To test whether this had some effect, data from only odd numbered quadrats of 60 m^2 were used to produce another ordination of microphanerophytes. This resulted in graphs very much like that produced from all the quadrat data, giving an identical interpretation. This also revealed the fact that transects 1 and 4 were oversampled--half of the number of quadrats would have been sufficient.

In the three layers whose species ordinations have been presented so far, six of the same species (but in different layers) are among the common ones along the diagonals in each figure: Cheirodendron trigynum, Coprosma rhyncocarpa, Ilex anomala, Metrosideros collina, Rubus hawaiiensis and Vaccinium calycinum. These are common epiphyte species which are also found as common seedlings (chamaephytes) growing on the ground and as common maturing shrubs or trees (microphanerophytes).

Mesophanerophytes

Fig. 14 shows the ordination of mesophanerophyte species in a three-dimensional representation. The left face is the yz plane and the right face is the xz plane.

One tight cluster of six species is indicated by a circle near the

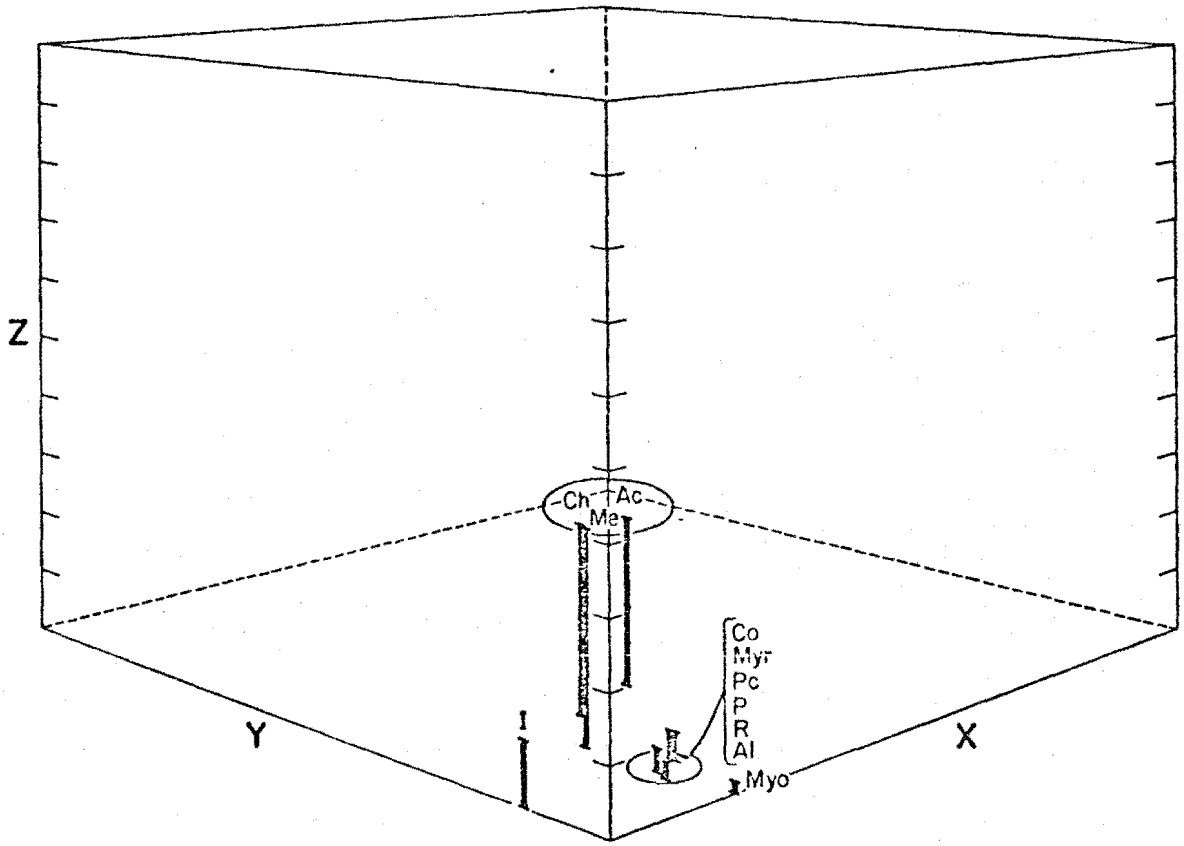


FIG. 14. Ordination of eleven mesophanerophyte species in three dimensions using the simple matching coefficient. Dissimilarity is based on species presence in 200 quadrats of 120 m^2 each. The following abbreviations for species names are used:

Ac = Acacia koa
Al = Alyxia olivaeformis (liana)
Ch = Cheirodendron trigynum
Co = Coprosma rhynchocarpa
I = Ilex anomala
Me = Metrosideros collina
Myo = Myoporum sandwicense
Myr = Myrsine lessertiana
PC = Pelea clusiaefolia
P = Pelea volcanica
R = Rubus hawaiiensis (shrub)

Two clusters of species are shown circled on the graph.

xy plane close to the x-axis (lower right). These species are the rarer ones occurring in less than 10% of the quadrats. They are mutually dissimilar to the other five, relatively common species. Three of these five species, Acacia koa, Cheirodendron trigynum and Metrosideros collina are clustered due to their similarity in distribution among the quadrats. These species represent a group markedly different in distribution from the other species.

The spatial arrangement of the common species is interpreted as heterogeneous with a recurring group. The arrangement of the rarer species is interpreted as homogeneous (or random) at this scale ($120\ m^2$).

The interpretation of this particular graph is difficult due to the inherent nature of the method, which may be inappropriate when only eleven species are involved. The construction of three axes depends on the choice of six reference species from the total of eleven. The results from later analyses will be helpful in understanding this graph and the arrangement of the species in this layer.

Another ordination of mesophanerophyte species was made using another similarity coefficient by which the relative distance between the species points was calculated. The coefficient is referred to as relative distance (RD) (Orlóci 1967) and the comparison of two individuals (in this case species), j and k, is as follows:

$$RD_{j,k} = \sqrt{[2(1-\sum_{h=1}^{p} x_{hj}x_{hk}/V_jV_k)]}\ ,$$

where p = the total number of attributes (in this case quadrats)

x_{hj} = the quantity for the h^{th} attribute of individual j

$V_j = \sqrt{[\sum_{h=1}^{p} x_{hj}^2\ ]}$

The coefficient has a theoretical range from 0 to $\sqrt{2}$. To convert this to the same range as the other coefficients (IS and SM) the values were divided by $\sqrt{2}$ and multiplied by 100. This represents the distance or dissimilarity between individuals. See Appendix D for a derivation of this coefficient and Appendix E for an example of the calculation. The ordination of eleven mesophanerophytes from 120 m^2 quadrats with relative distance was made using the Bray and Curtis method. Fig. 15 shows a three dimensional representation of this ordination. In the center is a cluster of four common species: Acacia koa, Cheirodendron trigynum, Ilex anomala and Metrosideros collina. The seven rarer species are spread out, separated from one another. This arrangement of rare species is in contrast to that in Fig. 14 where they are clumped. (The relative distance is professed to have this advantage in separating rare, but dissimilar individuals.)

Fig. 15 is interpreted as indicative of a heterogeneous spatial arrangement of mesophanerophytes. The four species, previously mentioned, represent a species group which recurs throughout the forest. This is in agreement with the interpretation of Fig. 14 except that the species Ilex anomala was not included in the group in that graph. An ordination using quadrats of 240 m^2 and the RD with qualitative data produced almost identical relationships as in Fig. 15.

On subsequent trips to the forest this one group of four species was actually observed throughout the study site. Cheirodendron trigynum and Metrosideros collina were found together very frequently and Acacia koa and/or Ilex anomala was present with them in many cases. The size of the quadrat in which this group could have been sampled was

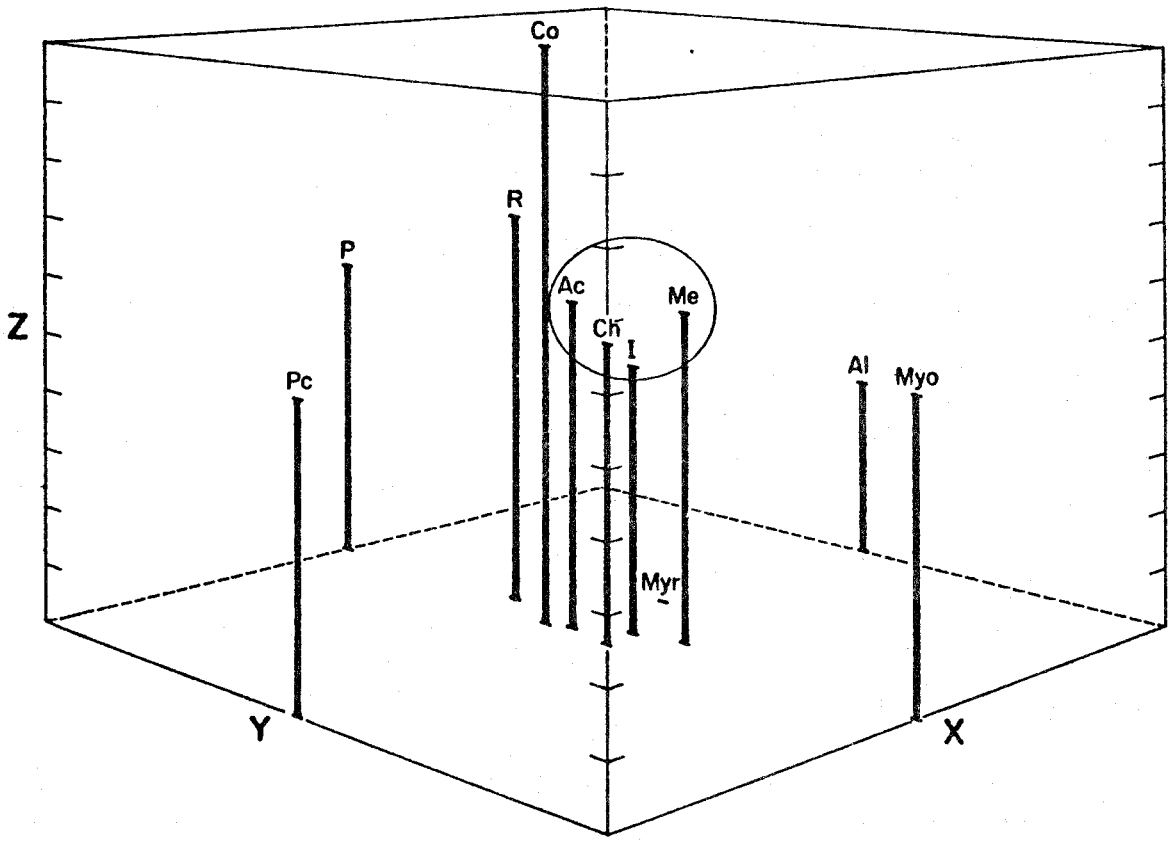


FIG. 15. Ordination of eleven mesophanerophyte species in three dimensions using the relative distance coefficient. Dissimilarity is based on species counts in 200 quadrats of 120 m^2 each. The abbreviations used for the species are the same as in FIG. 14.

approximately 120 to 240 m^2.

Metrosideros collina is the most numerous (745 sampled in 40 plots) large tree (mesophanerophyte) and is present in combination with most of the other species. Cheirodendron trigynum is the second most numerous (243 sampled) and is usually of much smaller size. Fewer Acacia koa individuals are present (64 sampled), but due to their large size they are more easily seen and therefore seem to be more numerous. Ilex anomala individuals are present in about the same numbers (72 sampled) as koa but since they are generally much smaller individuals (most only about 5 to 7 m high and less than 10 cm in diameter) with small crowns they are not as readily observed as the other three species.

Test for heterogeneity

Definitions

Heterogeneity involves a clumping of species into groups forming a mosaic. Within a homogeneous group the individual plants or smaller groups are randomly arranged and the quantities of different species are proportional. Assuming that there are measurable similarities in terms of their presence or quantity in different quadrats between species or between groups of species, a hierarchical class structure can be defined. If there are no such similarities then visual inspection can separate the groups; no dendrogram can logically be constructed.

If a random sample is taken of the vegetation, the similarities between species in the samples will estimate the similarities between

species in the vegetation. Hierarchies (dendrograms) constructed from the sample data will estimate the hierarchical class structure of the groups (assuming the method permits overlapping in groups). If a single hierarchy exists, implying inherent heterogeneity in the samples, then the sample dendrograms would be consistently similar (statistically indistinguishable). If, on the other hand, a homogeneous or very gradual continuum arrangement of species exists, then the dendrograms would possibly reflect chance arrangements and would be statistically dissimilar. The null hypothesis (H_o) to be tested then is that the sample dendrograms of species are indistinguishable against the alternative (H_1) that they are indeed distinguishable.

Test

Ten (an arbitrary number) random samples were taken from the available quadrats. Each sample consisted of 20% of the number of quadrats. The samples could overlap in terms of quadrats. The species of each sample were arranged in a dendrogram by the sum-of-squares clustering (Orlóci 1967; see below). From each dendrogram a topological distance matrix (Phipps 1971) was calculated by counting fusions. The matrices were compared by the minimum discrimination information statistic (m.d.i.s.) (Kullback, Kupperman, and Ku 1962) compared with Chi-square for significance. A low number of significant values would indicate that the dendrograms are sufficiently similar to indicate that H_o can be accepted. If there were many significant values H_o would be rejected and the analysis would terminate. This procedure is represented in a flow chart in Appendix H. The methods involved and the techniques used are discussed in detail in the following section.

Methods and techniques

Sum-of-squares.--The within-group sum of squares (Q_n) of a group of n individuals (visualized as points in an abstract space) is defined as the sum of squared distances of points from the group's centroid. The centroid is a pseudo-point representing the "average" individual of the group. The sum of squares can be calculated directly from the distances between points:

$$Q_n = (1/n) \sum_{i<j} RD_{ij}^2 ,$$

where RD_{ij} is the relative distance (as described previously) between the i^{th} and j^{th} points and $\sum_{i<j}$ denotes summation over all pairs of points, counting each pair only once.

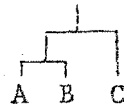
Two groups, with within-group sum of squares of Q_u and Q_v, are combined in the dendrograms if

$$Q_{uv} - (Q_u + Q_v) < \begin{matrix} Q_{uw} - (Q_u + Q_w) , \\ Q_{vw} - (Q_v + Q_w) , \end{matrix}$$

for all w (other groups). It can be seen from these expressions that the two groups are combined only if neither would combine better with some other group. The clustered pairs become new groups. At each step of the agglomeration all permissible combinations of groups are made before another cycle begins. The procedure is repeated over and over again until all individuals are contained within one group.

The hierarchy so established can be represented in the form of a dendrogram. A dendrogram is another type of graphical representation of the relationship between individuals. The individuals are shown as

clusters linked at different levels of similarity, for example:



where A, B, and C are individuals on which the cluster analysis is performed.

Topological distances.--Topology is defined by Phipps (1971) as the branching pattern relationship among individuals in a dendrogram. Topological distance is the total number of internodes (or fusions) between any two individuals counting both up and down in the dendrogram. The matrix of topological distances for A, B, and C in the previous example is:

	A	B	C
A	0	1	2
B	1	0	2
C	2	2	0

M.d.i.s.--The minimum discrimination information statistic (Kullback, et al. 1962) (see Appendix G) measures an information divergence which separates two dendrograms described by their topological distance matrices. The distribution of m.d.i.s. may be used to approximate the Chi-square distribution when the number of species is great. For the purposes of this study the probability distribution of m.d.i.s. was assumed to be representable by the Chi-square distribution and the calculated values were compared with the critical values in the Chi-square table. The calculated values greater than the critical Chi-square values were regarded as significant. Values less than the critical values, however, indicated indistinguishability. Whenever there are few significant values in the total number of comparisons (10(10-1)/2 in total), H_o is accepted.

When the number of species is low, it is recommended to calculate the values obtained from an artificial distribution under the current local conditions of sampling and cluster analysis similar to the simulation procedure of Orlóci (1971).

Procedures.--A computer subroutine for choosing random numbers was used to select the samples of quadrats at random. Ten samples were considered adequate, each comprising 20% of the total quadrats. The data set then consisted of species as individuals with quantities in quadrats as their attributes. The program of Goldstein and Grigal (1971) in FORTRAN IV* was used to produce the hierarchical classifications of the species in each sample based on the sum-of-squares method. Two additional programs* were written and used to calculate the topological distances (Phipps 1971) between species within each hierarchy and also to compare each pair of topological distance matrices with their m.d.i.s. values (see Appendix G for the formula).

The calculated values, totaling in number $10(10-1)/2 = 45$, where 10 is the number of sample dendrograms, were calculated by computer and printed. A sample printout is shown in Appendix J. The number of degrees of freedom for each m.d.i.s. is equal to the number of distance values compared in each of the matrices minus one, i.e. $[n(n-1)/2]-1$, where n is the number of individuals. The number of significant values of the 45 m.d.i.s. values at probability level 0.05 was counted and H_o was rejected if 95% or more of the values were significant. A lower percentage of significant values is interpreted as an indication to

*These programs are available in the Department of Botany, University of Hawaii.

accept H_o, and consequently, to declare heterogeneity of spatial arrangement for the species tested.

In the case where low significance, and therefore, acceptance of H_o resulted, an artificial random data set was produced (by a computer program which is listed in Appendix A) which was in turn tested for heterogeneity like each previous data set. These artificial data were comprised of the same number of species and individual plants of each species as in the actual data. The number of significant values resulting from this test was used as the critical number to compare with the number from the actual set of data collected from the field. If the latter was lower, then the H_o was accepted with reasonable confidence.

The data from the quadrats, 15 m^2 or 30 m^2 in area, were pooled to form sets of data for quadrats of double, quadruple, or octuple the basic size. Since it was known that the results depend on the size of the sampling unit, a few more quadrat sizes were tested.

The epiphyte presence data for 160 quadrats (16/plot X 10 plots) of 15 m^2 were combined to produce presence for 80 quadrats of 30 m^2. This new set of data was submitted for analysis. It was also condensed again to produce data for 40 quadrats of 60 m^2, which were in turn analyzed.

The chamaephyte cover data for 160 quadrats of 15 m^2 were combined and the average cover for 80 quadrats of size 30 m^2 was then calculated. These new data were submitted for analysis by the previously described program. Sixteen quadrats (20% of 80) were chosen at random in each of ten runs; ten dendrograms were generated and a topological distance

matrix for each dendrogram was calculated; the distance matrices were compared based on m.d.i.s. at the 0.05 level and [63(63-1)/2]-1 = 1952 degrees of freedom.

The count data for microphanerophytes in 200 quadrats of 30 m^2 were analyzed by the program for random samples, sum-of-squares clustering, and the statistical comparison. The data from every two quadrats were combined to produce total counts for 100 quadrats of 60 m^2 and this new set of data was also analyzed.

The mesophanerophyte count and basal area data for 800 quadrats of 30 m^2 were combined to produce total counts and basal area for 200 quadrats of 120 m^2, 100 of 240 m^2, and 50 of 480 m^2. These sets of data were also analyzed.

Results (Table 7)

Table 7 shows the resulting percentages of significant values for each layer at each particular quadrat size. (A sample printout of values for one data set is shown in Appendix J). The epiphyte, chamaephyte, and microphanerophyte species at each quadrat size all produced significant values (100%). This is interpreted as an indication that each of these layers consists of homogeneously or slightly continuously arranged species. The quadrat sizes chosen for an analysis were large enough to theoretically include all the different species of their respective layers. There was no difference in the results of different quadrat sizes of these three layers.

The mesophanerophyte species, however, produced fewer significant values at the quadrat sizes tested. At the top of Table 7 the quadrat size of 120 m^2 resulted in the lowest percentage of significant values;

TABLE 7. Summary of the results of the test for heterogeneity of species arrangement in each of the layers.

Layer	Quadrat size (m^2)	no. of quadrats used out of total	Percentage significant Chi-square values*			Result
			count data	qualitative data	basal area	
Mesophanerophytes	120	40/200	22	7	22	heterogeneous
Mesophanerophytes	240	20/100	29	44	44	heterogeneous
Mesophanerophytes	480	10/50		93		heterogeneous
Mesophanerophytes (without *Acacia koa*)	120	40/200		87		heterogeneous
Microphanerophytes	30	40/200		100		not heterogeneous
Microphanerophytes	60	20/100		100		not heterogeneous
Chamaephytes	30	16/80		100		not heterogeneous
Epiphytes	30	16/80		100		not heterogeneous
Epiphytes	60	8/40		100		not heterogeneous
Artificial random distribution of Mesophanerophytes	120	20/100		100		not heterogeneous

*Low percentage significant Chi-square values mean great heterogeneity.

this indicates the greatest heterogeneity. Mesophanerophytes in quadrats of 240 m^2 resulted in 44% significant values which also indicate heterogeneity. Quadrat size 480 m^2 resulted in a much higher percentage, but it is still not significant so it also indicates heterogeneity, but to a lesser degree. When Acacia koa values (at quadrat size 120 m^2) were excluded from the data set which was then tested the result was 87% significant values which still indicate heterogeneity but to a lesser degree than the same data set with koa (7%).

It seems to follow that the koa data adds to the heterogeneity of the layer. In other words, koa itself may be heterogeneously arranged. This conclusion is also supported from the mean distance data (presented in the section on plot ordinations) where it was found that koa is more widely spaced in transect 4 than transect 1. The cover data of koa (also in the plot ordination section) again lead to the same conclusion, at least with respect to the west and east sectors of the study site which differ significantly in cover values, therefore indicating heterogeneity of koa.

Species groupings

Whenever heterogeneity was indicated from the test, species data for all quadrats for that layer were clustered by the sum-of-squares method (see Appendix A for BASIC program listing) to produce one hierarchical classification (dendrogram) of the species. These species groups at any particular level should represent the actual species grouping in the field except for any overlapping species found in more than one group.

Since the mesophanerophytes were found to be heterogeneous which means a unique hierarchy exists, it is appropriate to produce a hierarchical classification of species groups. The dendrograms constructed using species data from all the quadrats for the mesophanerophytes are shown in Figs. 16 and 17. The data were from 100 quadrats of 240 m^2. These data indicated great heterogeneity when tested and were few enough for the convenient use of the computer (HP 2000E) available.

The level of 2.0 was chosen to draw a line across the dendrogram in Fig. 16. This level was sufficient to isolate the species group consisting of Acacia koa, Ilex anomala, Cheirodendron trigynum, and Metrosideros collina which were found in the ordination graph Fig. 15. Three other groups were also isolated: Myrsine lessertiana, Pelea clusiaefolia and Alyxia olivaeformis, Pelea volcanica and Rubus hawaiiensis, and Myoporum sandwicense and Coprosma rhyncocarpa. These three groups were not evident from Fig. 15, however, which suggests that these are perhaps overlapping groups and therefore not distinct from species in the main group (shown in Fig. 15 and observed in the field).

Fig. 17 shows slightly different groups if cut at the same level (2.0) as in Fig. 16. The largest group consists again of Acacia koa, Ilex anomala, Cheirodendron trigynum and Metrosideros collina. Others include Myrsine lessertiana, Pelea clusiaefolia, and Alyxia olivaeformis; and Pelea volcanica, Rubus hawaiiensis, and Coprosma rhyncocarpa.

The first and second group and part of the third group of the dendrogram in Fig. 16 using qualitative data are identical to the

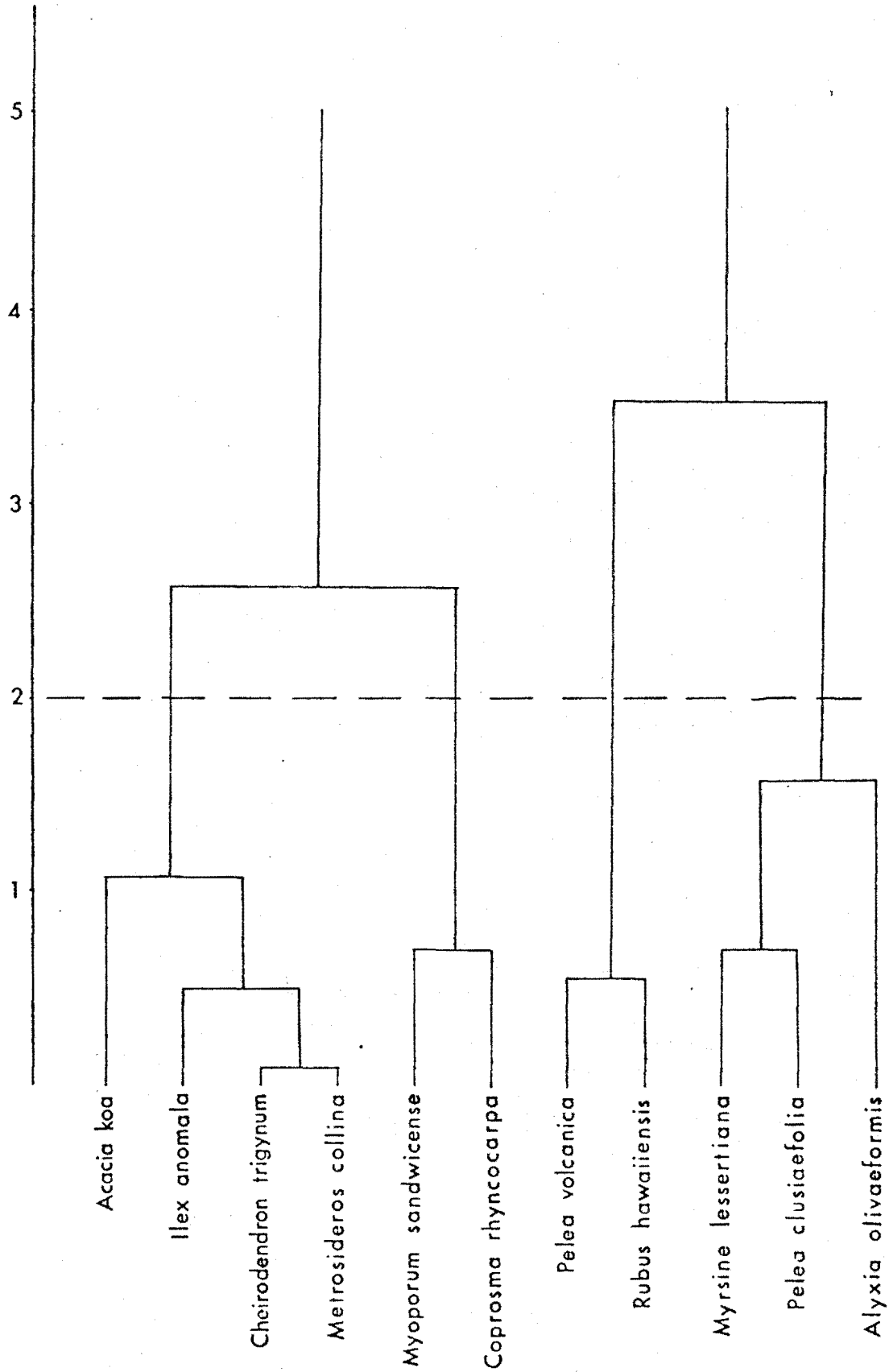


FIG. 16. Classification of mesophanerophyte species using qualitative data from 100 quadrats of 240 m^2 each. The sum-of-squares method with relative distances was used to produce this dendrogram. The vertical axis represents within-group dispersion of species (sum of squares). The two large groups of species come together at the 7.6 level (if the diagram were to be extended).

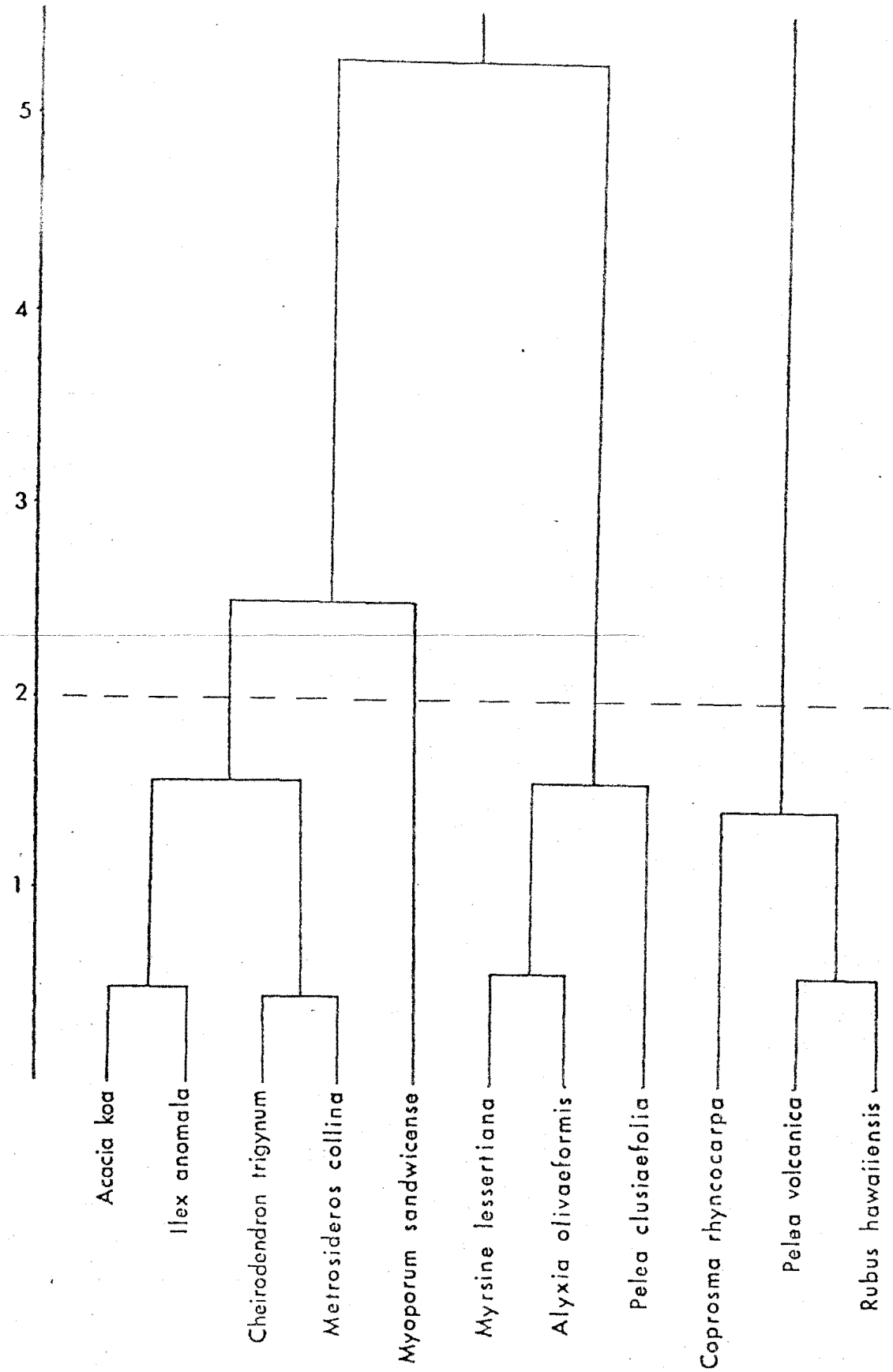


FIG. 17. Classification of mesophanerophyte species using count data from 100 quadrats of 240 m^2 each. The sum-of-squares method with relative distances was used to produce this dendrogram. The vertical axis represents within-group dispersion of species (sum of squares). The two large groups come together at the 8.1 level.

dendrogram in Fig. 17 based on (quantitative) count data. In other words both qualitative and quantitative data give very similar results.

The clustering technique of sum-of-squares is a non-overlapping method which cannot put the same species in two different groups (producing overlapping groups). Since the patches of vegetation have some of the same species, the groups are actually overlapping to some degree. Other methods do exist which produce overlapping groups (classes) and are discussed by Wirth, Estabrook, and Rogers (1966) and Jardine and Sibson (1968). These methods are, however, much more complicated to use and since no computer program was available to employ these techniques, they were not practical for this study. An alternative which was chosen to use here was the ordination of species. By this technique one can draw arbitrary lines and divide clusters of points. In this visual way overlapping groups can be estimated. The largest group of species found in the classifications was also found by the species ordination (Fig. 15). This group consisted of Acacia koa, Cheirodendron trigynum, Ilex anomala and Metrosideros collina. Depending on where one draws lines, this group represented by points on the graph could overlap with a nearby group of points representing Pelea volcanica and Rubus hawaiiensis because the point representing Acacia koa lies fairly near to this second group as well as to the first group. Other overlapping of groups appears less likely from the ordination.

DISCUSSION

The general purpose of this study, as stated in the Introduction, was to study the spatial arrangement of species in the superficially homogeneous rain forest and to find out whether there are any recurring associated species groups. It was hypothesized that there was variation (i.e. non-homogeneity) at some scale which could be detected and tests were devised to examine this hypothesis. The tests were in three parts: (1) ordinations of plots, (2) ordinations of species, and (3) tests of heterogeneity. They were performed for each layer. Species groups were then defined by cluster analysis in the layer in which heterogeneity was detected.

Variation in spatial arrangement in general and in this investigation was dealt with subjectively and objectively at several scales. The subjectivity existed in the choice of the 80 hm^2 study site. It was considered to be a "typical" site within the native montane koa rain forest. The choice of the exact plot locations was objective, since they were predetermined along transects.

Poore (1962) described the subjective method by which field ecologists choose a site as careful reconnaissance, followed by a selection of the "more uniform" or "homogeneous" areas and communities which occur frequently with more or less the same species composition. This procedure has been justified by its proven usefulness and the fact that the judgements of experienced ecologists tend to coincide.

Goodall (1954) was concerned with the method of visually deciding the "uniformity" of an area and warned that, "plant sociologists anxious to proceed with the work of . . . classification have been only too

willing to accept their own subjective evaluation of the situation, and have in general not troubled to go beyond their general visual impressions of homogeneity in the stands they are studying." This study has gone beyond the general visual impressions and has actually measured and tested for homogeneity (and the alternative spatial arrangements) on various scales.

Plot ordinations

The first step in testing homogeneity on a larger scale was plot ordination by layers. Gittins (1965) described plot ordination as "efficient and penetrating." The technique is powerful in testing the variation of floristic assemblages within a broader community. The variation was considered likely to be limited and therefore could be summarized and interpreted in terms of two dimensions.

Distinctly different plots would have been classified as belonging to a different community within a layer but such were not detected in this analysis. Though some variation was shown, no different species assemblages were detected within any of the layer communities.

The distribution and quantities of certain species were superimposed on each layer ordination graph. They showed certain trends in various directions, some or all of which may be related to environmental gradients. One environmental factor, soil depth, which was measured, did show a trend similar to that of three microphanerophyte species and was correlated with the presence of two mesophanerophyte species.

Species ordinations

The second part of the testing for variation was through species ordinations based on data from smaller scale quadrats. The size of the quadrats used in the ordination for each layer was chosen based on some knowledge of the size of the individual plants.

The results of the species ordinations of the epiphytes, chamaephytes, and microphanerophytes is interpreted as a gradually changing arrangement of common species with rare species interspersed randomly or in a homogeneous arrangement at the quadrat sizes tested. The mesophanerophytes are interpreted as having a heterogeneous arrangement of recurring species groups at the 120 m^2 quadrat size. One group of four species, Acacia koa, Cheirodendron trigynum, Ilex anomala, and Metrosideros collina, is clearly shown in the ordination.

As Poore (1968) did, the "common" species are discussed separately from the "rare" species. In this case, however, the lines between the two types were not always easy to see as was true in his case. (The lines which were subjectively chosen are shown in the ordination graphs in the Results.)

These results support the hypothesis that there is variation within the study site. This variation is exhibited in the species composition of common epiphytes, chamaephytes, and microphanerophytes changing gradually along a spatial gradient, and also in the heterogeneous arrangement of mesophanerophytes. The arrangement of species may be due to their varied response to habitat differences. If so, variation in species arrangement would be a result of some sort of variation in environment. This study covers only one environmental factor, soil

depth, and as previously discussed, plot values for it were correlated with plot density values of two mesophanerophyte species. Smaller scale quadrat depths and counts of mesophanerophyte species were, however, not correlated. Therefore, in this case, the large scale species arrangements are related to large scale (i.e. plot) variation in environment (soil depth), but the exact locations of species are not related to the small scale (i.e. quadrat) variation in environment.

Test for heterogeneity

The third part of the testing used the sum-of-squares clustering on random samples, which were subsequently compared by Chi-square tests. The results indicate that epiphytes, chamaephytes, and microphanerophytes, at the quadrat sizes examined, are not heterogeneous in arrangement. The mesophanerophytes are heterogeneous at quadrat sizes 120 m^2 to 480 m^2.

The interpretations of the species ordinations are somewhat compatible with the interpretations of the results of this test. From the ordinations, the three understody layers appear to consist of subcommunities merging into one another in a continuum. The heterogeneity test results indicate that these layers are not heterogeneous, including the possibility of a very gradual change or continuum. From the ordinations at quadrat size 120 m^2 the mesophanerophytes appear to be heterogeneous with one recurring associated species group evident. This agrees with the results of the heterogeneity test.

The original impression of the study site was one of homogeneity,

but upon closer examination by numerical methods it appeared substantially heterogeneous. The tests indicated both heterogeneous and continuously changing arrangement. However, these arrangements were just the opposite as originally supposed; heterogeneity was not detected in the understory species, but rather in the overstory.

One explanation why heterogeneity was not detected in the understory layers might be that the quadrats were not the proper size associated with the ground scale of the groups. More than one size was tested and the original size was chosen based on knowledge of the size of individuals and of observed groupings. Another explanation might be that there were so many species in each understory layer which were homogeneously arranged, as indicated by the clumps in the ordination graphs, Figs. 11-13, that the few species groupings which existed were "overshadowed" in the analysis. To overcome this problem some species would have to be eliminated. This subjective procedure would, however, defeat the purpose of the numerical analysis. The only other alternative I see is to accept the results as indicating the arrangement of all the species of each layer. In the chamaephyte layer, one species group of sedges and other herbaceous plants was observed, but occurred infrequently enough that all the species taken together were determined to be not heterogeneous in arrangement. In the microphanerophyte layer the tree ferns were observed to be absent in certain places, but for the most part the layer was not heterogeneous. The tree ferns may have been heterogeneous themselves, but were not associated in groups with other species.

Species groupings

The cluster analysis of the mesophanerophytes produced three species groups. The combination of four species, Acacia koa, Cheirodendron trigynum, Ilex anomala, and Metrosideros collina were found to recur within the study site by both qualitative and quantitative classifications and also by the species ordination (using relative distance). Other species groups consisted of Myrsine lessertinana, Pelea clusiaefolia, and Alyxia olivaeformis in one group and Pelea volcanica and Rubus hawaiiensis and possibly Acacia koa in another.

Ecological interpretation

The presence of the recurring groups of mesophanerophytes may be interpreted ecologically as a relationship to certain kinds of recurring site conditions or as a stability in these certain species combinations (cf. Poore 1964).

Goodall (1954) agrees that these patterns regularly repeating may be due to differences in the "inanimate environment" which cannot be attributed to the vegetation. The patterns can also arise through dynamic changes within the vegetation itself by regeneration and degeneration occurring throughout the area but not at the same time.

The author interprets the recurring species groups as resulting in part from recurring site conditions--not in the physical environment but rather indirectly from the vegetation by the presence of fallen logs. The patterns arising from this site condition do so also through the degeneration of old trees and the regeneration of new trees on the logs.

This regeneration takes place by a process which is described as beginning with an old, large Acacia koa or Metrosideros collina tree toppled by a strong wind or earthquake. At the same time many other smaller trees and tree ferns would also be knocked down by this large trunk and its branches as it falls. An even larger opening would then be created, providing light to small herbaceous plants and seedlings which had previously been shaded by the trees. The large trunk plus trunks of the smaller trees and tree ferns would lie on the ground with some on top of others. Over a short period of time (it was observed to occur in less than two years) the logs would become covered with bryophytes. Then herbaceous plants and tree seedlings would germinate in this substrate. Some trees still living, but in a horizontal position, might have one branch which would take over the function of the main trunk. Other horizontal trees might send out new sprouts. Subsequently, along the length of the horizontal logs, many new trees (branches, sprouts, or germinants) would begin. At the same time seedlings would also germinate on the ground below and existing roots would send up sprouts. The seedlings on the ground and on small logs, however, would likely be eaten, uprooted, or trampled by feral pigs which inhabit the forest in apparently large numbers. Many evidences of their activity on the ground were observed throughout the forest.

The common trees in the forest are Metrosideros collina, Cheirodendron trigynum, Acacia koa, and Ilex anomala, therefore many of the seedlings or sprouts on the logs would likely be of these species. (Most of these four species were recorded on logs.) These

species would therefore be likely to be associated in groups. They would have in common the same substrate. These species were the four species of the largest group which was detected. The description of regeneration also applies to another group detected which included Myrsine lessertiana, found equally on the ground and on logs, and Pelea clusiaefolia and Alyxia olivaeformis, both found mostly on logs. The third group detected consisted of rare species, Pelea volcanica and Rubus hawaiiensis, which are both found mostly on the ground. This vulnerable position (i.e. accessible to pigs) may have some effect on their relative rarity. In the classification using count data, Coprosma rhyncocarpa was included in this group. It is found on either the ground or logs. The only species not included in a group in the classification using count data (Fig. 17) and included with Coprosma in the qualitative classification was Myoporum sandwicense, which was almost always found on the ground. This was a relatively more common species. It does not fit the description of regeneration just given unless it perhaps is hardier as a seedling and is unfavorable as a food for the pigs, thus being protected and therefore not affected in the same way as the other species.

From this description and interpretation it follows that if in the past there had been no fallen logs, the present trees would have been homogeneously arranged (and also fewer in number). But instead, there were logs, and numerous trees germinated on the same logs, forming species groups.

If the large Acacia koa trees were to be logged, besides affecting the light conditions greatly, no fallen logs would be available in the

future for a substrate, affording protection from pigs, in which the new tree seedlings might succeed.

Suggestions

One limitation of the ordination method is that each different similarity coefficient will produce different relationships between individuals. One should be familiar with the distinctive features of a coefficient to use it effectively. For example, the simple matching coefficient allows rare species, which never occur together in the same quadrat, to be clumped; whereas the relative distance coefficient separates these rare species. Another limitation of ordination is that we are able to visualize the relationships between individuals presented in only two or three dimensions. The test for heterogeneity overcomes this limitation and considers all relationships in multi-dimensional space in determining the results. The test for heterogeneity, however, is limited by the statistic used. In cases in which the number of species is low, it is recommended to calculate the values obtained from an artificial distribution, as was done with the overstory layer, and compare these to the values obtained from the actual field data.

The results from this data analysis depend very much on the quadrat size used in sampling. Both Greig-Smith (1964) and Kershaw (1966) emphasized that the appearance of non-randomness in samples is not an absolute characteristic but, like frequency, is dependent on the size of the quadrats. Goodall (1954) stressed that at a scale near the size of the individual, homogeneity cannot be tested: "one knows *a priori* that at this scale there will be heterogeneity." The quadrat

size chosen for each layer was much larger than any of the individuals of that layer.

The effort spent in the field and in the lab work was optimal. For the ultimate description of the variation within the forest, the sampling and testing of numerous quadrat sizes might be used to show at what size heterogeneity begins and ends. There may be patches homogeneously arranged within larger patches and so on. Only numerous tests could reveal this. This was, however, not feasible at the degree of intensity used in this study.

If this study were to be continued, I would suggest that for the understory vegetation fewer quadrats, each of several different sizes, especially larger sizes which this study lacked, be sampled and tested by the techniques described. The next step could be a study of physical environmental factors affecting the presence of groups. If more environmental data on soil or microclimatic parameters were collected for each quadrat, the values could be compared to the plot ordinations of this study for evidence of trends (in the same way soil depth was analyzed). The interpretation of these results could be enhanced if more were known about the life-phases of the individual species in the recurring groups, in which case I would suggest future experimental studies on growth rates and growth requirements of these species.

CONCLUSIONS

In the four layers studied, the species of epiphytes, ferns and other herbaceous plants (chamaephytes), and shrubs and tree ferns (microphanerophytes) were found to consist of subcommunities merging into one another or randomly arranged species with no associated species groups. The species of the large tree (mesophanerophyte) layer were found to be heterogeneous in arrangement. The large tree species groups recognized in the course of the analyses included Acacia koa, Cheirodendron trigynum, Ilex anomala, and Metrosideros collina in one group, Myrsine lessertiana, Pelea clusiaefolia and Alyxia olivaeformis (a tall liana) in a second group, and Pelea volcanica and Rubus hawaiiensis (a tall shrub) and possibly Acacia koa in a third. A few observed species groups were not detected by the numerical approach, including herbaceous plants in open, wet areas and tree fern canopy gaps.

The methods used in this study could be applied to other similar studies where little is known about the spatial arrangement of plant species and about the physical environment affecting the spatial arrangement. The test for heterogeneity and the species ordinations both resulted in similar compatible interpretations of the nature of the spatial arrangements of the species. The cluster analysis produced groups which reflected the relationships shown in the ordinations.

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APPENDICES

APPENDIX A--COMPUTER PROGRAMS

1. Program in FORTRAN IV for Simulated Random Distribution of Mesophanerophytes 11 species, 200 quadrats

```
0001            DIMENSION LA(11),ME(11,200)
0002            IX=99999
0003            DO 510 J=1,11
0004            DO 510 K=1,200
0005          510 ME(J,K)=0
0006            READ (5,525) (LA(JJ),JJ=1,11)
0007          525 FORMAT (12(IX,13))
0008            DO 513 I=1,11
0009            JK=LA(I)
0010            DO 513 J=1,JK
0011            CALL RANDU (IX,IY,YFL)
0012            IX=IY
0013            I1=YFL*200
0014          513 ME(I,I1)=ME(I,I1)+1
0015            DO 514 K=1,11
0016            WRITE (6,526) (ME(K,L),L=1,200)
0017          514 WRITE (3,527) (ME(K,L),L=1,200)
0018          526 FORMAT (20(2X,I3)/)
0019          527 FORMAT (200I3)
0020            WRITE (6,125)
0021          125 FORMAT (1H1,'END OF JOB')
0022            STOP
0023            END
```

2. Sum of squares classification program in BASIC, written by L. Orlóci, using the method of Orlóci (1967).

```
10    PRINT "SUM OF SQUARES AGGLOMERATION"
20    PRINT
30    PRINT "NUMBER OF ROWS IN DATA MATRIX="
40    INPUT M
50    PRINT "NUMBER OF COLUMNS IN DATA MATRIX="
60    INPUT N
65    FILES TREEF
70    DIM X[100,11]
80    DIM V[11]
90    DIM R[11]
100   DIM L[11]
110   DIM T[11,2]
120   DIM D[11,11]
130   MAT L=CON
140   FOR K=1 TO N
142   FOR T=1 TO M
144   READ #1;X[T,K]
146   NEXT T
148   NEXT K
150   PRINT "TYPE 1 FOR RELATIVE DISTANCE OR 0 FOR ABSOLUTE DISTANCE"
160   INPUT T
170   IF T=0 THEN 250
180   FOR K=1 TO N
190   LET S=0
200   FOR Z=1 TO M
210   LET S=S+X[Z,K]↑2
220   NEXT Z
230   LET L[K]=SQR(S)
240   NEXT K
250   FOR K=1 TO N
260   FOR L=K+1 TO N
270   LET S=0
280   FOR Z=1 TO M
290   LET S=S+(X[Z,K]/L[K]-X[Z,L]/L[L])↑2
300   NEXT Z
310   LET D[K,L]=S
320   LET D[L,K]=S
330   NEXT L
340   LET D[K,K]=C
350   NEXT K
360   PRINT "TYPE 1 IF PRINTING OF DATA IS REQUIRED ELSE TYPE 0"
370   INPUT T
380   IF T <> 1 THEN 420
390   PRINT "DATA"
410   MAT PRINT X:
420   PRINT "TYPE 1 IF PRINTING OF DISTANCES IS REQUIRED ELSE TYPE 0"
430   INPUT T
```

```
440   IF T <> 1 THEN 480
450   PRINT "SQUARED DISTANCES"
470   MAT PRINT D;
480   LET A=0
490   FOR M=1 TO N
500   LET R[M]=1
510   NEXT M
520   LET K=N
660   PRINT "CLUSTERING PASS."
580   FOR M=1 TO K
690   LET Y=1.E+08
700   LET U=1.E+08
710   FOR L=1 TO K
720   IF M <> K THEN 740
730   IF L=K THEN 830
740   IF M <> L THEN 760
750   LET L=L+1
760   LET F=R[M]+B[L]
770   LET Z=(D[M,L]+D[M,M]+D[L,L])/F
780   LET Z=Z-D[M,M]/R[M]-D[L,L]/R[L]
790   IF Z >= U THEN 820
800   LET U=Z
810   LET H=L
820   NEXT L
830   FOR L=1 TO K
840   IF H <> K THEN 860
850   IF L=K THEN 950
860   IF L <> H THEN 880
870   LET L=L+1
880   LET F=R[H]+R[L]
890   LET Z=(D[H,L]+D[H,H]+D[L,L])/F
900   LET Z=Z-D[H,H]/R[H]-D[L,L]/R[L]
910   IF Z >= Y THEN 940
920   LET Y=Z
930   LET B=L
940   NEXT L
950   IF B <> M THEN 1000
960   LET T[M,1]=M
970   LET T[M,2]=H
980   LET V[M]=R[M]+R[H]
990   GOTO 1030
1000  LET T[M,1]=M
1010  LET T[M,2]=0
1020  LET V[M]=R[M]
1030  NEXT M
1040  LET W=0
1050  FOR M=1 TO K
1060  IF T[M,2] >= T[M,1] THEN 1080
```

```
1070  IF T[M,2]>0 THEN 1120
1080  W=W+1
1090  LET T[W,1]=T[M,1]
1100  LET T[W,2]=T[M,2]
1110  LET R[W]=V[M]
1120  NEXT M
1130  LET K=W
1140  LET A=A+1
1150  PRINT A
1170  FOR M=1 TO K
1180  LET J=T[M,1]
1190  LET E=T[M,2]
1200  IF E=0 THEN 1230
1210  LET D[M,M]=D[J,J]+D[E,E]+D[J,E]
1220  GOTO 1240
1230  LET D[M,M]=D[J,J]
1240  LET Y=D[M,M]/R[M]
1250  LET Z=Y/R[M]
1260  PRINT M;J;E;R[M];Y;Z
1270  NEXT M
1280  FOR M=1 TO K-1
1290  LET J=T[M,1]
1300  LET E=T[M,2]
1310  FOR L=M+1 TO K
1320  LET G=T[L,1]
1330  LET C=T[L,2]
1340  IF E+C=0 THEN 1380
1350  IF E+C=C THEN 1400
1360  IF E+C=E THEN 1420
1370  GOTO 1440
1380  LET Z=D[J,G]
1390  GOTO 1450
1400  LET Z=D[J,G]+D[J,C]
1410  GOTO 1450
1420  LET Z=D[J,G]+D[E,G]
1430  GOTO 1450
1440  LET Z=D[J,G]+D[J,C]+D[E,G]+D[E,C]
1450  LET D[M,L]=Z
1460  LET D[L,M]=Z
1470  NEXT L
1480  NEXT M
1490  IF K>1 THEN 660
1520  PRINT "MESOPHANEROPHYTES 240 SQM"
9000  END
```

APPENDIX B--AVERAGE PLOT VALUES FOR EACH LAYER

TABLE 8. Forest floor components, three substrates and plant cover, in each plot (size 6 x 40 m = 240 m^2) estimated in percentage of total ground area. The substrate values in each plot add to approximately 100. The plants were found growing on any of the three substrates.

Substrate	Plots									
	Transect 1					Transect 4				
	1	2	3	4	5	16	17	18	19	20
Rotting wood and lying logs	18.7	33.8	26.3	19.8	32.8	22.0	20.3	23.1	20.3	22.5
Humus and mineral soil	75.3	63.2	66.2	75.5	65.9	76.8	73.9	71.9	76.2	74.9
Rocks	6.1	3.1	7.6	5.3	1.3	1.3	5.8	5.0	3.5	2.0
Bryophytes and herbaceous plants	19.5	32.5	26.9	24.7	33.1	27.5	22.2	39.7	17.8	23.4

TABLE 9. Frequency of epiphytes in each plot. The values are the percentage of sixteen 15 m^2 quadrats, in which a species is present.

Species	Plots									
	Transect 1					Transect 4				
	1	2	3	4	5	16	17	18	19	20
1 Acacia koa PE	0.0	12.5	0.0	0.0	0.0	6.3	0.0	6.3	0.0	0.0
2 Adenophorus tripinnatifidus ChE	0.0	12.5	0.0	0.0	12.5	37.5	37.5	18.8	18.8	50.0
3 Alyxia olivaeformis PE	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	50.0
4 Asplenium contiguum ChE	0.0	0.0	0.0	0.0	6.3	6.3	43.8	0.0	0.0	12.5
5 Asplenium lobulatum ChE	12.5	12.5	0.0	0.0	31.3	0.0	12.5	18.8	0.0	0.0
6 Asplenium normale ChE	0.0	0.0	0.0	0.0	0.0	18.8	0.0	0.0	0.0	0.0
7 Asplenium schizophyllum ChE	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0
8 Astelia menziesiana ChE	0.0	6.3	0.0	6.3	0.0	37.5	25.0	18.8	12.5	37.5
9 Athyrium microphyllum ChE	0.0	0.0	6.3	6.3	18.8	43.8	50.0	31.3	31.3	43.8
10 Athyrium sandwichianum ChE	6.3	0.0	6.3	0.0	0.0	6.3	12.5	0.0	0.0	18.8
11 Broussaisia pellucida PE	0.0	12.5	0.0	0.0	0.0	6.3	18.8	12.5	6.3	12.5
12 Carex alligata ChE	0.0	0.0	0.0	6.3	0.0	6.3	0.0	0.0	0.0	0.0
13 Carex macloviana ChE	6.3	12.5	0.0	6.3	0.0	12.5	37.5	6.3	0.0	18.8
14 Cheirodendron trigynum PE	18.8	37.5	6.3	25.0	43.8	75.0	87.5	37.5	56.3	75.0
15 Cibotium chamissoi PE	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	6.3
16 Cibotium glaucum PE	0.0	12.5	0.0	6.3	0.0	12.5	18.8	0.0	18.8	25.0
17 Coniogramme pilosa ChE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
47 Coprosma ochracea PE	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0
18 Coprosma rhyncocarpa PE	0.0	12.5	0.0	6.3	6.3	31.3	25.0	12.5	18.8	12.5
19 Ctenitis rubiginosa ChE	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0
20 Cyanea sp. PE	0.0	0.0	0.0	0.0	0.0	12.5	43.8	6.3	0.0	6.3
21 Dryopteris glabra ChE	6.3	6.3	12.5	0.0	12.5	31.3	68.8	12.5	12.5	12.5
22 Dryopteris paleacea ChE	12.5	0.0	25.0	6.3	0.0	25.0	12.5	0.0	12.5	18.8

TABLE 9. (Continued) Frequency of epiphytes in each plot. The values are the percentage of sixteen 15 m^2 quadrats, in which a species is present.

Species	Plots									
	Transect 1					Transect 4				
	1	2	3	4	5	16	17	18	19	20
24 Elaphoglossum hirtum ChE	0.0	25.0	0.0	6.3	6.3	25.0	25.0	12.5	6.3	12.5
23 Elaphoglossum wawrae ChE	6.3	0.0	0.0	0.0	6.3	25.0	12.5	6.3	0.0	6.3
25 Gouldia sp. PE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
26 Grammitis hookeri ChE	18.8	31.3	31.3	0.0	25.0	56.3	50.0	25.0	37.5	43.8
27 Ilex anomala PE	6.3	12.5	6.3	12.5	6.3	43.8	25.0	25.0	25.0	75.0
29 Lycopodium serratum ChE	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0
30 Marratia douglasii ChE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
31 Metrosideros collina PE	25.0	50.0	43.8	18.8	43.8	50.0	68.8	62.5	75.0	56.3
32 Myoporum sandwicense PE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0
33 Myrsine lessertiana PE	0.0	6.3	0.0	0.0	0.0	6.3	0.0	0.0	6.3	25.0
34 Nertera depressa ChE	0.0	0.0	0.0	0.0	0.0	6.3	0.0	12.5	18.8	0.0
35 Pelea clusiaefolia PE	0.0	6.3	0.0	0.0	0.0	18.8	12.5	25.0	6.3	43.8
36 Peperomia leptostachya ChE	18.8	18.8	0.0	6.3	12.5	25.0	31.3	6.3	0.0	0.0
37 Pipturus hawaiiensis PE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0
38 Pleopeltis thunbergiana ChE	6.3	0.0	0.0	6.3	0.0	31.3	25.0	0.0	0.0	6.3
39 Polypodium pellucidum ChE	0.0	6.3	0.0	12.5	0.0	0.0	0.0	0.0	0.0	0.0
40 Rubus hawaiiensis PE	18.8	18.8	12.5	12.5	6.3	12.5	43.8	18.8	12.5	31.3
41 Sadleria pallida ChE	0.0	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.3
42 Sphaerocionium obtusum ChE	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0	0.0	0.0
43 Stenogyne calaminthoides ChE	0.0	0.0	0.0	0.0	0.0	0.0	6.3	0.0	0.0	0.0
44 Vaccinium calycinum PE	12.5	62.5	6.3	31.3	12.5	62.5	81.3	68.8	50.0	75.0
45 Vandenboschia davallioides ChE	0.0	0.0	0.0	0.0	0.0	6.3	6.3	0.0	6.3	12.5
46 Xiphopteris saffordii ChE	0.0	0.0	0.0	0.0	0.0	31.3	18.8	18.8	12.5	0.0

TABLE 10. Frequency (F) and cover (C) of chamaephytes* in each plot. Both are expressed as percentages. The cover values are the averages of the sixteen 15 m^2 quadrats.

Species	Plots																			
	Transect 1										Transect 4									
	1		2		3		4		5		16		17		18		19		20	
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C
1 Acacia koa	31.3	0.02	6.3	0.00	12.5	0.01	37.5	0.00	68.8	0.02	6.3	0.01	18.8	0.01	31.3	0.02	0.0	0.00	0.0	0.00
2 Adenophorus tripinnatifidus	62.5	0.35	56.3	0.04	62.5	0.19	12.5	0.01	93.8	0.39	56.3	2.38	37.5	0.02	68.8	0.05	81.3	0.06	37.5	0.02
3 Alyxia olivaeformis	0.0	0.00	0.0	0.00	6.3	0.00	6.3	0.01	18.8	0.01	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	12.5	0.00
4 Asplenium contiguum	6.3	0.01	0.0	0.00	6.3	0.01	0.0	0.00	12.5	0.00	18.8	0.01	43.8	0.18	0.0	0.00	6.3	0.00	0.0	0.00
5 Asplenium lobulatum	25.0	0.17	6.3	0.16	18.8	0.00	6.3	0.01	31.3	0.16	0.0	0.00	12.5	0.01	18.8	0.00	0.0	0.00	0.0	0.00
6 Asplenium normale	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	18.8	0.02	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
7 Astelia menziesiana	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.16	6.3	0.00	25.0	0.01	18.8	0.00	12.5	0.01	37.5	0.01
8 Athyrium microphyllum	62.5	0.04	68.8	0.03	87.5	0.08	68.8	0.06	81.3	1.30	75.0	0.37	62.5	0.36	75.0	1.30	62.5	0.06	50.0	0.03
11 Cheilanthes sandwichianum	25.0	0.16	18.8	0.00	75.0	0.36	87.5	0.37	25.0	0.00	50.0	0.04	12.5	0.01	37.5	0.18	62.5	0.51	62.5	0.03
12 Dryopteris pellucida	25.0	0.02	0.0	0.00	18.8	0.01	12.5	0.00	0.0	0.00	18.8	0.94	31.3	0.02	18.8	0.01	6.3	0.00	25.0	0.01
13 Carex alligata	0.0	0.00	56.3	0.79	37.5	0.33	43.8	0.34	31.3	0.32	25.0	0.96	0.0	0.00	50.0	14.69	0.0	0.00	0.0	0.00
14 Carex macloviana	100.0	0.55	81.3	0.67	93.8	1.62	81.3	0.37	68.8	0.81	81.3	0.83	62.5	0.96	68.8	0.66	62.5	0.33	50.0	0.68
15 Chirodendron trigynum	68.8	0.05	75.0	0.07	75.0	0.05	68.8	0.06	100.0	0.10	50.0	0.04	81.3	0.07	75.0	0.06	81.3	0.08	87.5	0.07
16 Cibotium chamissoi	0.0	0.00	18.8	0.17	0.0	0.00	0.0	0.00	12.5	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
17 Cibotium glaucum	62.5	0.06	56.3	0.19	81.3	0.21	31.3	0.01	43.8	0.32	31.3	0.33	12.5	0.01	50.0	2.98	25.0	0.16	31.3	0.16
18 Cyrtandra rhyncocarpa	0.0	0.00	18.8	0.02	18.8	0.00	25.0	0.01	81.3	0.02	50.0	0.02	68.8	0.04	37.5	0.01	68.8	0.02	31.3	0.03
19 Dicranopteris linearis	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	18.8	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
20 Dryopteris sp.	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.00	12.5	0.00	0.0	0.00	0.0	0.00
21 Dubautia lyallii	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
22 Elaphoglossum emarginata	0.0	0.00	0.0	0.00	25.0	0.02	6.3	0.00	0.0	0.00	0.0	0.00	6.3	0.01	25.0	0.00	0.0	0.00	6.3	0.00
23 Elaphoglossum glabra	62.5	0.06	18.8	0.00	25.0	0.02	0.0	0.00	68.8	0.06	37.5	0.18	25.0	0.02	0.0	0.00	31.3	0.02	18.8	0.01
24 Elaphoglossum paleaceum	37.5	0.02	50.0	0.19	25.0	1.11	62.5	2.61	18.8	0.16	62.5	3.92	25.0	2.04	37.5	1.11	31.3	0.00	25.0	0.16
25 Elaphoglossum sp.	18.8	0.01	0.0	0.00	0.0	0.00	12.5	0.16	0.0	0.00	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
27 Elaphoglossum hirtum	0.0	0.00	12.5	0.00	12.5	0.00	25.0	0.02	6.3	0.01	18.8	0.01	0.0	0.01	18.8	0.01	0.0	0.00	6.3	0.00
26 Elaphoglossum wawrae	0.0	0.00	6.3	0.00	18.8	0.01	0.0	0.00	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
28 Hedyotis oligodentata	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	12.5	0.01	0.0	0.00	0.0	0.00
29 Erechtites valerianifolia	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	18.8	0.00	0.0	0.00	18.8	0.16
4 Gnaphalium sp.	6.3	0.00	0.00	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
30 Gouldia sp.	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.00	0.0	0.00
31 Grammitis hookeri	56.3	0.05	18.8	0.01	43.8	0.03	0.0	0.00	31.3	0.02	50.0	0.04	56.3	0.05	18.8	0.01	75.0	0.06	68.8	0.06

*Includes herbaceous plants and seedlings of woody plants less than 0.5 m in height.

TABLE 10. (Continued) Frequency (F) and cover (C) of chamaephytes* in each plot. Both are expressed as percentages. The cover values are the averages of the sixteen 15 m^2 quadrats.

Species	Plots																			
	Transect 1										Transect 4									
	1		2		3		4		5		16		17		18		19		20	
	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C
[illegible] sp.	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.16	0.0	0.00	0.0	0.00
[illegible] ple sibthorpioides	0.0	0.00	6.3	0.01	18.8	0.01	31.3	1.88	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
[illegible] javanicum	0.0	0.00	0.0	0.00	6.3	0.01	25.0	1.26	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
[illegible]	62.5	0.06	6.3	0.00	31.3	0.01	62.5	0.05	56.3	0.05	37.5	0.02	37.5	0.02	37.5	0.01	68.8	0.04	50.0	0.04
[illegible] lium	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	25.0	0.16	0.0	0.00	0.0	0.00
[illegible]	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	37.5	3.08	0.0	0.00	0.0	0.00
[illegible]	0.0	0.00	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.01	6.3	0.00	12.5	0.01	0.0	0.00	0.0	0.00
[illegible] vegetatum	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.00	12.5	0.00	6.3	0.00	0.0	0.00	0.0	0.00	6.3	0.00
[illegible] saujauii	6.3	0.00	6.3	0.00	0.0	0.00	0.0	0.00	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
40 Hypericum collina	100.0	0.10	93.8	1.17	93.8	0.24	81.3	0.07	68.8	0.07	50.0	0.04	37.5	0.04	81.3	0.23	81.3	0.07	43.8	0.04
41 [illegible] mandioense	12.5	0.00	0.0	0.00	6.3	0.00	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
42 [illegible] lessertiana	6.3	0.01	6.3	0.00	0.0	0.00	0.0	0.00	6.3	0.01	12.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.00
43 [illegible]	6.3	0.01	18.8	0.01	0.0	0.00	0.0	0.00	12.5	0.16	12.5	0.16	31.3	1.11	50.0	1.12	50.0	0.05	0.0	0.00
44 Rubus chamaemorus	12.5	0.01	12.5	0.01	0.0	0.00	0.0	0.00	0.0	0.00	12.5	0.01	18.8	0.00	37.5	0.02	6.3	0.00	25.0	0.01
45 [illegible] volcanica	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	12.5	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
46 [illegible] leptostenya	0.0	0.00	0.0	0.00	6.3	0.00	12.5	0.01	25.0	0.32	6.3	0.01	31.3	0.01	12.5	0.01	0.0	0.00	0.0	0.00
47 [illegible]	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
[illegible]	18.8	0.02	0.0	0.00	0.0	0.00	18.8	0.01	0.0	0.00	6.3	0.01	18.8	0.02	6.3	0.00	6.3	0.01	6.3	0.01
[illegible]	18.8	0.01	6.3	0.00	0.0	0.00	6.3	0.00	6.3	0.00	12.5	0.16	0.00	0.00	0.0	0.00	0.0	0.00	0.0	0.00
[illegible]	0.0	0.00	12.5	0.16	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
[illegible]	68.8	0.06	68.8	0.06	81.3	0.04	75.0	0.07	50.0	0.05	37.5	0.02	68.8	0.04	68.8	0.05	68.8	0.21	43.8	0.03
52 Rubus rosaefolius	0.0	0.00	0.0	0.00	6.3	0.01	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	18.8	0.47	0.0	0.00	0.0	0.00
53 [illegible] pallida	0.0	0.00	43.8	0.04	43.8	1.26	25.0	0.17	31.3	0.17	0.0	0.00	18.8	0.94	18.8	0.47	0.0	0.00	0.0	0.00
54 [illegible] obtusum	6.3	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
55 [illegible]	0.0	0.00	6.3	0.00	12.5	0.01	6.3	0.00	0.0	0.00	0.0	0.00	6.3	0.00	6.3	0.01	0.0	0.00	0.0	0.00
56 [illegible] calaminthoides	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
57 Vaccinium calycinum	87.5	0.08	100.0	0.09	93.8	0.09	37.5	0.04	93.8	0.09	56.3	0.06	68.8	0.07	68.8	0.07	62.5	0.06	68.8	0.06
58 [illegible] devalliodes	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.94	6.3	0.01	0.0	0.00	6.3	0.01	12.5	0.01	18.8	0.17
60 Veronica plebeia	0.0	0.00	31.3	0.17	18.8	0.17	12.5	0.01	6.3	0.00	6.3	0.01	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00
61 Veronica serphyllifolia	0.0	0.00	25.0	0.32	31.3	1.89	31.3	1.89	12.5	0.01	18.8	0.17	0.0	0.00	25.0	0.32	0.0	0.00	0.0	0.00
62 Xiphopteris saffordii	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0	0.00	6.3	0.01	0.0	0.00	6.3	0.00	6.3	0.01	0.0	0.00

*Includes herbaceous plants and seedlings of woody plants less than 0.5 m in height.

TABLE 11. Cover of microphanerophytes* in each plot. The percentage values are the average of the cover for the length of the plot (100 m). (Other species belonging to this layer did not have crowns intercepting the transect line.)

Species	Plots									
	Transect 1					Transect 4				
	1	2	3	4	5	16	17	18	19	20
1 Acacia koa	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
2 Broussaisia pellucida	2.0	0.0	0.2	0.5	0.0	1.0	1.5	5.0	0.3	0.0
3 Cheirodendron trigynum	2.5	0.6	1.4	2.0	1.3	4.5	1.2	0.5	1.0	0.0
4 Cibotium glaucum	77.0	90.0	77.0	49.9	72.0	84.0	74.0	76.5	83.5	89.5
5 Coprosma rhyncocarpa	0.0	0.0	1.0	0.0	0.0	2.2	2.0	0.0	0.0	3.0
6 Cyrtandra lysiosepala	0.0	0.0	1.5	0.7	0.0	0.0	0.0	0.0	0.0	0.0
7 Ilex anomala	0.0	0.7	0.7	1.0	0.0	0.0	0.0	0.7	0.0	1.0
8 Metrosideros collina	0.0	2.0	0.8	1.0	0.0	0.5	0.5	0.4	0.0	0.0
9 Myrsine lessertiana	0.0	0.0	0.2	0.0	0.0	2.0	0.0	0.0	0.0	0.0
10 Pelea clusiaefolia	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.4	0.5
11 Rubus hawaiiensis	0.0	0.0	0.0	0.0	0.2	0.0	3.5	0.0	4.5	1.0
12 Vaccinium calycinum	0.0	0.2	2.7	0.5	0.0	0.0	0.0	0.0	0.0	2.0

*Includes the shrubs and trees 0.5-5 m in height.

TABLE 12. Frequency (F) and density (D) of microphanerophytes in each plot. Frequency is the percentage of twenty 30 m^2 quadrats in which a species is present and density is the total number of individuals per hm^2.

Species	Transect 1 Plots										Transect 4 Plots									
	1		2		3		4		5		16		17		18		19		20	
	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D	F	D
1 Acacia koa	5	17	5	17	5	17	0	0	0	0	0	0	0	0	0	0	5	17	5	17
2 Alyxia olivaeformis PL	5	33	0	0	0	0	5	17	30	117	0	0	0	0	0	0	0	0	35	133
3 Broussaisia pellucida	20	100	10	33	20	83	20	83	0	0	25	83	35	200	25	167	15	67	20	67
4 Cheirodendron trigynum	75	617	70	800	80	800	55	350	80	650	60	633	65	817	60	550	80	683	65	450
5 Cibotium chamissoi	5	33	5	33	0	0	5	17	15	67	0	0	5	33	5	17	0	0	5	17
6 Cibotium glaucum	100	2417	95	2517	100	2833	90	1500	100	2200	100	3000	100	2300	100	2633	100	2567	100	2850
7 Clermontia hawaiiensis	5	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8 Coprosma rhyncocarpa	0	0	0	0	10	33	10	33	0	0	15	50	15	50	20	67	5	17	15	67
9 Cyrtandra lysiosepala	10	33	0	0	5	17	5	17	0	0	0	0	0	0	0	0	0	0	0	0
10 Gouldia sp.	0	0	0	0	0	0	0	0	0	0	5	17	0	0	20	83	0	0	5	17
11 Ilex anomala	20	83	30	317	30	133	45	267	35	317	20	83	10	67	55	467	45	283	65	783
12 Metrosideros collina	65	433	45	217	40	183	40	200	35	167	45	200	35	200	80	750	40	250	25	117
13 Myoporum sandwicense	15	67	10	50	0	0	10	83	0	0	0	0	0	0	0	0	0	0	5	17
14 Myrsine lessertiana	0	0	0	0	10	33	5	17	30	117	30	133	0	0	5	17	5	17	15	50
16 Pelea clusiaefolia	25	100	20	100	10	33	0	0	0	0	35	217	50	233	30	133	25	100	55	283
17 Pelea volcanica	0	0	5	17	0	0	5	17	10	33	5	17	0	0	0	0	10	33	0	0
18 Rubus hawaiiensis	5	17	15	50	5	33	5	17	20	67	10	33	30	150	15	50	15	50	15	133
19 Rubus rosaefolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	67	0	0	0	0
20 Vaccinium calycinum	20	100	30	200	30	167	0	0	10	33	25	83	20	117	20	200	10	33	15	83

TABLE 13. Frequency of mesophanerophytes* in each of 10 primary plots (1-5 in transect 1 and 16-20 in transect 4). (Two other species of mesophanerophytes were found in other plots.)

Species	Plots									
	Transect 1					Transect 4				
	1	2	3	4	5	16	17	18	19	20
Acacia koa	0	10	5	15	15	0	5	0	0	0
Cheirodendron trigynum	45	25	25	10	30	15	20	10	10	45
Coprosma rhyncocarpa	0	0	0	0	10	0	5	5	0	0
Ilex anomala	5	5	5	10	5	0	0	10	5	0
Metrosideros collina	20	30	35	40	40	45	50	10	30	60
Myoporum sandwicense	5	5	0	0	0	0	0	0	0	0
Myrsine lessertiana	0	5	5	0	0	5	0	0	0	10
Pelea clusiaefolia	0	0	0	0	0	0	0	0	0	5
Pelea volcanica	0	0	0	0	5	0	0	0	0	0

*Includes trees greater than 5 m in height and any other life form which reaches this height.

APPENDIX C--SOIL DEPTHS

TABLE 14. Average soil depths (cm) along four transects. Twenty measurements were made from each plot at 5m intervals. Forty plots (6 X 100 m) are numbered consecutively with 10 plots per transect (see Fig. 7). The ten primary plots of some analyses are numbered here as 2, 4, 6, 8, and 10 and 32, 34, 36, 38, and 40.

	Plot	Depth	Standard deviation
Transect 1	1	24.25	14.74
	2	30.00	14.09
	3	24.75	12.49
	4	29.60	15.07
	5	25.40	9.85
	6	41.35	15.79
	7	28.50	12.55
	8	50.40	28.86
	9	54.70	25.89
	10	60.80	23.34
Transect 2	11	28.30	10.33
	12	20.75	10.27
	13	29.20	10.96
	14	36.35	18.10
	15	37.45	13.22
	16	39.55	15.80
	17	36.35	20.78
	18	43.25	15.07
	19	35.10	12.06
	20	48.00	22.70
Transect 3	21	25.60	10.20
	22	29.70	6.99
	23	31.60	12.84
	24	40.45	14.67
	25	40.11	12.15
	26	33.00	10.63
	27	32.80	13.47
	28	26.90	9.34
	29	32.75	13.61
	30	31.85	12.97
Transect 4	31	65.95	17.10
	32	51.40	14.47
	33	36.95	13.68
	34	40.55	11.88
	35	40.15	11.31
	36	46.95	15.77
	37	39.78	14.51
	38	39.45	15.20
	39	34.55	13.59
	40	33.20*	7.69

*Only 5 measurements were recorded.

APPENDIX D--DERIVATION OF TWO FORMULAE USED IN THE TEXT

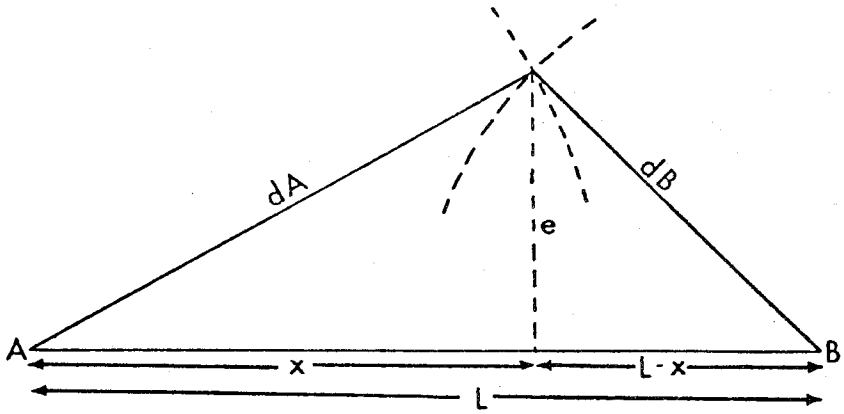


FIG. 18. Geometrical representation of the x-coordinates of the points in an ordination. From this Beal's (1960) formulae were derived:

$$x = \frac{L^2 + dA^2 - dB^2}{2L} \quad \text{and} \quad e^2 = dA^2 - x^2.$$

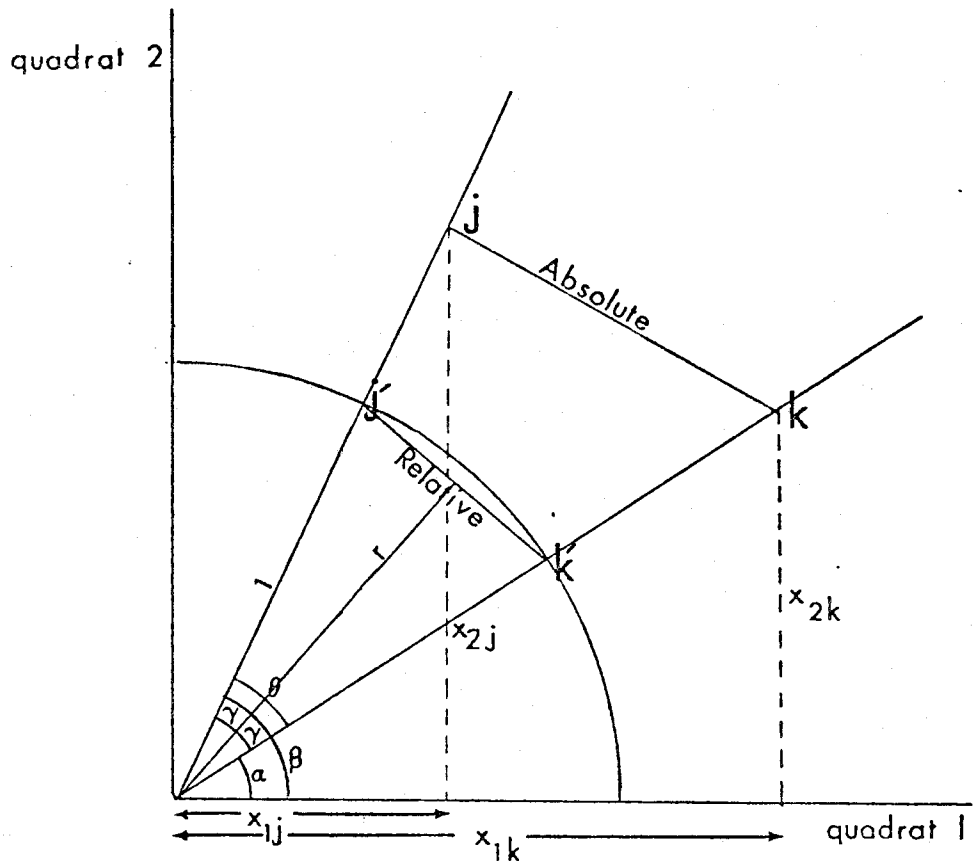


FIG. 19. Absolute and relative distance between two species points j and k in two dimensions (quadrats 1 and 2). Any species which lie anywhere along those two same lines have the same relative distance. The formula for relative distance is derived from this figure.

The distance from point j to point k is the absolute or Euclidean distance which in two-dimensional space can be calculated from the formula:

$$D_{j,k} = \sqrt{[(X_{1k} - X_{1j})^2 + (X_{2k} - X_{2j})^2]}$$

If j and k are in r-dimensional space their distance becomes:

$$D_{j,k} = \sqrt{[\sum_{i=1}^{r}(X_{ik} - X_{ij})^2]}$$

If these points represent individual species with r attributes (quantities in r quadrats) the absolute distance does not give a realistic measure of resemblance between the two species which are in identical quadrats if the quantities in those quadrats are greatly different. It also may give a small distance between two species which never occur together in the same quadrat but whose quantities are generally low.

To overcome this problem a standard or relative distance can be calculated between points j' and k' which are located on the vectors through j and k at the points where the arc of the unit circle (radius=1) intersects (Orlóci 1967). This distance ($D'_{j,k}$) is the chord of the arc intersected. If the angle (θ) formed by the two vectors is bisected each of the smaller angles has $\cos \gamma = r/1$ and

$$\sin \gamma = 1/2\ D'_{j,k}.$$

Also:

$$\cos\theta = \cos(2\gamma) = \cos\gamma \cos\gamma - \sin\gamma \sin\gamma$$

and substituting:

$$\cos\theta = r^2 - (1/2\ D'_{j,k})^2$$

also:

$$1^2 = r^2 + (1/2\ D'_{j,k})^2$$

subtracting:

$$\cos\theta - 1 = -2(1/2\ D'_{j,k})^2$$

or

$$D'_{j,k} = \sqrt{[2(1 - \cos\theta)]}$$

This angle (θ) is equal to $\beta-\alpha$ (see Fig. 19) where:

$$\cos\alpha = X_{1k} / \sqrt{[X_{1k}^2 + X_{2k}^2]}$$

and

$$\cos\beta = X_{1j} / \sqrt{[X_{1j}^2 + X_{2j}^2]}$$

and

$$\cos\theta = \cos(\beta-\alpha) = \cos\beta \cos\alpha + \sin\beta \sin\alpha$$

$$= [X_{1k}/\sqrt{(X_{1k}^2+X_{2k}^2)}] . [X_{1j}/\sqrt{(X_{1j}^2+X_{2j}^2)}] + [X_{2k}/\sqrt{(X_{1k}^2+X_{2k}^2)}] . [X_{2j}/\sqrt{(X_{1j}^2+X_{2j}^2)}]$$

Therefore:

$$D'_{j,k} = \sqrt{[2(1 - \cos\theta)]}$$

can also be described as:

$$= \sqrt{2}[1 - (X_{1k}X_{1j}+X_{2k}X_{2j})/\sqrt{([X^2_{1k} + X^2_{2k}][X^2_{1j}+X^2_{2j}])}]$$

For more than two dimensions (up to $\underline{p}$), then:

$$D'_{j,k} = \sqrt{2}[1 - (\sum_{h=1}^{p} X_{hk}X_{hj})/V_kV_j]$$

where the quantity $V_j = \sqrt{[\sum_{e=1}^{p} x^2_{ej}]}$

is the length of the $\underline{j}^{th}$ position (column) vector. V_k is similarly defined.

This resulting formula is Orlóci's (1967) formula for relative distance as used for one ordination (Fig. 15) and in the sum-of-squares clustering in this paper.

APPENDIX E--EXAMPLE OF THE CALCULATION OF THE COEFFICIENTS USED IN THE TEXT

Sample data matrix A (4 X 5)

	quadrats			
species	1	2	3	4
a	20	25	30	10
b	5	0	5	0
c	10	5	10	20
d	20	15	20	20
e	5	10	0	10

When the individuals being compared are the quadrats 1 and 2 and their attributes are the species (a-e) which occur in them:

Spatz's (1970) coefficient (see Results for description)

$IS_{1,2}=[\Sigma(Mw/Mg)/(a+b+c)][Mc/(Ma+Mb+Mc)][100]$

$=[(20/25+5/10+15/20+5/10)/(1+0+4)][110/(5+0+110)][100]$

$=48.8\%$

distance (dissimilarity) = 100 - 48.8 = 51.2%

Simple matching coefficient (Sokal and Sneath 1963)

$SM_{1,2}=[(a+d)/n][100]=[(4+0)/5][100]$

$=80.0\%$

distance = 100 - 80.0 = 20.0%

Relative distance (Orlóci 1967)

$RD_{1,2}=\sqrt{[2(1-\sum_{h=1}^{p} x_{h1}x_{h2}/V_1V_2)]}$

$=\sqrt{[2(1-[500+0+50+300+50]/\sqrt{[400+25+100+400+25]}\sqrt{[625+0+25+225+100]})]}$

$=0.36$

percentage of total distance = $[0.36/\sqrt{2}][100] = 25.5\%$

Sample data matrix B (5 x 4) (= A transposed)

	species				
quadrats	a	b	c	d	e
1	20	5	10	20	5
2	25	0	5	15	10
3	30	5	10	20	0
4	10	0	20	20	10

When the individuals being compared are the species a and b and their attributes are the quadrats (1-4) in which they occur:

$IS_{a,b}$ = [(5/20+5/30)/(2+0+2)][60/(35+0+60)][100] = 6.6%

distance = 100% - 6.6% = 93.4%

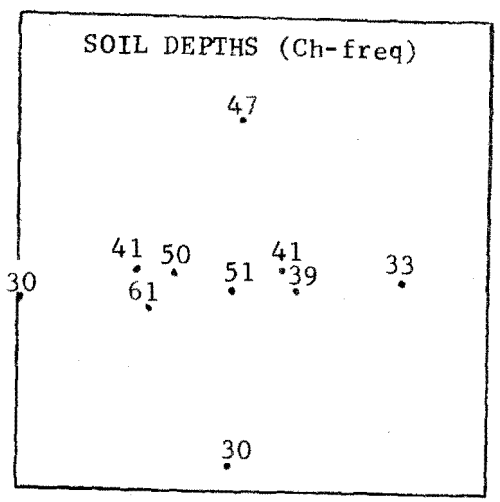
$SM_{a,b}$ = [(2+0)/4][100] = 50.0%

distance = 100 - 50.0 = 50.0%

$RD_{a,b}$ = $\sqrt{}$[2(1-[100+0+150+0]/$\sqrt{}$[400+625+900+100]$\sqrt{}$[25+0+25+0])]

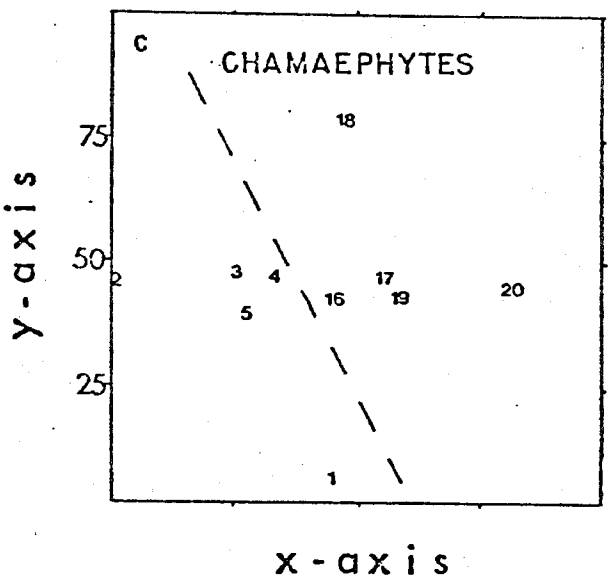
= 0.43

% distance = (0.43/$\sqrt{}$2)(100) = 30.3%



In the original copy, this figure appeared as a transparent overlay by which the soil depths were placed in the positions of their respective plot numbers in the chamaephyte graph shown on the next page.

APPENDIX F--PROCEDURE FOR DETERMINING TRENDS IN SOIL DEPTH VALUES ON PLOT ORDINATION GRAPHS *



* This procedure can also be used to determine trends of individual species quantities.

APPENDIX G--MINIMUM DISCRIMINATION INFORMATION STATISTIC (m.d.i.s.)

The m.d.i.s. for categorical data in its simplest form (Kullback, et al., 1962) is:

$$2\hat{I} = 2\sum_{i=1}^{c} f_i \ln(f_i/np_i)$$

where c is the total number of categories, p_i is the probability of an observation from the i-th category under the null hypothesis, $p_1 + p_2 + \ldots + p_c = 1$, f_i is the observed frequency of occurrence of the i-th category, $f_1 + f_2 + \ldots + f_c = n$, and ln is the natural logarithm. $0 \ln 0 = 0$.

Since f is the observed frequency (O) and np is the expected frequency (E), then with $\sum_i O_i = \sum_i E_i$,

$$2\hat{I} = 2\sum_i O_i \ln(O_i/E_i) \approx \sum_i (O_i - E_i)^2/E_i.$$

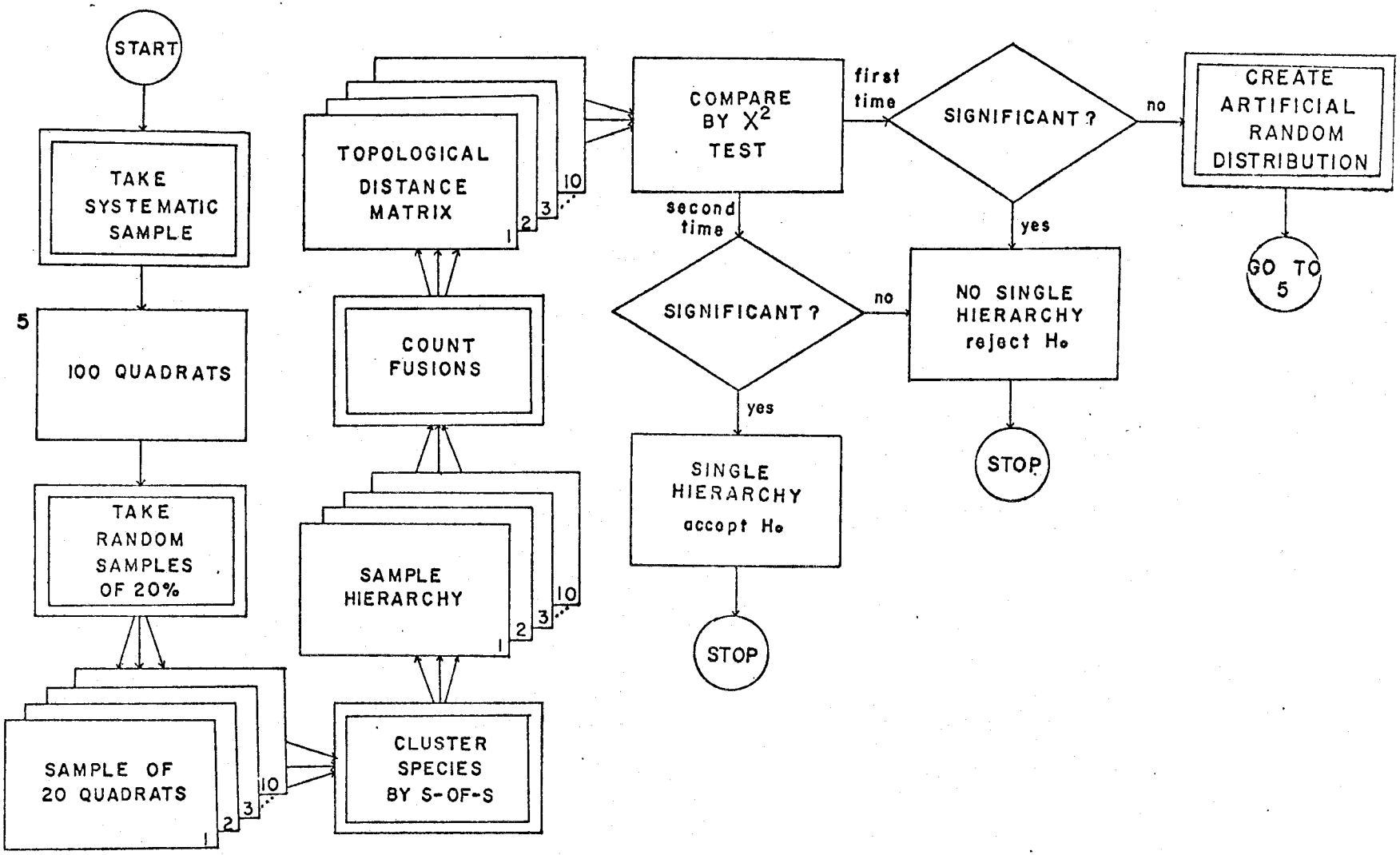
This last expression is the familiar χ^2 statistic. In large samples the m.d.i.s. and χ^2 are equivalent and neither has an advantage. In small samples the m.d.i.s. is preferred.

This formula can be simplified for our specific case where the entries of two topological matrices j and k are being compared. The observed values of each of the two paired entries are f_j and f_k. The expected values of each is $(f_j + f_k)/2$. The formula becomes:

$$2\hat{I} = 2\sum_{h=1}^{p-1} \sum_{i=h+1}^{p} [f_{jhi} \ln 2f_{jhi}/(f_{jhi}+f_{khi}) + f_{khi} \ln 2f_{khi}/(f_{jhi}+f_{khi})]$$

where p is the number of rows and columns in each of the matrices.

APPENDIX H--PROCEDURES FOR THE TEST OF HETEROGENEITY



APPENDIX I--REGRESSION EQUATIONS

TABLE 15. Crown diameter (m) as a function of trunk diameter (cm) and substrate of germination of six tree species.*

1. *Metrosideros collina*	$y = 1.3 + 0.1x$
2. *Myoporum sandwicense*	$y = 2.0 + 0.1x$
3. *Ilex anomala*	$y = 0.9 + 0.2x$
4. *Coprosma rhyncocarpa*	$y = 2.6 + 0.03x_1 + 0.3x_2$
	x_1 = trunk diameter
	x_2 = substrate of germination (soil = -1, log = 1)
5. *Myrsine lessertiana*	$y = 1.0 + 0.2x$
6. *Cheirodendron trigynum*	$y = 0.8 + 0.2x$

*The regression equations were derived by the standard procedures for regression from numerous (20-70) measurements of trunk and crown diameters and substrates of each species.

APPENDIX J--SAMPLE PRINTOUT OF THE RESULTS OF CHI-SQUARE TEST FOR HETEROGENEITY

TABLE 16. Chi-square values for ten species of mesophanerophytes (without koa).

I	J	CHI-SQ
1	2	72.36 **
1	3	101.96 **
1	4	95.71 **
1	5	85.12 **
1	6	83.28 **
1	7	81.28 **
1	8	81.22 **
1	9	68.26 **
1	10	101.26 **
2	3	90.17 **
2	4	96.51 **
2	5	76.82 **
2	6	80.72 **
2	7	55.27
2	8	80.44 **
2	9	54.78
2	10	87.33 **
3	4	96.02 **
3	5	87.62 **
3	6	91.60 **
3	7	86.46 **
3	8	93.92 **
3	9	71.46 **
3	10	77.25 **
4	5	102.54 **
4	6	51.84
4	7	80.06 **
4	8	85.14 **
4	9	78.45 **
4	10	60.75 *
5	6	106.37 **
5	7	100.64 **
5	8	77.75 **
5	9	89.16 **
5	10	99.62 **
6	7	68.97 **
6	8	80.08 **
6	9	81.34 **
6	10	58.75
7	8	94.87 **
7	9	59.33
7	10	55.63
8	9	90.75 **
8	10	87.40 **
9	10	75.79 **

Degrees of freedom = (n n-1 /2)-1, where n is the number of species.

In this example, n = 10, so d.f. = (10[10-1]/2)-1 = 44

Table χ^2	Probability
60.2	0.05
66.9	0.01

Percentage of significant values =

$$\frac{\text{number of significant values}}{\text{total values}} \times 100 = \frac{39}{45} = 86.7\%$$

*Significant at the 0.05 level.
**Significant at the 0.01 level.

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