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Comparative vegetation analysis on the wet slopes of two tropical mountains: Mt. Haleakalā, Hawaii and Mt. Kinabalu, Borneo

Kitayama, Kanehiro, Ph.D.

University of Hawaii, 1992

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COMPARATIVE VEGETATION ANALYSIS
ON THE WET SLOPES OF TWO TROPICAL MOUNTAINS:
MT. HALEAKALĀ, HAWAII AND MT. KINABALU, BORNEO

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN BOTANICAL SCIENCES (BOTANY)

MAY 1992

BY

KANEHIRO KITAYAMA

Dissertation Committee:

Dieter Mueller-Dombois, Chairperson
Clifford W. Smith
Gerald D. Carr
Haruyoshi Ikawa
Thomas W. Giambelluca

ABSTRACT

An altitudinal transect analysis was conducted on the wet slopes of two biogeographically contrasting mountains: Haleakalā (3055 m) on the oceanic island of Maui and Kinabalu (4101 m) on the continental island of Borneo. The flora of Haleakalā is much impoverished as compared to Kinabalu due to Haleakalā's geographic isolation. Two principal questions asked were: 1) are vegetation zones floristically definable, and if so what environmental parameters control the zones on each mountain; and, 2) how do the differences in the regional floristic richness between the mountains relate to the quantitative importance of species in individual sample stands, to beta diversity, and to discreteness, number and range of floristic vegetation zones?

Results suggested that altitudinal vegetation zones were floristically definable, discrete, and coincidental with certain climatic zones on both mountains. The vegetation boundaries were correlated with thermal and atmospheric moisture changes along the slopes. Alpha diversity of major canopy/subcanopy tree species was much higher on Kinabalu than in thermally comparable zones of Haleakalā. Beta diversity of the tree species using the half-change index was 0.81 for trees ≥2 m height on Haleakalā, and 11.83 for trees ≥10 cm DBH on Kinabalu. The number of the floristic vegetation zones was similar on both mountains despite the striking difference of the beta index. This surprising result is explained by the facts that: 1) there was a similar number of differential-species groups, indicating the presence of homologous climatic zones on the mountains; 2) on Haleakalā, a high proportion of species of different plant life forms extended over a broad altitudinal range upslope but there was also a sufficient number of range-restricted species with diagnostic value as indicators of climatic zones; 3) by contrast, on Kinabalu, a high proportion of tree genera was differentiated into parapatric altitudinal congeners. The prevalence of wide-ranging species as well as the presence of more range-restricted species groups on Haleakalā necessitated a strongly hierarchical arrangement of the vegetation units on this mountain. It seems that the altitudinal species radiation on Haleakalā is less advanced than on Kinabalu. This hypothesis is supported by the occurrence of disproportionately fewer parapatric congeners on Haleakalā than on Kinabalu.

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PREFACE

My first introduction to Bornean rain forests was on Mount Kinabalu in 1983. In this year I was assigned to the Sabah Campus of the National University of Malaysia as Japanese Overseas Cooperative Volunteer.

While teaching at the University, I organized a project to map and classify the vegetation on Kinabalu. This project was continued for three years from 1983 to 1986. It became the start of my dissertation research, which was later completed in Hawaii.

As the survey proceeded, I became interested in the Quaternary history of the subalpine coniferous forest on the mountain. Field observations suggested that many elements of the subalpine coniferous forest have close affinities in lower zones of the same mountain. I hypothesized that these high altitude elements are specialized forms of low-altitude taxa, which have ascended after the last glacial period. I named this pattern "altitudinal vicarism."

In 1985 I travelled through the major part of the Sunda Islands from Sumatra to Lombok. One objective was to find mountains which have the same vicarious vegetation patterns as Kinabalu. Unfortunately, I could not find such a phenomenon on this journey, because most mountains in the Sunda Islands are recent volcanoes and do not support old-growth forests.

When I came to Hawaii in 1986, my intention was to continue investigating the putative "vicarism" of subalpine zones, and to extend my study area into the New Guinean high mountains. Unlike most Sunda mountains, many New Guinean mountains are non-volcanic. Some articles suggested that the New Guinean vegetation zonation is very similar to that on Kinabalu.

Disappointingly, a transect study on Mount Haleakalā was suggested as my dissertation research topic in Hawaii in complement to my Kinabalu work. This was against my first strong impression that the floristically and structurally impoverished Hawaiian rain forest would have no comparable similarity. Later, I found that there are many similarities in the spatial vegetation patterns on Haleakalā with those on Kinabalu. Further, I learned that Haleakalā is one of the best mountains where ecologists can study altitudinal organization of vegetation patterns and develop hypotheses on speciation, which in turn can be tested by genetic and physiological methods.

Indeed, K. M. Aradhya, another Ph.D. student in vegetation ecology became interested in a population genetics study of the dominant canopy species along the same transect on Haleakalā. His dissertation can be considered a companion study, where he presents genetic evidence of altitudinal conspecific differentiation in accord with my vegetation analysis.

I dedicate this volume to Dr. Dieter Mueller-Dombois, my mentor, and to my wife Reiko Kitayama, who assisted in every aspect of this dissertation research.

PART I. BACKGROUND

CHAPTER 1. LITERATURE REVIEW AND WORKING HYPOTHESES FOR DISSERTATION RESEARCH

INTRODUCTION

This literature review provides the background for a comparative study of the vegetation on two tropical mountains. One of these is on an oceanic island, i.e. Haleakalā Mountain (3055m) on the island of Maui in the Hawaiian Islands, the other is Mount Kinabalu (4101m) on the continental Asian island of Borneo. In both cases the analysis relates to the wet slope of each mountain and to transects that extend from near sea level to the summit areas. Each transect includes lowland, montane and tropical alpine vegetation.

The two mountains are strikingly different from each other in regional floristic richness. The oceanic mountain is in a biogeographically very isolated area. This mountain, therefore, has a naturally impoverished flora (Hubbell 1968; Carlquist 1974), whereas the continental island mountain occurs in the highly diverse floristic region of Malesia (Whitmore 1975). Despite the difference in overall floristic richness and the long distance between them, there are relatively many genera common to both mountains. Most ancestors of the present native Hawaiian flora are believed to have been derived from the Malesian flora (Wagner et al. 1990). Moreover, because of general similarities in climate, one may expect a certain convergence in the physiognomy and life form structure of the vegetation on these two mountains.

In studies of high mountain vegetation systems, four basic questions have generally been asked: 1) what species are found on mountains; 2) how are they distributed; 3) are vegetation zones recognizable; and, 4) what factors govern the distributions of the species and vegetation zones? In relation to these questions, the following reviews two concepts of plant community organization, the methodology to recognize vegetation zones, and examples of altitudinal vegetation studies done on tropical mountains. These are pertinent to the working hypotheses presented later.

TWO CONTRASTING VIEWS OF COMMUNITY ORGANIZATION

The concepts

There are two schools of thought on community organization which have been debated among vegetation ecologists for some time. One viewpoint considers vegetation to change abruptly at certain places along environmental gradients showing distinctively associated species groups. The other considers vegetation to change gradually along environmental gradients, showing a continuum.

The first viewpoint is known as the community unit theory. This holistic view which sees the plant community as a unit is attributed to F. E. Clements (Mueller-Dombois & Ellenberg 1974). Braun-Blanquet (1932, translated edition in 1965) was based on a similar thought primarily for classifying plant communities. The theory and its technique by Braun-Blanquet (1965) have been applied to many studies of plant community classification often referred to as the Zürich-Montpellier school of plant sociology. The community unit concept states that a vegetation unit is recognized by distinctive species associations, delimited by clear boundaries. Distinctive species groups are used as diagnostic species for characterizing site factors, and for mapping (Mueller-Dombois & Ellenberg 1974).

The second viewpoint, known as the individualistic community theory (Gleason 1926) or the continuum theory (Curtis 1955), denies the presence of distinctive species associations. This perspective of vegetation was theoretically founded by Ramenskij in 1924 (cited by Moravec 1989). In this view, individual species are understood to have their own spatial distributions, relating to their unique physiological constitutions.

According to the individualistic view, species form a somewhat cohesive group in a multi-species plant community. However, by enlarging the area of investigation on plant communities, the individualistic nature of vegetation emerges. No two species have exactly the same distribution.

Multi-species plant communities are theoretically conceived in a multidimensional coordinate space where ecological factors have varied influences along each axis (Hutchinson 1957; Whittaker 1972, 1975). Therefore, according to the individualistic view, vegetation forms a continuum with scattered species distributions in the coordinate space. An objective community classification is therefore considered arbitrary (Whittaker 1962).

In the 1950's, a continuum of vegetation was demonstrated with the inventive methods of direct gradient analysis by Whittaker (1956, 1960), and of ordination by Curtis and his collaborator (Curtis 1955, Bray & Curtis 1957).

Species distribution patterns along altitudinal gradients

Whittaker's four hypotheses

Species distributions can be represented by bell shaped curves along gradient (i.e. by the Gaussian response model; Whittaker 1972, 1973, 1975; van der Maarel 1976). The length of the curves indicates the species distribution ranges along the gradient. The mode of the curves indicates the quantitative maximum of a species and its most optimal habitat.

Whittaker devoted much effort to clarifying spatial community turnover patterns by analyzing transects along altitudinal gradients in the Great Smoky Mountains (Whittaker 1956), the Siskiyou Mountains (Whittaker 1960) and the Santa Catalina Mountains (Whittaker & Niering 1965, 1968) of temperate North America. He plotted species distributions with such biomass parameters as density along two primary gradients (altitudinal and moisture gradients) and displayed them as bell-shaped curves. By visual inspection, he concluded that species curves generally do not coincide with one another and instead are individually distributed. His results apparently argue against any species association, and instead confirm the existence of a continuum of species ranges and modes along each of his mountain gradients investigated.

Later, Whittaker (1975) postulated four models of spatial distribution. These are shown in Fig. 1.1. Three of these, he attributed to interpretations of other authors and one model to be best applicable to his own data. The chief causal factors in these distribution models were considered to be competition among species and/or coadaptation of subsidiary species to a certain dominant species.

According to Pielou (1975, 1977, 1978), the species distribution patterns can be clarified in terms of upper and lower boundaries. At an arbitrarily set starting point along a gradient, the upper boundary is that point where a single species distribution begins. The lower boundary is that point where a single species distribution ends. The four models are restated by Dale (1986) with presence/absence lines rather than curves as shown in Fig. 1.2.

The community unit theory predicts clustered boundaries by means of associated species curves (model 1 in Figs. 1.1 and 1.2). Here, competing dominant species exclude each other. Other species become coadaptive to the dominant species. Consequently, overlapping distributions of associated species are formed with sharp boundaries between competing groups.

The continuum theory predicts randomly scattered upper or lower boundaries of species ranges (model 4 in Figs. 1.1 and 1.2). According to this theory, competition does not result in sharp boundaries between species along gradients. Species are predicted to evolve into independent distributional curves with separate modes along the gradient implying reduced interspecific competition (Whittaker 1972).

Whittaker's other two models, the second and the third models (Figs. 1.1 and 1.2) can be explained similarly using upper and lower boundaries. Model 2 shows random species limits with coincident upper and lower boundaries. Here, competing species exclude each other, but coadaptation into assemblages of species is not formed. Model 3 shows clustered species limits and non-coincident upper and lower boundaries. Here, competition does not result in sharp boundaries between dominant species. However, other species become associated with dominant species through coadaptation.

Methodological problems in Whittaker's approach

Whittaker's gradient analyses in temperate North America have strongly influenced the views of ecologists. Whittaker's work has built support for the individualistic and the continuum theory of plant communities (Moravec 1989). His influence can be seen not only in chorology but also in other domains of ecology, for example the individualistic approach in studies of the vegetation dynamics as emphasized by Drury & Nisbet (1973). Influence of his view is seen also in recent methods of vegetation pattern analysis. Some computer programs are based on his random-assortment hypothesis and are widely used among ecologists probably without knowing so. In the computer programs DECORANA (detrended correspondence analysis, Hill 1979; Hill & Gauch 1980) and GRADBETA (beta diversity computation, Wilson & Mohler 1986), the ecological axes are arbitrarily rescaled so that species become randomly or regularly distributed along the axes. Thus ordinated scattered species or relevés are manipulated to conform more strongly to a continuum than to clusters.

However, Whittaker's direct gradient analysis suffers from its subjectivity. Whittaker has failed to use probability statistics (see the next section) in judging the non-existence of community boundaries (Shipley & Keddy 1987).

Furthermore, his data presentation may not be able to demonstrate concrete species distributions. His species curves are based on a composite transect. In altitudinal gradient analysis, Whittaker lumped several sampling sites together, which were closely placed relevés within a certain predefined altitudinal belt. From these, he computed composite species abundances. The composite transect, consisting of composite sample sites or relevés, consequently depicted average species abundances. This computation resulted in smoothing out species distribution curves on the gradient axis. This effect in part gives researchers a bias toward supporting the individualistic distributions of species. Also, when an ecologically meaningful and distinct boundary line (e.g. timberline) has a wavy configuration and does not follow an altitudinal contour line, lumping multiple relevés may obscure the actual boundary. An absolute value from one transect should be used in the gradient analysis instead of an average value from composite sites. This is because composite transects include a further level of abstraction.

Whittaker also failed to specify the essence of the altitudinal gradient in his mountain transect studies. No measurement of environmental factors was conducted on the gradient. The species correlation analysis is not unconditionally applicable to altitudinal gradients unless environmental parameters are evaluated along the altitudinal gradients as well. His thought on the altitudinal gradient is that the gradient is comprised of multiple environmental factors and is therefore a "complex gradient." However it was not demonstrated whether the complex altitudinal gradient changes always in a smoothly continuous fashion with increasing altitude. As perceptively stated by Shipley & Keddy (1987), when a boundary clustering correlates with a change of one of several abiotic factors over a short distance, do we interpret this correlation to agree with the individualistic theory? When some abiotic factors change abruptly along a gradient and only a few boundaries of species distributions are shown, does this support the continuum view of community organization? Shipley & Keddy (1987) argue that the application of the continuum theory is equivocal and ecologically meaningless when physical factors in a complex gradient are not evaluated.

Also, species admitted to the test were selected in Whittaker's gradient analysis. Not all plant life forms were included. This is highly subjective. Species associations according to Braun-Blanquet's (1965) definition may include species from different life forms or synusiae.

Probability statistics to test the discreteness of vegetation

Dale's simpler line model (Fig. 1.2) has an advantage in that it allows for an effective analysis of randomness and non-randomness of species distribution boundaries. When one visually examines scattered curves, the judgement will most likely be affected by a preconceived view or by an impression from field observations. A statistical test is necessary, when research objectives are to test the discreteness of vegetation units.

Statistical methods have been developed by Pielou (1977, 1978) to detect the patterns of species distribution using simplified line models (Fig. 1.2). Several authors have applied Pielou's technique to their data (Underwood 1978; Dale 1984, 1986; Shipley & Keddy 1987). Pielou's null hypothesis is that boundaries of species distributions are randomly distributed over a gradient. This assumes that the individualistic theory is correct, and that the average numbers of boundaries in short gradient segments are randomly distributed. The mean deviation of the observed numbers of boundaries from the expected numbers of boundaries per interval is tested for departures from random expectation, which is zero. A significant deviation greater than zero indicates regular dispersion of boundaries, while a significant deviation less than zero indicates a cluster of boundaries.

The application of this principle (Pielou 1977) to broader geographic ranges of seaweed species along an latitudinal gradient of the Atlantic Ocean showed that congeneric species overlap one another strongly. However, the ranges were located independently of one another and were not influenced by species competition. Thus the results primarily supported the fourth model of Whittaker, i.e. random distributions of species, but congeneric species were closely associated.

In the example of a transect on an intertidal rock platform in Britain, upper boundaries of intertidal organisms were found to be randomly distributed (Underwood 1978). Likewise, distribution data of seaweeds on rocky intertidal shores in Nova Scotia (Dale 1986) suggested no evidence for the existence of associated groups of species. However, a narrow zone of transition between partially overlapping species was found.

In terrestrial ecosystems, for example in wetland plant communities of prairie marshes in eastern South Dakota, visually distinct zones were noted but the species formed a continuum along a gradient (Johnson et al. 1987). In larger wetland the vegetation was sharply discontinuous between two distinct environments. Here, interspecific competition was considered less important than physical environmental factors in the formation of zonal pattern. The data from a gradient analysis of a freshwater marsh community in Canada by Shipley and Keddy (1987) showed clustered lower boundaries (i.e. limits where the distributions begin along an arbitrary set direction) supporting the community unit theory. However, the upper boundaries (i.e. limits where the distributions end) in contrast to the lower ones, were diffuse, contradicting the community unit theory. Thus, a reciprocal test of one data set could not consistently confirm either of the community theories. In this study, they concluded that the dichotomy of the community unit versus the continuum was too limited.

The statistical analyses introduced in this section are advantageous in objectively testing the degree of discreteness of plant communities. Nevertheless, they are not sensitive to identify the location of boundaries and the number of species clusters from the results. In the following section, methods to recognize vegetation zones (units) are reviewed.

METHODS TO RECOGNIZE ALTITUDINAL VEGETATION ZONES

The direct and indirect gradient approaches

Methods to describe spatial vegetation patterns may be categorized into two approaches, the direct gradient and the indirect gradient approaches (Whittaker 1973; Mueller-Dombois & Ellenberg 1974; Itow 1977). The direct gradient approach analyzes the sequence of species and vegetation segments across habitats along a preconceived and pre-established environmental gradient (i.e. transect). The indirect approach attempts to ordinate or classify species and samples based only on vegetation attributes independently of underlying factors (gradients). Subsequently, a correlation is sought between emerged species/sample clusters or continuum and environmental factors. Therefore, characterization of vegetation by environmental parameters is *a priori* in the former but *a posteriori* in the latter. Both approaches have been used widely and equally among ecologists. Whittaker's studies on North American mountains are among examples of the direct gradient approach.

The following techniques are categorized as a numerical application of the direct gradient analysis with transects. They are sensitive in identifying locations of community boundaries along gradients: 1) the coefficient of dissimilarity performed by Beals (1969); 2) the moving split-window distance technique of Ludwig & Cornelius (1987); and, 3) the gradient rescaling method by Wilson & Mohler (1983).

The three techniques are based on the same theory but they use different mathematical procedures. The first method by Beals (1969) is an application of the dissimilarity index based on community coefficient of two adjacent relevés along a gradient. A relatively sharp boundary in species composition is identified by a high dissimilarity. This technique was applied to an east African mountain.

In the second technique by Ludwig & Cornelius (1987), an environmental gradient was partitioned into even intervals (windows) with two or more relevés in each interval. Splitting a window into two equal subgroups, the squared Euclidean distance was calculated between these two subgroups. A curve indicating Euclidean-distance changes over an entire span of the gradient was subsequently drawn by moving the window from one end to the other. A sharp rise of the curve indicated a boundary in vegetation. This technique was used in a study on relationships between vegetation and eight soil-series zones in the northern Chihuahua Desert (see Ludwig & Cornelius 1987).

In the third technique, Wilson & Mohler (1983) computed species turnover rates over infinitesimal intervals of a gradient to identify discontinuity of vegetation. A sudden change of vegetation composition was expressed as a high turnover rate. They applied this technique to field data on distributions of tree species obtained earlier by Whittaker (1960). These trees were sampled along an altitudinal gradient on quartz diorite substrate in the Siskiyou Mountains, Oregon. The results were in agreement with Whittaker's field observations. The greatest rate of change was found above 1800 m a.s.l. where Whittaker indicated a broad subalpine-montane border. In line with this technique, a computer program, GRADBETA is distributed by Wilson & Mohler (1986) for the computation of unit turnover and turnover rate.

By contrast, the numerical application of the indirect gradient approach is more diverse in number and background theory. Three types of analysis and data display are included in the indirect approach: 1) Braun-Blanquet's synthesis table technique; 2) ordination technique; and, 3) cluster analysis (Whittaker 1973; Mueller-Dombois & Ellenberg 1974). Braun-Blanquet's synthesis table technique is a divisive method, i.e. divide a given data set into a hierarchical dichotomy. Ordination is a method to sort samples or species along several putative ecological gradients. Cluster analysis can be either divisive or agglomerative, but outcomes of the analysis are always expressed in form of dendrogram. In a given dendrogram, both the abscissa and ordinate can be considered an ecological gradient along which samples or species are ordinated, whereas overall clustering patterns in the coordinate can be used for classifying the samples or the species. Therefore, cluster analysis has a combined ordination and classification.

Several modified techniques have been invented in each of the three types. Examples of studies of vegetation zonation on tropical mountains using these direct and indirect approaches will be discussed in the following section.

Previous studies of vegetation patterns on tropical high mountains

Some authors suggested that the community unit concept may be applicable to slopes of tropical high mountains where species richness is far higher than on temperate mountains. Holdridge (1967) empirically recognized groups of species, which relate to altitudinal climatic zones based on air temperature, rainfall and potential evapotranspiration in Costa Rica. Thus altitudinal vegetation zones were thought to be delimited by relatively distinct boundaries whose altitudes correlate with meaningful bioclimatic thresholds. Based on Holdridge's bioclimatic zones, MacArthur (1972) suggested that vegetation on tropical high mountains may show altitudinal zones which are defined by associated species. Mountain-gradient analyses conducted in the tropics are discussed below.

Direct approach along transects

From his study in Ethiopia, Beals (1969) concluded that the degree of spatial association of species and sharpness of boundary between species groups along an altitudinal gradient was dependent on the steepness of the slope of the mountain. He placed numerous relevés adjacently along the mountain slope and grouped always five adjacent ones by computing a composite species abundance. These adjacent groups were then compared as to their indexes of dissimilarity (ID). Here, a smooth modal dissimilarity curve supports the continuum view of organization, while a high peak protruding from a smooth curve would indicate a discrete boundary of plant communities (Fig. 1.3). In this way he found boundaries with large ID values between adjacent groups of relevés, and these occurred on the steep sections of the slope.

Itow (1990) computed species turnover rates along the north and south slopes of Santa Cruz Island in the Galápagos Islands. He did not discuss the question of vegetation discontinuity/continuity. His results, however, indicate a sharp compositional turnover at 623 m a.s.l. on the north slope. He recognized several vegetation zones based on dominant species. Altitudinal moisture regimes related to the trade winds were thought to determine the vegetation zones. It is not known whether the sharp compositional turnover correlates to a limit of a moisture regime.

These two studies are probably the only examples of the numerical application of the direct gradient analysis to tropical mountains.

Indirect approach along transects

On the mountains of east Africa, two independent indirect gradient analyses were conducted with altitudinal transect by Hamilton & Perrott (1981) and by Woldu *et al.* (1989). Hamilton & Perrott (1981) applied a cluster analysis to the montane vegetation on Mt. Elgon. Vegetation zones were numerically definable on the mountain. However, the number of zones varied from two to four, when different values were applied for threshold of their dendrogram. Upper boundaries of the vegetation zones were thought to be set by temperature-related factors.

Woldu *et al.* (1989) applied the probabilistic similarity coefficients to an extensive altitude gradient in Bale Mountains National Park, Ethiopia. They identified six types of stratocoena (synonymous with synusiae) for the tree-shrub layer and also six types for the herb layer. The hierarchical relationships of the identified stratocoena were displayed as dendrogram, with stratocoena aligned on the altitude gradient. Subsequently, the degree of discontinuity was hierarchically identified in terms of similarity index along the gradient.

Baruch (1984) applied classification and ordination to a vegetation transect through the paramo of the upper Venezuelan Andes. This study demonstrated that vegetation changes are primarily related to a complex of climatic and edaphic factors associated with altitude. The vegetation generally showed a gradation. A major disjunction in vegetation occurred at 3500m a.s.l., seemingly caused by the glacial history and the occurrence of frequent night frosts.

A cluster analysis was conducted on the high altitude scrub vegetation in the eastern Cordillera of Peru by Crawford et al. (1970). Results suggested that two clusters of stands (two community types) were present. These were altitudinally sorted, but a gradual transition was evident between them.

Hoffman & Hoffman (1982) applied a cluster analysis to an altitude transect in the subalpine zones of central Chile. They found that vegetation changes are generally gradual in the subalpine zones. An abrupt change was observed at one elevation demarcated by a clear boundary. The change was associated with an altitudinal shift of life forms from phanerophytes to chamaephytes. One factor for the abrupt vegetation change was the duration of snow cover.

These three South American studies were done only at the upper segments of altitudinal gradients.

On Mauna Loa, located on the isolated oceanic island, Hawaii, Mueller-Dombois & Spatz (1981) employed a modified two-way table technique with an application of the reciprocal averaging, and a cluster analysis for recognizing plant community and zones along an altitudinal transect. Resulting groups of relevés and species from the two-way table technique, and clusters of relevés from the cluster analysis were sorted independently along the altitudinal transect. Zonal boundaries were drawn where at least two cluster limits were coincident. The obtained zonal patterns were the same for the two different techniques.

In addition, they investigated the applicability of Whittaker's four models to the island's altitude gradient. The results supported the third model of Whittaker (i.e. interpenetrating or overlapping but associated groups of species). However, some dominant tree species showed the fourth pattern (i.e. random distributions). Besides these, they supplemented two further spatial models: 1) bi-modal groups and individuals being recognized in some native shrubs and trees; and, 2) species with high modal similarity, but low range similarity, being recognized in exotic plants. These patterns were considered by the authors to be related to a substrate discontinuity and substrate disturbance, respectively. Therefore, these two models appear to indicate a strong relationship to substrate which overcompensates for interspecific competition and a gradual change of climate.

Vegetation zones based on species check lists

The following two authors investigated upper and lower limits of species from such secondary data sources as Floras, check lists, and herbarium specimens. Van Steenis (1984) analyzed altitudinal ranges of most montane plant species in the entire Malesian floristic region. The upper limits congregated at certain elevational points. These were in agreement with the boundaries of physiognomically recognized vegetation zones. However, this analysis lumped mountains from a large geographic area, which included volcanic mountains of various height with different geological states. It is, therefore, rather surprising that he found coinciding elevational boundaries for such different mountains. Hamilton (1975) analyzed the forest vegetation in Uganda using the same method as van Steenis. Hamilton concluded that altitudinal vegetation zones defined by floristic disjunctions are lacking from the forests in Uganda. Therefore, his analysis supported the continuum concept.

Two methodological problems are apparent in these studies. One is that influences of local environmental factors are ignored. Another is that biological interactions are not taken into account. Analyzed species ranges are probably more expanded than those in communities, because Floras usually indicate upper- and lower-most limits of species including those of solitary occurrences.

Altitudinal transect studies without numerical analyses

In the following examples, the altitudinal sequence of vegetation was investigated using transects. However, the question on the range, mode and limit of species, and on the clustering pattern of associated species is not asked. Emphasis is placed on floristic enumeration, productivity, and structural changes in relation to soil nutrient regimes from warm lowland to cooler high altitude region: on Mt. Pangrango, Java, Indonesia (Yamada 1975, 1976a, 1976b); on Volcan Barva, Costa Rica (Marrs et al. 1988; Heaney & Proctor 1990); on the ultramafic mountain of Gunung Silam, Sabah, Malaysia (Proctor et al. 1988); in Manusela National Park, Maluku, Indonesia (Edwards et al. 1990).

Transect studies of van der Hammen et al. (1983) and of van der Hammen & Ruiz (1984) are comprehensive and include vegetation, bryophytes, soil macro and micro fauna in the Colombian Andes. Geological, pedological, meteorological and archeological observations have also been made along the transects. These transect studies belong to a more inclusive research program, called the "Ecoandes-Project." Numerical gradient analysis has not been performed for investigating spatial species patterns in this research program.

Vegetation zonation based on physiognomy

Physiognomical criteria and dominant species were primary keys for recognizing vegetation zones in the following studies. In Africa such studies were conducted on Mt. Muhavura, Uganda, by Snowden (1933); on Mt. Kilimanjaro by Salt (1954); on Mt. Kenya by Coe (1967); on Mt. Cameroon by Hall (1973); on east African mountains by Hedberg (1969, 1986). On Andean mountains, accounts on the physiognomic vegetation zones were made in the "Eco-Andes Project" (van der Hammen et al. 1983; van der Hammen & Ruiz 1984; van der Hammen et al. 1989a). In Malesia, vegetation zones were described on Mt. Makiling, the Philippines (Brown 1919-cited in Richards 1952); on Mt. Wilhelm, Papua New Guinea (Wade & McVean 1969); on mountains of New Guinea (Hope 1976; van Royen 1980; Johns 1982); on Mt. Kerinci, Sumatra (Ohsawa 1982; Ohsawa et al. 1985); on mountains in Malaya (Whitmore 1975); and, on Mt. Kinabalu, Borneo (Hotta 1974; Cockburn 1978; Kitayama 1987; Menzel 1988). Vegetation zonation on tropical mountains was discussed globally by Troll (1958, 1968,1973).

Physiognomic classification may be the best method for a first description of altitudinal vegetation zones. It is a rapid field technique. Results are easily comprehensible by other people. However, it is a subjective method, and is affected by researchers' emphasis and experience. Fig. 2.2 (see chapter 2) depicts physiognomic vegetation zones described by four authors on the same slope of Mt. Kinabalu. The number of zones and the altitudes of boundaries vary. The differences seem to be related to different research perspectives and emphases.

VEGETATION STUDIES CONDUCTED ON HALEAKALĀ AND KINABALU

There are only a few vegetation studies done on the windward slope of Haleakalā. Holt (1988) reassessed the dieback problem in the lowland region 80 years after the problem was first noted by Lyon (1909). Holt's study included floristic classification of dieback stands and an analysis of regeneration in the dieback stands. Vogl & Henrickson (1971) studied the vegetation of an alpine bog. Whiteaker (1983) mapped the vegetation in the crater district. No vegetation studies have been conducted on the mid-slope, and the details of the floristics and structure of the mid-slope rain forests remain unknown.

On Kinabalu, physiognomic vegetation zones were described by Hotta (1974), Cockburn (1978), Kitayama (1987) and Menzel (1988). The floristics of physiognomically identified alpine herbaceous communities was described by Smith (1970). Plant communities above 3200 m a.s.l. were floristically classified and environmentally characterized by Smith (1980). The vegetation of the entire Kinabalu Park was mapped at the scale of 1:100 000 using physiognomical criteria by Kitayama (1978, 1991). Floristic and structural sequence of the vegetation along an altitudinal gradient has never been quantitatively investigated on the mountain.

CONCLUSIONS

Whittaker's altitudinal transect studies on temperate North American mountains demonstrated a random pattern of the modes and limits of species distribution curves along gradients. With the results supporting the vegetation continuum concept, he concluded that vegetation units are products of arbitrary categorization. However, in this review several problems were pointed out in his highly schematized diagrams of species curves and in his study methods. One of his assumptions was that an altitudinal gradient is a unidirectionally changing sequence of factor complex. For this, he did not provide any evidence.

Vegetation patterns along mountain slopes have been variously described in the tropics. From the review of previous studies, it is evident that recognition of vegetation patterns is affected largely by the type of methods used. Agglomerative and divisive techniques with cluster analyses always identify vegetation units along altitudinal gradients even where vegetation changes gradually. Furthermore, the number of recognized units varies when different threshold values are applied (e.g. Hamilton & Perrott 1981). One reason is that the cluster analysis uses only the between-sample similarities (i.e. the Q technique, Mueller-Dombois & Ellenberg 1974). Conversely, ordination techniques tend to emphasize a vegetation continuum with scattered plots (Itow 1977; Shipley & Keddy 1987; Barkman 1990).

It is suggested that the factual description of vegetation patterns substantiated by characterization with environmental factors be a primary purpose of gradient studies. An unbiased vegetation sampling (e.g. transect method, van der Hammen et al. 1989b) followed by the indirect analysis using Braun-Blanquet's synthesis table technique is suggested to be used in such studies. The synthesis table technique is based on the simultaneous application of the Q and R techniques (Hill 1979). It produces both species and sample groups. The method, therefore, allows an ecological characterization of the sample groups by species groups and of the species groups by the sample groups.

In spite of the strong support for Whittaker's continuum view of species distributions along temperate mountain gradients, the results of the Mauna Loa transect study and a number of studies of physiognomically classified altitudinal vegetation zones in other tropical mountains reviewed here imply the existence of distinctive vegetation units associated with physiognomy. Yet, few transect studies encompassing entire altitudinal ranges have been carried out to test this possibility in detail on continental tropical high mountains. Moreover, the transect study on Mauna Loa relates to a geologically very young oceanic mountain. If either or both of the two distribution concepts are of general applicability as distribution principles, they must be tested also on old tropical mountains in floristically very diverse areas by application of comparable methods. This includes the measurement of environmental factors along with the analysis of species distribution.

WORKING HYPOTHESES

In plant communities, interspecific competition may be focussed on the situation where two or more species of the same synusia grow together. Species of a synusia may be limited by the same quality and quantity of resources such as light, water, and nutrients (Arthur 1987). When the species are nearly identical to one another in ecological characteristics (i.e. closely overlapping niches *sensu* Hutchinson 1957) and their demography is density dependent, certain species that have a slightly better fitness or adaptability to resource factors in the limited environment are favored over the rest. Such intra-synusial competition results in the differential dominance values of species.

Competitive exclusion in plant communities can be specified as the demand for common limiting resources among the members of a synusia. This form of competition has been termed "exploitative competition" by Arthur (1987).

The following dissertation research does not investigate autoecological aspects of species. It accepts the theory that the number of tree species in a similar synusia (cf. Volterra 1928-cited in Arthur 1987) can express the intensity of interspecific competition.

Whittaker (1972) has hypothesized based on his altitudinal transect analyses on North American mountains: that "given a resource gradient in a community, species evolve to use different parts of this gradient; competition between them is thereby reduced (rephrased after him)." Whittaker conceived the relationships among species in a plant community to be displayed in a multidimensional coordinate system. The coordinate consists of multi-environmental gradients which define axes of the coordinate.

With relevance to this study, a multi-species community is simplified here into a two-dimensional coordinate system rather than a multi-dimensional one as shown in Fig. 1.4. Such a simplified two-coordinate presentation was used by several authors including Whittaker (1972) and Shmida &

Wilson (1985). The x-axis represents a changing altitudinal gradient, and the y-axis the species biomass at a given altitude. In reality, however, the x-axis consists of a complex of environmental factors. This is what is meant by "composite gradient" sensu Whittaker (1956). Further, as evolutionary processes proceed, species diverge in autoecological characteristics and increase in number. Their distributional ranges become increasingly narrower along the x-axis. At the same time, the y values (biomass) of species at a given x value (altitude) also change. Therefore, competitive exclusion affects species along two axes; namely it results in narrower altitudinal ranges (x-axis) and reduced relative biomass values (y-axis).

Spatial species composition changes along the x-axis refers to "beta diversity" according to Whittaker (1972). Species number and representativeness along the y-axis at a given x value are referred to as "alpha diversity" by Whittaker (1972). The number of species at a given x-value indicates richness, and the representativeness indicates evenness of species quantity. It is apparent that an increase in the number of species in the coordinate system (i.e. an increase in regional floristic richness) can result in an increase in either beta or alpha diversity, or in both indexes, if Whittaker's hypothesis is applicable here.
Thus, the following working hypotheses are suggested for the dissertation research.

1. Plant communities on Haleakalā have lower values of alpha diversity than those in the comparable vegetation zone on Kinabalu because the regional species richness on Haleakalā is lower than on Kinabalu.

2. Each of the plant communities on Haleakalā is characterized by a greater dominance value of and a fewer number of leading dominant species than those on Kinabalu.

3. The lower regional floristic richness on Haleakalā leads to a lower spatial species turnover along its altitudinal gradient as compared to that on Kinabalu.

4. If vegetation zones are floristically definable by associated species groups, the zones on Haleakalā are fewer in number and wider in distribution than those on Kinabalu.

The view that consequences of interspecific competition in a multi-species community can be represented in a two-dimension coordinate is based on Whittaker's suggestion. Adequacy of this simplified view will be discussed after testing these working hypotheses.

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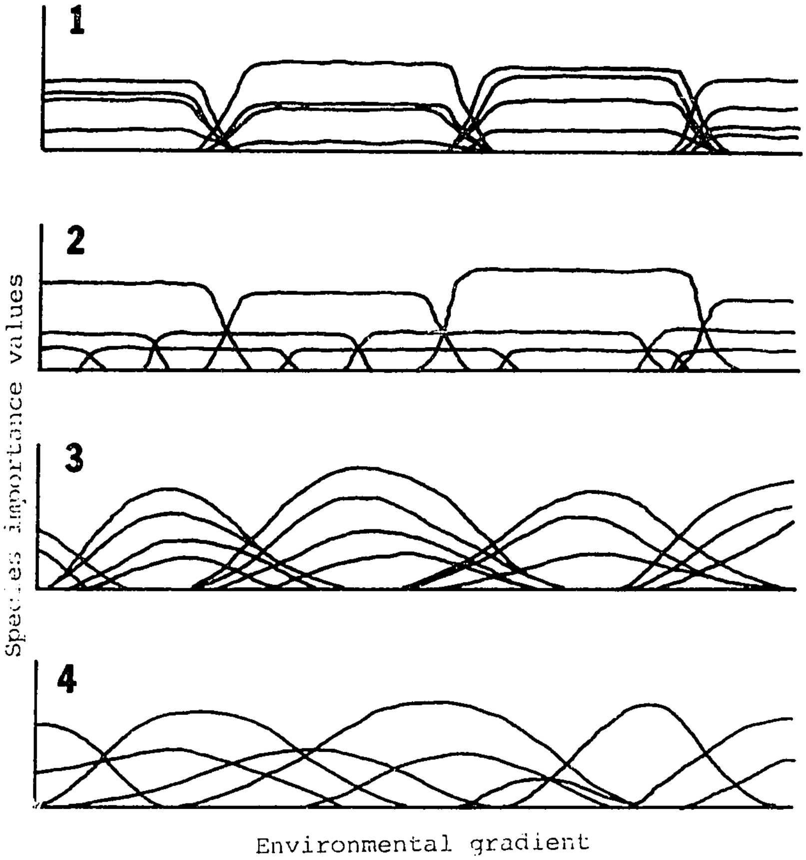

Fig. 1.1. Whittaker's four models of community organization along environmental gradients (after Whittaker 1975).

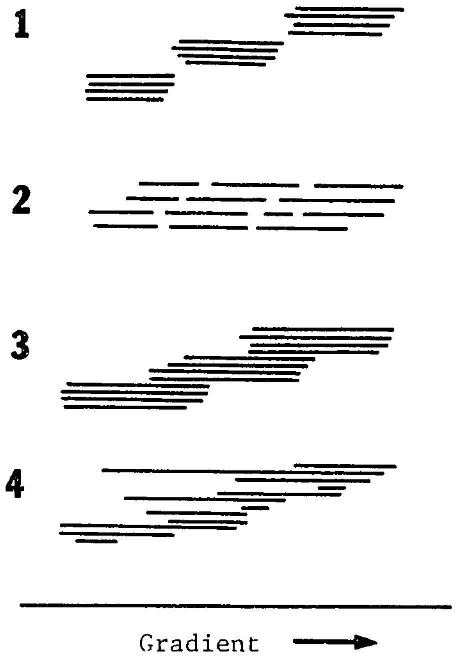

Fig. 1.2. Whittaker's four models restated with distribution limits shown by lines instead of curves (after Dale 1986).

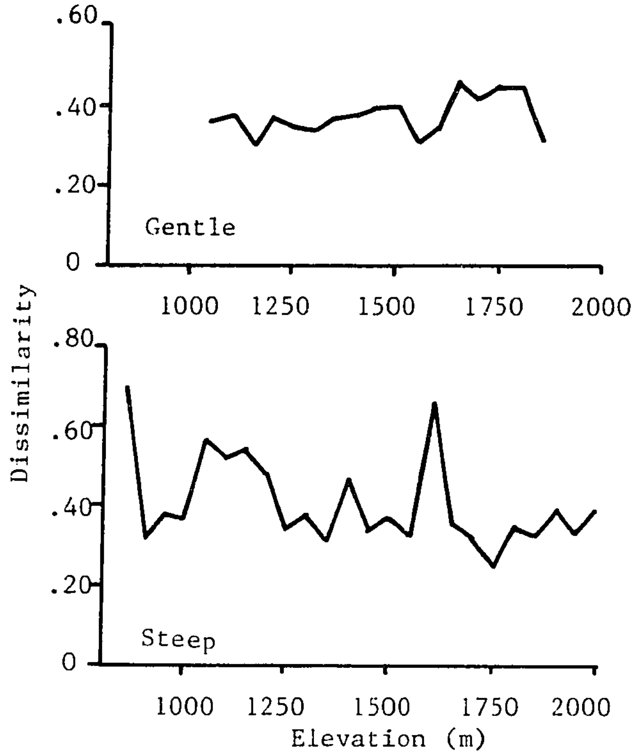

Fig. 1.3. Dissimilarity of adjacent segments of the altitudinal gradient along the gentle and the steep slopes on an African mountain. High values indicate rapid vegetation turnover, low values indicate slow turnover (after Beals 1969, the explanation is his).

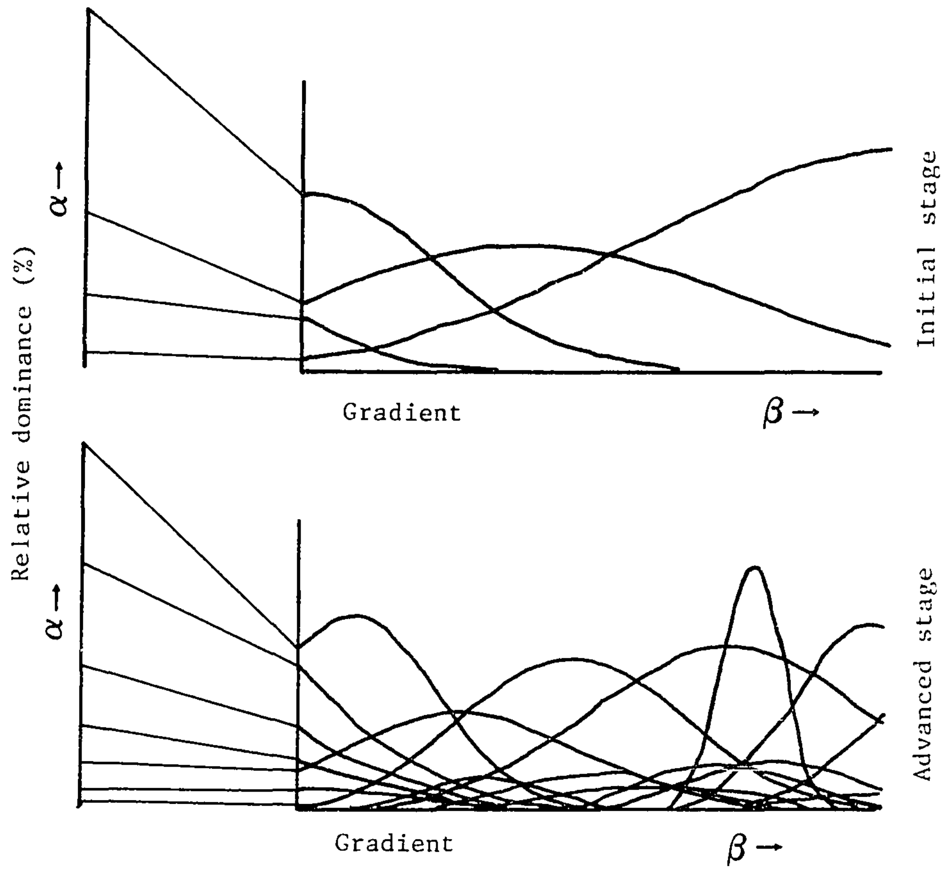

Fig. 1.4. Two-dimensional coordinate system representing plant communities organized along a hypothetical altitudinal gradient (x-axis). The plant communities are indicated by species distributional curves. The y-axis expresses absolute species biomass at a given altitudinal point. The extended lines to the left of the y-axes express relativized species biomass (=relative dominance values). Evolutionary process proceeds from the upper to the lower diagram, and results in the increase in alpha (along the y-axis) and beta (along the x-axis) diversities.

PART II. ORIGINAL RESEARCH

CHAPTER 2. AN ALTITUDINAL TRANSECT STUDY OF THE VEGETATION ON MOUNT KINABALU, BORNEO

ABSTRACT

A quantitative transect analysis of altitudinal sequences of forest canopy species from 600 to 3400 m on Mt. Kinabalu (4101 m), Borneo, resulted in four discrete altitudinal vegetation zones. These were made up of mutually exclusive species groups for lowland (<1200 m), lower montane (1200 to 2000-2350 m), upper montane (2000-2350 to 2800 m), and subalpine (2800 to the forest line, 3400 m) zones. The number of tree layers successively decreased by one per zone from six to three upslope, and this reduction in number was correlated with the floristic zonal vegetation changes. Zonal soil types were also correlated with the vegetation zones. In upslope sequence, these were: lowland Oxisols, montane Histosol/Spodosol complex, and subalpine Inceptisols. The highest contents of organic carbon, extractable phosphorus, and exchangeable magnesium and potassium were recorded in the lower and upper montane zones. The upper boundaries of the lowland, upper montane and subalpine zones coincided with thermal thresholds of latitudinal bioclimatic zones: 18°C TMIN (Köppen's tropical), WI 85 (Kira's warm temperate), and WI 45 (Kira's cool temperate), respectively. The upper limit of the lower montane zone was correlated with an abrupt increase of water surplus estimated from the annual rainfall minus annual potential evaporation. These climatic characteristics appear to define ecological altitudinal turnover points, so called "critical altitudes," where groups of associated species are displaced by other groups.

Keywords: Altitudinal gradient, Bioclimatic zone, Controlling factor, Critical altitude, Edaphic zone, Forest zone.

Abbreviations: DBH=diameter at breast height, TMAX=Mean daily maximum air temperature, TMIN=Mean daily minimum air temperature, TWINSPAN=Two-way indicator species analysis, WI=Warmth index.

Nomenclature: Nomenclature follows the index of the herbarium, Sepilok Forest Research Center (SAN), Sabah, Malaysia.

INTRODUCTION

Tropical mountains are attractive for the study of vegetation/environmental relationships because significant variations are compressed into short distances. Researchers have described altitudinal vegetation "zones" on tropical mountains. Salt (1954) and Hedberg (1986) studied African mountains; van der Hammen _et al_. (1983), and van der Hammen & Ruiz (1984) conducted the "Ecoandes Project"; Whitmore (1975), van Steenis (1984) and Ohsawa _et al_. (1985) studied Malesian mountains. Troll (1958) compared tropical mountains globally.

A zone is a belt of homogeneous vegetation bounded by relatively narrow boundaries. Although it has been implied that there are "critical altitudes," i.e. points where vegetation and/or some environmental attributes change abruptly (Hamilton 1975), the concept has not been widely substantiated with quantitative data.

The question of zonation and critical altitudes relates to contrasting unit versus continuum concepts of vegetation (Moravec 1989). Whittaker (1956, 1960, 1972, 1975) described vegetation as a continuum with staggered and random modes of Gaussian species distributions on temperate mountains. MacArthur (1972), however, suggested that associated species groups can be typified for species-rich tropical mountains on the basis of Holdridge's life-zone concept (Holdridge 1967). Mueller-Dombois et al. (1981) recognized both random and associated species assortments on a species-poor Hawaiian mountain. Beals (1969), Hamilton & Perrott (1981), and Woldu et al. (1989) found vegetation discontinuities on mid-slopes of African mountains. However, floristic/numerical studies have not yet been done to test Whittaker's findings along an entire species-rich tropical mountain from base to summit.

As part of a broader study on Malaysian mountain ecosystems, the present preliminary transect study has been conducted on Mt. Kinabalu (4101 m), Borneo. On this species-rich mountain, a closed-canopy forest occurs continuously from the base to the upper-elevation forest line. This situation contrasts with the African and Andean mountains, where distinct dry, non-forested zones mark the foothills. This paper presents results of the transect study and provides evidence for altitudinal turnover points in line with the concept of "critical altitudes."

The following questions have guided this study: (1) are canopy species organized into altitudinally differentiated groups? (2) How does forest structure relate to the floristic changes? (3) How are the changes in vegetation and soil related to climate along the mountain slope?

STUDY AREA

Kinabalu (4101 m) is the highest mountain in South-East Asia between the Himalayas and New Guinea. It is located at the northern tip of Borneo at 6°5'N and 160°33'E, and forms a conspicuously isolated mountain away from the central ranges.

The mountain is non-volcanic, extremely precipitous, rising sharply from the undulating low foothills (Fig. 2.1). The steep physiography with granitic bedrocks above c. 2700 m was formed by an intrusion of adamellite pluton during the Pleistocene (1.5 million years ago) into the surrounding Tertiary sedimentary rock. The latter consists of the Trusmadi Formation from the Eocene and the Crocker Formation from the Eocene-Oligocene (Jacobson 1970). Interspersed on the surface of these Tertiary rocks is more recent Quaternary sedimentary rock (early Pleistocene), which covers a small portion of the south face at c. 2000 m, and the entire Pinosuk Plateau. In addition, intrusions of ultrabasic rock occur around the massif (Brunotte & Kitayama 1987). The present summit is denuded, and shows effects of erosion by a late Pleistocene glacier as low as 3000 m (Jacobson 1970).

Currently, the mountain with its adjacent mountainous areas to the north is one of Sabah's state parks. The park headquarters (PHQ) are on the south face at 1680 m. A trail connects the PHQ through the south face with the summit.

The mountain has a humid tropical climate (Table 2.1). The mean monthly air temperature is c. 20°C throughout a year at 1680 m (PHQ), with a daily fluctuation of 7-9°C. The annual TMAX and TMIN (1975-83) at this elevation are 22.2°C and 14.4°C, respectively. The yearly course of monthly rainfall shows slight reductions twice a year under an average condition in April and September, which may lead to water deficits (Brunig 1969). The year-to-year rainfall fluctuates greatly, ranging from 2000 to 3800 mm (1975-83). Prolonged dry spells result in severe droughts (1979, 1981 and 1983 from Table 2.1). Drought years have been found to occur periodically (Beaman et al. 1985), and result in severe stress on the mountain vegetation (Lowry et al. 1973). A cloud belt envelopes the mid-slope daily year-round. No detailed study of the summit climate has ever been done.

The vascular flora is not completely known. Beaman & Beaman (1990) estimate c. 4000 species of vascular plants native to the mountain. The biogeography of selected species has been studied (van Steenis 1964; Meijer 1964; Corner 1978). From these accounts, Mt. Kinabalu supports plants from Indo-Malaysian, East Asian and Austral-Antarctic floristic regions. While Indo-Malaysian elements are prevailing and are diverse in the hot lower altitudes (e.g.

Dipterocarpaceae), East Asiatic elements (e.g. Fagaceae) progressively become more diversified upslope. Austral-Antarctic elements (e.g. *Ranunculus*, *Dacrycarpus* and *Leptospermum*) are found at higher elevations (Hotta 1974). Van Steenis (1964) considers Mt. Kinabalu the "stepping stone" linking the Southern Hemisphere to the north, through which southern temperate elements migrated northward in the Cretaceous. The invasion of temperate elements found at high altitudes has now been demonstrated to have begun in the Pleistocene (Smith 1986). Several genera are extremely speciose: 98 species *Ficus*, 66 *Syzygium* (=*Eugenia* *s.l.*), 53 *Litsea*, and 46 *Lithocarpus* (Beaman & Beaman 1990). Endemic species are numerous, notably neoendemic, and mostly localized (Beaman & Beaman 1990).

Plant communities have been described by Smith (1970, 1980) and Kitayama (1987). The vegetation formations of Kinabalu Park were mapped by Kitayama (1991). On the south face, the forest is fragmented below *c.* 1600 m due to ongoing rice and vegetable cultivation. The forest vegetation is, however, intact on the east and north slopes, where it forms a continuous cover down into the lowland (*c.* 500 m). The highest closed forest line is found at 3400 m, above which forest becomes naturally fragmented. Individual trees thrive as high as at 3700 m (tree line). Closed-canopy scrub ascends to 4000 m. In the summit area they form small mosaics in pockets of accumulated soil interspersed in a vast alpine rock-desert. There are a few extremely stunted shrubs near the peak, indicating that the peak is still below the climatic shrub line. A comparison (Fig. 2.2) of previously described vegetation zones on Mt. Kinabalu (Hotta 1974; Cockburn 1978; Kitayama 1987; Menzel 1988) demonstrates inconsistencies in designating zones on Kinabalu.

METHODS

Vegetation analyses

Van der Hammen et al.'s (1989) transect method was employed to investigate altitudinal changes of vegetation, climate and soil. The south face and the east ridge were selected for the investigation because of their relatively easy accessibility. The transect consisted of two discontinuous segments through undisturbed primary forest. The lower transect segment started at 600 m at Poring Hot Spring and ascended on the eastern shoulder to an elevation of 1800 m. The upper transect started from 2000 m near the Power Station and extended through the south face to the closed-forest line at 3400 m (Fig. 2.1). Fieldwork was conducted from March to July 1989.

A total of 14 vegetation sampling plots were located at 200 m altitudinal intervals. Efforts were made to avoid geological anomalies (e.g. ultrabasic substrate) and topographic extremes (e.g. ridge tops or valley bottoms) when selecting the plots. At 2200 m no stands were appropriate for sampling due to steep topography. The plots between 600 and 2600 m were underlain by Tertiary sedimentary rock, except for one at 2000 m where Quaternary gravel was found. Those above 2800 m were underlain by granitic rock.

At each plot, a secondary transect parallel to contour lines and intersecting the altitudinal transect was established. Along this secondary transect, the point-centered quarter method (Mueller-Dombois & Ellenberg 1974) was applied to trees ≥10 cm DBH, which were arbitrarily defined as canopy trees. Sampling points were systematically placed on the secondary transect at intervals of 10 m in low-density tree plots, and at intervals of 5 m in high-density tree plots. The tree closest to the point was measured for DBH in each quarter, and for distance from stem mid-point to the sampling point. The enumeration was continued until the same species repeatedly occurred and the number of newly added species became substantially low. An area of approximately 1 ha was considered a minimal size for the species-richest stand at 600 m.

For the structural analysis, the height of the canopy layer was measured at each plot with a clinometer. Using measured canopy height for reference, the height of lower layers and coverage were visually estimated. A layer is here defined as a visually recognizable, relatively continuous row of tree and shrub crowns.

Voucher specimens were collected from every tree and identified to species, based on vegetative morphology, at SAN. However, since a number of specimens remained unidentified, a series of running numbers were given to all enumerated morpho-species for data processing.

At each plot, mean area per individual tree was calculated by a square of the mean distance between the sampling points and the closest trees. This approximation is accurate when trees are randomly distributed (Mueller-Dombois & Ellenberg 1974). The total area of a plot was computed by multiplying the total tree number by the mean area. The tree density per ha was obtained by dividing 10 000 by the mean area (m^2).

Floristic/numerical classification of vegetation was performed using the computer program TWINSPAN (Hill 1979) on the relative species basal areas. Fourteen samples (plots) with a total of 425 canopy species were analyzed. TWINSPAN uses the reciprocal averaging for classifying samples and species into a hierarchical dichotomy. Clustered, selected species are numerically derived indicators for the classified vegetation types.

Soil analysis

At each of the vegetation plots except at 1000 m, one soil pit was excavated under closed canopy. A total of 13 pits were described for horizons based on the system of U.S.D.A. Soil Management Support Services (1986); soil colors were determined with Munsell color charts. Soil samples were collected from every horizon for chemical analysis, which was done by the Soil Chemist at the Tuaran Agricultural Research Center, Sabah.

Soil acidity (pH) was measured on a solution of fresh soils in deionized water. The weight ratio of soil to water was 1:2.5. Organic carbon was determined by the Walkley and Black rapid titration method. Total nitrogen was determined by the Kjeldahl digestion method followed by semimicro distillation in a Markham apparatus. Exchangeable cations (Ca, Mg, K and Na) were analyzed by atomic absorption spectrophotometry after extraction by M ammonium acetate solution at pH 7. Cation exchange capacity was analyzed by leaching the soil with M ammonium acetate solution at pH 7, and the amount of ammonium ions retained in the soil was determined by the semimicro Kjeldahl digestion method. Extractable phosphorus was extracted by a hydrochloric acid-ammonium fluoride solution, and determined colorimetrically. Bulk densities were not determined. Results were calculated on an oven dry weight basis.

Climate analysis

Data for demonstrating altitudinal changes of air temperature and humidity were gathered from two hygrothermographs. These were placed at five altitudes; 10, 500, 1680, 3200 and 3780 m. The station at 10 m was situated near the ocean in Kota Kinabalu, 100 km west of the main massif. Others were positioned along the transect (Fig. 2.1). One at 1680 m (PHQ) was monitored continuously for a four-month period, another was successively shifted (see Table 2.2 for duration). The continuous hygrothermograph readings were reduced to hourly air temperature and relative humidity. Hourly saturation vapor pressures (Es) were calculated with Lowe's polynomial (Lowe 1976) using the hourly air temperatures. The polynomial approximation is highly accurate with a mean percentage error of 0.007% in the temperature range of 0-35°C. Hourly actual vapor pressures (E) were calculated by:

$$E = Es \times \text{Relative Humidity}/100,$$

hourly saturation deficits (SD) by:

$$SD = Es - E.$$

In addition, four hand-made atmometers were installed in the same manner, but at closer intervals (10, 500, 1000, 1680, 2600, 3200 and 3780 m, see Fig. 2.1). The atmometer used consisted of a plastic reservoir with an evaporating surface made from a dark, porous carborundum stone (152.4 mm in diameter), and a clear plastic cover set 10 cm above the evaporating surface (Ekern 1983). The evaporating surface was located 1.3 m above the ground. One at 1680 m (PHQ) was continuously monitored for water loss during four months, the rest were shifted among other observation points (Table 2.2). Thus, the station at 1680 m served as a standard point. The climatic measurement was carried out in a relatively wet period of the year.

RESULTS

Altitudinal climate changes

Daily oscillations of the air temperature, actual vapor pressure and saturation deficit decrease upslope (Fig. 2.3). Saturation deficit maxima appear at 12:00 below 500 m, however at progressively earlier times with increasing altitude. This pattern suggests that a convective uplift of clouds results in condensation earlier upslope. Night saturation deficits decrease to the same value (c. 2 hPa) at all stations. Daily maximum deficit is the highest at 10 m (17 hPa), and progressively decreases upslope to the lowest value of 2 hPa at 3780 m. Maxima of actual vapor pressures are delayed to later hours than the temperature maxima due to radiative heating and subsequent increase in evapotranspiration.

The correlations between altitude m (X-axis) and air temperature °C (Y-axis) is given in Fig. 2.4. Mean air temperature decreases linearly upslope ($Y=27.45-0.0055X$, $r^2=0.999$). The temperature lapse rate is $0.55\pm0.01°C \cdot 100\ m^{-1}$ ($27.5\pm0.3°C$ at 0 m). This is slightly lower than the often used lapse rate of $0.6°C \cdot 100\ m^{-1}$ (Sarmiento 1986, Smith & Young 1987). Similarly, TMAX and TMIN are well correlated with altitude. The daily temperature difference diminishes with increasing altitude. This phenomenon has been described by other authors (Sarmiento 1986; Halloy 1989), and is due to the greater lapse rate of TMAX ($0.62°C \cdot 100\ m^{-1}$, 32.36°C at 0 m) than TMIN ($0.49°C \cdot 100\ m^{-1}$, 23.85°C at 0 m).

The regressions obtained from this short-term observation lead to an estimate of temperature ranges which fit mean air temperatures determined from long-term measurements (1975-83, Table 2.1). The short-term estimates are $21.94\pm1.35°C$ and $15.62\pm1.30°C$, respectively, for TMAX and TMIN at 1680 m, while the long-term values are 22.2°C and 14.4°C. The short-term measurements give a slightly higher value for TMIN than the long-term does.

The mean saturation deficit is depressed at mid-slope (Fig. 2.5), and indicates effects of the prevailing clouds. Fig. 2.6 shows altitudinal changes of estimated potential annual pan-evaporation. Conversion of the measured evaporation to standard pan-evaporation values was made using a conversion factor of 0.5533 obtained by Giambelluca et al. (1991, unpubl.). The potential evaporation decreases linearly upslope with a reduction rate of 27.85 mm·100 m^{-1} (1316 mm at 0 m, r^2=0.904). Evaporation values show a slight depression at 2600 m as do the saturation deficit values. However, the measured evaporation conforms closer to a linear correlation than does the saturation deficit.

Mean annual rainfall values are available at four altitudes in the vicinity of the transect. Annual water surpluses in rainfall equivalent, estimated from the annual rainfall minus the potential annual pan-evaporation, are +1348 mm at 10 m, +2011 mm at 1500 m, +1994 mm at 1680 m, and +3342 mm at 2150 m (Fig. 2.6). These values approximate the estimates made by Burnham (1974) in the same area. There exists a steep moisture gradient between 1680 and 2150 m, a consequence of the frequent presence of the lower cloud level.

Altitudinal soil changes

Several altitudinal changes are notable from the soil profile information (Fig. 2.7). An upslope reduction of the soil depth is evident from a deep (>1.5 m) lowland solum to a shallow one (c. 0.3 m) at higher altitudes. Thick organic horizons (Oa) develop above 1200 m. The Oa horizons between 1200 m and 2600 m are mors and fibrous, while above 2800 m they become mulls. Those at 2800 and 3000 m, are incorporated with a considerable amount of mineral matter, and are categorized as A horizons.

Eluviated horizons (E), brown to light gray in color, are prominent in some mid-slope soils between 1200 and 2600 m. These suggest effects of leaching. Fine silicaceous sands seem to be the dominating mineral components in the E horizons.

Oa or A horizons abut consolidated granitic rock above 2800 m, suggesting relative recency of soil accumulation. It seems that glacial erosion removed soils as low as this elevation. Lesser amounts of mineral particles are incorporated with organic matter at 3200 and 3400 m than at 2800 and 3000 m.

Chemical properties of the top soils, where most roots occur, are shown in Table 2.3. Each value is from a single sample. I assumed that the extent of internal site variation is lower than their altitudinal differences between plots. The assumption is valid as will be shown.

Associated with the profile changes, some chemical properties also show distinct altitudinal patterns. The mid-slope top soils (1200-2600 m) have higher amounts of organic carbon (19.9-40.4%), total nitrogen (0.98-1.87%), and extractable phosphorus (except for 2600 m, 15-37 ppm) than in the lower and upper slopes. Exchangeable magnesium and potassium, and cation exchange capacity become higher also on the mid-slope. They are, respectively 2.20-8.73 m-equiv. (except for 1400m), 1.05-1.76 m-equiv., and 46.8-114 m-equiv. between 1200 and 2600 m. The increased humus, which is indicated by higher organic carbon values, is responsible for the increase of other chemical properties.

The higher C/N ratios in some mid-slope soils indicate a lower nitrogen mineralization than other soils. Ratios >20 are found at 1600, 1800 and 2600 m. The nitrogen availability for plants may be limited in these soils. The ratio of Ca/Mg, which is an index of leaching (Askew 1964), is generally low in the soils below 2600 m indicating advanced leaching below this elevation.

Soil acidity does not show any consistent altitudinal pattern. Soils are acidic to weakly acidic throughout the slope. This is contrary to the expected pattern that humid mid-slope soils would be the most acidic.

Two profiles at 2000 and 3000 m have higher pH than the rest, respectively 4.9 and 5.4. These high values are reflected in the strikingly high base saturations, 54% and 64%, respectively. An explanation for the high base saturation, and the outstanding soil depth at 2000 m could be that substrate was derived from the geologically recent tilloid of the early Quaternary (Jacobson 1970).

Altitudinal vegetation changes

A total of 425 morpho-species (trees≥10 cm DBH) were recorded in the 14 plots on the transect. The species number per stand (Table 2.4) exponentially decreases with increasing altitude, ranging from 153 (600 m) to 11 (3400 m). The total basal area tends toward greater upslope, ranging from 27.5 $m^2 \cdot ha^{-1}$ (1000 m) to 57.4 $m^2 \cdot ha^{-1}$ (3200 m). The tree density increases upslope, and ranges from 333 $trees \cdot ha^{-1}$ (600 m) to 1950 $trees \cdot ha^{-1}$ (3000 m). An abrupt, twofold increase in the density is notable at 1400 and 2800 m. The changing patterns, and values of the parameters (Table 2.4) are closely comparable to those on a Costa Rican mountain (Heaney & Proctor 1990).

Association patterns

TWINSPAN output was transcribed to a differential table (Table 2.5). Indicator species are shown with their relative basal area (%) classes:

5, 20-100 %; 4, 10-19 %; 3, 5-9 %; 2, 2-4 %;
and, 1 <1 %.

The complete species composition at each plot is given in Appendixes 1.1 to 1.14.

Classified sample groups are well correlated with altitude (Table 2.5). Accordingly, they are considered altitudinally defined vegetation zones. The fourteen samples are divided into two major groups at the first level: the samples from 600 to 2000 m; and those from 2350 to 3400 m. A major compositional boundary is drawn between 2000 and 2350 m. They are further partitioned into four sample groups at the second level. The hierarchy is weakly expressed because the number of associated species are low at the first level (i.e. the groups I and IV in Table 2.5). I tentatively conclude that the sample groups correspond to the lowland, the lower montane, the upper montane, and the subalpine zones, respectively (sensu Grubb 1974).

Floristics

The lowland zone is differentiated by the greatest number of species among the four zones. A total of 30 species in group 1a (Table 2.5), and 16 species (group 1b) indicate the zone. The latter is weaker in the association with the zone. The lowland indicators are largely of pantropical or of Malesian floristic elements. The Malesian elements are represented by the genus Shorea. Families which occur in the lowland canopy and are absent from upper zone canopies include: Dipterocarpaceae, Sapindaceae, Fabaceae, Xanthophyllaceae, Moraceae, Gonystylaceae, Meliaceae, Rubiaceae, Burseraceae, Bombacaceae, and Rutaceae. These families provide the main canopy species in the lowland forest, but may appear in the understory of upper zones, e.g. Moraceae. A few species of

Dipterocarpaceae occur in the montane zone, but the family is one of the most dominant lowland elements.

The lower montane zone is indicated by groups 2a and 2b, the first of which is more strongly associated with the lower montane zone than the second. These indicators are represented largely by species of Fagaceae, Lauraceae, Theaceae, Myrtaceae and Elaeocarpaceae. In contrast with the lowland indicator families, none of the lower-montane families are characteristic for this zone. This lower montane zone together with the upper montane zone is comparable to what was described by van Steenis (1964) as the lauro-fagaceous zone. However, the families Lauraceae and Fagaceae are rather generalistic on Kinabalu, and have broad altitudinal ranges extending both to the lowland and the subalpine zone.

The upper montane zone is indicated by four associated species (group 3): *Ascarina philippinensis* is preponderant at 2350 m but occurs also at 1600 m. *Eugenia punctilimba*, *Olea rubrovenia* and *Ilex zygophylla* are more restricted in distribution. The latter two species occur as shrubs on nearby ultrabasic substrate.

The subalpine zone is indicated by ten associated species (group 4), most of which are sclero/micro-nanophyllous. *Leptospermum recurvum* has very small leaves (leptophylls). Several species extend beyond the closed-forest line (3400 m) into open forest, and closed-canopy scrub, i.e. *Dacrycarpus kinabaluensis*, *Leptospermum recurvum*, *Eugenia kinabaluensis*, *Schima brevifolia*, *Symplocos buxifolia*, *Eugenia ampullaria*, *Rhododendron buxifolium*.

It is noteworthy that some of the indicator species for the subalpine zone have close congeneric affinities in lower zones. *Dacrycarpus kinabaluensis*, *Leptospermum recurvum* and *Schima brevifolia* are subalpine species congeneric with *D. imbricatus*, *L. flavescens* and *S. wallichii* in the montane zone.

With increasing altitude above the lowland zone, a higher number of Austral affinities (van Steenis 1964) or Austral-Antarctic elements (Meijer 1964) prevails: A single Austral element *Phyllocladus hypophyllus* (group III) indicates the montane and subalpine zones. Other Austral species include *Dacrycarpus imbricatus*, *D. kinabaluensis*, *Ascarina philippinensis*, and *Leptospermum recurvum*.

Cluster analysis

Cluster analysis defined the same relationships among the 14 samples as did TWINSPAN (Fig. 2.8). The dendrogram construction employed a quantitative similarity index PS:

$$PS=2Mw/200$$

where Mw=sum of the smaller relative basal area values of the common species between two samples.

Sample similarities are generally below 59%. Relatively high similarities between 600 and 800 m (45.3%), and between 3000 and 3200 m (59%) are due to the presence of dominant species common to each sample pair, respectively *Shorea leprosula* and *Dacrycarpus kinabaluensis*.

Four vegetation zones are also discernible at the 10% threshold line shown in the dendrogram. Internal variation in composition within each zone is very high, indicated by the overall similarity at the highest rank of each zone (the lowland, 12.4%; the lower montane, 17.2%; the upper montane, 21.4%; the subalpine zone, 30%). Internal variation becomes progressively less upslope, implying reduced species numbers, reduced species dispersion, and increased relative dominance by leading species within upslope zones.

Forest structure

There is a successive reduction in the number of layers by one per zone (Table 2.6). This pattern coincides with another series of altitudinal forest formations in Malaya described by Robbins & Wyatt-Smith (1964 cited in Whitmore 1975).

The canopy height decreases upslope from 50 m (600 m a.s.l.) to 6 m (3400 m a.s.l.). Each floristic zone has a characteristic layer structure. Emergent trees are characteristic for lowland forests as also noted by Whitmore (1975). Except at 1200 m, the lowland forest has a six-layered structure. The forest becomes five-layered between 1200 and 2000 m, four-layered between 2350 and 2600 m, and three-layered above 2800 m.

DISCUSSION

Zonation and critical altitudes

Four floristically defined altitudinal zones emerged from this study (Table 2.5). The results of the floristic classification agreed with the cluster analysis (Fig. 2.8). The floristic zones were closely correlated also with the changes in the forest structure (Table 2.6). Therefore, the four vegetation zones tentatively named in the previous section seem to be valid. This zonal scheme closely agrees with the four "formation types" defined by Grubb (1974, 1977) using structural and physiognomic vegetation characteristics.

As to vegetation boundaries, a laboratory examination of air photographs showed emergent trees in close proximity to the plot at 1200 m. This suggests that the forest at 1200 m is transitional from the lowland to the montane zone. Yet, a rather sharp boundary between the two may be drawn near 1200 m. Furthermore, field observations demonstrated an abrupt change in forest structure at 2800 m on the south face, the elevation marking the upper limit of the upper montane zone. Such an abrupt structural change was not found for the upper limit of the lower montane zone between 2000 and 2350 m.

The altitudinal changes in the soil profiles (Fig. 2.7) and in the chemical properties (Table 2.3) indicate that the limits at c. 1200 and c. 2800 m are boundaries also for edaphic zones (Table 2.7). The indicated edaphic zones in Table 2.7 are identified tentatively by comparing results of this study with diagnostic properties of Askew (1964) and Burnham (1974).

Thus, critical altitudes do exist on Kinabalu, where plant species composition abruptly changes by the replacement of indicator species groups. The critical altitudes are further substantiated by forest-structural and edaphic changes which correlate with floristic changes at the same altitudes.

Controlling factors

Temperature: comparison with bioclimatic zone

The following discussion compares latitudinal lowland bioclimates with Kinabalu's altitudinal climates. The vegetation zones are displayed with altitudinal environmental components in Fig. 2.9. Information on zones above 3400 m is cited from Kitayama (1987). Air temperatures are estimated from the regressions (Fig. 2.4) at the vegetation boundaries. The classification of altitudinal climates are based on the threshold values of Köppen's thermal system (Köppen 1936) and Kira's system (Kira 1976). These bioclimatic systems were derived from empirical criteria as related to latitudinal vegetation zones.

Köppen's thermal climate system uses as threshold values mean monthly temperatures of the coldest and the warmest months. Kira's system uses the warmth index (WI) based on temperature summation:

$$WI=\sum_{1}^{n}(t-5)$$

where n= number of months with mean air temperature (t) exceeding 5°C. Therefore, the WI index consists of the cumulated mean monthly temperatures >5°C, whereby 5°C is considered a threshold temperature for plant growth (Kira 1976).

An application of these latitudinal bioclimatic indices to Kinabalu's diurnal thermal regime became valid by the following procedure. For the application of Köppen's climate zones, TMAX and TMIN were used as threshold values instead of mean monthly temperatures of the warmest and the coldest months because the mountain vegetation experiences greater temperature differences in the daily cycle than in the yearly cycle. For Kira's climate zones, mean daily temperatures were used instead of monthly means in the equation given before.

According to the temperature lapses obtained, Köppen's tropical climate (set by TMIN >18°C) appears below 1200 m on Kinabalu (Fig. 2.9). Temperate climate (TMAX >10°C, and 18°C>TMIN>-3°C) appears in a broad zone between 1200 and 3610 m. Polar climate (TMAX <10°C) directly abuts the temperate zone. Although Köppen has recognized a cold climate between the temperate and the polar zones in his latitudinal scheme, a homologous climate zone (TMAX >10°C, and TMIN <-3°C) does not appear on Kinabalu. This absence is due to: 1) an year-round equable tropical climate, and 2) the diurnal temperature difference between TMAX and TMIN diminishing upslope on Kinabalu (Fig. 2.4).

Kira set his WI >240 as the limit for latitudinal tropical climate, 240>WI>180 for subtropical, 180>WI>85 for warm temperate, 85>WI>45 for cool temperate, 45>WI>15 for subpolar, and 15>WI>0 for polar tundra. All climate zones based on Kira's WI appear on the slope, but they are markedly compressed in distribution as compared to Köppen's zones (Fig. 2.9).

A close correlation exists between floristic vegetation boundaries and altitudes of bioclimatic thermal thresholds (Fig. 2.9). The upper boundary of the lowland coincides with the threshold of Köppen's tropical climate (TMIN 18°C). The upper boundaries of the upper montane and subalpine zones coincide with those of Kira's warm temperate (WI 85) and cool temperate climates (WI 45), respectively.

Another important thermal factor on the transect is the daily ground-frost line (Fig. 2.9). This line coincides closely with the tree line (=the upper limit of the open-canopied subalpine forest). Noguchi et al. (1987) estimated a temperature difference of 3 to 4°C between the standard screen level at 1.5 m and the ground surface. Using the 4°C deduction from TMIN at the screen level, the lowest daily ground-frost line is estimated to appear at 3680 m. Ohsawa (1990) has concluded that tree lines on South and East Asian mountains are set by WI 15 regardless of latitude. Indeed, Kinabalu's tree line occurs in the proximity of this value (Fig. 2.9). The threshold of Köppen's temperate climate (TMAX >10°C) also conforms closely to the tree line. Among these the ground-frost line shows the closest occurrence with the tree line.

The lowland vegetation zone on Kinabalu extends up to WI=190, internally encompassing Kira's latitudinal tropical and subtropical climates. Kira's tropical climate (WI >240) may correspond to what Symington (1974) calls the lowland dipterocarp zone, differentiated from the hill dipterocarp zone within the lowland. According to Hotta (1974) this zone occurs below 600 m on Kinabalu, i.e. WI >230 corresponding to Kira's tropical climate. Whether a major species turnover appears at 600 m was not investigated in the study, because the transect began at 600 m. Unfortunately the vegetation below 600 m was already disturbed.

Sakai & Larcher (1987) emphasize that latitudinal and altitudinal plant distributions are often restricted by physiologically stressful absolute low temperatures during the coldest season. For example, the potential frost resistance of timberline trees on Mt. Wilhelm, New Guinea, is -3 to -5°C regardless of species (Sakai & Larcher 1987). This explains why trees can not extend beyond a certain altitude. By contrast, Ohsawa (1990) suggests that the forest limits on tropical Asian mountains south of 20°N are set by the shortage of heat, the so called "requirement limit." He hypothesizes that the coincidence of the forest limits with the threshold value of WI 15 on the mountains is an indication of the heat deficiency for treeline species. This hypothesis is in line with the accounts by Troll (1973) and Su (1984).

Whether plant distributions on continental tropical mountains are in general restricted by absolute minimum temperatures or by the shortage of heat is controversial. Results of this study (Fig. 2.9) suggest that the upper limit of the lowland zone and the tree line are set by absolute minimum temperatures because they coincide with TMIN=18°C and the daily ground-frost line, respectively;

but, the upper limits of the upper montane and subalpine (lower) zones are set by the shortage of heat.

Temperature: implication for the zonal differentiation

One remarkable difference between tropical and seasonal temperate high mountains is that evergreen broad-leaved trees occur at the forest lines in the tropics (Troll 1973; Ohsawa *et al*. 1985; Ohsawa 1990). On Kinabalu the evergreen broad-leaved and the Austral-Antarctic coniferous elements have extremely wide generic altitudinal ranges. The middle diagram of Fig. 2.9 schematically depicts two groups of wide-ranging floristic elements along the slope, i.e. (a) the latitudinal lowland tropical floristic group represented by *Shorea*, and (b) the latitudinal lowland temperate group represented by *Schima*. The two groups may partially overlap with one another.

Upon considering the discrepancy between Köppen's broader and Kira's compressed climate zones in Fig. 2.9, the following explanation for the differentiation of the vegetation zones is suggested. The upper limit of the lowland and the tree line may be the two most important turnover points on Kinabalu's altitudinal gradient. The latitudinal lowland tropical elements (group a) and the latitudinal lowland temperate elements (group b) largely drop out respectively at the two turnover points, set by the minimum temperatures. These two floristic groups occur over a wide altitudinal range due to the mountain's yearly equable thermal regime, and correspond respectively to Köppen's tropical and temperate zones. Consequently, some widespread floristic elements are constrained by the deficiency of heat near their upper limits, and split into altitudinal congeners (e.g. Eugenia of group b). The adaptation to the altitudinal heat-thermal regimes results in the subdivision of the two zones into finer altitudinal vegetation zones as correlated to Kira's climate zones (Fig. 2.9).

Atmospheric humidity

Based on dew point calculation, Burgess (1969) predicted the lifting condensation level to occur at 1200 m on the Malayan main ranges. At this elevation on Kinabalu, moss cover becomes prominent on standing trees. Results from atmospheric humidity measurements further indicate that the condensation level fluctuates daily and is frequent at the higher altitude of c. 2000 m (Fig. 2.6).

The upper montane forest zone is not as distinct as other zones in that its diagnostic canopy species are few. Although the zone has a higher floristic similarity with the subalpine zone (Fig. 2.8), it may be considered an impoverished subtype of the lower montane forest, where a number of canopy species drop out and only a few indicator species are added. This interpretation may be corroborated by the fact that both lower and upper montane zones conform to the same altitudinal warm temperate zone (Fig. 2.9). The abrupt increase of water surplus above c. 2000 m (Fig. 2.6) may be responsible for the floristic impoverishment of the upper montane forest.

The excessive water surplus leads to soil saturation and a consequent anaerobic state (Grubb 1974). This creates lowered soil nutrient availability, as will be shown in the following section. The frequent cloud cover creates physiological stresses, such as reduced transpiration (Leigh 1975, Ash 1987) and photosynthetically active radiation (Grubb 1977; Körner *et al*. 1983).

Kitayama (1987) recorded irregular relative humidity oscillations at 3260 m, which were not detected in the present study. From January to March 1986, very dry air, as low as 20% relative humidity, alternated frequently with near-saturated air there. A probable explanation is subsidence of upper air masses. McVean (1974) reported a similar phenomenon on Mt. Wilhelm, New Guinea. Occurrence of air mass subsidence seems to be seasonal on Kinabalu, probably corresponding to the movement of the intertropical convergence zone. If so, plants in the high altitude environments may be subjected to seasonal water deficits. Small leaves and sclerophylly of high-altitude trees may be a consequence of morphological adaptation to several stress factors, among which the putative seasonal water deficits may be important.

Soil: comparison with other tropical mountains

Edaphic factors seem to be of secondary importance in controlling vegetation zones on Kinabalu. Several workers suspected that soil nutrient deficiencies are related to upslope reduction in the forest height and to tree-morphology changes on some tropical mountains. Emphases were often placed on differences between lowland and montane forests. Montane species may in general be better adapted to relatively poor nitrogen and phosphorus supply than are lowland species (Grubb 1977; Tanner 1985; Marrs et al. 1988; Vitousek et al. 1988; Tanner et al. 1990). Deficiency of copper and potassium was proposed for the montane forest, respectively in Malaya and Puerto Rico (Grubb 1977).

Chemical data on montane soils from selected tropical mountains are compared with results from Kinabalu (Table 2.8). This demonstrates representativeness of the single-sample analysis of this study. Geometric means of the chemical properties in the montane soil on Kinabalu (1200-2600 m except at 2000 m) generally fit in the ranges obtained from other mountains. Overall, the montane soil on Kinabalu is similar to that of Jamaican mor ridge forest at 1600 m (Tanner 1977) with only minor differences.

Furthermore, the altitudinally changing pattern in the chemical properties on Kinabalu largely agrees with results from a transect study in Costa Rica (100-2600 m) done by Marrs et al. (1988). The Costa Rican transect shows that organic carbon, total nitrogen, and exchangeable cations (K, Ca and Mg) increase with altitude, and that there are no significant altitudinal changes in pH and extractable phosphorus. Therefore, departure from Kinabalu's results is found only in calcium and extractable phosphorus. These are found to decrease and increase, respectively, in the montane zone on Kinabalu. This calcium reduction in the montane zone (as expressed in a low Ca/Mg ratio) seems to be typical for the peaty montane soils underlain by granitic substrate in the Malayan main range and on Kinabalu (Askew 1964, Burnham 1974).

Soil: nutrient availability

Mineral nutrients are apparently not poorer in Kinabalu's montane zone than in the upper and lower zones, except for exchangeable calcium, and probably nitrogen. Because soil pH is similar along the entire transect (Table 2.3), pH restriction on nutrient availability should remain nearly constant along the slope.

Although there is a large nitrogen reserve accumulated in the montane zone, a considerable fraction may not be available to plants as indicated by higher C/N ratios.

Unfortunately, the nitrogen turnover rate, which is critical for determining the potential nitrogen availability, is not known from Kinabalu. In the Costa Rican transect study, both nitrogen mineralization and nitrification rates linearly decreased with altitude (Marrs et al. 1988). Some montane soils, however, show a moderate nitrogen turnover (Table 2.8), e.g. 35 $\mu g \cdot g^{-1}$ mineralization per 14 days in the Jamaican mor ridge forest (Tanner 1977), whose soil chemical properties resemble those of Kinabalu. The data suggest a considerable site-to-site variation in nitrogen turnover.

Another factor for mineral nutrient limitation is a mechanism which suppresses the uptake. Such a mechanism could be the highly saturated air which retards transpiration (Fig. 2.6). The correspondingly lowered mass flow reduces the nutrient uptake (Leigh 1975; Ash 1987). This suppression of uptake is more likely to occur for nitrates, which are mobilized largely by the mass flow (Foth 1984). Grubb (1977), however, argues that nutrient uptake is reduced rather by the shortage of photosynthates where photosynthetically active radiation is lowered due to the mid-slope cloud cover. Also, he states that certain cations (e.g. potassium) are transported to plant roots largely by diffusion rather than mass flow. A further investigation including foliar analysis and nutrient turnover will be needed on Kinabalu to clarify this argument.

Marrs _et_ _al_. (1988) have found that nitrogen mineralization in the montane zone in Costa Rica is restricted by increased soil moisture rather than by altitudinal temperature reduction. The mid-slope humus increase, and associated changes in soil properties are primarily a consequence of the cloud incidence, and probably of the reduced temperature coefficient. There is no doubt that climatic factors govern both edaphic properties and plants along the transect of Mt. Kinabalu.

CONCLUSIONS

The floristic/numeric vegetation analysis has clearly defined four floristic forest zones along an altitudinal gradient below the closed-forest line on Kinabalu. The zones are distinct and discrete. Each zone has multiple indicator species which are all displaced by those of the next zone only with limited overlap at the boundaries. These results are different from the pattern hypothesized from North American mountains, that evolutionary adaptation and competitive exclusion result in random species distributions along an environmental gradient (Whittaker 1972, 1975). The discrete pattern on Kinabalu agrees with the results from relatively species-rich African mountains (Hamilton & Perrott 1981; Woldu _et_ _al_. 1989), and from species-poor Hawaiian mountains (Mueller-Dombois et al. 1981).

The upper limit of the lowland vegetation, and the tree line coincide with Köppen's minimum temperature for latitudinal vegetation zones, and the daily ground-frost line. The upper boundaries of the upper montane and subalpine zones coincide with Kira's WI threshold values. The upper boundary of the lower montane zone seems to be related to a sharp moisture increase. The implication from these results is that the upper boundaries are largely controlled by climatic factors. Thus, results in part agree with the hypothesis, that upper limits of species are set primarily by temperature and lower limits by species competition (Grubb 1977). An experimental approach is needed to examine the role of species competition in setting lower limits.

ACKNOWLEDGEMENTS

This study was conducted as part of an investigation of the mountain ecosystems of Sabah, Malaysia, supported by the Toyota Foundation (grant 88-I-036). The following persons and institutes assisted in the study: Reiko Kitayama in fieldwork and all aspects of data analysis; Sabah Parks in fieldwork; the Sepilok Forestry Research Center in specimen identification; and the Tuaran Agricultural Research Center

in soil chemical analysis. I am grateful to each for these contributions, and to Dr. D. Mueller-Dombois, Univ. of Hawaii, for his invaluable advice throughout the study.

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Table 2.1. Climate of Mt. Kinabalu. (a) Monthly mean daily maximum and minimum air temperatures (°C) at the Park Headquarters (1680 m) from 1975-83. (b) Monthly rainfall (mm) at the same station.

(a)

Month	1	2	3	4	5	6	7	8	9	10	11	12	Mean
Max.t	21.1	21.7	23.0	23.6	23.4	22.4	22.1	21.5	22.0	21.7	22.1	21.6	22.2
Min.t	13.6	13.6	13.8	14.3	15.2	14.9	14.6	14.9	14.9	14.8	14.6	13.7	14.4

(b)

	Month												
Year	1	2	3	4	5	6	7	8	9	10	11	12	Total
1975	232	194	586	65	414	202	229	279	312	315	424	577	3828
1976	420	63	133	112	334	225	306	285	193	327	258	191	2846
1977	325	547	80	192	284	306	335	296	195	355	297	155	3365
1978	180	139	65	192	173	257	209	234	213	503	421	183	2770
1979	33	32	194	56	171	349	402	136	314	608	262	224	2780
1980	150	148	309	126	183	246	191	302	123	314	279	462	2833
1981	340	147	18	80	219	140	274	64	89	333	189	112	2004
1982	269	117	105	122	266	263	178	315	142	216	144	260	2397
1983	59	8	30	8	73	369	192	332	281	215	381	323	2270
Mean	223	155	169	106	235	262	257	249	207	354	295	276	2788

Table 2.2. Duration of climatic measurements at seven stations established along the transect on Mt. Kinabalu in the 1989 field survey.

Station (Alt. m)	Temperature	Vapor pressure (Humidity)	Evaporation
Kota Kinabalu (10)	8-22 May	8-22 May	10 Apr-22 May
Poring (500)	17 Apr-8 May	17 Apr-8 May	17 Apr-22 May
Kg. Teburi (1100)	_	_	1 Jun-17 Jul
PHQ (1680)	17 Apr-17 Jul	17 Apr-17 Jul	30 Mar-17 Jul
RTM (2600)	_	_	25 May-17 Jul
Laban Rata (3260)	23 May-12 Jun	23 May-12 Jun	6 Apr-12 Jun
Sayat-Sayat (3780)	12 Jun-17 Jul	12 Jun-17 Jul	12 Jun-18 Jul

Table 2.3. Chemical properties of top soils at the study plots along the transect on Mt. Kinabalu: soil acidity pH (H_2O); contents (oven-dry weight basis) of organic carbon (o-C), total nitrogen (t-N), exchangeable calcium, magnesium, potassium and sodium, total bases, and extractable phosphorus (P); C/N and Ca/Mg ratio; cation exchange capacity (CEC); and base saturation (BS). Two profiles observed at 600 m. Soil at 1000m not analyzed.

Alt. (m)	Depth (cm)	pH	o-C (%)	t-N (%)	C/N	Exchangeable elements (m-equiv.·100 g^{-1}) Ca	Mg	K	Na	CEC	Total Bases	BS (%)	P (ppm)	Ca/Mg
600	2-5	4.2	7.6	0.53	14	0.91	1.85	0.43	0.12	18.1	3.31	18	3	0.49
600	2-5	3.9	6.4	0.53	12	0.90	1.22	0.50	0.09	23.3	2.71	12	n.d.	0.74
800	2-5	3.8	9.5	0.55	17	0.09	0.79	0.34	0.06	23.3	1.28	5	10	0.11
1200	4-15	4.1	33.4	1.87	18	0.32	2.20	1.68	0.35	66.5	4.55	7	28	0.15
1400	2-37	3.5	33.6	1.81	19	0.25	0.45	1.37	0.34	91.5	2.41	3	29	0.56
1600	5-30	3.7	40.4	1.41	29	0.46	2.76	1.05	0.44	114	4.71	4	15	0.17
1800	2-12	4.1	31.4	1.58	20	0.61	2.49	1.76	0.37	97.5	5.23	5	31	0.25
2000	2-7	4.9	19.9	1.14	17	15.23	8.73	1.36	0.22	46.8	25.54	54	34	1.75
2350	2-10	3.9	34.6	1.96	18	0.51	8.17	1.17	0.23	78.7	10.08	13	37	0.06
2600	2-10	3.9	38.0	0.98	39	4.08	7.21	1.17	0.42	79.6	12.88	16	4	0.57
2800	3-20	4.6	7.7	0.45	17	0.40	0.27	0.26	0.10	9.8	1.03	10	13	1.48
3000	1-5	5.4	15.5	0.83	19	18.30	2.42	0.63	0.20	33.4	21.55	64	9	7.56
3200	5-10	3.9	11.6	0.91	13	1.07	1.09	0.68	0.18	34.3	3.02	9	28	0.98
3400	2-30	4.7	8.8	0.56	16	3.41	0.47	0.40	0.21	22.1	4.49	20	11	7.26

n.d.: not detected

Table 2.4. Area, number of species, total basal area (BA) per ha, and density per ha for trees ≥10 cm DBH at the study plots along the transect on Mt. Kinabalu. Sampled areas are estimated by a square of mean distance that is obtained from the point-centered quarter method. Basal areas are based on DBH at 1.3m.

Alt. (m)	Study area (m^2)	Species number	Total BA ($m^2 \cdot ha^{-1}$)	Density ($trees \cdot ha^{-1}$)
600	11 188	153	33.4	333
800	8063	102	29.8	372
1000	5636	93	27.5	369
1200	4027	79	34.0	447
1400	2477	70	46.6	759
1600	3707	58	33.2	572
1800	3441	41	39.0	593
2000	4907	50	36.7	497
2350	1439	26	59.5	778
2600	1700	13	49.2	659
2800	1034	16	26.4	1044
3000	574	17	55.4	1950
3200	932	14	57.4	1202
3400	542	11	45.0	1844

Table 2.5. Kinabalu's floristic altitudinal forest zones, and indicator species differentiated by TWINSPAN. Each vertical column under A - D represents one of the 14 samples. Each entry represents a cover class (see text). (A) the lowland zone, (B) the lower montane zone, (C) the upper montane zone, and (D) the subalpine zone. Species running numbers are given by the author for data processing. *Eugenia* (=*Syzygium sensu stricto*).

```
          A     B    C    D
         ____  ____  __  ____
   A     6811  1112  22  2333
   l     0002  4680  36  8024
   t     0000  0000  50  0000
  (m)      00  0000  00  0000
                               Species name (Running no.)
Lowland (1a)
         452-  ----  --  ----  Shorea leprosula (585)
         423-  ----  --  ----  Lithocarpus hallieri (716)
         33--  ----  --  ----  Shorea parvistipulata (587)
         33--  ----  --  ----  Shorea laevis (583)
         21--  ----  --  ----  Palaquium rostratum (568)
         21-1  ----  --  ----  Eugenia elliptilimba (887)
         113-  ----  --  ----  Nephelium lappaceum (685)
         11-1  ----  --  ----  Aporusa acuminatissima (641)
         111-  ----  --  ----  Castanopsis sp. (727)
         111-  ----  --  ----  Fordia coriacea (686)
         12--  ----  --  ----  Xanthophyllum affine (610)
         111-  ----  --  ----  Artocarpus sp. (559)
         12-1  ----  --  ----  Gonystylus consanguineus (735)
         12-1  ----  --  ----  Eugenia sp. (533)
         1-11  ----  --  ----  Chisocheton sp. (823)
         111-  ----  --  ----  Dysoxylum rugulosum (811)
         111-  ----  --  ----  Timonius flavescens (833)
         11-1  ----  --  ----  Actinodaphne sp. (869)
         12--  ----  --  ----  Dacryodes costata (846)
         111-  ----  --  ----  Xanthophyllum griffithii (612)
         1111  ----  --  ----  Aglaia sp. (825)
         11-1  ----  --  ----  Knema cinerea (625)
         -2-1  ----  --  ----  Canarium littorale (844)
         --4-  ----  --  ----  Durio cf. graveolens (494)
         --31  ----  --  ----  Calophyllum teysmannii (512)
         --21  ----  --  ----  Eugenia cf. acuminatissima (894)
         --21  ----  --  ----  Lithocarpus cf. cantleyanus (708)
         --21  ----  --  ----  Helicia fusco-tomentosa (569)
         --12  ----  --  ----  Vatica dulitensis (614)
         ---4  ----  --  ----  Madhuca glabrescens (777)
```

Table 2.5. -continued.

Lowland (1b)

111-	-1--	--	----	Albizia sp. (542)
1112	1---	--	----	Eugenia cf. festigiata (889)
1--1	1---	--	----	Drypetes microphylla (616)
1111	1---	--	----	Myristica iners (622)
1-11	1---	--	----	Chionanthus cf. cuspidata (680)
1111	1---	--	----	Castanopsis clemensii (724)
1-11	1---	--	----	Ternstroemia cf. magnifica (658)
11--	-1--	--	----	Garcinia caudiculata (779)
1-22	-11-	--	----	Tetractomia tetrandra (351)
-112	1---	--	----	Eugenia filiformis (888)
-111	1---	--	----	Eugenia sp. (886)
--11	1---	--	----	Eugenia sp. (430)
--11	1---	--	----	Pternandra coerulescens (529)
--13	11--	---	---	Tristania obovata (770)
--11	1---	--	----	Garcinia sp. (749)
---2	1---	--	----	Dissochaeta sp. (531)

Lowland & lower montane (I)

11--	-11-	--	----	Litsea castanea (870)
1-11	2---	--	----	Eugenia cf. valdevenosa (901)
1-1-	---2	--	----	Cinnamomum griffithii (407)

Lower montane (2b)

11-4	45--	--	----	Palaquium gutta (570)
--11	211-	--	----	Eugenia cf. confertum (896)
--1-	1--1	--	----	Lithocarpus lampadarius (705)
--11	1111	--	----	Eugenia sp. (903)
---2	1--2	--	----	Litsea sp. (854)

Lower montane (2a)

---2	2212	--	----	Adinandra clemensiae (654)
---1	1111	--	----	Schima wallichii (653)
---1	3-34	--	----	Lithocarpus cf. elegans (710)
---1	11-1	--	----	LAURACEAE sp. (546)
---1	11-1	--	----	Elaeocarpus cf. fulvo-tomentosus (595)
----	51--	--	----	Lithocarpus ewyckii (702)
----	21--	--	----	Lithocarpus cf. confragosus (707)
----	11-1	--	----	LAURACEAE sp. (853)
----	124-	--	----	Calophyllum garcinioides (511)
----	112-	--	----	Horsfieldia glabra (620)
----	11-1	--	----	Dacrycarpus imbricatus (483)
----	1121	--	----	Garcinia coriacea (522)
----	112-	--	----	Eugenia subdecussata (257)
----	133-	--	----	Eugenia cf. subdecussata (963)
----	1111	--	----	Prunus arborea (366)
----	111-	--	----	Neolitsea sp. (856)
----	-123	--	----	Ternstroemia cf. coriacea (659)
----	-112	--	----	Madhuca endertii (492)
----	-114	--	----	Eugenia sp. (431)
----	---4	--	----	Eugenia valdevenosa (902)

Table 2.5. -continued.

```
       Montane (II)
             ---1 ---1 1- ---- Litsea sp. (860)
             --11 1113 53 ---- Magnolia carsonii (354)
             ---1 1-1- 11 ---1 Rapanea affinis (58)
             ---- --11 3- ---- Horsfieldia sp. (832)
             ---- -11- 31 ---- Elaeocarpus sp. (347)

       Upper montane (3)
             ---- -1-- 4- ---- Ascarina philippinensis (509)
             ---- ---- 35 ---- Eugenia punctilimba (287)
             ---- ---- 13 ---- Olea rubrovenia (66)
             ---- ---- 14 ---- Ilex zygophylla (5)

       Montane & subalpine (III)
             ---- 1351 13 4135 Phyllocladus hypophyllus (913)

       Upper montane & subalpine (IV)
             ---1 ---- 12 5--- Lithocarpus havilandii (280)
             ---- --1- -1 --11 Microtropis wallichiana (50)
             ---- ---- 12 -2-- Polyosma sp. (205)
             ---- ---- 1- --4- Prunus mirabilis (151)
             ---- ---- 1- 12-- Eugenia houttuynii (26)
             ---- ---- -1 213- Symplocos pendula (2)

       Subalpine (4)
             ---- ---- -- 4553 Dacrycarpus kinabaluensis (962)
             ---- ---- -- 3122 Leptospermum recurvum (252)
             ---- ---- -- 34-- Eugenia kinabaluensis (256)
             ---- ---- -- 3443 Schima brevifolia (147)
             ---- ---- -- 32-- Myrica javanica (536)
             ---- ---- -- 23-- Polyosma hookeri (3)
             ---- ---- -- 11-3 Symplocos buxifolia (18)
             ---- ---- -- -22- Daphniphyllum glaucescens (337)
             ---- ---- -- --35 Eugenia ampullaria (22)
             ---- ---- -- --14 Rhododendron buxifolium (338)

Level 1      0000 0000 11 1111
Level 2      0000 1111 00 1111
```

Table 2.6. Layer structure at the study plots along the transect on Mt. Kinabalu. Height (H) and coverage (C) of each layer are shown: E, emergent trees; T1, first tree layer; T2 second tree layer; T3, third tree layer; S, shrub layer; and Hb, herb layer.

Altitude	Hb		S		T3		T2		T1		E	
(m)	H m	(C%)	H m	(C%)	H m	(C%)	H m	(C%)	H m	(C%)	H m	(C%)
600	0.5	(5)	2	(20)	6	(20)	15	(70)	30	(60)	50	(30)
800	0.5	(40)	3	(20)	7	(25)	15	(60)	25	(70)	45	(60)
1000	0.5	(5)	2.5	(20)	7	(30)	15	(70)	30	(60)	40	(40)
1200	0.5	(20)	2	(60)	7	(20)	17	(40)	30	(70)		
1400	0.5	(20)	2	(30)	6	(40)	15	(80)	25	(20)		
1600	0.5	(30)	2	(40)	6	(30)	20	(70)	30	(50)		
1800	0.5	(20)	2	(30)	5	(25)	15	(70)	25	(60)		
2000	1	(25)	2.5	(30)	8	(80)	20	(70)	30	(30)		
2350	1	(80)	3	(25)			10	(10)	20	(70)		
2600	1.5	(95)	4	(10)			10	(5)	20	(60)		
2800	1	(70)	3	(30)			10	(90)				
3000	1	(40)	4	(25)			10	(80)				
3200	1	(40)	2.5	(30)			15	(75)				
3400	0.5	(20)	2	(20)			6	(100)				

Table 2.7. Tentative edaphic zones on Mt. Kinabalu (this study) in comparison to those in Malaya and on Mt. Kinabalu described by Burnham (1974). Nomenclature follows the system of the United States Department of Agriculture (U.S.D.A.).

Altitude (m)	U.S.D.A. soil group or order	
250- 500 Malaya	Typic haplorthox	by Burnham (1974)
1050 and 1310 Malaya	Typic haplohumox	
1430 Malaya	Typic humitropept	
1615-2030 Malaya	Histic placaquod (steep slopes) Troposaprist (gentle slopes)	
3000-3200 Mt. Kinabalu	Lithic humitropept	
600-800 (1000)	Oxisols	Mt. Kinabalu: this study
1200-2600	Histosol/Spodosol complex	
2800-3400	Inceptisols	

Table 2.8. Comparison of soil chemical properties from montane zones of Mt. Kinabalu (this study), Jamaica (mor ridge forest, Tanner 1977), Costa Rica (Volcan Barva, Marrs *et al.* 1988), New Guinea (Edward & Grubb 1982) and Hawaii (organic bogs, Balakrishnan & Mueller-Dombois 1983): soil acidity pH; contents (oven-dry weight basis) of organic carbon (o-C), total nitrogen (t-N), exchangeable cations, and extractable phosphorus (P); cation exchange capacity (CEC); C/N ratio and Ca/Mg ratio; and nitrogen turnover indicated by nitrate production (ppm 14 day) on oven-dry weight basis.

Site		o-C	t-N	C/N	Exchangeable cations (m-equiv. 100·g^{-1})					Ca/Mg	P	Nitrate
(Alt. m)	pH	(%)	(%)		Ca	Mg	K	Na	CEC		(ppm)	ppm 14day
Kinabalu# (1200-2600)	3.9	35.1	1.6	22.8	0.6	2.7	1.3	0.4	86.7	0.2	19.6	n.a.
Jamaica (1600)	3.0	47.4	1.6	30.0	2.6	10.2	1.0	0.9	185	0.3	n.a.	35*
Costa Rica (2600)	4.5	25.8	1.9	14.5	9.2	4.9	1.2	0.3	n.a.	1.9	55.0	3**
New Guinea Site I (2480)	5.7 -6.2	12.6 -20.0	1.3 -1.5	9.5 -13.4	8.0 -25.7	2.2 -7.1	0.6 -1.1	0.5 -0.6	61	3.7	6.9 -39.2	n.a.
Site V (*c.*2500)	6.4 -6.5	10.9 -18.9	1.1 -1.6	9.8 -11.9	12.1 -40.6	4.7 -13.7	1.1 -1.8	0.5 -0.6	64	2.9	6.4 -37.0	n.a
Hawaii R.17 (1190)	4.8	37	2.0	18.8							69	3.5***
R.2 (1160)	5.1	32	2.2	14.7							26	19.6***

geometric means of six samples, sample at 2000 m excluded

* laboratory incubation at 26-29°C

** field incubation

*** laboratory incubation at 17°C

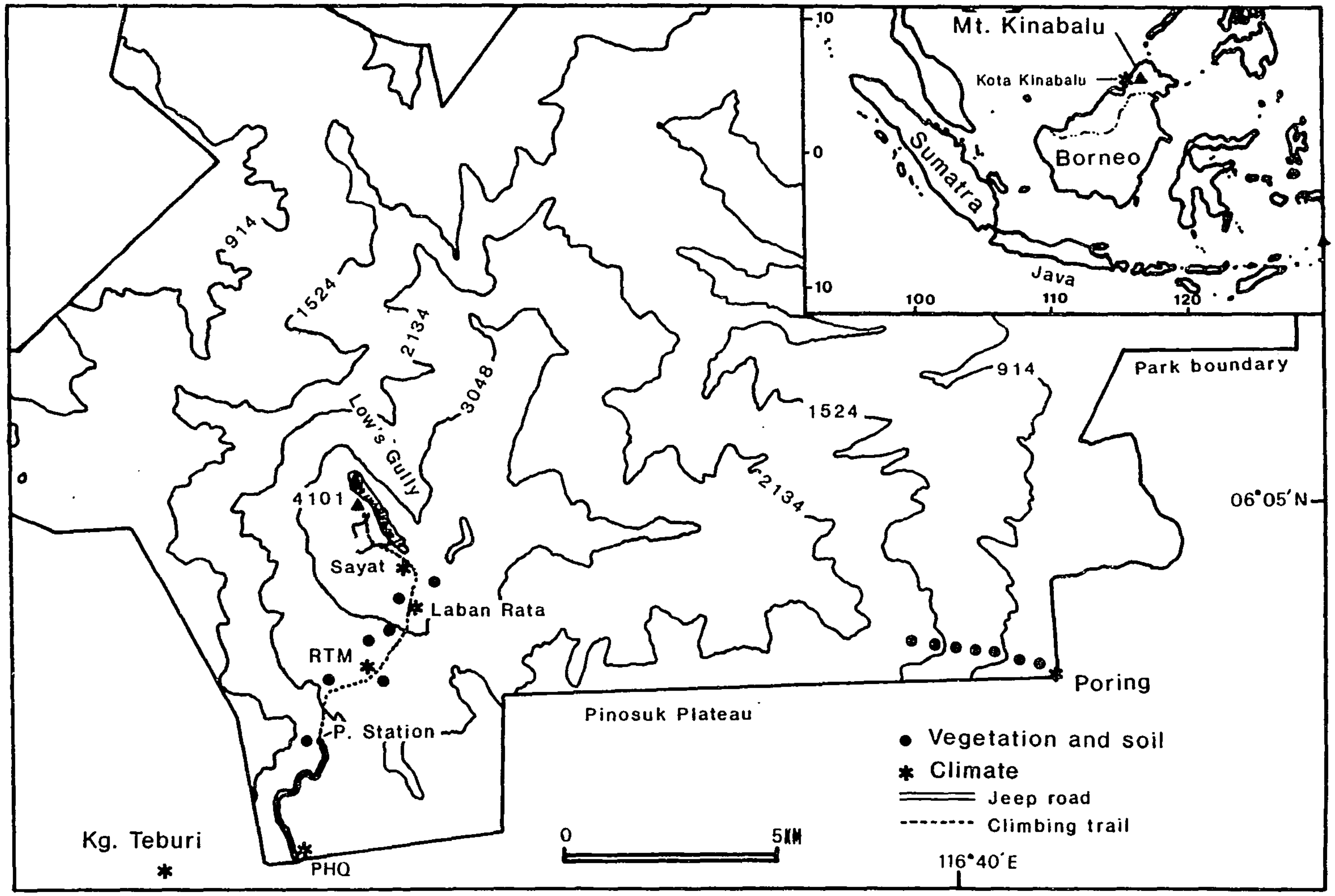

Fig. 2.1. Map showing topography of Mt. Kinabalu, and location of transect segments and climate stations.

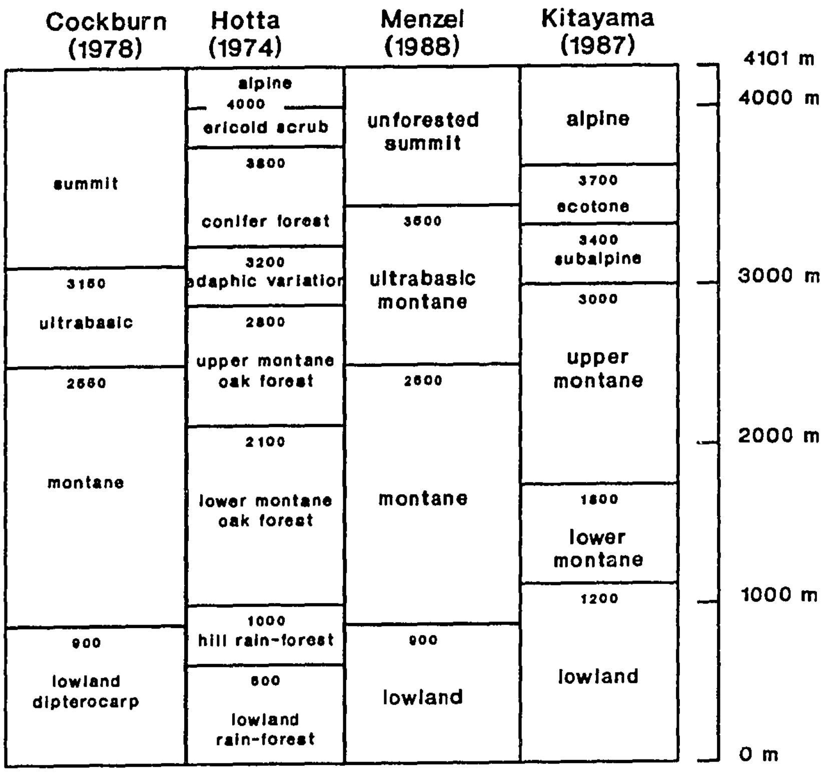

Fig. 2.2. Comparison of vegetation-zonation schemes described by previous authors on Mt. Kinabalu.

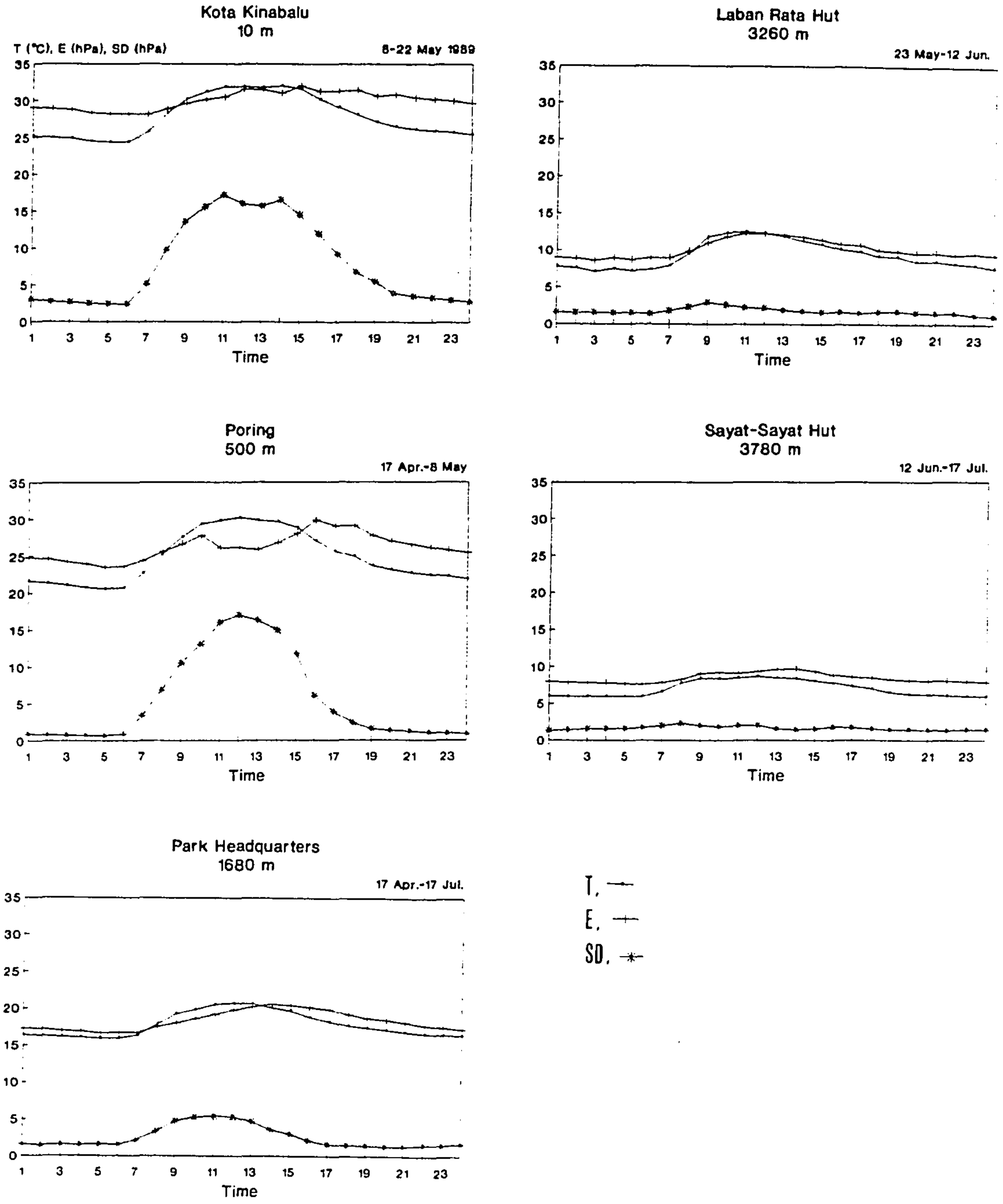

Fig. 2.3. Hourly changes of mean air temp. (T ,°C), actual vapor pressure (E , hPa) and saturation deficit (SD, hPa) at five stations along the transect.

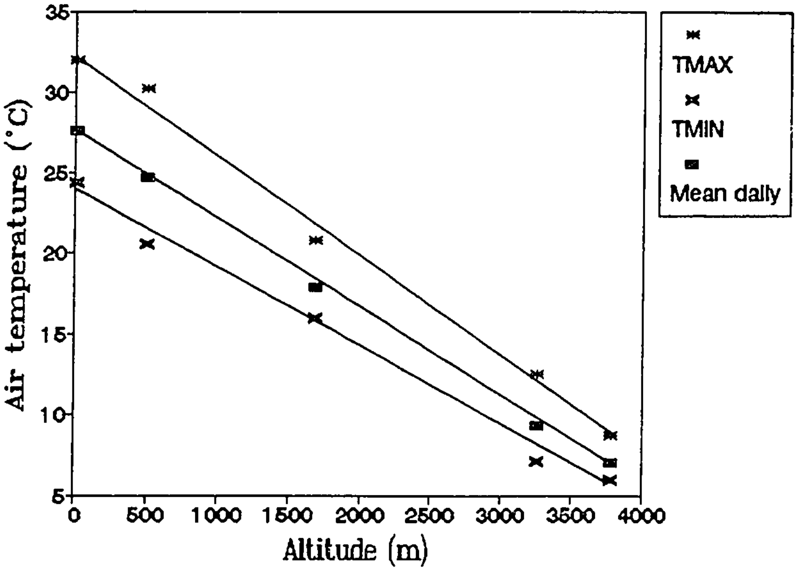

Fig. 2.4. Altitudinal air temp. (°C) reduction on Mt. Kinabalu. Mean daily max. temp. (TMAX), mean daily min. temp. (TMIN), and mean daily temperature.

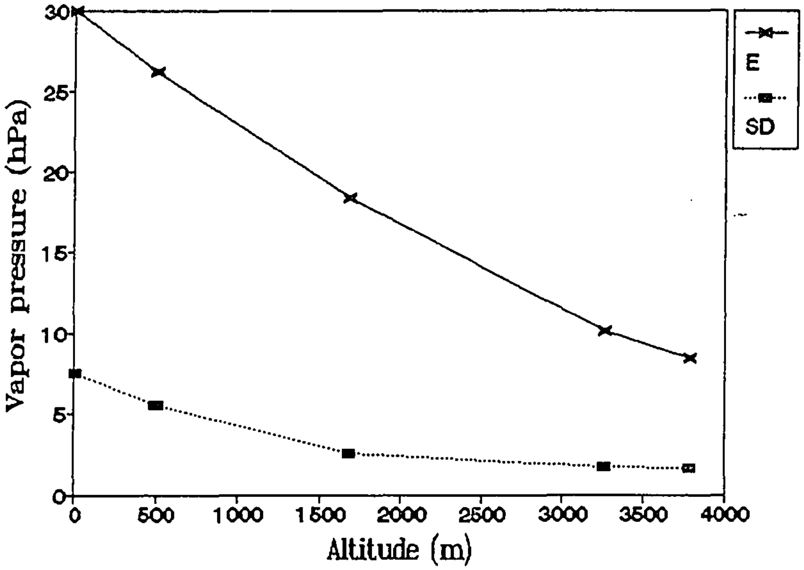

Fig. 2.5. Altitudinal reduction of vapor pressures (hPa) on Mt. Kinabalu. Actual vapor pressure (E) and saturation deficit (SD).

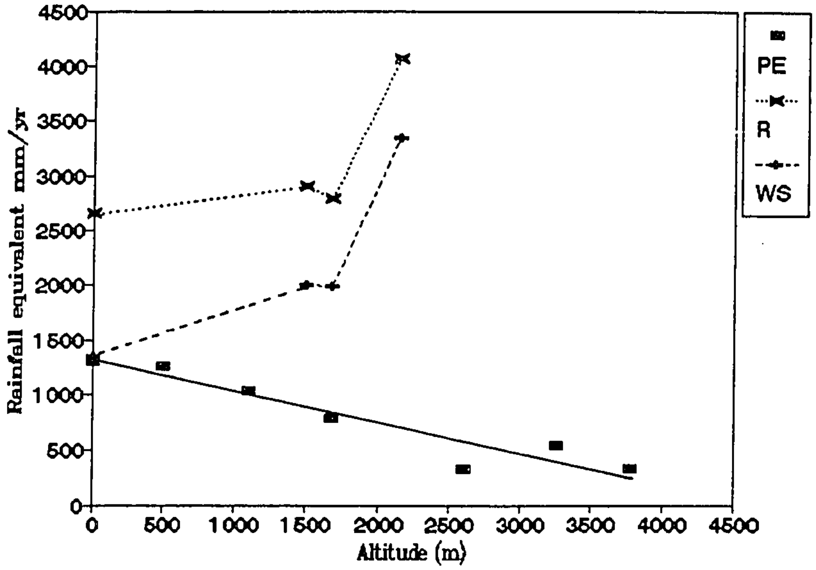

Fig. 2.6. Estimated water budgets (mm·yr^{-1}) on Mt. Kinabalu. Water surplus (WS) is obtained from mean annual rainfall (R) subtracted by the estimated potential pan-evaporation (PE).

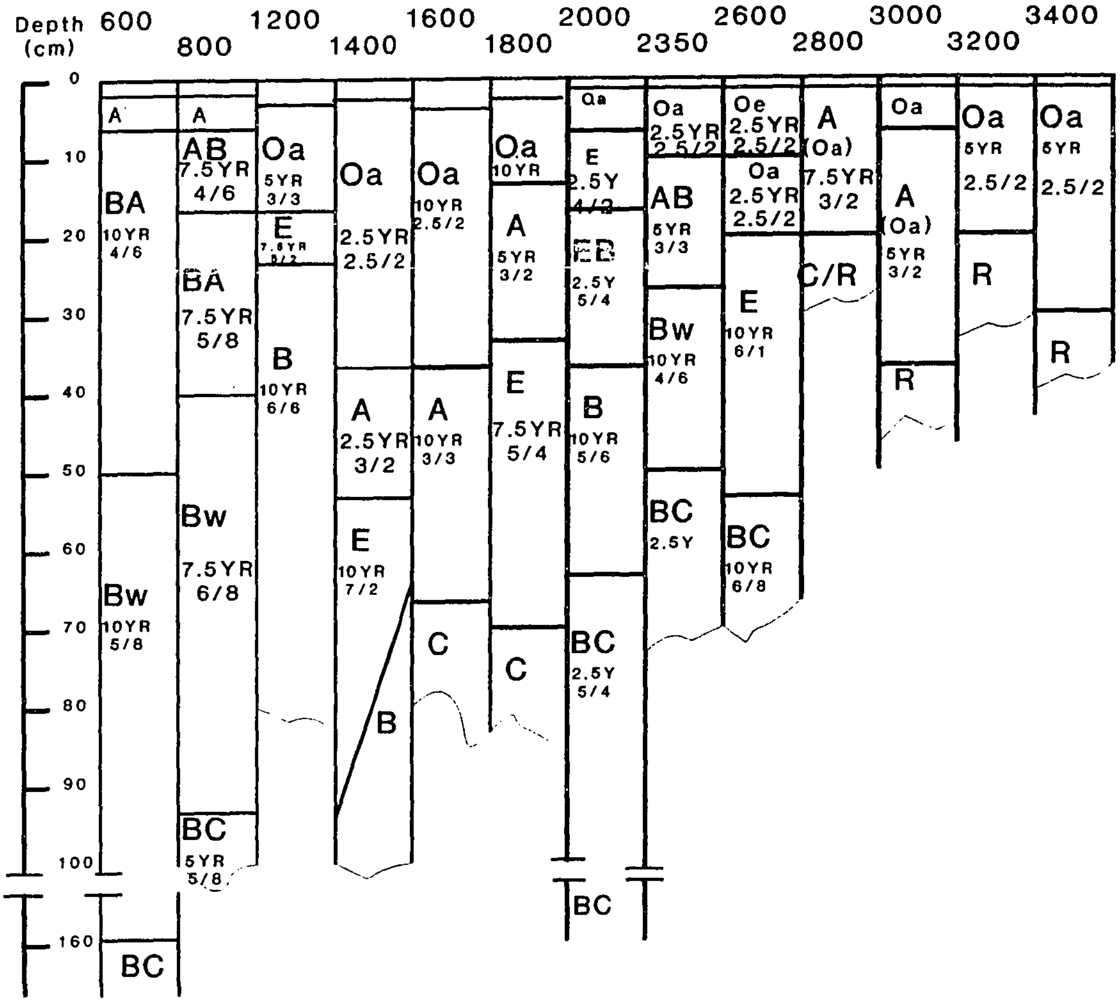

Fig. 2.7. Altitudinal sequence of soil profiles along the transect on Mt. Kinabalu. Horizons and soil colors indicated by codes of S.M.S.S. (1986) and of Munsel color charts, respectively.

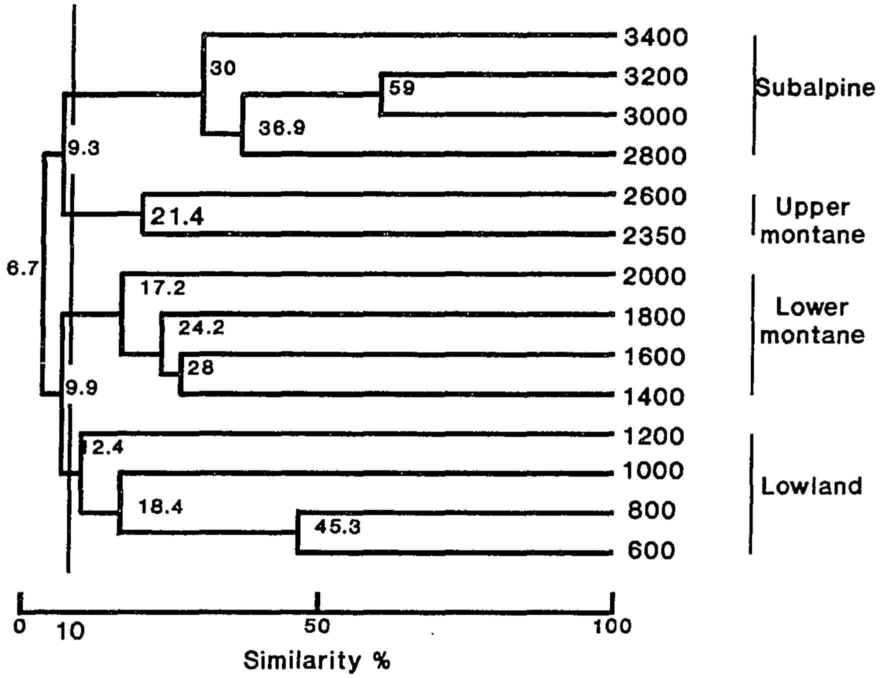

Fig. 2.8. Dendrogram showing relationships among 14 samples (sites) collected along the transect on Mt. Kinabalu. Four clusters are recognizable at 10% threshold.

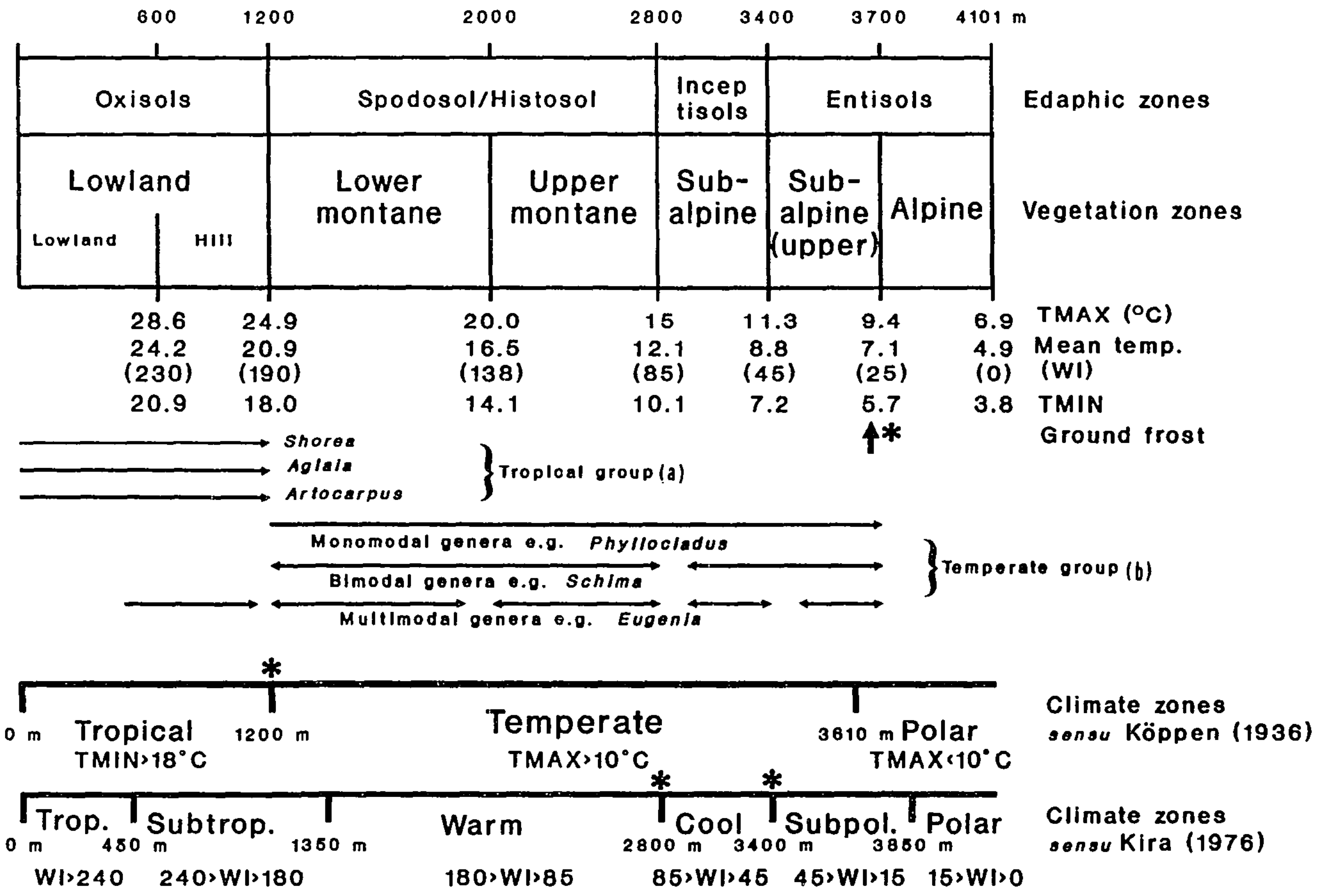

Fig. 2.9. Altitudinal vegetation zones differentiated in this study, and empirical latitudinal lowland climate systems applied to the slopes of Mt. Kinabalu. Significant correlations between boundaries and thresholds are indicated by (✱). The ground-frost line is indicated by (↑).

CHAPTER 3. VEGETATION OF THE WET WINDWARD SLOPE OF MT. HALEAKALĀ, MAUI, HAWAII

ABSTRACT

The plant community organization along a transect between 350 m and the summit (3055 m) on the wet windward slope of Haleakalā was studied. The plant communities classified by Braun-Blanquet's synthesis table technique showed a strong hierarchical arrangement, and were correlated with altitude. At the top of the hierarchy, the rain forest and the treeless high-altitude vegetation were differentiated by two major species groups. At the next level, the two wide-ranging types were subdivided into three vegetation units, corresponding to the lowland, montane, and high altitude zones. The three units were further partitioned into seven plant communities which indicated six altitudinal subzones and one dieback belt. The rain forest is dominated by a single endemic tree species, <u>Metrosideros polymorpha</u>, with one broad-ranging and three zonally discrete morpho-varieties. DBH and height of this species increased upslope to the closed-forest line. Climate analysis suggested that there were three altitudinal disjunctions where thermal/moisture factors abruptly changed: relatively persistent lower and upper cloud limits, and winter ground-frost line. They coincided with the upper limits of the lowland, montane, and subalpine zones, respectively. Soil profiles and chemical properties showed evidence of strong water-logging in the lowland, improving drainage on the mid-slope, and a xeric regime above the inversion. The availability of some soil nutrients increased upslope. These soil changes appeared to be responsible for the increase in DBH and height of the dominant tree species upslope.

Keywords: Altitudinal climate, Classification, Soil-water regime, Transect, Vegetation zones.

Abbreviations: DBH=diameter at breast height, PAR=Photosynthetically active radiation

Nomenclature: Flowering-plant names follow Manual of the Flowering Plants of Hawaii by Wagner et al. (1990). Pteridophyte names follow an unpublished checklist by Wagner & Wagner (Revised Checklist of Hawaiian Pteridophytes 1987).

INTRODUCTION

The Hawaiian Islands, biogeographically the world's most isolated archipelago, have a highly endemic flora (of 956 flowering plant species 89% are endemic, Wagner *et al.* 1990). The extreme isolation acted as a sieve allowing only a limited number of species to cross the ocean and become established. As a result, the flora is disharmonic (Hubbell 1968). For instance, species with large disseminules are not very common in the native inland forests in Hawaii. The flora is also depauperate, and the number of potential canopy species is low (Mueller-Dombois 1987).

These two features related to extreme isolation, i.e. taxonomic disharmony and relative biotic impoverishment, resulted in widespread monodominance of the native rain forests by *Metrosideros polymorpha* (Mueller-Dombois 1981a); a myrtaceous tree species with capsular fruits with very small wind-dispersed seeds. The species dominates the wetter Hawaiian habitats (Mueller-Dombois 1987).

The monodominance over multiple habitats has been considered the result of reduced species competition (Mueller-Dombois 1981b). The implication is that other component species may also have as wide distributional amplitudes as *Metrosideros*. If so, distributional patterns of plant communities on the Hawaiian high mountains should be substantially different from those on continental high mountains where species competition is presumably higher.

This chapter presents results from an altitudinal transect analysis on one of the three Hawaiian high mountains, Haleakalā on the island of Maui. The following questions guide this study: 1) Does a depauperate flora become organized into altitudinally definable communities? 2) If definable, are such altitudinal communities broader and fewer in number than in floristically richer areas? 3) How are the plant distribution patterns related to the altitudinal environmental gradient?

STUDY AREA

Haleakalā is a shield shaped volcano of early Pleistocene origin (0.8 million years) and now quiescent. It is the third highest mountain in Hawaii (after Mauna Kea 4205 m and Mauna Loa 4169 m). The summit (3055 m), located at 20°45'N and 156°15'W, has a huge caldera-like structure (12 km long, 4 km wide) with cinder cones on its floor and exposed pyroclastic materials on the outer walls. The northeast slope is covered with recent (late Pleistocene) volcanic rocks of the Kula volcanic series. There are also still younger (Holocene) rocks from the Hana volcanic series. The study area is located on the Kula volcanic series. The parent rock is largely from alkalic basalt (Stearns 1985).

The topography consists of a very gently rising slope below 700 m, and a somewhat steeper slope above. The slope is dissected by numerous streams running parallel to one another downslope. The lateral dissections become steeper and wider near the coast, where they form deeply sliced V-shaped valleys.

The study area is a belt transect. It starts at 350 m near Kailua and extends upward on the interfluves of either side of Waikamoi Stream to the summit (Fig. 3.1). The projected horizontal length of the transect is 17 km, while it rises 2700 m from the low end.

The belt transect traverses three protected areas: a watershed forest (350-1600 m) managed by the East Maui Irrigation Company, the Waikamoi Preserve (1600-2100 m) of The Nature Conservancy Hawaii, and the summit area (2100-3055 m) in Haleakalā National Park. Currently, the vegetation is relatively well protected. The summit area has been severely influenced by feral ungulates, particularly by goats (Stone 1985). But control efforts have suppressed their activity. Feral pigs are the current major disturbance factor in the wetter forests (Stone 1985). The vegetation below 350 m has largely been converted to plantation forests.

Widespread forest dieback was noted in the lower segment of the transect and adjacent areas early in this century by Lyon (1909). Holt (1988) reassessed the same area. The vegetation of the summit crater was mapped by Whiteaker (1983).

Climate

There are great climatic changes over short distances associated with three factors: the altitudinal reduction of air temperature, the mid-slope increase in cloudiness, and the occurrence of the trade wind inversion. The climate at the low end of the transect may be classified as Af in Köppen's system, and is warm-tropical and perhumid year-round. The summit climate, which may be classified as Cs in Köppen's system, is cool-tropical with a dry summer season.

The mean annual air temperature at the Kailua meteorological station (213 m) is 21.5°C (Fig. 3.2). The mean monthly temperature is 22.9°C in the warmest month (August), and 20.1°C in the coldest month (February). Thus the thermal regime is equable year-round with only a small annual change (2.8°C). This indicates a maritime climate regime. By contrast, its diurnal fluctuation is nearly 10° C. Mean air temperature decreases upslope probably in accordance with the lapse rate of 0.55°C per 100 m, the rate estimated on Mauna Loa of the neighboring island of Hawaii by Blumenstock (1961). Actual temperature reduction diverges from the estimated lapse at altitudes where the trade wind inversion occurs. This inversion layer oscillates frequently betweeen 1800 and 2400 m a.s.l. (Mendonca & Iwaoka 1969; Noguchi et al. 1987), as will be shown later. At the summit (3055 m), the monthly mean air temperature is c. 6°C in the coldest month, and slightly exceeds 10°C in the warmest month.

The moisture regime of the northeast slope is largely controlled by the trade winds and the trade wind inversion (Lyons 1979). The orographic uplift of the trade winds results in high rainfall below the inversion. Rainfall rapidly increases upslope from 4000 mm at 350 m a.s.l., reaching a maximum mean annual amount of 6500 mm at c. 1000 m a.s.l. (Giambelluca et al. 1986, Fig. 3.2). A dry area occurs above the inversion because clouds are prevented from moving upwards by the inversion; the mean annual rainfall at 2000 m a.s.l. is 2000 mm and becomes less than 1000 mm at the summit (3055 m). In the mid-slope area, fog may add a substantial amount of precipitation to the annual rainfall (Juvik & Ekern 1978). The monthly rainfall pattern shows a maximum value (>600 mm month) in March-April, and a minimum (c. 350 mm month) twice per year in June and in September-October (nearby West Honomanu station at 900 m a.s.l., Giambelluca et al. 1986).

Soil

The soils of the study area were mapped in a reconnaissance survey by the Soil Conservation Service, USDA (1972). The dominant map units below 1900 m a.s.l. are the Honomanu-Amalu association and the Amalu peaty silty clay, while that above 1900 m is very stony land. The Honomanu-Amalu association occurs below 850 m a.s.l. but also occurs between 1500 and 1900 m a.s.l. The Amalu peaty silty clay occurs on the midslope between 850 and 1500 m a.s.l.

The Honomanu-Amalu association is composed of the Honomanu soil (about 60%), a Hydrudand, and the Amalu soil (about 40%), a Placaquept. The former is situated on better-drained slopes and the later on less sloping and poorly drained ridge tops and interfluves.

A recent soil survey along the transect by Ikawa et al. (1991) suggests the occurrence of Histic Tropaquepts at 600 and 1000 m a.s.l., Acrudoxic Hydrudands at 1400 and 1800 m a.s.l., and Pachic Haplustand at 2200 m a.s.l.

METHODS

The transect method was employed to analyze altitudinal changes of vegetation, soil and climate following the manual written by van der Hammen et al. (1989). Analytical methods and sampling design for each parameter follow.

Vegetation

Two sampling techniques were involved in vegetation analysis: the relevé and the count-plot methods (Mueller-Dombois & Ellenberg 1974). The former was used for classifying plant communities along the transect, while the latter for investigating structural changes of forest communities.

The belt transect was stratified into even altitudinal intervals of 100 m to locate sample plots (i.e. relevés). In each interval, relevé analyses were performed in several stands of 20x20 m by a system of stratified sampling. One relevé was sampled in the most developed stand on a gentle slope, and several additional relevés under various canopy conditions ranging from widely opened to closed. In these relevés, species composition, species cover using the Braun-Blanquet cover-abundance scale, layer structure, and physical environments were recorded. The quadrat size of 20x20 m was chosen to allow direct comparisons to other Hawaiian rain forest studies done with the same quadrat size. This size exceeded the minimal area. Some low-growing stands were sampled with 10x10 m quadrats, which also satisfied the minimal area requirement.

One relevé within the most structurally developed stand was selected at 450 and 1900 m and every 200 m in altitude between 600 and 2000 m a.s.l. for the forest structural analysis. Trees (≥5 m height) of the dominant canopy species, Metrosideros, were measured for height and DBH in the same quadrats as the relevé analysis (20x20 m). DBH and height of saplings (2≤ height <5 m) were measured in four belts of 3x20 m, which were systematically placed in each of the quadrats. Because they were widely scattered at these elevations, trees and saplings at 450 and 2000 m were investigated using 50x50 m quadrats

Soil

A soil profile was examined and described in each of the count-plot quadrats, i.e. at 200 m altitudinal intervals. Designation of master horizons was according to the procedure described by the Soil Management Support Services, USDA (1986). Soil color, pH, texture, structure, presence of mottling, plant root distribution and other noticeable properties were then recorded. Soil colors were determined using Munsell Color Charts. The acidity, pH, was measured in the laboratory on a mixture of fresh soil with deionized water (1:1 dilution).

Five soil profiles were selected for further laboratory chemical and physical analyses at intervals of 400 m between 600 and 2200 m a.s.l. These soils were judged to best represent an altitudinal sequence of edaphic properties despite the wide altitudinal intervals.

An adequate amount of soil was collected from each horizon. An additional pH measurement was made with 1:1 N potassium chloride dilution. Organic carbon was determined by the modified Walkley-Black wet digestion method (Heanes 1984). Total nitrogen was determined by the micro Kjeldahl procedure after digestion with concentrated sulfuric acid and measurement of ammonia by the indophenol blue method on an autoanalyzer. The exchangeable calcium, magnesium and potassium were extracted with N ammonium acetate (pH 7.0) and analyzed by atomic absorption spectroscopy. Aluminum was extracted with N potassium chloride and analyzed by the catechol violet method (Dougan & Wilson 1974). Phosphorus was extracted with the modified Truog solution, made up of 0.02 N H_2SO_4 and $(NH_4)_2SO_4$ acidified to pH 2.04 (Ayers & Hagihara 1952) and analyzed by the molybdenum blue method on an autoanalyzer.

Bulk density was determined by means of a core sampler. Soil minerals were identified by X-ray diffraction analysis of the powdered soil samples using copper radiation; identification of mineral species was based on Brindley & Grown (1980).

The chemical analysis, except for soil acidity, was performed by the Agricultural Diagnostic Service Center, University of Hawaii at Manoa. The X-ray diffraction analysis was made by H. Ikawa at the Department of Agronomy and Soil Science of the same University. The other analyses were performed by the author.

Climate

Climate analysis consisted of two sets of measurements: long-term and short-term. The short-term measurement investigated altitudinally changing air temperature and vapor pressures during summer, the season when atmospheric dryness becomes highly contrasting between high/low and mid altitudes. The long-term measurement included other climate parameters and focused on month-to-month variations at selected altitudes. In total, five climate stations were established at 450, 950, 1300, 1900 and 2400 m a.s.l., ranging from the lowland to the subalpine environments (Fig. 3.1). These sites were selected by noting the availability of open deforested or shrubby land along the transect.

The long-term monitoring was done at the altitudes of 1300 and 1900 m (representing a cloud-laden belt and a belt where the trade wind inversion presumably frequently occurs), and at 2400 m (an arid subalpine belt). Each of the stations consisted of a CR-21 micrologger system (Campbell Scientific Inc.), which supported five to six sensors connected to a data logger kept inside a raintight shelter. Measured climatic parameters included air temperature and relative humidity (Campbell 201 Thermistor &

RH probe), global radiation (LI-COR pyranometer), PAR (photosynthetically active radiation) (LI-COR quantum sensor), and wind speed and direction (Met One wind speed and direction sensors). Reading was instantaneous, but successively reduced to means or totals over two intervals: 30 min and 24 h. Data were continuously recorded by a portable cassette tape recorder left inside the shelter, and regularly retrieved by visiting the sites. The measurements were begun in January 1990, and were continued for more than one year.

The seasonality of relative drought was estimated based on the monthly rainfall minus the monthly potential evapotranspiration at the three altitudes. Monthly median rainfall values from nearby climate stations (data source Giambelluca et al. 1986) were used in the computation. The monthly evapotranspiration values were estimated using the fundamental energy-budget equation:

$$Rn = S + H + LE$$

where Rn=net radiation, S=soil heat flux, H=atmospheric heat flux, LE=latent heat of vaporization. Here, S and H were neglected for a first approximation following the suggestion by Thornthwaite & Mather (1955 -cited in Mather 1974). Net radiation was approximated from the actually measured global radiation multiplied by the factor of 0.67 (Ekern 1965). The same factor was applied to all altitudes. This may be justified by the counterbalance effects between outgoing longwave radiation and albedo: outgoing longwave radiation increases with altitude, while albedo probably decreases upslope due to reducing rain forest cover (Noguchi _et_ _al_. 1987).

The short term observation was conducted at all five altitudes. The climate stations at 450, 950 and 2400 m each consisted of a hygrothermograph and an atmometer. At 1300 and 1900 m, each station consisted of a CR-21 and an atmometer. Because it was not possible for the investigator to visit all stations on the same day, four atmometers were placed alternately during different periods at the five stations (see Table 3.1 for duration). Each of the atmometers (Ekern Atmometer) consisted of a plastic reservoir with an evaporating surface made from a porous grinding stone (152.4 mm diameter), and a clear plastic cover 10 cm above the stone surface (Ekern 1983). They were placed directly on the ground. Reading of water loss was undertaken weekly. One of the atmometers was continuously monitored at 1300 m for ten weeks, and served as a standard. Weekly evaporation often overran the capacity of the atmometer at some stations, and the water level in the reservoir became lower than the undersurface of the stone. Calibration on the overrun evaporation values was made later based on a correlation between the values from an overrun atmometer and the mean values from three adequately monitored atmometers placed at the same site (r^2=0.95, n=13).

The hygrothermographs, sheltered in hand-made screens set 1.5 m above the ground, were used for investigating air temperature and relative humidity. Saturation vapor pressures were calculated from the hourly air temperatures using the polynomial equation by Lowe (1976). Further, saturation deficits were computed from the saturation vapor pressures and the relative humidity values. This short-term observation was done from June to August 1988.

In addition, seven max-min mercury thermometers were left at these stations and additionally at 1800 and 2000 m for six days (13-19 June 1988) to detect the trade wind inversion. After termination of the monitoring, readings of the thermometers were compared with those of a properly calibrated Tele-Thermometer (Yellow Springs Instrument) under various temperatures in a water bath. Calibration was based on the linear regressions (r^2=0.99 for all max-min thermometers, n=6) obtained from the comparison.

Monthly altitudes where the lowest ground-frost line is expected on the windward slope was deduced based on the difference in daily minimum temperatures between Haleakalā Ranger Station (2140 m) and Summit Station (3035 m) (data source NOAA 1973, 1974). The summit station often showed higher temperatures than at Haleakalā Ranger Station evidently due to the occurrence of the trade wind inversion above Haleakalā Ranger Station. Such higher values were excluded from this analysis. Noguchi _et_ _al_. (1987) suggested the temperature difference of 3-4°C between the screen and the ground surface. Assuming a linear temperature reduction between the two stations, monthly temperature lapse rates were calculated based on the daily minimum-temperature differences. Subsequently, using the lapse rates obtained, the monthly altitudes where air temperatures become 4 and 3°C at the screen level were estimated ($p=0.05$). In this procedure, Haleakalā Ranger Station was considered as reference point using its monthly means of daily minimum temperatures during 1980-91 (data source NOAA 1980-91).

RESULTS

Altitudinal climatic changes

The trade wind inversion

After calibration, air temperature maxima and minima during 13-19 June 1988 were plotted along the altitudinal gradient (Fig. 3.3). Mean daily wind speed during this period at 1300 m ranged from 2.14 to 4.04 $m \cdot s^{-1}$. The values indicate that the mountain slope received slightly weaker trade winds than an average summer condition (cf. 4.1 $m \cdot s^{-1}$ at 700 mb level during summer, given by Lyons 1979).

The maxima show a distinct temperature inversion with a sharp increase of 4-5°C between 1800 and 2000 m, indicating the presence of the trade wind inversion. The altitude of c. 1900 m, where the inversion has been recorded, agrees closely with the average inversion level in the free atmosphere of Hawaii (Mendonca & Iwaoka 1969). The inversion is, however, said to fluctuate synoptically along the slope resulting in substantial temporal weather changes (Lyons 1979; Noguchi *et al*. 1987).

Estimation of ground-frost line

The ground-frost line appears below the summit during winter (Fig. 3.4). 4°C-reduction estimates the lowest winter ground frost line at c. 2400 m. The line appears at c. 2700 m when 3°C-reduction is applied. Noguchi *et al*. (1987) estimated the occurrence of ground frost to be 187 days per year at the summit assuming 4°C difference between the screen-level and the ground-level temperatures, and 121 days for 3°C difference. The results of this study agree closely with their estimate.

Altitudinal changes of measured evaporation

The measured evaporation (Fig. 3.5) demonstrates an altitudinally asymmetric atmospheric drying power. Here, the station at 1300 m was considered as the standard point. The altitudinal evaporation change is expressed by the ratio of mean daily water loss at each station to that at 1300 m during the same measurement period.

The depicted pattern clearly indicates the presence and saturation effects of mid-slope clouds. The ratio of the measured evaporation to the standard (1300 m) is 1.81 at 450 m and 2.42 at 2400 m. Atmospheric aridity is markedly higher in the high altitude environment than in the lowland during the summer.

It is not known whether the potential evaporation changes abruptly at a certain altitude, because the stations were so widely separated. Nevertheless, as suggested by Lyons (1979), the upper cloud limit corresponds to the inversion frequently in the morning, but ascends later in the afternoon driven by the convective force. Therefore, the altitude of _c._ 1900 m may be a turnover point in atmospheric moisture, above which the moisture fluctuates daily, and the cumulative effects of moisture decreases gradually with altitude.

The low limit of near-saturated atmosphere corresponds to the lifting condensation level, and is dependent on the moisture and temperature of the orographically ascending air mass. In field observations, the low limit frequently appeared at _c._ 900 m. Therefore, the depicted pattern seems to well represent a typical altitudinal change in the cumulative potential evapotranspiration during summer.

Hourly fluctuation in atmospheric moisture

Fig. 3.6 depicts hourly changes in measured saturation deficit during 26-31 July 1988. Mean daily wind speed during this period at 1300 m ranged from 3.38 to 4.09 $m \cdot s^{-1}$. Wind direction at the same altitude changed generally from ENE during the day to SE-ESE during the night. These values suggest that wind speed was a near-average of summer weather, and that the wind flow became anabatic during day and katabatic during night due to the mountain effect as demonstrated by Lyons (1979). Thus, this period can represent a typical summer day with diurnal moisture changes in association with the anabatic and katabatic cloud pattern on the windward slope.

The hourly values of saturation deficit repeat distinct diurnal cycles at 450 and 950 m, i.e. modes always appear at midday. The hourly pattern at 1300 m suggests a near-saturated atmosphere throughout day. By contrast, those at 1900 and 2400 m show irregular and great diurnal changes probably due to the combined effects of the synoptic-scale oscillation of the trade wind inversion and of the local-scale convective uplift of cloud. The altitudinal change of the mean deficit values during 26-31 July 1988 (6.9 hPa at 2400 m, 4.2 hPa at 1900 m, 1.2-1.3 hPa at 950 and 1300 m, and 2.7 hPa at 450 m) corresponds well to the altitudinal change of measured evaporation (Fig. 3.5). The absolute maximum of 20 hPa at 2400 m is slightly lower than that of

25 hPa which was measured at 2000 m on the same slope during spring 1988 by Leuschner & Schulte (1991).

Seasonal relative drought

The results of the computation based on limited information indicate the midslope station at 1300 m is perhumid year-round (Fig. 3.7). The inversion station at 1900 m shows a short-term relative drought in May-July. By contrast, the relative drought at the high altitude station (2400 m) is prolonged (April-November), and severe in magnitude.

Monthly changes in photosynthetically active radiation (PAR)

All three stations show a summer maximum and a winter minimum in the 1990 PAR (μ Einstein$\cdot m^{-1} \cdot s^{-1}$) (Fig. 3.8). A sharp increase in January-February 1991 at all stations is believed to be rather atypical. PAR values are almost identical between 1900 and 2400 m throughout the year. Mean daily PAR values in winter are slightly lower at 1300 m than those at the two higher altitudes. However, the difference in PAR between 1300 and the two higher altitudes sharply increases during summer. The midslope reduction in PAR is a reflection of the suppressed radiation incidence due to cloud cover.

Altitudinal soil changes

Soil profiles

The soil-water regime is highly contrasting between the profiles below 1900 m and those above (Fig. 3.9). In general, the soils below 1900 m are wet and histic. Such histic soils characteristically have gleyed horizons with an overlay of thick mors (5-30 cm); these soils are highly acidic with pH values between 3 and 4 in the top horizons. By contrast, the soils above 1900 m are drier, and soil acidity becomes weaker with pH values >5.

The most strongly reduced horizon (gray in color) is found throughout the lowland below 1000 m. The reducing condition is particularly prominent on flat interfluves at 450 and 600 m. Roots are restricted to surface organic horizons. The gleys at 450 and 600 m are probably related to the gently sloping topography which prevents rain water from lateral drainage, and in turn aggravates the anaerobic condition.

The profile at 450 m shows a placic horizon of iron hardpan beneath the B horizon. The hardpan is thin, wavy and discontinuous, but it may effectively lower percolation of water. It is also notable that the organic horizon is nearly absent from this profile. Here, the reduced horizon is found directly below live mosses and a very thin Oi horizon; consequently, tree roots are restricted to the upper few centimeters.

The montane soils between 1200 and 1800 m are characterized by moderately gleyed horizons still indicating water-logging. The reducing condition does not seem as strong as those in the lowland soils. However, plant roots are effectively absent or rare in these gleyed horizons. Organic materials are highly decomposed to the extent that fibers are hardly visible unlike the lowland soils. These thick peaty organic horizons (Oa) are typical for the montane zone. Some profiles at relatively better drained sites in the montane zone show clearly eluviated horizons, e.g. E horizon at 1400 m (dark grayish brown in color), suggesting strong leaching and lower water tables whose levels may fluctuate only below the eluviated horizon. Concave montane slopes are completely saturated.

Soils gradually become better drained toward the inversion where thin gley horizons are still recognizable (1800 m). At 1900 m evidence of water-logging is not found any more. Here, friable crumb structure is observed in mineral horizons unlike the saturated profiles at lower altitudes.

The soils above 2000 m are less developed, exhibit diffused boundaries, and are devoid of thick organic horizons. The dominating soil texture is sandy clay loam to sandy loam between 2000 m and 2700 m. Darker colored horizons alternately appear on each of the profiles at 2200 and 2400 m, and indicate several buried horizons.

The land above 2700 m is stony, and soil texture becomes predominantly sandy. The soils can be placed in the order of Entisols. They lack pedogenic horizons and incorporated organic matters may be low.

Bulk density and clay minerals

The bulk density of mineral horizons is consistently low, ranging from 0.25 to 0.80 $g \cdot ml^{-1}$ (Table 3.2). The only exception to this is the Bg horizon (1.01 $g \cdot ml^{-1}$) at 1000 m. The low values suggest that the mineral horizons have been derived largely from volcanic ash deposition (Ikawa *et al*. 1991) throughout the transect.

Results of the X-ray diffraction (Table 3.2) indicate an altitudinal disjunction in soil mineral composition at 1800 m. Quantification of mineral species was based on the total intensity. Except for the materials amorphous to X-ray, the most abundant soil mineral below 1800 m is quartz and above 1800 m magnetite. The horizons at 1800 m are transitional and both quartz and magnetite occur. The quartz materials are believed to be eolian, originated from the Asiatic continent, and sedimented by rain droplets (Jackson *et al*. 1971). Thus, the abundance of quartz suggests a prolonged and stable pluvial environment below 1800 m. This elevation parallels closely with the altitude where a trade wind inversion was demonstrated earlier (Fig. 3.3).

Chemical and physical properties

Several altitudinal changes in the chemical properties (Table 3.3) are related to the soil-water regime which becomes drier upslope.

The organic carbon content in the surface horizons is extremely high (>40%) below 1800 m and becomes less than 10% at 2200 m. At this altitude (2200 m), organic carbon increases toward the bottom horizon, unlike other profiles at lower altitudes, suggesting more than one deposition of volcanic ash.

The content of total nitrogen is correlated with organic carbon. It is high (2.16%-2.48%) in the organic horizons below 1800 m and becomes low (0.82%) in the surface soil at 2200 m. The C/N ratio in the surface horizon decreases upslope and indicates increasing rates of N-mineralization and nitrification.

Below 1800 m, the exchangeable calcium and magnesium are high in the Oe horizons (respectively, 1.46-15.56 m-equiv. and 1.38-16.1 m-equiv.) but decrease considerably in the mineral horizons. By contrast, calcium and magnesium are consistently high in every horizon at 2200 m (≥10.97 m-equiv and ≥1.42 m-equiv., respectively). The content of exchangeable potassium in the top horizon decreases with increasing altitude. The content of extractable phosphorus is high (≥32 ppm) in every horizon at 2200 m.

Extractable aluminum is extremely high in some gleyed horizons below 1800 m indicating strong acidification. A value ≥15 m-equiv. is found at 600 m and 1400 m. It becomes almost negligible at 2200 m.

The Ca/Mg ratio, an index of leaching in exchangeable cations (Askew 1964), increases with altitude ranging from 0.63 (600 m) and 0.11 (1000 m) to 7.73 (2200 m) in the top horizon. This suggests that the effects of leaching decrease upslope.

Altitudinal vegetation changes

Classification

Using a total of 111 relevés comprising 189 taxa, the vegetation along the transect was hierarchically classified by the Braun-Blanquet synthesis table technique (Mueller-Dombois and Ellenberg 1974). However, the designation of abstract communities into a hierarchical ranking was not attempted. What follows is a local classification along the transect.

The criterion of fidelity (Braun-Blanquet 1965) was applied for selecting diagnostic species. Selected species have constancy values relevant to fidelity degrees 4 and 5. The plant communities classified have not been compared floristically with similar vegetation types found from other Hawaiian islands. Therefore, the nomenclature for the diagnostic species in the following description does not connote the traditional terms: groups of differential species may contain both character and differential species.

At the first level, two vegetation types contrasting in physiognomy (forest versus treeless vegetation) are differentiated by mutually exclusive species. This results in two major differential species groups. At the second level, the forest vegetation is subdivided into two units, while the treeless vegetation remains one unit. At the third level, these three units are further partitioned into seven plant communities: one of these is split into two subunits, yielding a total of eight units (noda). The subunit is a floristic variation of a community, and is diagnosed by a group of species which are absent only in other subunits of the same community. The classified plant communities are named by their leading species. They are shown in the summarized differential table with constancy values (Table 3.4, see inside back cover).

The floristically classified vegetation units are well correlated with altitude (Fig. 3.10). The three broader units are identified by three species groups, the Elaphoglossum crassifolium group, the Vaccinium calycinum group and the Dubautia menziesii group. These correspond to three broad ecological zones, respectively the lowland, the montane, and the high altitude zone. The seven plant communities in the lower hierarchy are defined by seven species groups with more restricted amplitudes, which indicate finer zonal arrangements of vegetation within the broader altitudinal zones.

Most alien species (indicated with ** in Table 3.4) are sporadic in distribution, and remain unclassified. However, several alien species appear preferentially in certain zones, have high constancy values, and are assembled in associations.

Description of altitudinal floristic zones

I. Forest Vegetation

Forest vegetation extends over the lower two-thirds of the slope (from 350 to 1950 m). The forest line (1950 m) coincides with the level where the trade wind inversion appears most frequently.

Fourteen endemic taxa (Metrosideros polymorpha v. glaberrima, Cheirodendron trigynum, Vaccinium dentatum, Myrsine lessertiana, Broussaisia arguta, Athyrium microphyllum, Astelia menziesiana, Carex alligata, Polypodium pellucidum, Hedyotis terminalis, Athyrium sandwichianum, Sadleria pallida, Myrsine sandwicensis and Smilax sandwicensis), five indigenous species (Elaphoglossum hirtum, Ilex anomala, Pleopeltis thunbergiana, Asplenium lobulatum and A. polyodon), and one alien species (Rubus *argutus*) are associated with each other. They differentiate the forest vegetation from the treeless vegetation. These species have extremely broad altitudinal distributions spanning either the entire or most of the forested zone. Of the 20 differential species, only *M. polymorpha* v. *glaberrima* (a glabrous leaved variety of *M. polymorpha*), *I. anomala* and *C. trigynum* are potential canopy trees, and the rest of the species are understory components. Therefore, in this forest vegetation even the undergrowth taxa in lower layers or those with lower cover values have broad altitudinal distributions.

The tree cover is dominated in its entire range, by a single species *M. polymorpha*, in spite of various habitat types encountered within the forest range. *C. trigynum* is persistent in the canopy but low in cover. Trees of *Metrosideros* commonly, except at the upper limit of closed forest, show gnarled tree forms which may indicate oligotrophy (Grubb 1977). Most of the trees are perched on fallen logs or on mounds of peats underlain by water-logged soils. Saplings and seedlings of *Metrosideros* are common in canopy gaps, but they are scarce under closed canopies.

Effects of exotic plants are evident in the lower forest zone as seen in other parts of Hawaii (Vitousek *et al*. 1987). The mid and upper segments are almost purely native.

The forest vegetation is floristically partitioned into two units: A) *Elaphoglossum crassifolium* unit and B) *Vaccinium calycinum* unit.

A. *Elaphoglossum crassifolium* unit (lowland zone)

The *Elaphoglossum crassifolium* unit occurs below 1000 m corresponding to the lowland zone. Four endemic species (*E. crassifolium*, *Adenophorus hymenophylloides*, *Antidesma platyphyllum* and *Tetraplasandra oahuensis*), four indigenous species (*Psilotum complanatum*, *P. nudum*, *Huperzia phyllanthum* and *Nephrolepis cordifolia*), and four alien species (*Paspalum conjugatum*, *Cyperus halpan*, *Rubus rosifolius* and *Setaria palmifolia*) are associated with each other, and differentiate this unit.

The following two types are distinguished in this unit: A1) *M. polymorpha* v. *glaberrima*-*Odontosoria chinensis* community, and A2) *M. polymorpha* v. *glaberrima*- *Adenophorus pinnatifidus* community.

A1) *M. polymorpha* v. *glaberrima*-*Odontosoria chinensis* community (lowland dieback belt, stunted open-canopy evergreen scrub)

The *M. polymorpha* v. *glaberrima*-*Odontosoria chinensis* community, differentiated by two indigenous species (*O. chinensis* and *Machaerina mariscoides*) and six alien species (*Andropogon virginicus*, *Psidium cattleianum*, *Centella* *asiatica*, *Sacciolepis indica*, *Tibouchina herbacea* and *Clidemia hirta*), occurs between 450 and 600 m.

The canopy is stunted (4-6 m) in height and open (10-40%) in cover; the understory is dense (100% cover). The stunted *Metrosideros* trees are of vegetatively low vigor with dead or defoliated branches. Their roots are restricted to a few cm of surface soils, or directly abut on the soil surface covered with mosses. Such trees are typically stilted by aerial roots. These trees show reproductive vigor by producing abundant flowers. However, regeneration is only sporadic, probably due to the paucity of such substrates as fallen logs, on which seedlings can establish themselves, as stated also by Holt (1988). *Dicranopteris linearis* and *A. virginicus* dominate the ground. Weeds are abundant both in cover and species number. In the differential species group, *A. virginicus*, *P. cattleianum* and *C. hirta* are listed among the twelve worst weeds in Hawaii by Smith (1990).

The community lies entirely in the dieback area, initially described by Lyon (1909), and more recently by Holt (1983, 1988). Dieback is widespread on the lowland flat interfluve along the transect. This stunted plant community is underlain by saturated soils. There is a possibility that the stand reduction due to dieback in turn further aggravates soil water-logging (Mueller-Dombois 1988). A similar process in a more recent stand-reduction dieback on Mauna Kea with soil degradation was termed bog formation dieback by Mueller-Dombois et al. (1977) and Mueller-Dombois (1980).

A2) M. polymorpha v. glaberrima-Adenophorus pinnatifidus community (intact lowland zone, partially open to closed canopy evergreen rain forest)

The M. polymorpha v. glaberrima-Adenophorus pinnatifidus community is differentiated by six endemic species (Adenophorus pinnatifidus, Psychotria mariniana, Peperomia obovatilimba, P. hirtipetiola, Syzygium sandwicensis and Labordia hedyosmifolia) and two indigenous species (Freycinetia arborea and Diplopterygium pinnatum). Most stands of this community occur between 600 and 1000 m with the exception of a few stands on lower ridge crests at 350 m, where lateral drainage is better than the surrounding flat interfluves. The lower ridge crests support the better preserved forest fragments in the dieback territory.

The vegetation is low to tall (7-12 m) and widely open to closed (30-80% in the canopy cover). The shrub layer is 5 m tall, sparse to dense (30-80% cover), and dominated by Dicranopteris linearis, Cibotium chamissoi and C. glaucum. The herb layer is 1 m tall, sparse to dense (20-100% cover), and dominated by the same species as those of the shrub layer on imperfectly drained soils or by Paspalum conjugatum, Cyperus halpan and Juncus planifolius on saturated soils. Trees become progressively mossy, and epiphytic ferns become abundant toward the upper altitudinal limit.

B. Vaccinium calycinum unit (montane zone)

The Vaccinium calycinum unit is distributed in the middle segment of the slope between 1200 and 1950 m., corresponding to the montane zone. Eight endemic species (V. calycinum, Elaphoglossum wawrae, Coprosma ochracea, Rubus hawaiiensis, Dryopteris subbipinnata, D. glabra, Ctenitis rubiginosa and Adenophorus tripinnatifidus) and two indigenous species (Dryopteris wallichiana and Uncinia uncinata) differentiate this unit.

Three plant communities are distinguished in this unit: B1) M. polymorpha v. glaberrima-Nertera granadensis community, B2) M. polymorpha v. glaberrima-Pelea clusiifolia community, and B3) M. polymorpha v. glaberrima-Sadleria cyatheoides community. These three communities correspond to the lower montane zone (B1), the upper montane zone (B2) and the forest line (B3), respectively.

B1) M. polymorpha v. glaberrima-Nertera granadensis community (lower montane zone, closed canopy evergreen moss forest)

The M. polymorpha v. glaberrima-Nertera granadensis community, differentiated by 11 endemic taxa (M. polymorpha

v. *incana*, *Peperomia expallescens*, *P. macraeana*, *Xiphopteris saffordii*, *Labordia venosa*, *Cyrtandra hashimotoi*, *Adenophorus montanus*, *Psychotria hawaiiensis*, *Cyrtandra platyphylla*, *Thelypteris sandwicensis* and *Dryopteris acutidens*) and three indigenous species (*Nertera granadensis*, *Grammitis hookeri* and *Korthalsella complanata*), occurs between 1200 and 1700 m. Clouds persistently envelope this altitudinal zone. Consequently, epiphytic mosses and ferns grow abundantly in all strata, forming mossy forests. *Metrosideros polymorpha* v. *incana* (a pubescent variety of *M. polymorpha*) intermixes with *M. polymorpha* v. *glaberrima* with various cover degrees in the canopy. Both varieties are sclerophyllous.

The canopy is tall (10-15 m) and closed or partially open. The shrub layer (3-5 m tall) is generally dense (50 to 80% cover); there is no single-dominant shrub species, however *Vaccinium dentatum*, *V. calycinum*, *Broussaisia arguta* and the forb *Astelia menziesiana* are abundant. The herb layer is dense (near 90% in cover) and dominated by *Carex alligata* on saturated soils. It becomes sparser (less than 70%) and more mixed with other herbaceous species on somewhat better drained soils. Epiphytic ferns (*Elaphoglossum hirtum*, *E. wawrae*, *Mecodium recurvum*, *Sphaerocionium lanceolatum*), terrestrial ferns (*Dryopteris* and *Asplenium*) and *Peperomia* are abundant among low-growing shrub species in the herb layer. Invasion by alien weeds is rarely seen in most stands. However, along the flume, where the forests were cleared and regulary visited by man, alien graminoids such as Juncus planifolius are abundant.

Canopy dieback is locally evident in this montane zone where soils are saturated, however dieback stands are not distinguishable floristically from intact stands in the differential table. In such stands, fallen trees are often piled up on forest floors, or buried without much decay. These fallen logs serve as substrates for seedlings to establish themselves in the otherwise saturated and anaerobic condition.

B2) M. polymorpha v. glaberrima-Pelea clusiifolia community (upper montane zone, closed canopy evergreen rain forest)

The M. polymorpha v. glaberrima-Pelea clusiifolia community, differentiated by three endemic species (P. clusiifolia, Asplenium normale and Peperomia membranacea), occurs between 1750 and 1950 m. This community marks the upper limit of closed forest beyond which forest canopies become open. The mosses no longer prevail, and epiphytic mosses are largely replaced by lichens, suggesting intermittent drying out. The canopy layer is tall (15 m) and closed. Acacia koa becomes codominant near the upper limit of the community range (1900 m). The canopy trees are ground-rooted, unlike those at lower elevation. The shrub layer is sparse (5% over); Coprosma ochracea, Vaccinium calycinum and P. clusiifolia are frequently encountered. The herb layer is dense (100% cover), predominated by Athyrium sandwichianum interspersed with other terrestrial ferns such as Dryopteris, Asplenium and Ctenitis. The dense fern layer and the occurrence of ground-rooted trees are related to the well-drained soils. Invasion by weeds into the community is rarely seen.

B3) M. polymorpha v. glaberrima-Sadleria cyatheoides community (forest line, ecotone community between the upper montane forest and the subalpine scrub)

The M. polymorpha v. glaberrima-Sadleria cyatheoides community occurs in the forest line between 1900 and 1950 m. The differential species group includes four endemic taxa: Sadleria cyatheoides, M. polymorpha v. polymorpha, Oreobolus furcatus and Polystichum bonseyi. The forest structure consists of a low (5-8 m tall) and partially to widely open canopy layer (5-60% cover), and a dense herb layer (70-100% cover). Metrosideros polymorpha v. polymorpha (a tomentose leaved variety of M. polymorpha) intermixes with M. polymorpha v. glaberrima in the canopy at the lower limit of the community, but forms pure stands at the upper limit. Acacia koa is another canopy tree species which locally becomes abundant. The herb layer is dominated by either Dryopteris wallichiana or S. cyatheoides, with two alien grass species (Anthoxanthum odoratum and Holcus lanatus) as codominants. The community can be considered an ecotone between the closed upper montane forest and the subalpine scrub. Several subalpine elements such as Vaccinium reticulatum, Coprosma ernodeoides and Deschampsia nubigena consistently occur in the community.

II. Treeless Vegetation

C. Dubautia menziesii unit (high altitude zone)

Sparse vegetation characterizes the landscape above 1950 m. Mutually exclusive with the forest vegetation, a single endemic species differentiates the Dubautia menziesii unit which entirely lies in the subalpine and alpine treeless vegetation.

Tall trees are absent from this vegetation type. The only exception are widely scattered M. polymorpha v. polymorpha trees, which range from the forest line to the tree line at 2200 m.

This unit contains the following two plant communities which are physiognomically and floristicaly distinct: C1) Sophora chrysophylla community, and C2) Tetramolopium humile community.

C1) Sophora chrysophylla community (subalpine zone, tropical subalpine scrub)

The Sophora chrysophylla community, differentiated by three endemic shrubs (S. chrysophylla, Coprosma montana and

Geranium cuneatum ssp. tridens) and one endemic sedge (Carex wahuensis), occurs between 1950 and 2700 m. The canopy shrub layer is low (1.5-3 m in height) and widely open (5-50% cover). The herb layer is relatively dense (40-90% cover). The differential shrub species and Styphelia tameiameiae prevail in the shrub layer. In the herb layer, endemic species (Coprosma ernodeoides, Deschampsia nubigena, Vaccinium reticulatum and Luzula hawaiiensis) and alien species (Hypochoeris radicata, Anthoxanthum odoratum and Holcus lanatus) are prevalent. The community shows some xeromorphic adaptations to the arid environment as reflected in sclero-microphylly.

The community is further subdivided into two subunits: C1a) Prunella vulgaris subunit and C1b) Trisetum glomeratum subunit. The P. vulgaris subunit is differentiated by Prunella vulgaris, Epilobium billardierianum ssp. cinereum and Coprosma ernodeoides. These species occur in the lower segment of the subalpine zone (1950-2400 m). The T. glomeratum subunit is differentiated by Trisetum glomeratum, Rumex acetosella, Pellaea ternifolia, Asplenium adiantum-nigrum, A. trichomanes and Dodonaea viscosa, occurring at higher elevation (2300-2700 m), and marking the shrub line.

C2) Tetramolopium humile community (alpine zone, tropical alpine desert)

The Tetramolopium humile community, differentiated by two endemic species (T. humile ssp. haleakalae and Argyroxiphium sandwicensis ssp. macrocephalum), occurs above 2700 m. The substrates are pyroclastic ashes and rocks. The community is very sparse with less than 5% cover, low (< 1 m in height except when Argyroxiphium flowers) and rather barren in physiognomy. Argyroxiphium sandwicensis ssp. macrocephalum (silversword) is a monocarpic giant rosette of the Compositae, a characteristic life form of tropical alpine zones elsewhere, e.g. in the Afroalpine zones and Andean mountains. The other constituents include the native species of Dubautia menziesii, Trisetum glomeratum, Asplenium adiantum-nigrum, A. trichomanes, Styphelia tameiameiae, and Deschampsia nubigena, and one alien species Hypochoeris radicata.

Structural changes in the forest vegetation

Fig. 3.11 depicts altitudinal changes in the DBH/height relationships of Metrosideros polymorpha ≥2 m height sampled in each of the count-plot quadrat (20x20 m). All varieties of the species are included in the analysis. Because saplings <5 m height were measured in four of 3x20 m belts per quadrat (240 m^2 total), one dot <5 m height in Fig. 3.11 is equivalent to 1.7 (=400/240) individuals.

Maxima of height and DBH of Metrosideros increase with altitude between 450 and 1200 m. Above 1200 m, DBH increases upslope to the elevation of 1800 m, while maximum tree heights remain relatively similar. The stand at 1900 m shows a slight decline in the maximum height and DBH as compared to those at 1800 m. Above the tree line, Metrosideros trees abruptly decline in size.

Metrosideros canopy trees at 1900 m are overgrown by Acacia koa which is not included in the analysis. Thus the biomass of canopy trees at 1900 m is greater than the indicated in Fig. 3.11.

Most canopy trees are relatively even-sized in DBH below 1200 m, whereas above 1400 m they consist of a wide range of DBH classes, e.g. c. 20 to 70 cm DBH at 1800 m.

Species Richness along the Transect

The numbers of species in the communities are shown in Table 3.5. The total number of species per community ranges from 14 in the alpine desert (unit C2 in Table 3.4) to 103 species in the lower montane forest (B1). The mean species number per stand ranges from 7.3 species (4-10) in the alpine desert to 43.5 species (31-55) in the lower montane forest.

The lower montane forest is relatively more diverse in flora than the lowland intact forest (A2). The lowland dieback community (A1) has a lowered species richness (21 species per stand), comparable to that of the forest line community (B3, 23.2 species per stand).

Quantitative relationships between the classified communities

Fig. 3.12 depicts community relationships among the eight classified units in the form of a dendrogram. While the hierarchical ranking shown in Table 3.4 was based on the selection of diagnostic species, the depicted relationships in Fig. 3.12 are based on the species quantities of all constituents in each unit. The calculation of community similarities is based on species constancy values (%) per unit, using Sorensen's similarity index modified for quantitative application:

$$IS=2Mw/(MA+MB)$$

Where Mw=sum of the smaller constancy values of the species common to two communities; MA and MB=sum of the constancy values of all species in each of the two communities.

Overall, the communities share relatively high similarities despite the differences in their environments. The lower subalpine scrub (unit C1a in Table 3.4) and the upper subalpine scrub (C1b) have the highest similarity since they are subunits of the same community. The lowland intact forest (A2) has a higher similarity with the lower montane forest (B1) than with the lowland dieback community (A1), although A1 and A2 are parts of the same unit in the hierarchy (Table 3.4 and Fig. 3.10). This is because the lowland intact forest shares more species with the lower montane forest than with the lowland dieback community. The lowland dieback community has low similarities with any of the intact forest communities (A2,B1,B2 and B3) (joining them at the level of 24.2%), suggesting that canopy dieback in that zone impoverished the species composition.

The similarity between the alpine (C2) and subalpine (C1a and C1b) communities is relatively high despite the low species richness of the alpine community. Several common alien species, spanning both zones, are responsible for this high similarity.

DISCUSSION

Altitudinal vegetation zones

Previous workers (Egler 1939; Krajina 1963; Knapp 1965; Mueller-Dombois & Spatz 1981; and Gagné & Cuddihy 1990) have variously described and characterized altitudinal vegetation zones of the Hawaiian Islands. The results of this strictly floristically defined study show altitudinal zones comparable to those of Knapp, Mueller-Dombois & Spatz, and Gagné & Cuddihy. Moreover, the number of altitudinal zones agrees with those of continental tropical high mountains described by Grubb (1974), who used vegetation structure and physiognomy as the principal classifying criteria.

An important difference to the previous studies is the hierarchical arrangement of vegetation in this study (see Fig. 3.10). Species groups that differentiate lower units in descending order of the hierarchy consist mostly of herb and shrub species (except of Syzygium sandwicensis and M. polymorpha v. incana), while canopy tree species segregate the forest from the non-forest vegetation. Therefore, any finer altitudinal differentiation in the forest vegetation is floristically recognizable only by understory species. This fact contrasts with continental tropical mountains (Whitmore 1975; cf. chapter 2) where zonal differentiation is often evident through changes in canopy species composition.

Altitudinal con-specific/generic segregation

The results show a conspecific segregation of M. polymorpha into zonal varieties (Fig. 3.13). Metrosideros polymorpha is present with three morpho-varieties (Fig. 3.14) along the transect. Variety glaberrima occupies the broadest range; overlapping with this, variety incana is confined to the lower montane zone; variety polymorpha is sharply separated from the first variety, and occurs above the inversion.

Stemmermann (1983) states that the pubescent character is heritable.

Moreover, within the glabrous variety (glaberrima) a large coriaceous leaf variant and a small sclerophyllous leaf variant are discernable (see Fig. 3.14). These morphological leaf variants are respectively confined to the lowland and to the montane zone. The variants may be ecotypic (Corn & Hiesey 1973), and are likely in the process of altitudinal segregation.

The morphological altitudinal segregation is supported by an isozyme analysis on Metrosideros populations along the same transect by Aradhya (1992). He found three genetic entities with three altitudinally clustering populations which coincide with the two leaf variants and the morpho-variety polymorpha. The three genetic entities coincide also with three vegetation units of this study.

In addition to Metrosideros, altitudinal segregation of mutually related taxa is commonly seen also at the specific level. Examples of genera showing such species segregations along the altitudinal gradient include Coprosma, Vaccinium, Asplenium, Peperomia, Adenophorus, Dryopteris and Pelea. Among these, the genera Coprosma, Vaccinium and Asplenium have exceedingly broad ranges, 600-2700 m, 600-2800 m and 600-3000 m a.s.l., respectively. Figure 3.13 depicts altitudinal species distributions of a few representative angiosperm genera. In these genera, constituent species are probably genetically closely related. Morphological resemblance and mutually exclusive distributions in Pelea haleakalae and P. clusiifolia, and in Coprosma pubens, C. ochracea and C. montana, indicate their vicarious or ecotypic relationships.

Congeneric segregation has been reported also from the Mauna Loa transect study (Mueller-Dombois 1981b). The pattern may indicate that individual species of the genera initially widely occurred, being limited only by environmental constraints, and subsequently radiated into related congeneric taxa with narrower amplitudes.

Synthesis

The floristically differentiated vegetation zones are compared with altitudinal climatic and edaphic changes in Fig. 3.15. Abiotic factors form an environmental gradation from low to high elevations. However, some of the factors change abruptly at certain altitudes. These altitudes coincide closely with the differentiated vegetation boundaries where groups of associated species are displaced by other groups.

Climatic factors

There are three climatic turnover points which correspond significantly with vegetation boundaries: 1. the lower cloud limit (i.e. the lifting condensation level) at c. 900-1000 m; 2. the upper cloud limit set by the lower trade wind inversion at c. 1900 m; and, 3. the winter ground-frost line at c. 2700 m. These correspond with the upper limits of vegetation units A, B and C1, respectively.

The persistent midslope cloud cover between c. 1000 m (the lifting condensation level) and c. 1900 m (the trade wind inversion) seems to have profound ecological effects on the vegetation and soils. Within the cloud belt, hourly saturation deficit is always low (Fig. 3.6), and climate is perhumid throughout the year (Fig. 3.7). Under these conditions plants would experience suppressed transpiration, and consequent reduced mass flow which may restrict the uptake of soluble nutrients (Leigh 1975; Ash 1987). Another adverse effect of the cloud cover is the reduction of PAR (Fig. 3.8), which consequently suppresses photosynthetic assimilation.

Conversely, the suppressed transpiration may be advantageous in reducing the uptake of soluble toxic substances (e.g. manganese), which may be taken up rapidly by plants in the atmospherically drier lowland. Further, the persistent year-round saturated condition favors sciophytic and epiphytic plants. Indeed such sciophytic ferns are abundant among the differential species of vegetation units B1 and B2. Here, species richness becomes maximum largely due to the increase of sciophytic pteridophyte species (Table 3.5).

In contrast to the wet montane condition, the lowland (A) and the high altitude environment (C) is atmospherically drier (Fig. 3.5). The former (A) is underlain by saturated soils, but the latter (C) is edaphically also xeric. Furthermore, unit C is subjected to diurnally highly oscillating saturation deficits during summer (Fig. 3.6), and to a long summer drought which alternates with wet winter months (Fig. 3.7). In global vegetation classification, the summer-drought regime typically supports maquis which is microphyllous, sclerophytic, and open-canopied scrub (Walter 1979). The change in vegetation physiognomy at 1900 m (i.e. the closed forest changing into a scleromorphic maquis-like scrub), agrees with the demonstrated change in the atmospheric moisture regime which abruptly becomes xeric with summer drought above 1900 m. Therefore, the closed-forest line is thought to be set primarily by water deficits. This hypothesis agrees with Leuschner & Schulte (1991) who suggest the importance of drought for setting the timberline on Haleakalā.

Sclerophylly and pachyphylly of high altitude environments in the tropics have been considered a mechanism which maximizes CO2 uptake relative to water loss (Grubb 1977). Furthermore, there is evidence that some dryland-adapted species can maintain high turgor pressure by osmotic adjustment (Robichaux & Canfield 1985). It is an important mechanism that maintains high stomatal conductance for photosynthesis in spite of dry atmosphere (Turner & Jones 1980; Robichaux & Canfield 1985).

It is known that there are great differences in the capacity of turgor maintenance among phylogenetically closely related congeners which grow in different moisture-regimes (Canfield 1984; Robichaux *et al*. 1984; Robichaux & Canfield 1985). The congeneric species distributed over diverse moisture-regimes displayed in Fig. 3.13 may have such differential water-potential capacities, resulting in a wide generic ecological amplitude.

When a 3°C-difference is assumed between the screen level and the ground (Fig. 3.4), the estimated winter ground-frost line coincides well with the upper boundary of vegetation unit C1 (=C1b, 2700 m). When a 4°C-difference is assumed, it becomes coincidental with the lower boundary of C1b (*c.* 2400 m). In reality, the ground-frost level may fluctuate between 2700 and 2400 m during the coldest month. Indeed, daily minimum air temperatures below 3°C at the screen level were recorded on five days at 2400 m in January-March 1991. The upper boundary of C1 may be clearcut due to the persistent winter ground-frost. The freeze-thaw activities on the ground may be occasional in the distributional range of C1b, while null or very rare in C1a. Ground-frost is one of the most distinct temperature effects regulating the upper limits of plants on tropical mountains (Sakai & Larcher 1987). On Mauna Loa, the upper boundary of the subalpine zone was found to coincide with the nocturnal ground-frost line by Mueller-Dombois (1967); its altitude (2700 m) agrees with the estimated winter ground-frost line of Haleakalā by 4°C-difference.

Altitudinal temperature reduction must have significant effects on plant physiology. Because of the effects of the oscillating trade wind inversion, the estimation of accurate temperature lapse rate has not been attempted in this study.

Edaphic factors

The observed altitudinal changes in the soil profile and chemical properties are a consequence of altitudinal climatic changes. Effects of the vegetation on soil formation may be of secondary importance because: 1) the parent materials are commonly volcanic ash across the transect (this study, Table 3.2; Ikawa et al. 1991); 2) edaphic changes are correlated with soil water regimes which are largely governed by the topography and mid-slope cloud; and, 3) there is altitudinal differentiation in edaphic chemical and physical properties under the rain forest canopy dominated by the same tree species. The inverse may also be true; edaphic factors probably do not directly control the vegetation zones, but rather influence the growth and morphology of individual plants within each of the vegetation zones which are set by climate.

Although annual rainfall shows a symmetric pattern along the slope with a maximum value at c. 900-1000 m (Fig. 3.2), the most reduced soil seems to be in the lowland (unit A). Downward run-in may add a fair amount of rain water to the water budget in the lowland. There, an almost flat topography prevents rain water from draining laterally. With increasing altitude, the slopes become steeper. The atmospheric drying power is low in the midslope, but gradually becomes greater above. The combined effect of increasing steepness and atmospheric dryness results in gradually improving soil-water drainage upslope to the forest line. Above the line the soil-water regime abruptly becomes xeric. The change of moisture-regime is clearly reflected in soil chemical properties (Table 3.3).

Strong acidification in the mineral horizons at 600 and 1000 m has resulted in extremely low Ca/Al ratios (Table 3.3). These low values suggest direct toxic effects of soluble aluminum on plant roots or indirect effects in impeding nutrient uptake (Balakrishnan & Mueller-Dombois 1983; Huettl 1989).

Factors limiting tree-root penetration in the lowland and lower montane zones are thought to be: 1) direct effects of reduced soil aeration which limits gas exchange in the root zone (Armstrong 1975), and 2) indirect or direct effects of such soil toxins as aqueous solution of Al, Fe and Mn (Armstrong 1975; Huettl 1989). It is not readily known which is most responsible for limiting root penetration. Metrosideros trees and other native canopy trees do not seem to have developed physiological adaptive mechanisms to exclude such toxins. The maintenance of natural Metrosideros populations on the saturated soils appears to be related rather to its ecological adaptations, i.e. perching on fallen logs, aerial roots, and vegetative propagation.

Increasingly better soil drainage upslope is probably responsible for the unusual pattern of tree-size increase with altitude (Fig 3.13). The better drainage upslope increases both the quantity and availability of mineral nutrients. In other parts of the world where soil water-logging is not a major stress factor, inorganic nitrogen and/or available phosphorus are believed to decrease with altitude (Grubb 1977; Tanner 1985; Marrs et al. 1988; Vitousek et al. 1988; Tanner et al. 1990). Unlike these previous studies, C/N ratios in this study suggest increasing nitrogen availability with altitude (Table 3.3). Furthermore, improved soil water-drainage and appearance of dry months at high altitudes probably favor nitrogen-mineralization and nitrification (Marrs et al. 1988; Marrs et al. 1991). The greater DBH increment of Metrosideros trees in the upper montane zone where a short summer relative-drought period occurs (Fig. 3.11) supports this hypothesis.

Species competition

Grubb (1977) suggested that upper limits of species on tropical mountains are set primarily by thermal factors and lower limits by competition. He further suggests that other such adverse effects as soil nutrient deficiencies, waterlogging and reduced light in the cloud zone depress the potential distribution limits.

The question of whether lower limits are set by species competition is intricate. This question can only be resolved by an experimental approach. In this study, Styphelia tameiameiae, which has the most individualistic distribution, seems little affected by species competition. By contrast, the lower limits of heliophytic subalpine species, Coprosma ernodeoides, Sadleria cyatheoides and Vaccinium reticulatum, appears to be controlled by competition with montane trees. The latter three species, being indicators of the dry higher altitudes, are found further downslope in anthropogenically cleared wet areas and naturally along gully walls. The implication is that the physiological amplitudes of these native species are much wider than the realized distributions in community assemblage as displayed in Fig. 3.10.

ACKNOWLEDGEMENTS

I thank Reiko Kitayama and Yutaka Kitayama for their excellent assistance in fieldwork and data analysis. Dr. H. Ikawa assisted in and provided valuable comments on soil analysis, and generously permitted the use of his X-ray diffraction data in this paper. Dr. T. Giambelluca is acknowledged for valuable comments on climate analysis. I am grateful to Dr. D. Mueller-Dombois for his invaluable advice throughout the study. This project was in part supported by a grant from the East-West Center.

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Table 3.1. Duration of evaporation measurement at the five altitude points along the transect in 1988.

Altitude (m)	Period of measurement
450	6 June - 31 July
950	27 June - 15 August
1300	6 June - 15 August
1900	22 July - 18 August
2400	1-18 August

Table 3.2. Bulk density (BD), and mineral species identified by X-ray diffraction analysis.

Hor.	Depth (cm)	BD (g·ml^{-1})	Mineral		
			Dominant	Moderate -small	Small -trace
600 m					
Oi	0- 10				
Oe	10- 18	0.12	O/Amo	Qz	
Oa	18- 24	0.13	O/Amo	Qz	Ha,Il
Ag	24- 39	0.59	Amo	Qz	Ha,Il,Ma
Bg	39- 70	0.80	Amo	Qz	Ha,Il,Ma
1000 m					
Oi	0- 1				
Oe	1- 10	0.10	O/Amo	Qz	
Bg	10- 15	1.01	Amo	Qz	Ha,Il, Ma
Bg	15- 39	0.78	Amo	Qz	Ha,Il
1400 m					
Oe	0- 11	0.14	O/Amo	Qz	
Oa	11- 18	0.14	O/Amo	Qz	
E	18- 30	0.60	Amo	Qz	
Bg	30- 60	0.28	Amo	Qz	Il
Abg	60- 80	0.25	Amo	Qz	Il
CBg	80- 90	0.30	Amo	Qz	Il
1800 m					
Oe	0- 8	0.19	O/Amo	Ma	Qz,Hm
Oa1	8- 19	0.14	O/Amo	Ma	Qz,Hm
Oa2	19- 31	0.18	O/Amo	Ma	Qz,Hm
Ag	31- 37	0.33	Amo	Ma	Qz,Hm
B	37- 67	0.29	Amo	Ma	Qz,Hm
Bb	67->115	0.47	Amo	Ma	Qz,Hm
2200 m					
A	0- 14	0.56	Amo	Ma	Hm,Qz
AB	14- 25	0.33	Amo	Ma	Hm,Qz
Ab	25- 34	0.32	Amo	Ma	Hm,Qz
ABb	34- 55	0.29	Amo	Ma	Hm,Qz

Ha=halloysite, Hm=hematite, Il=ilmenite, Ma=magnetite, O/Amo=organic and/or amorphous materials (include materials of low crystallinity), Qz=quartz

Table 3.3. Chemical properties of selected soil profiles along the transect of Mt. Haleakala, Maui: contents of organic carbon (o-C), total nitrogen (t-N), extractable phosphorus (P) and aluminum (Al), and exchangeable calcium (Ca), magnesium (Mg) and potassium (K); soil acidity (pH); C/N, Ca/Mg, and Ca/Al (mol) ratios.

Hor.	Depth (cm)	pH KCl	pH H2O	o-C (%)	t-N (%)	C/N	Ca	Mg	K	Al	P	Ca/Mg	Ca/Al
							(m-equiv. 100 g^{-1})				(ppm)		(mol)
600 m (HK-42)													
Oi	0- 10												
Oe	10- 18	2.80	3.81	47.2	1.35	35	10.2	16.1	1.5	2.6	26.0	0.6	5.9
Oa	18- 24	3.09	3.81	37.8	2.16	18	2.7	4.6	1.1	1.8	35.0	0.6	2.3
Ag	24- 39	3.11	4.01	7.1	0.24	29	0.54	0.53	0.15	15.0	1.5	1.0	0.05
Bg	39- 70	3.63	4.38	2.7	0.10	27	0.36	0.17	0.10	6.8	2.1	2.1	0.08
1000 m (HK-36)													
Oi	0- 1												
Oe	1- 10	2.91	3.72	41.3	2.65	16	1.46	13.17	1.84	3.6	34.0	0.1	0.6
Bg	10- 15	3.39	4.02	2.4	0.16	15	0.26	0.21	0.07	3.0	3.3	1.2	0.1
Bg	15- 39	3.55	4.56	1.1	0.10	11	0.32	0.12	0.11	4.8	6.0	2.7	0.1
1400 m (HK-10)													
Oe	0- 11	2.91	3.71	51.4	2.56	20	15.56	6.50	1.54	0.42	34.0	2.4	55.6
Oa	11- 18	3.12	3.74	46.0	2.69	17	1.34	0.92	0.49	5.0	7.8	1.5	0.4
E	18- 30	3.32	4.07	4.5	0.25	18	0.46	0.20	0.22	15.6	2.4	2.3	0.04
Bg	30- 60	4.21	4.42										
	Subsample 9(brown)			14.9	0.45	33	0.25	0.03	0.05	1.5	40.0	8.3	0.3
	Subsample 8(gley)			11.5	0.35	33	0.24	0.04	0.12	1.1	43.0	6.0	0.3
Abg	60- 80	4.60	4.72	18.9	0.76	25	0.26	0.03	0.06	0.17	39.0	8.7	2.3
CBg	80- 90	4.72	4.81										
1800 m (HK-5)													
Oe	0- 8	3.39	3.75	29.7	2.48	12	3.19	1.38	0.82	9.1	6.3	2.3	0.5
Oa1	8- 19	4.10	4.25	20.6	1.45	14	0.40	0.18	0.29	4.3	1.2	2.2	0.1
Oa2	19- 31	4.36	4.52	23.0	1.33	17	0.32	0.06	0.10	1.8	22.0	5.3	0.3
Ag	31- 37	4.38	4.38	11.2	0.52	22	0.30	0.06	0.08	1.9	2.1	5.0	0.2
B	37- 67	4.53	4.75	9.8	0.48	20	0.26	0.05	0.06	0.81	2.7	5.2	0.5
Bb	67->115	4.90	4.70	8.7	0.44	20	0.24	0.04	0.04	0.14	35.0	6.0	2.6
2200 m (HK-60)													
A	0- 14	5.00	5.95	9.3	0.82	11	10.97	1.42	0.21	0.03	35.0	7.7	514
AB	14- 25	5.06	5.84	10.0	0.97	10	14.76	1.81	0.15	0.02	34.0	8.2	1384
Ab	25- 34	5.10	5.85	11.9	1.03	12	15.36	1.81	0.09	0.02	32.0	8.5	1152
ABb	34- 55	5.03	5.62	13.4	0.88	15	11.77	1.65	0.09	n.d.	42.0	7.1	infi.

n.d.: not detected

Table 3.5. Species richness of the classified plant communities. Total number of plant per community, and mean species number per stand for each community are shown. The communities are indicated by codes:

A1. Lowland dieback
(*M. polymorpha* v. *glaberrima*-*O. chinensis* community)
A2. Lowland intact forest
(*M. polymorpha* v. *glaberrima*-*A. pinnatifidus* community)
B1. Lower montane forest
(*M. polymorpha* v. *glaberrima*-*N. granadensis* community)
B2. Upper montane forest
(*M. plymorpha* v. *glaberrima*-*P. clusiifolia* commnity)
B3. Forest line
(*M. polymorpha* v. *glaberrima*-*S. cyatheoides* community)
C1a. Lower subalpine scrub
(*S. chrysophylla* community, *P. vulgaris* subunit)
C1b. Upper subalpine scrub
(*S. chrysophylla* community, *T. glomeratum* subunit)
C2. Alpine desert
(*T. humile* community)

	LOWLAND		MONTANE			HIGH ALTITUDE		
PLANT COMMUNITY	A1	A2	B1	B2	B3	C1a	C1b	C2
Total Number	47	100	103	52	56	28	26	14
Mean per Stand	21	38.4	43.5	24.7	23.2	14.2	15.2	7.3
(Range)	19-25	14-54	31-55	15-31	13-32	11-17	11-18	4-10

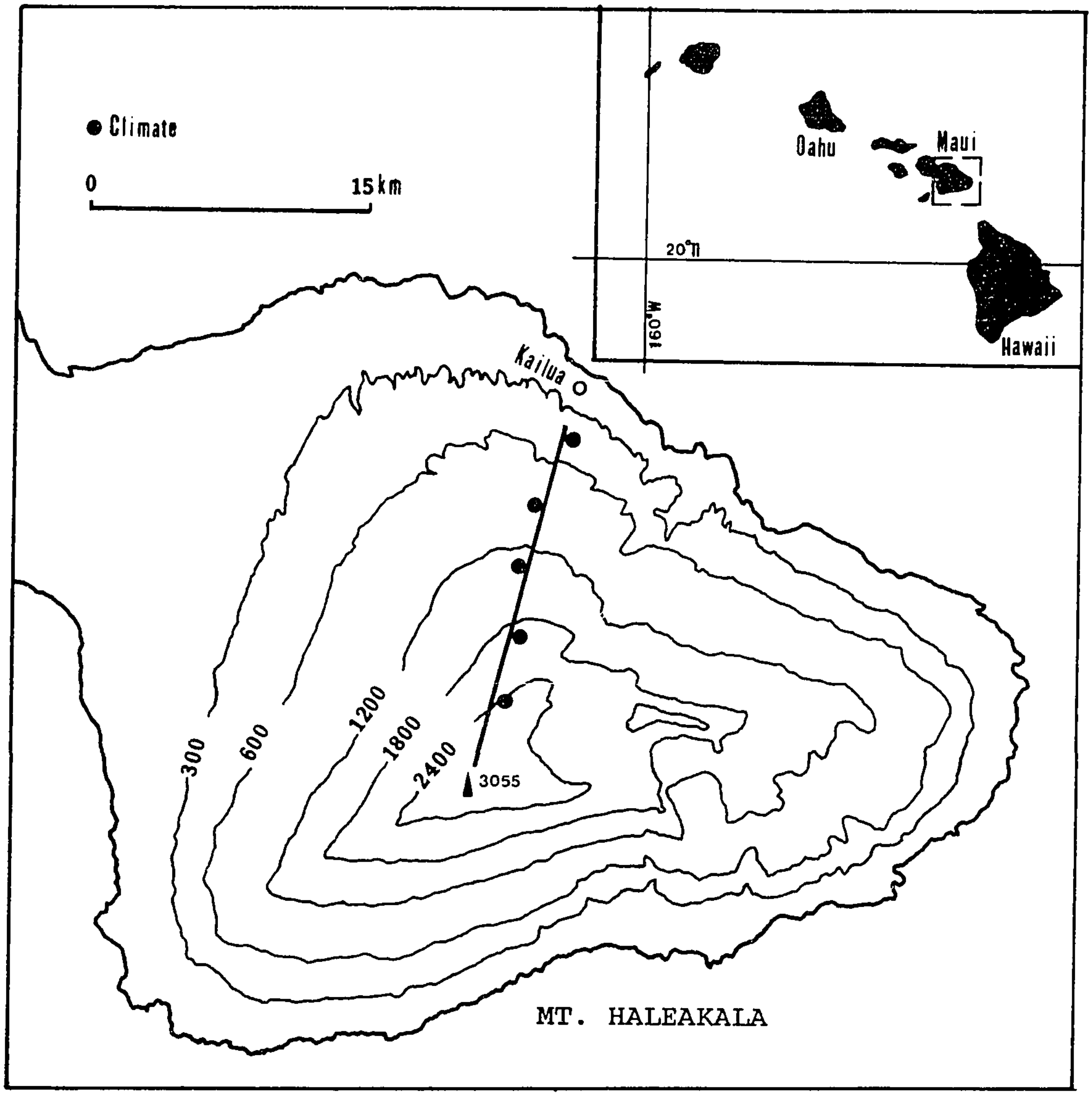


Fig. 3.1. Topography of the study area and location of the transect.

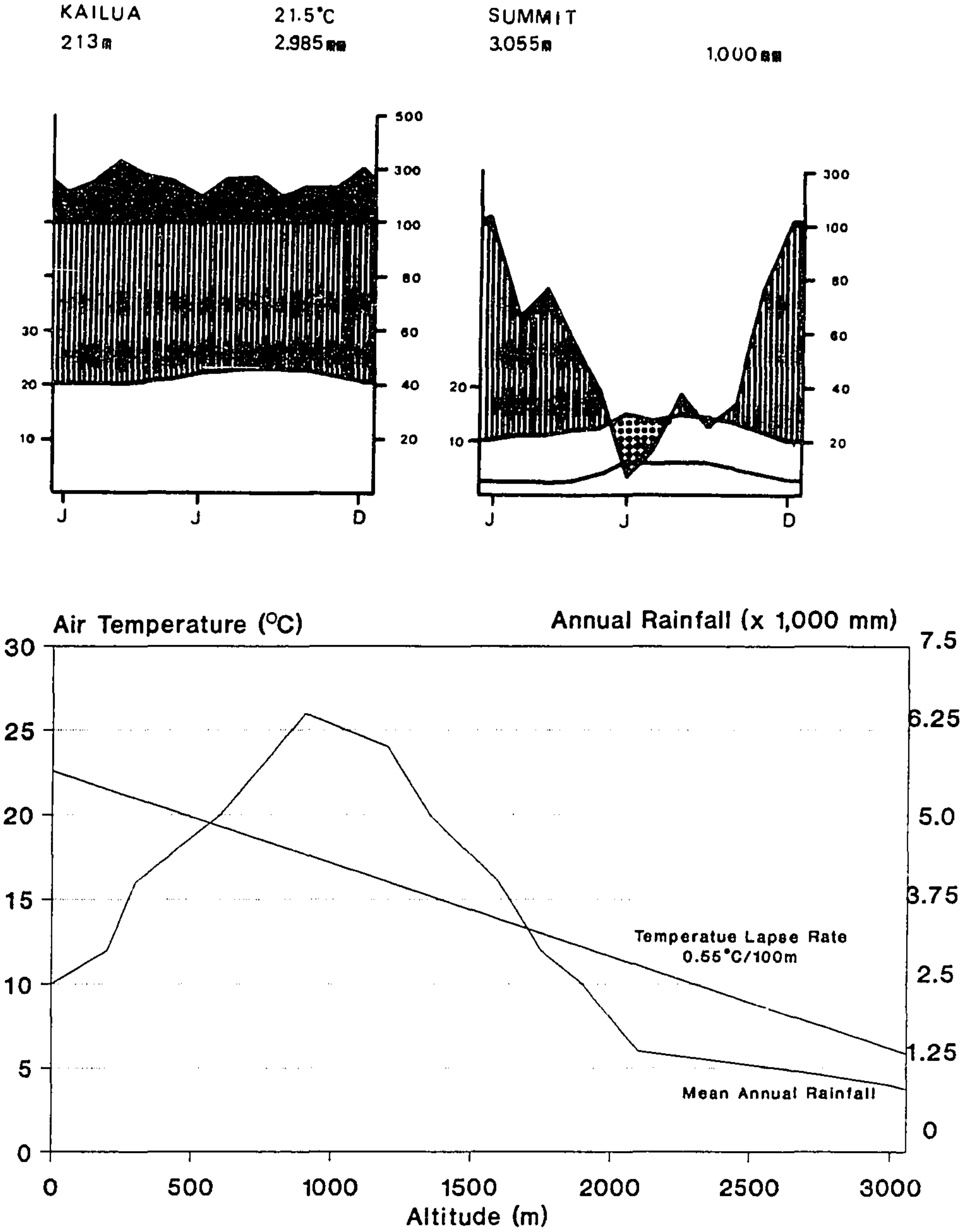


Fig. 3.2. Climate along the transect. The climate diagram of Haleakala's summit is shown with monthly mean daily maximum and minimum air temperatures.

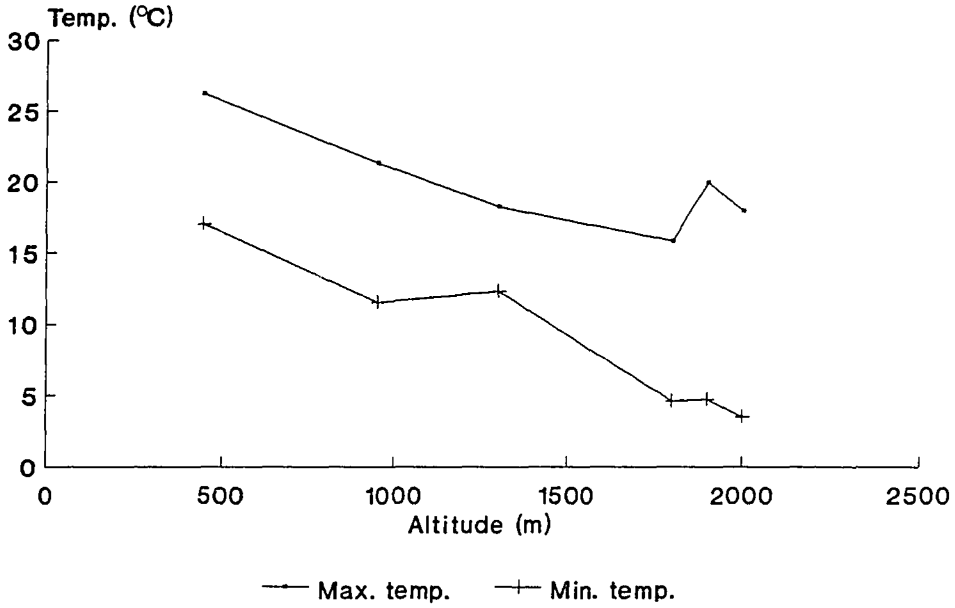


Fig. 3.3. Absolute maximum and minimum air temperatures along the transect during 13-19 June 1988.

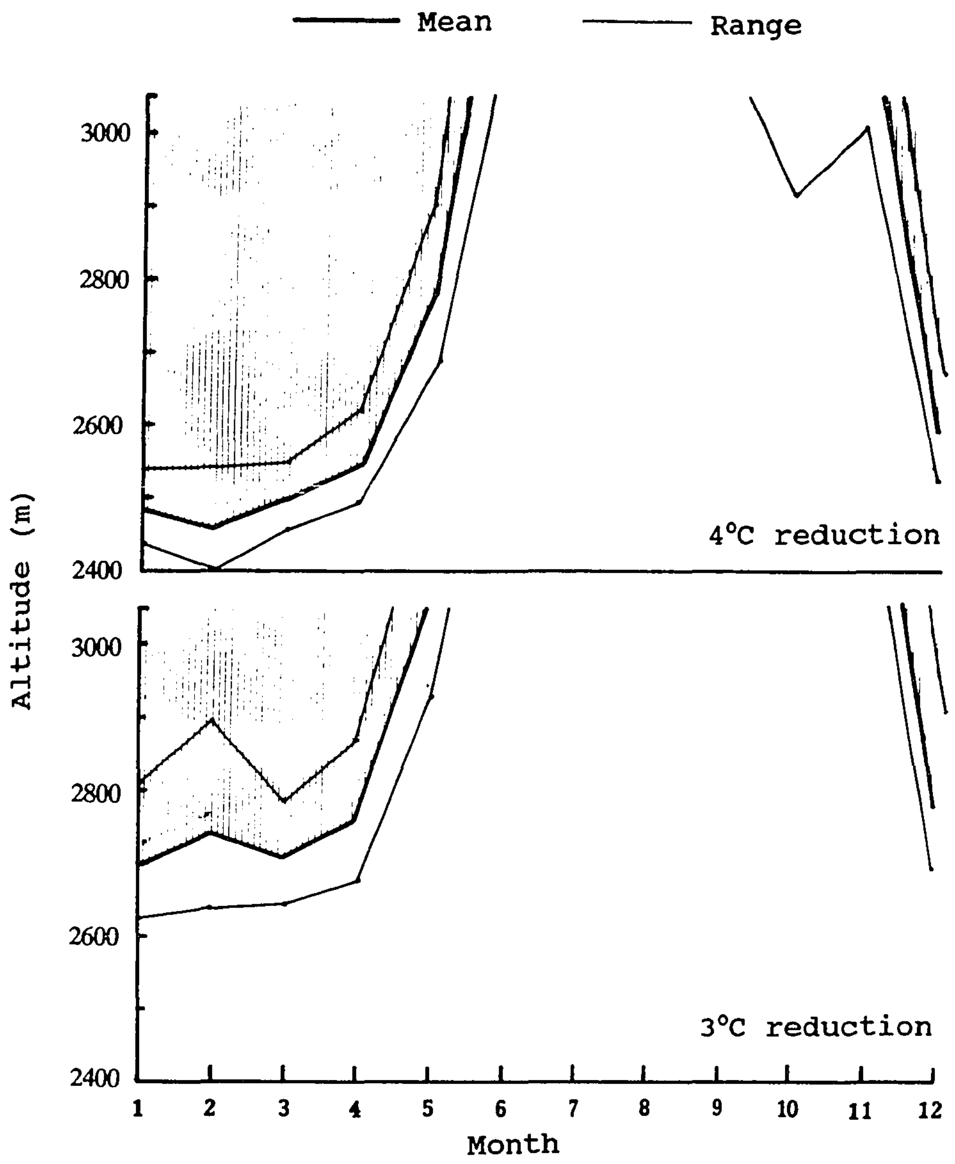


Fig. 3.4. Monthly altitudinal changes of the ground-frost line on Haleakala, which were estimated based on the temperature differences between the screen level and the ground surface: Upper, 4°C difference assumed; lower, 3°C difference assumed. The mean and range of the frost line are shown. Shaded area indicates the period and altitude where the ground frost occurs below the summit.

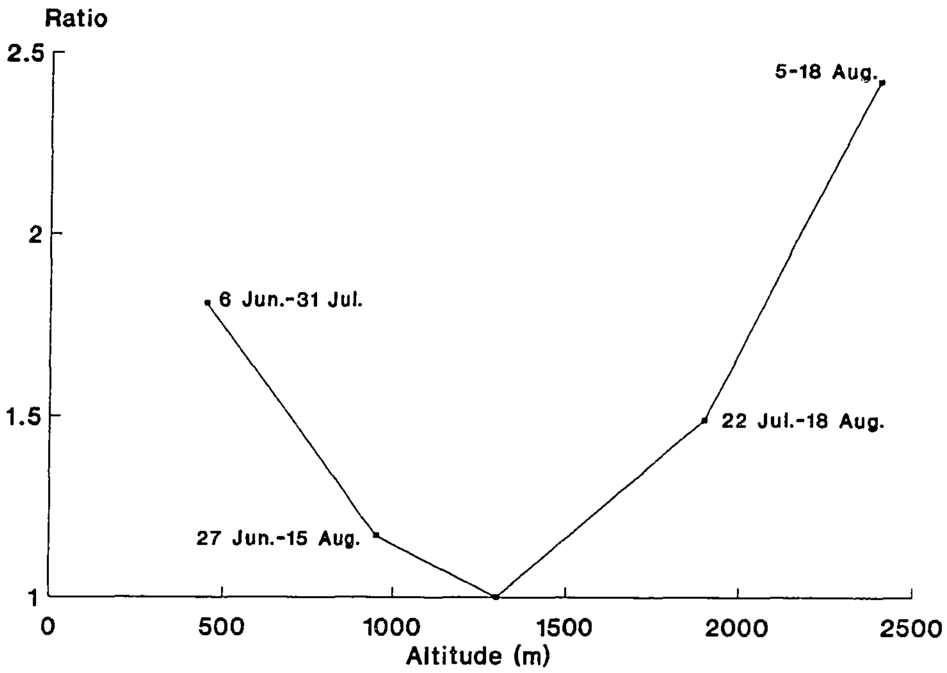


Fig. 3.5. Altitudinal evaporation change along the transect. Ratios of measured evaporation to that at the standard altitudinal point (1300 m asl) are indicated. Dates indicate measurement period at each station.

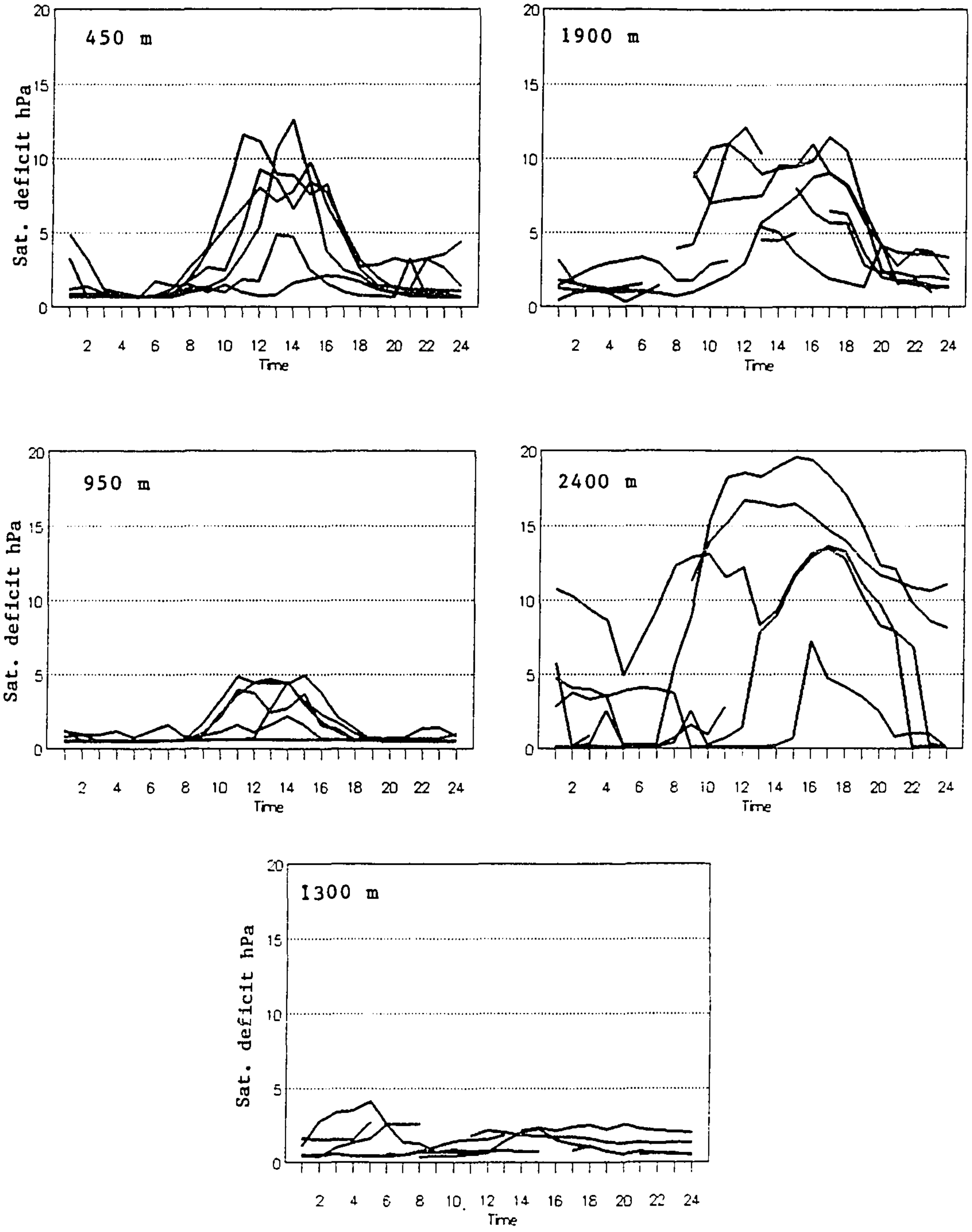


Fig. 3.6. Hourly changes in measured saturation deficit during 26-31 July 1988.

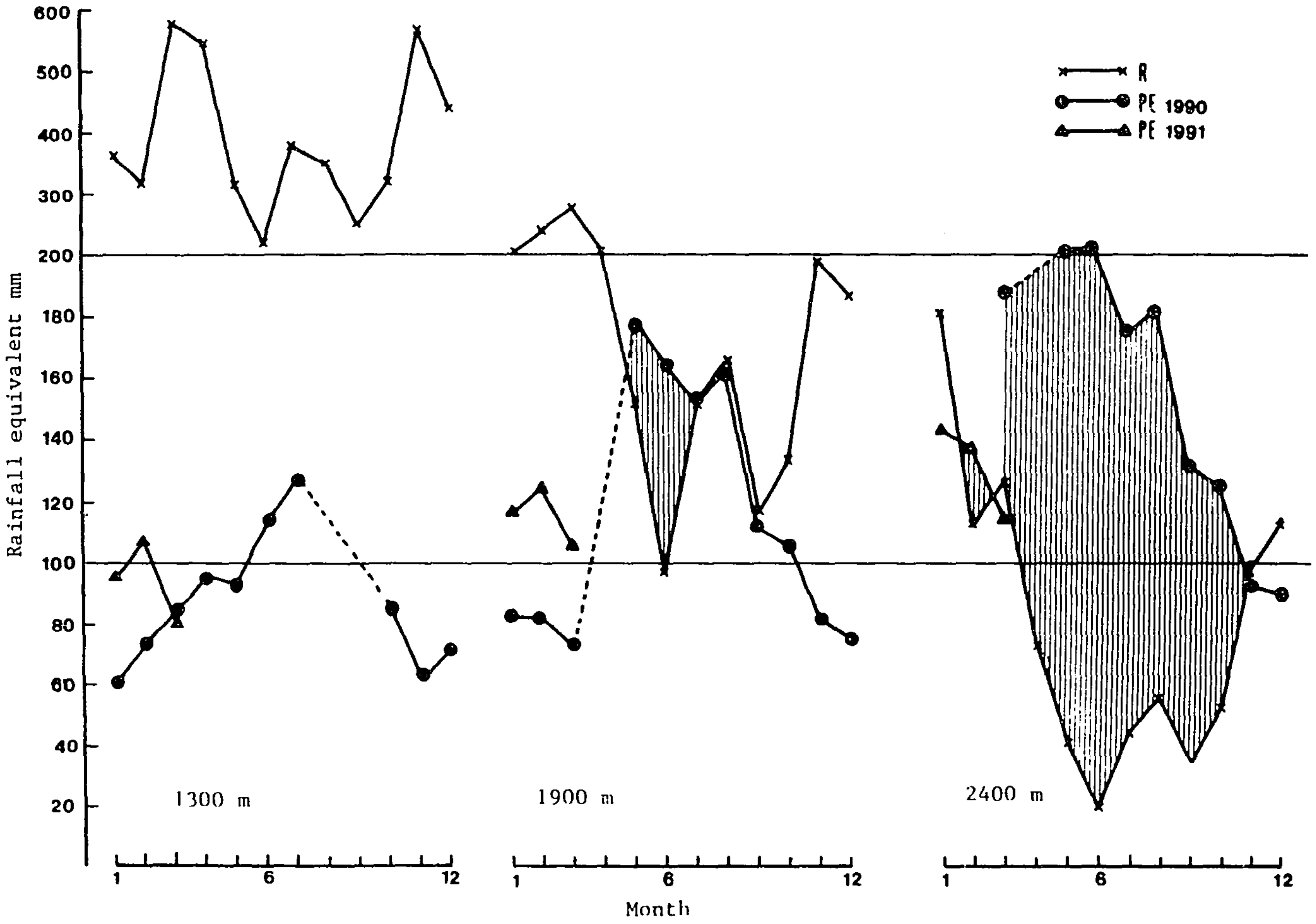


Fig. 3.7. Monthly water budgets at three altitudes along the transect. Drought period (shaded) is defined by the negative water budget = monthly rainfall (R) - monthly potential evapotranspiration (PE).

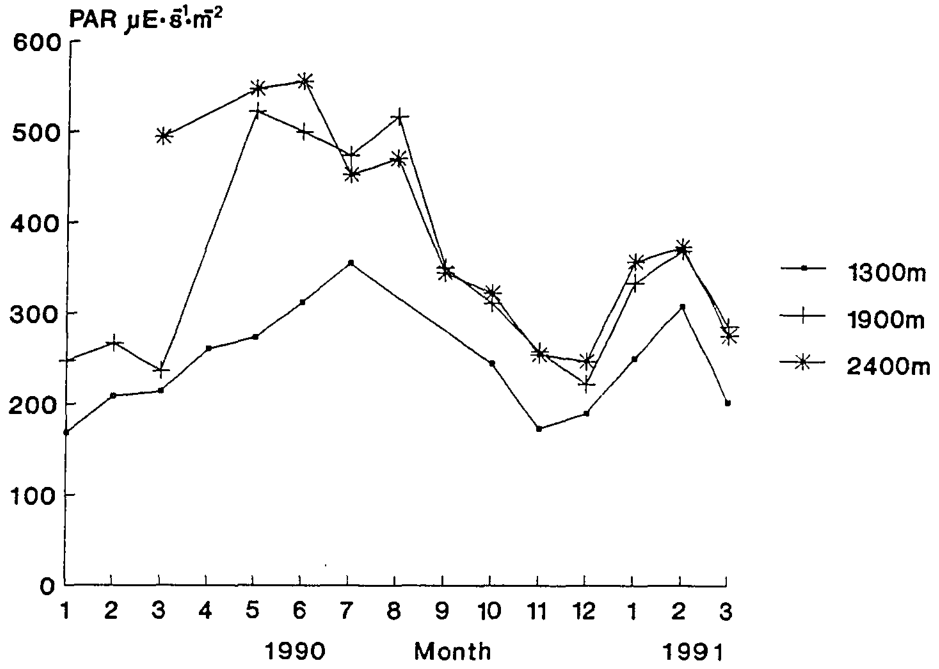


Fig. 3.8. Monthly changes in mean daily photosynthetically active radiation (PAR) at three altitudes along the transect.

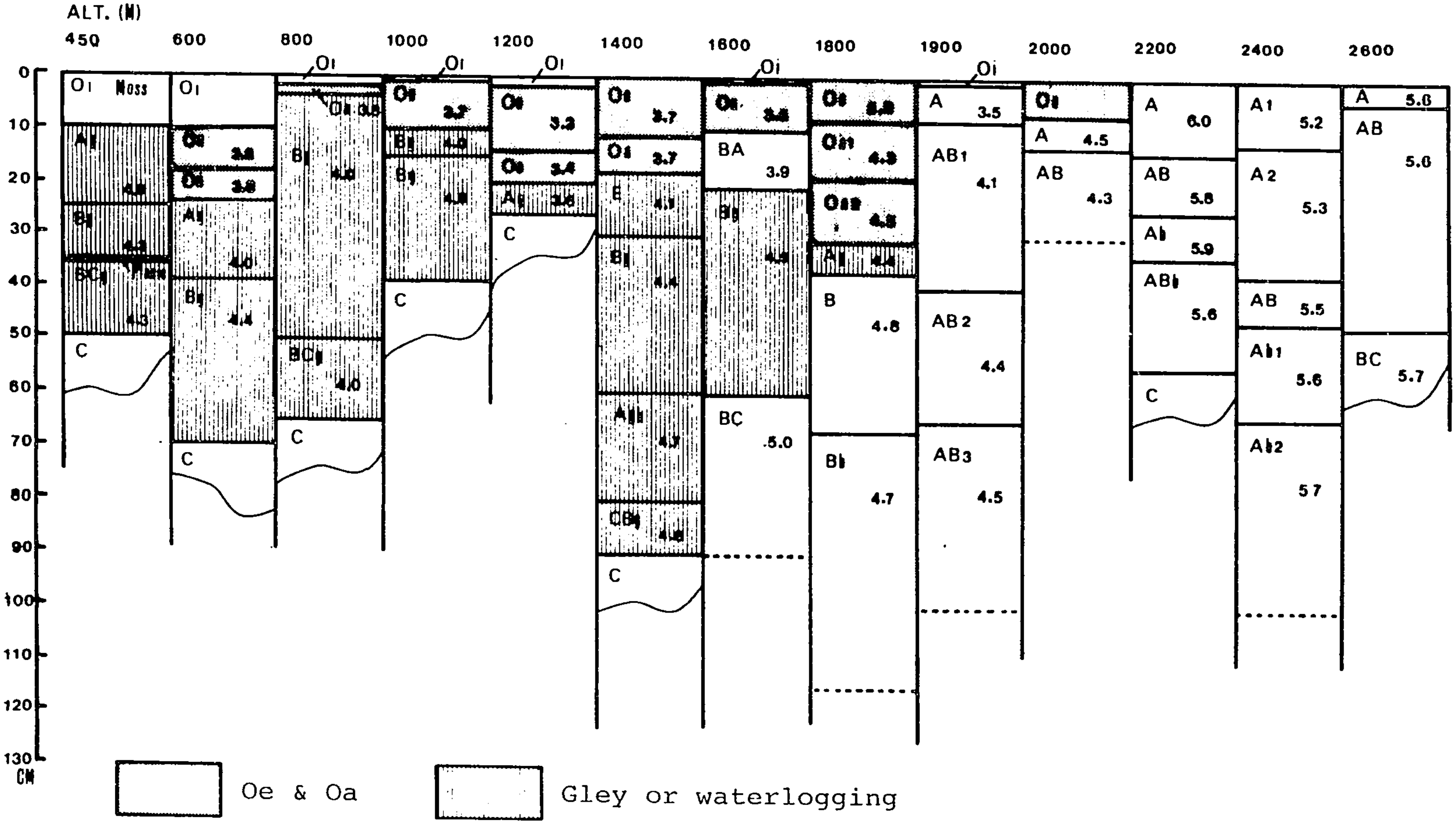


Fig. 3.9. Soil profiles along the transect. Figures are pH (H_2O) values.

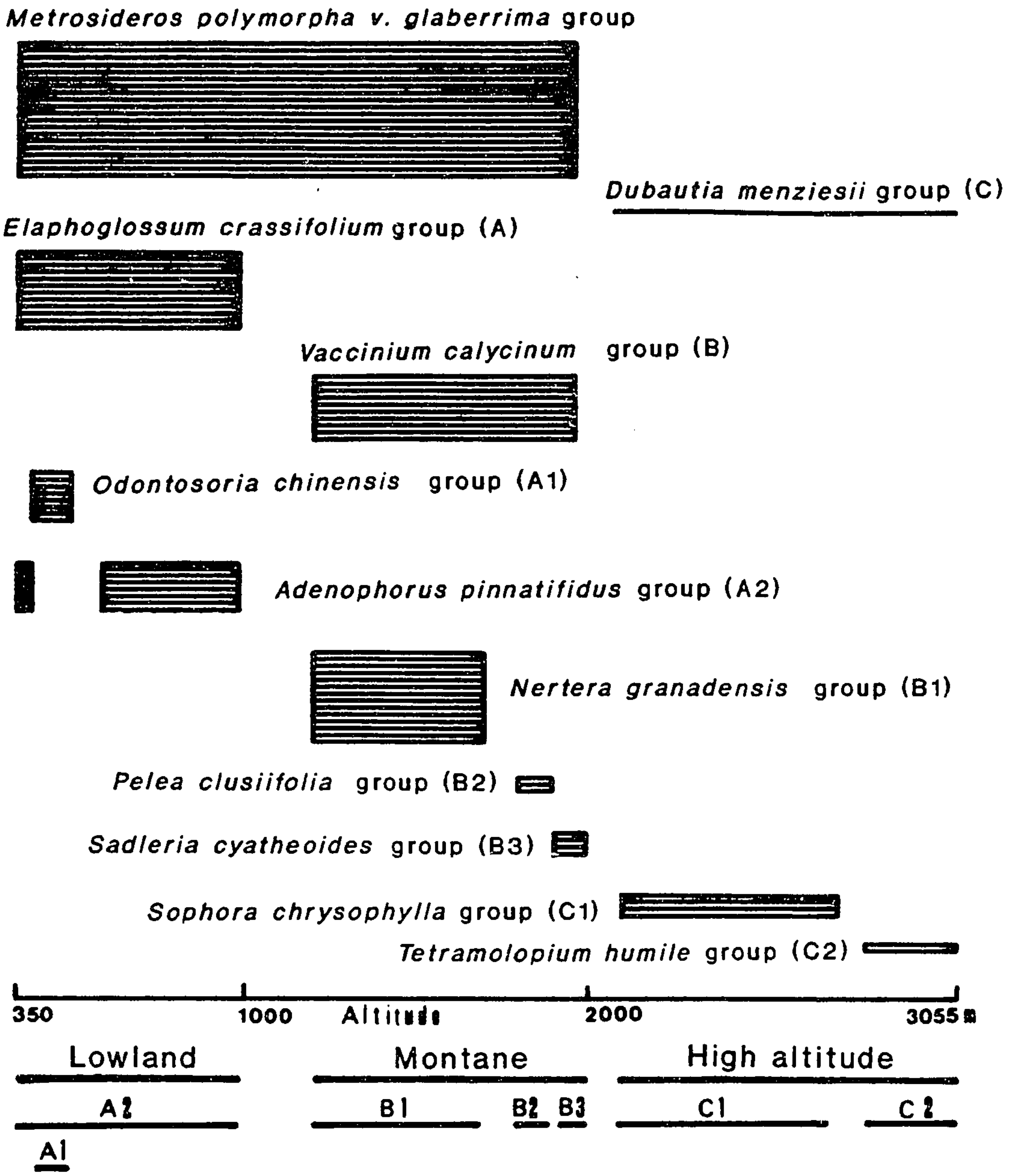
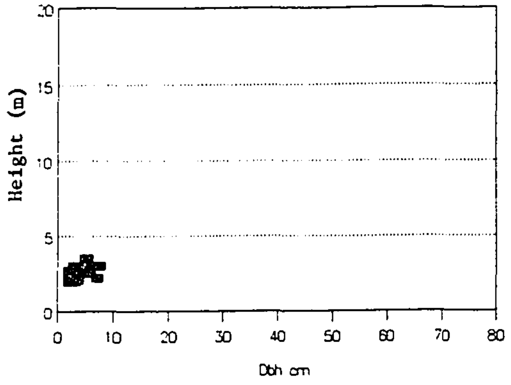
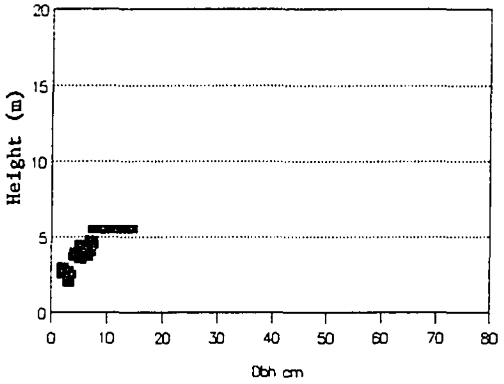


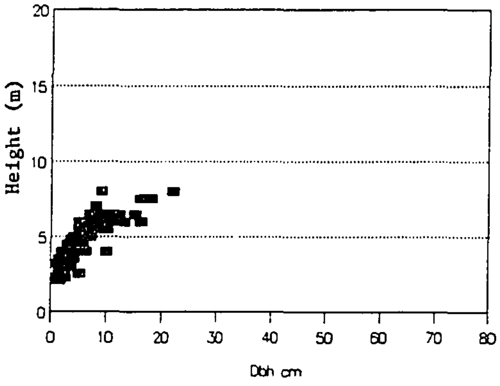
Fig. 3.10. Altitudinal distributions of selected differential species along the transect. The number of lines in each cluster indicates the number of its differential species.



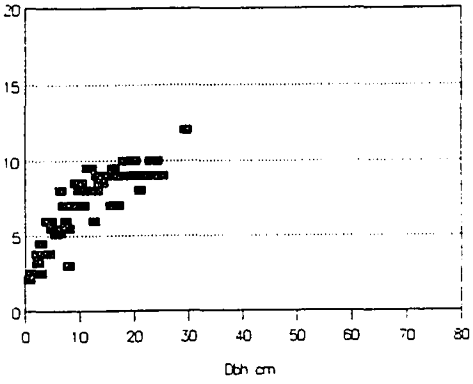
450 m



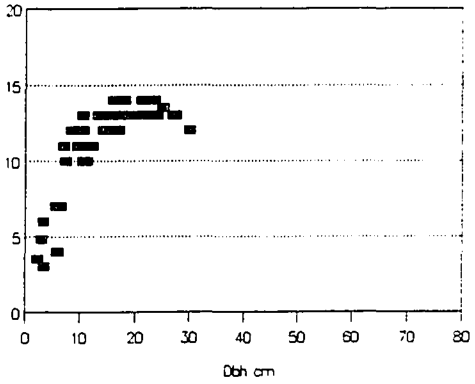
600 m



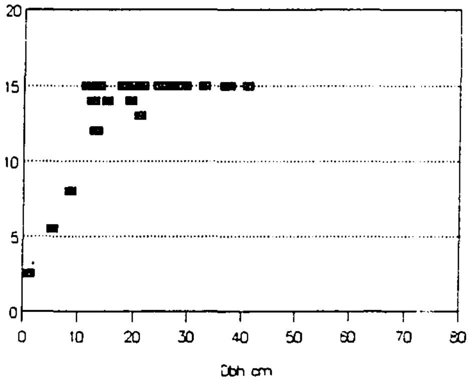
800 m



1000 m



1200 m



1400 m

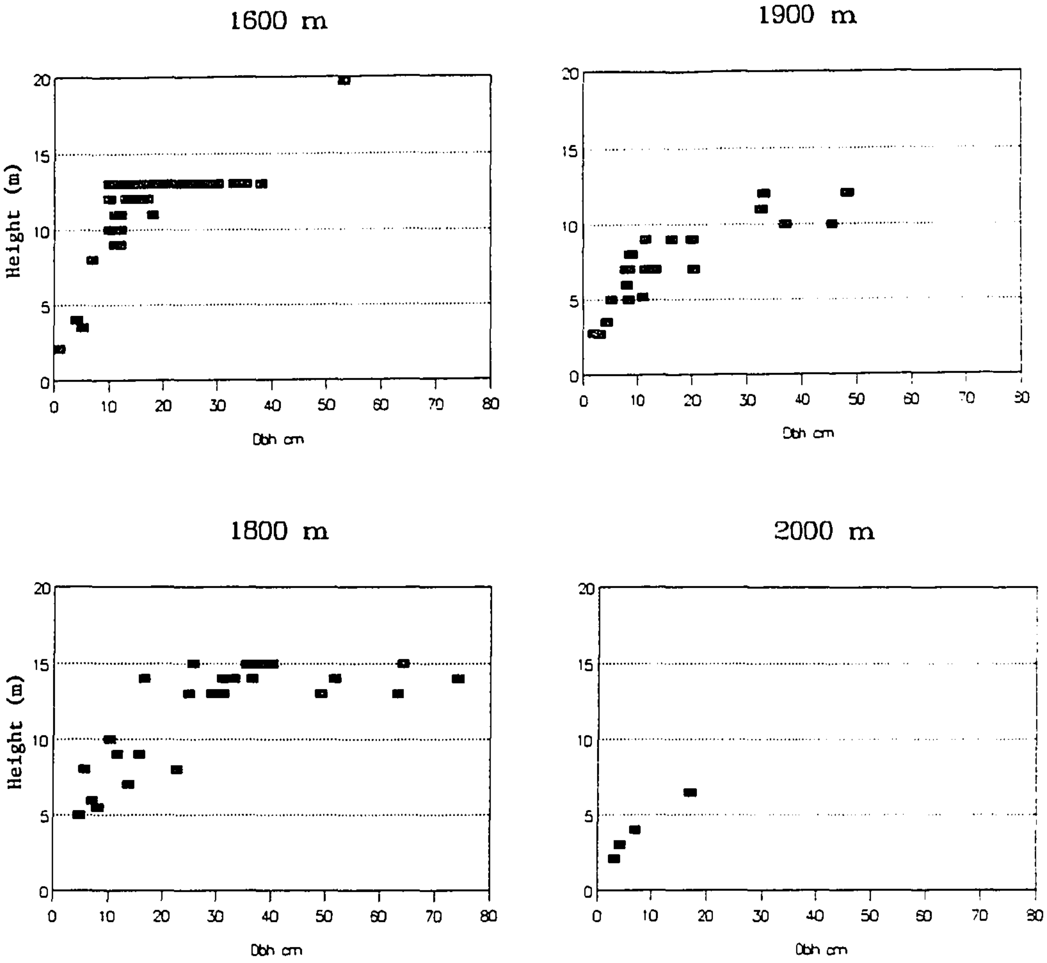


Fig. 3.11. DBH-height relationships of Metrosideros trees ≥2 m height along the transect.

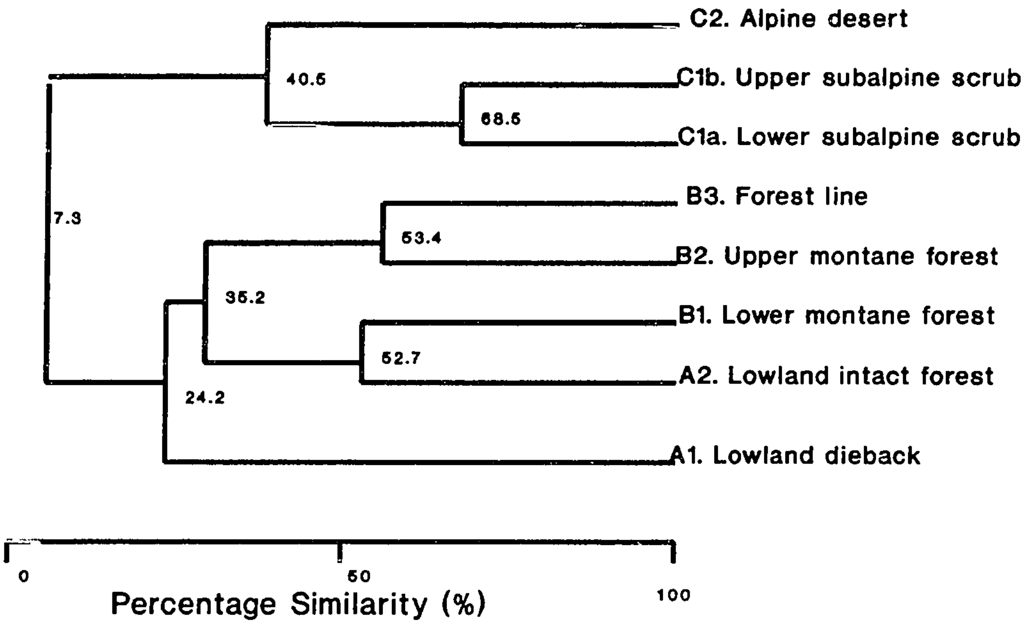


Fig. 3.12. Dendrogram showing relationships among the classified plant communities.

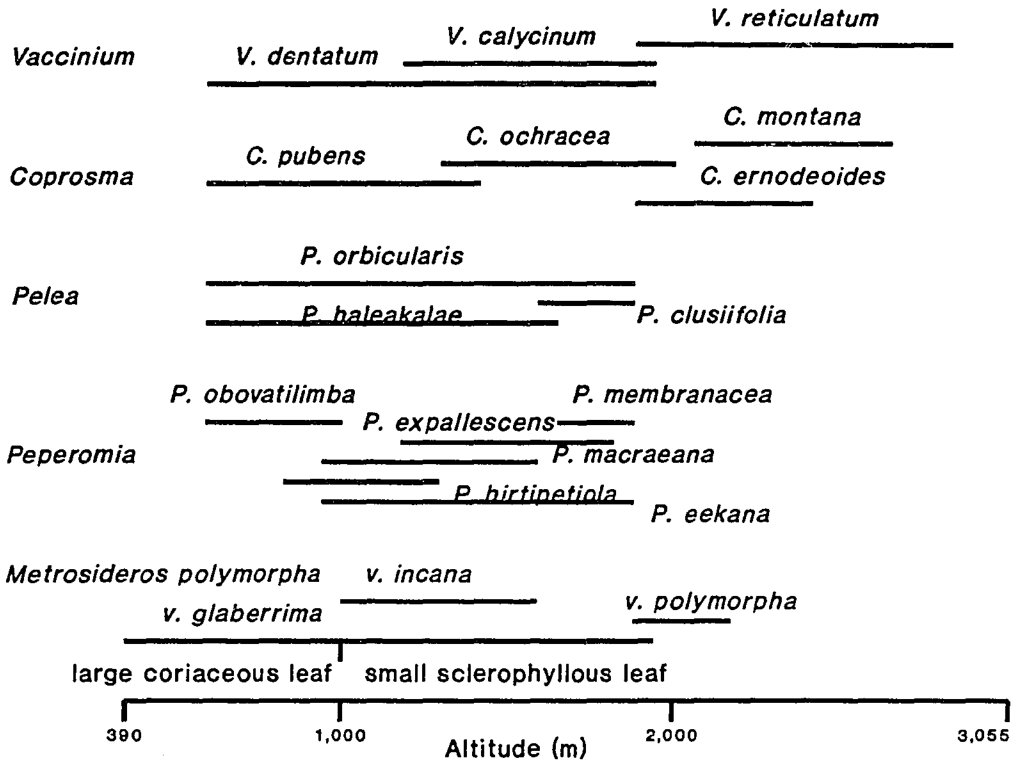


Fig. 3.13. Altitudinal distribution patterns of selected conspecific/generic taxa along the transect.

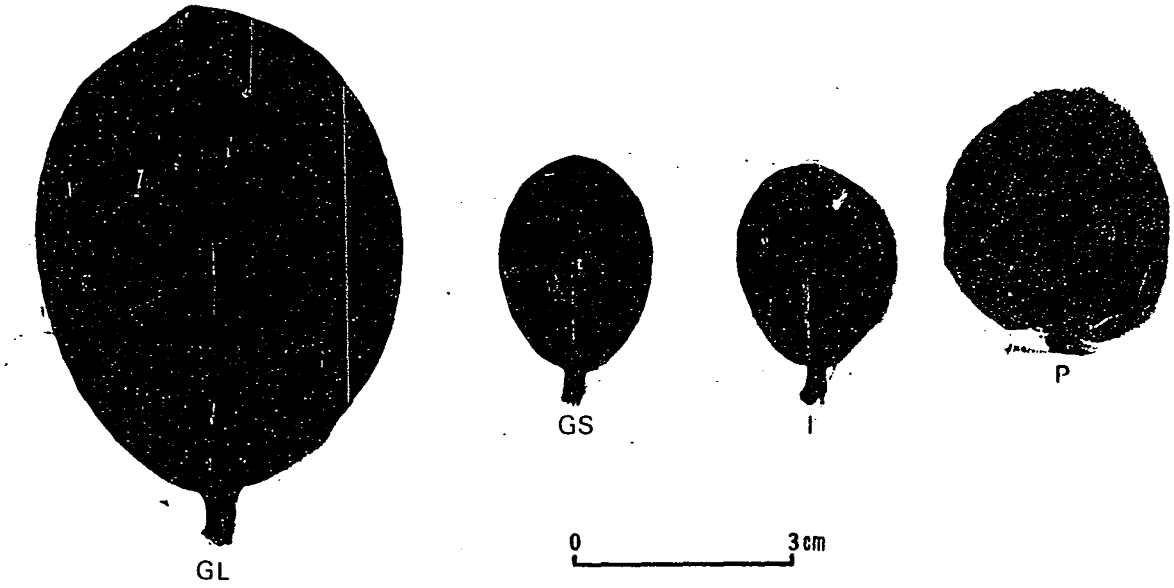


Fig. 3.14. Variations in *Metrosideros* leaves representing three morpho-varieties, and two leaf-variants in one of the varieties: GL, large leaf variant of variety *glaberrima*; GS, small leaf variant of variety *glaberrima*; I, variety *incana*; P, variety *polymorpha*.

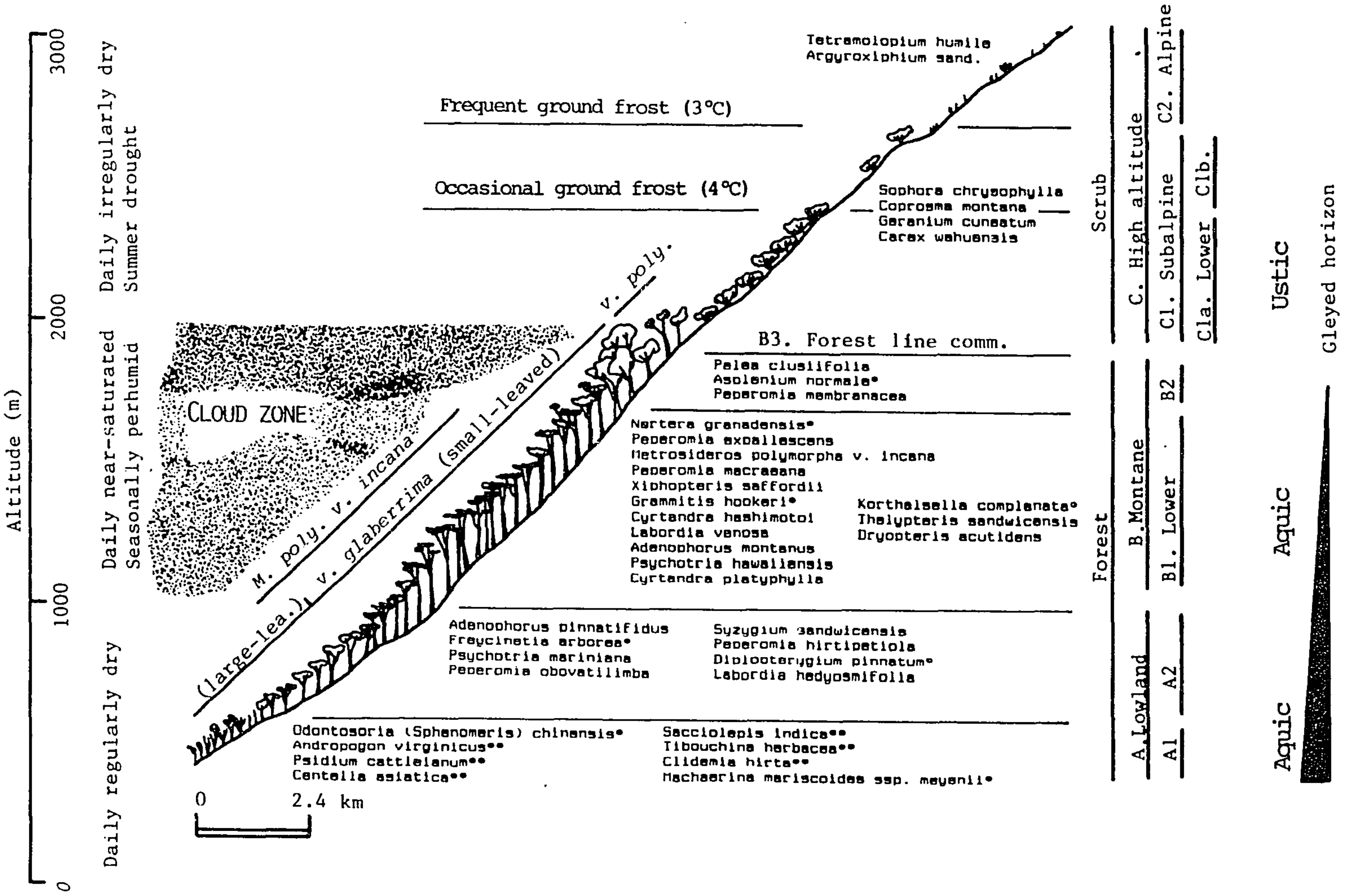


Fig. 3.15. Altitudinal floristic vegetation zones with some important climatic and soil parameters along the transect.

CHAPTER 4. COMPARATIVE VEGETATION ANALYSIS ON THE WET SLOPES OF TWO TROPICAL MOUNTAINS: MT. HALEAKALĀ, HAWAII AND MT. KINABALU, BORNEO

ABSTRACT

The vegetation on the wet slope of Mt. Haleakalā on the oceanic island of Maui was compared with that of Mt. Kinabalu on the continental island of Borneo in order to examine the effects of the geographic isolation on Haleakalā's altitudinal vegetation patterns. The two mountains are similar in their equable tropical climate, generic and high level floristic elements, and age of summit regions, but contrast strongly with each other in regional floristic richness. Alpha diversity (richness and evenness) of major canopy/subcanopy tree species was much higher on Kinabalu than in thermally comparable zones of Haleakalā. Beta diversity of the tree species using Whittaker's half-change index was 0.81 for trees ≥2 m height on Haleakalā; on Kinabalu, the value was 11.83 for trees ≥10 cm DBH. Floristically defined altitudinal vegetation zones were distinct and discrete on both mountains. The number of the zones was the same on both mountains despite the striking difference in beta diversity. This surprising result is explained by the facts that: 1) there was the same number of differential-species groups, indicating the presence of homologous climatic zones between the mountains; 2) on

Haleakalā, a high proportion of species extended over a broad altitudinal range upslope; and, 3) by contrast, on Kinabalu, a high proportion of genera was differentiated into parapatric altitudinal congeners. The ubiquity of wide-ranging species as well as the presence of more range-restricted species groups on Haleakalā was reflected in a strong hierarchical arrangement of vegetation units. It is hypothesized that the altitudinal species radiation on Haleakalā is less advanced than that on Kinabalu.

Keywords: Altitudinal species radiation, Geographic isolation, Impoverished flora, Species diversity, Species turnover, Vegetation zones.

Abbreviations: DBH=Diameter at breast height, HC=Half-change, IA=Internal association, TWINSPAN=Two-way indicator species analysis.

INTRODUCTION

Oceanic islands are considered biogeographically different from continental islands in several evolutionary and ecological aspects. With regard to evolutionary aspects, Carlquist (1974) states that there are several unique botanical syndromes found on oceanic islands. One prominent example among the syndromes is adaptive radiation. Further, certain morphologically distinct congeneric species on oceanic islands have a high genetic identity comparable to that of conspecific populations in continents (Carr 1987).

In synecological aspects, some substituted plant communities consisting of alien species monopolize islands' landscape over more than one habitat type (Egler 1939). Mueller-Dombois (1981a) states that the dominant rain forest tree species in Hawaii, _Metrosideros polymorpha_, has a wide ecological amplitude ranging from newly created lava flows to old growth forest. The rain forest dominated by this species shows a divergent phenomenon also in its dynamics: i.e. stand-level canopy dieback (Mueller-Dombois 1988). This spatially and successionally divergent phenomenon is found also in another oceanic island chain, the Galápagos Islands (Itow & Mueller-Dombois 1988). These synecological characteristics have been described as "ecological release" by Shimizu & Tabata (1991).

All of the above ecological characteristics relate in some way to the islands' lessened interspecific competition which is expressed in their impoverished floras. Spatial patterns in natural vegetation may also be divergent between oceanic and continental islands, reflecting the difference in regional floristic richness. Except for theoretical/ mathematical consideration in island ecology (MacArthur & Wilson 1967; MacArthur 1972), such vegetation comparisons have been limited to a few parametric analyses as made by Itow (1988).

The following analysis numerically compares the vegetation on the wet slope of Mt. Haleakalā (3055 m) on the oceanic island of Maui with that of Mt. Kinabalu (4101 m) on the continental island of Borneo. The former has a naturally impoverished flora, while the latter has a very rich flora. Kinabalu is perhaps the most floristically diversified mountain in the circum-Pacific region. The vegetation of each mountain was described in the preceding chapters.

Four working hypotheses have been empirically established, and/or theoretically derived from some earlier hypotheses of other authors (see the theory in chapter 1). The working hypotheses (H0) are summarized:

H01. Alpha species diversity: Alpha species diversity based on the number of species relative to the number of individuals is lower on Haleakalā than in comparative zones on Kinabalu.

H02. Space preemption and the number of dominant species: The low regional floristic richness on Haleakalā leads to disproportionately higher relative dominance by fewer dominant species on Haleakalā than on Kinabalu.

H03. Beta diversity: Spatial species turnover is less along the slope on Haleakalā than on Kinabalu.

H04. Floristic zonal assemblage: Floristic vegetation zones are wider in range and fewer in number on Haleakalā than on Kinabalu.

STUDY AREAS

Haleakalā (Fig. 4.1) is a dormant volcano, while Kinabalu is non-volcanic. Thus, their geological substrates are rather different (Table 4.1). The entire slope of Haleakalā is covered with basaltic volcanic materials of early Pleistocene origin (Stearns 1985). The lower slope of Kinabalu (<c. 2700 m) is covered with the sedimentary rock, deposited in the Eocene and uplifted in the upper Miocene; the upper slope (>c. 2700 m) is made up of granitic rock uplifted in the early Pleistocene (Jacobson 1978). Therefore, the upper part of Kinabalu is very similar in geological age with the entire slope of Haleakalā, but the lower part of Kinabalu is much older.

While the height difference between Haleakalā (3055 m) and Kinabalu (4101 m) is striking, their high-altitude habitats are compensated by a difference in latitudinal location: Haleakalā, though lower, supports a hot tropical climate at the base and a cold climate at the summit as does Kinabalu. The two mountains have an equable thermal climate throughout the year (Table 4.1) with almost identical temperature lapse rates ($0.55°C \cdot 100\ m^{-1}$, chapters 2 and 3). Therefore, altitudinal climatic zones are identical in range along the slopes. However, the same thermal zones start at different altitudes, and Kinabalu's lowest climatic zone is hotter because it is closer to the equator.

The most striking difference is found in floristic richness (Table 4.1); the numbers indicating floristic richness are from wider areas than those studied. The total number of vascular species is c. 4000 in the entire region of Kinabalu, while on Haleakalā there are only several hundred. Haleakalā's flora consists largely of elements derived from the Malesian region, the biogeographic region of Mt. Kinabalu. Furthermore, in Hawaii there are many species of Australasian affinities, which occur also at the higher altitudes on Kinabalu (Meijer 1964, Hotta 1974). Consequently, a large number of native genera are common to both mountains.

SAMPLING METHODS

The comparative altitudinal transect method was used on both mountains following the IUBS manual written by van der Hammen _et_ _al_. (1989). An attempt was made to unify the sampling layout on both mountains as much as possible. Two altitudinal transects were laid out through undisturbed primary vegetation with a maximal length below the uppermost forest line. Both represent a narrow belt along wet mountain slopes, thus environmental variations were expressed only altitudinally. However, the use of different sampling methods was unavoidable because of logistic restrictions and differences in the vegetation structure and species complexity of the two mountains.

The count-plot method and the relevé method were used on Haleakalā. On Kinabalu the point-centered quarter method, a plotless sampling method, was used. The results, however, are directly comparable because the plotless measurements were converted to area samples (see below).

The Haleakalā transect

The transect on Haleakalā started at 350 m a.s.l. and extended into the summit at 3055 m a.s.l. (see chapter 3). Along the transect, the relevé analysis (Mueller-Dombois & Ellenberg 1974) was done in 100 m altitudinal intervals with several quadrats of 20x20 m per interval. Thus, multiple relevés were horizontally arranged at one altitudinal level, less than 1 km width in a belt-shaped transect. All vascular plants present in each relevé were enumerated, and species cover values were visually estimated using the Braun-Blanquet cover-abundance scale. A total of 111 relevés were analyzed, which together contained 189 taxa. The relevés were then used for investigating vegetation zonation corresponding to the fourth hypothesis.

Every 200 m in altitude, the relevé with the most developed forest stand containing the tallest canopy and richest species assemblage was selected for the quantitative analysis. In each of the selected forest relevés, trees ≥5 m height were measured for DBH throughout the entire quadrat (20x20 m), while DBH for shrubs 2 to 5 m tall were measured in only four of 3x20 m belts which were systematically placed within the quadrat. In one relevé at 450 m, trees ≥5 m were sampled using the enlarged quadrat of 50x50 m because they were low in density. DBH was measured to determine dominance values of species ≥2 m height. A total of nine stands were analyzed, and they were comprised of 33 taxa. Species dominance values were used for testing the first, second and third hypotheses, which relate to alpha species diversity and turnover.

The Kinabalu transect

The altitudinal transect on Kinabalu consisted of two separate segments. The lower segment extended from 600 to 1800 m a.s.l. along the eastern shoulder of the mountain (see chapter 2). The upper segment started at 2000 m and extended to 3400 m a.s.l. (the closed-forest line) on the south face. The two segments were further stratified into altitudinal intervals of 200 m, and one sampling plot was established in each interval. Geological anomalies and topographic extremes were avoided for sampling sites. At each of the plots, a secondary transect parallel to the contours was established to intersect with the altitudinal transect. Along this secondary transect, trees ≥10 cm DBH were enumerated by the point-centered quarter method (Mueller-Dombois & Ellenberg 1974). Sampling points were placed at 10 m intervals for low-density forests but 5 m intervals for dense forests. Distances from a sampling point to the stem mid-point of a closest tree per quarter were measured, as was DBH of the tree. The enumeration was continued until the same species repeatedly occurred and newly added species became substantially reduced. This criterion was used to extract a representative tree species composition.

Each area of the sampling plots was determined according to the methods of Mueller-Dombois & Ellenberg

(1974): Mean area per individual tree was obtained by a square of the mean distance between sampling points and the closest trees. Subsequently, the total area per plot was computed by multiplying the total tree number by the mean area.

Above 3400 m (the closed-forest line), the forest became naturally fragmented, and the same sampling method could not be applied to the fragmented stands. There, the altitude of the uppermost fragmented forest stand was noted for comparing the treeline with that on Haleakalā.

A total of 14 samples, comprised of 425 taxa, were obtained by the point-centered quarter method. The data refer only to trees ≥10 cm DBH. They were used for testing hypotheses 1 through 4.

Analyses and computation procedures

Alpha species diversity

The values of alpha species diversity were obtained using Fisher's equation (Itow & Miyata 1977):

$$S=\alpha\ln(1+\frac{N}{\alpha})$$

where S is the total number of species per stand, and N is the total number of individuals per stand.

Species representativeness: space preemption

In each of the stands (plots), species dominance values were calculated by relativizing the species basal areas so that the sum of the species dominance values became 100 per stand (see results in Appendices 1.1-1.14 for Kinabalu and 2 for Haleakalā).

For analyzing species representativeness (a Whittaker term relating to quantitative importance of species in individual sample stands or relevés), species were sequentially sorted along the x-axis in descending order of relative dominance and plotted against the logarithmic relative dominance on the y-axis in each stand. The theory and mathematical considerations underlying this analysis are given in Fig. 4.2.

A leftmost dot in each graph (Fig. 4.2) represents the most dominant species in the stand, and a rightmost is the least important one. The length of a curvilinear tail projected on the x-axis equals the total species number of the stand. The slope of a curve indicates species representativeness (evenness sensu Whittaker 1972) or the allocation pattern of basal area among species per stand. Thus, it is a measure of how the total basal area (100%) is split and preempted among the constituent species.

An average fraction of space preemption by a given species was computed using the linear least-square regression analysis between the species sequence and the logarithmic relative dominance values. This fraction was tentatively termed the "space allocation ratio" by the author, which refers to the fraction of space occupied by the species in question measured in basal area. The space allocation ratio indicates the evenness of the species representativeness based on an average slope of the species sequence-relative dominance curve. It may be used to predict the relative dominance value of the i-th species (i=1-----n) in the descending order in a given stand. The more linear the species sequence-relative dominance curve is, the more accurate the prediction is. The details of its definition and theory are given in Fig. 4.2.

Species representativeness: the number of dominant species

The following analysis determines how many species are said to be dominant species in each stand. The analysis uses the equation of the dominance analysis by Ohsawa (1984):

$$d=\frac{1}{N}\left[\sum_{i\in T}(X_i-X)^2+\sum_{j\in u}X_j^2\right]$$

where X_i is the relative dominance value(s) (basal area %) of leading dominant species (the number of dominant species: T=1, 2, 3----); X is the expected relative dominance values of T and expressed as 100/T; X_j is the relative dominance values of the remaining non-dominant species (U); N is the total number of species per stand.

When only one dominant (T=1) is present, it is expected to occupy nearly 100% (=100/T) of the stand, and the rest become near-zero asymptotically. When two species codominate equally (T=2), they are expected to share 50% (=100/T) of the stand, and the rest become near-zero asymptotically. Following the equation, the calculations are iterated successively from T=1 until the deviation (d) reaches to a minimum value. At this point, the deviation of actual relative dominance values from the expected values becomes least. Thus, the T value at this point is accepted as the number of dominant species.

Species turnover

The extent and pattern of spatial changes in species composition along environmental gradients are expressed in two ways: 1) unit species turnover, and 2) species turnover rate (Itow 1990). Two units have been coined for expressing unit turnover: one is "half-change (HC)" (Whittaker 1960), the other is "gleason" (Wilson & Mohler 1986) in honor of the pioneering community ecologist. The following analysis uses only the unit of HC because the gleason unit may be more sensitive to the number of species included in a computation. Hence, it is inadequate for this comparison where the total number of species is so different due to biogeographic factors.

The theory and basic consideration in computation of HC are given in Fig. 4.3. The procedure of computing internal association (IA; see Fig. 4.3), HC and turnover rate follows:

1. Percentage similarities (PS) were calculated among the collected samples (stands) using the relative species basal areas (Appendixes 1.1-1.14 and 2) based on Motyka's equation (Mueller-Dombois & Ellenberg 1974):

$$PS=(2Mw/200) \times 100$$

where Mw is the sum of the smaller basal areas of the species common to two samples. The computed similarity matrixes are shown in Table 4.2 for each of the mountains.

2. The altitudinal transect (gradient) below the closed-forest line on each mountain was scaled so that the length becomes 100. Relative location of the stands were plotted on the scaled gradient (Fig. 4.4). Here, it was assumed that altitude can correctly represent a composite gradient consisting of multiple environmental factors, and that the rate of altitudinal changes of the composite gradient is entirely constant.

3. Altitudinal gradient distances between any two given samples (from Fig. 4.4) were plotted on the x-axis against their PS similarity (from Table 4.2) on the y-axis. A logarithmic scale was used on the y-axis because similarities of two-sample pairs usually decrease exponentially as their distance increases (Whittaker 1972).

This procedure resulted in the scatter diagrams of Fig. 4.5. The diagrams indicate a trend of how sharply stand similarities decrease with increasing altitude (i.e. increasing x value).

4. The linear least-square regression analysis was done to find the best-fitting line among scattered points, hence an average reduction rate of similarity values. The regression analysis was done only for x values <50 in the Kinabalu series, and those <80 in the Haleakalā series. These thresholds were arbitrarily set from the scatter patterns in Fig. 4.5 but later justified by the highest r^2 values among other thresholds.

5. A theoretical IA value was derived from the y-coefficient with which the regression lines intercept on y-axis. Average species turnover rate was given by the value of the x-coefficient from the obtained linear regressions. The HC value was derived from the equation of Wilson & Mohler (1986):

$$HC=[\ln(IA)-\ln\frac{IA/2}{b}]^{-1}\times 100$$

This is a modified Whittaker's equation given in Fig. 4.3, where b is the x coefficient of linear regression, and IA the theoretically extrapolated value.

Differentiation of floristic zones

Two different analytical methods were used for differentiating floristic vegetation zones. Braun-Blanquet's synthesis table technique (Mueller-Dombois & Ellenberg 1974) was applied to the set of relevé data from Haleakalā (111 relevés), while the reciprocal averaging technique using the computer program TWINSPAN (Hill 1979) was applied to the data set from Kinabalu (14 samples). The former is based on the presence/absence of species, while the latter is based on quantitative species values. Both methods generate sample and species groups, although the process and theory of classification are different. Details on the classification procedure and description of the classified vegetation units are given in the preceding chapters.

RESULTS

The mean number of taxa per plot is 3.8 for trees ≥2 m height on Haleakalā, and 30.4 for trees ≥10 cm DBH on Kinabalu (Table 4.3). The table does not include data from the floristic relevé analysis of Haleakalā.

Table 4.4 shows basic statistics on sample area, species number, tree density, and total basal area derived from DBH. The adequacy of using different lower size limits for comparative purposes on the two mountains (≥10 cm DBH for Kinabalu versus ≥2 m height for Haleakalā) may be questioned. However, the difference in forest-canopy heights can make up for the difference in the threshold values. On Kinabalu trees ≥10 cm DBH represent the canopy, subcanopy and upper shrub strata, while on Haleakalā trees ≥2 m height represent the canopy, subcanopy and shrub strata. Therefore, the sampled trees are representative of comparable forest strata on the two mountains.

HO 1: Alpha species diversity

Fisher's alpha index of diversity (Table 4.5) decreases exponentially with altitude from 97.3 at 600 m to 3.2 at 3400 m on Kinabalu. On Haleakalā it ranges from 0.5 to 5.0; the maximum value of 5.0 appears on the mid-slope at 1000 m, and is comparable to that of the subalpine zone on Kinabalu. The values of Fisher's index are based on trees ≥10 cm DBH for Kinabalu, while trees ≥2 m height are used for Haleakalā.

Species diversity values, based on Fisher's alpha index, at any altitude on Haleakalā are comparable to those of high altitudes on Kinabalu. The altitudinal change of the diversity index shows a normal curve with a mode on the midslope on Haleakalā but an exponential reduction with increasing altitude on Kinabalu. Thus, the first hypothesis is accepted.

HO 2: Species representativeness

The species sequence-dominance relationship

On Haleakalā, the species sequence-relative dominance relationship conforms to a somewhat straight line at all altitudes (Fig. 4.6). However, the linear pattern on Haleakalā is not distinct, because the species number per stand is very low. On Kinabalu, the relationship results in a near-sigmoid curve in the stands below 1800 m, while above it becomes linear (Fig. 4.7).

Results of the space allocation ratio are shown in Table 4.6. The regression on which the computation of the ratio was based is given for each altitude in Fig. 4.6 for Haleakalā and Fig. 4.7 for Kinabalu.

The space allocation ratio on Kinabalu increases with increasing altitude from 3.2% at 600 m to a maximum value of 32.1% at 2600 m (Table 4.6). Above 2800 m, the values of the ratio randomly fluctuate. On Haleakalā, the values of the ratio are >35% across altitudes and do not show an altitudinally consistent pattern (Table 4.6).

The value of 3.2% (600 m on Kinabalu) means that species are expected to preempt the remaining space (basal area) on an average of 3.2% successively from the most to the least dominant species; the first species occupies 3.2% =100 x 0.032 of the stand, the second one 3.1% =0.032 x (100-3.2), the third one 3.0% =0.032 x (100-3.2-3.1), etc.

The obtained values in Table 4.6 represent only the "expected" allocation ratio based on an average of actual species dominance values. Indeed, the curves depicted in Figs. 4.6 and 4.7 suggest that leading dominant species considerably deviate above the obtained regression lines. The deviation suggests that such species are occupying more space than the "expected" fraction based on the space allocation ratio. However, it is not known from the figures how many species occupy disproportionately more space than expected.

Number of dominant species

Table 4.7 shows how many species occupy disproportionately more space than expected in each plot with the results of the iterations and obtained d values. The numbers of dominant species so derived differ strongly between Haleakalā and Kinabalu. On Haleakalā, only one to three species dominate a stand regardless of altitude. On Kinabalu, the number of dominant species is greater at any altitude than on Haleakalā, and decreases generally with increasing altitude, ranging from 23 to four.

Many species occupy more space than expected at lower altitudes on Kinabalu, and share relatively similar, low dominance values. The number of dominant species decreases upslope, and the space allocation ratio increases upslope with sharper slope of the species sequence-relative dominance curves. Consequently, species evenness decreases with increasing altitude. By contrast, on Haleakalā, only a single or a few species occupy more space than expected and become dominant with high relative dominance values. This pattern of diminished number of dominants does not change with altitude on Haleakalā. Therefore, the second hypothesis that the lower regional floristic richness leads to higher predominance by fewer leading species per a stand is accepted.

HO 3: Spatial species turnover

The results from the computation of species turnover are indicated in Tables 4.8 (see step 4 in the computation procedure) and 4.9 (step 5). The unit species turnover is 0.81 HC on Haleakalā between 450 and 1900 m, and 11.83 HC on Kinabalu between 600 and 3400 m (Table 4.9). The average turnover rate, which is expressed by the logarithmic reduction of percentage similarity (PS), is 0.0385 $\ln(PS)\cdot 100\ m^{-1}$ on Haleakalā, and 0.2927 $\ln(PS)\cdot 100\ m^{-1}$ on Kinabalu. These values mean that for an IA to become cut in half, the altitude span of 1799 m is needed on Haleakalā, but only 236 m on Kinabalu.

In conclusion, both unit turnover and turnover rate of forest trees are much lower on Haleakalā than on Kinabalu. It may be argued that the values are not directly comparable between the mountains because the transect length below the forest line is longer on Kinabalu. However, the regression analysis was based on the relative gradient length <50% on Kinabalu (where the absolute length is longer), but <80% on Haleakalā (where the absolute length is shorter). Therefore, the conclusion is justified by the use of different thresholds, and the third hypothesis (spatial species turnover is less along the slope of Haleakalā than on Kinabalu) was accepted.

HO 4: Comparison of altitudinal zonation

Figure 4.8 schematically depicts the vegetation zones which are defined by the distributions of the associated-species groups differentiated in the classification analyses (see also Table 2.5 in chapter 2 for Kinabalu and Table 3.4 in chapter 3 for Haleakalā). Mean annual air temperatures estimated using the lapse rate of $0.55^{\circ}C \cdot 100\ m^{-1}$ are also indicated along the altitudinal gradients to characterize the vegetation zones. Information on the vegetation zones above the closed-forest line on Kinabalu is taken from Kitayama (1987, 1991). There, the open-canopied-forest line was considered the upper limit of the upper subalpine zone. The zones are named using the conventional terms by earlier workers in each region such as Grubb (1974, 1977) in Malesia and Gagné & Cuddihy (1990) in Hawaii. These conventional terms were used also in the previous chapters.

There are several differences in the zonation between Haleakalā and Kinabalu:

1) The forest line is depressed c. 700 m below the winter ground-frost line on Haleakalā, while on Kinabalu the forest line (the open-canopied-forest line) coincides clearly with the daily nocturnal ground-frost line;

2) The subalpine zone is scrub-dominated on Haleakalā, whereas on Kinabalu the zone is forested;

3) The upper and lower montane zones of Haleakalā are compressed in altitude relative to those on Kinabalu, and the same two zones on Haleakalā correspond to a single, upper montane zone on Kinabalu;

4) What is termed the "lowland" on Haleakalā parallels the "lower montane" zone on Kinabalu in terms of mean annual air temperature at their boundaries.

The mean annual air temperatures at the upper limits of the subalpine and montane zones are surprisingly similar between the two mountains. However, the within-year fluctuations of mean monthly temperatures are noteworthy. On Haleakalā there is a 3-4°C temperature seasonality, while on Kinabalu the temperature curve is almost a straight line through year (see Table 4.1). Therefore, the given temperatures in Fig. 4.8 are expected to fluctuate in altitude on Haleakalā, but are relatively persistent on Kinabalu.

Furthermore, it has been hypothesized that the moisture factor is more important in setting altitudinal limits of the montane zone on Haleakalā than the thermal factors (chapter 3). Nevertheless, the close similarities in mean annual temperatures at the vegetation boundaries suggest that the subalpine and montane zones are climatically homologous between the two mountains despite the physiognomic differences.

In conclusion, the number of differentiated floristic vegetation zones is only one fewer on Haleakalā (above 350 m) than on Kinabalu (above 600 m). The zones are similar in altitudinal range, and homologous in the temperature thresholds at the zonal boundaries between the two mountains. The reduced number on Haleakalā is attributable only to its lower-temperature regime at the base of the mountain which in turn is a function of the higher latitudinal position of the mountain. Thus, the hypothesis 4, that vegetation zones on Haleakalā are more expanded in distribution, and fewer in number than those on Kinabalu, is rejected.

DISCUSSION

The depression of the forest line on Haleakalā

The depression of Haleakalā's forest line (Fig. 4.8) can be explained by two biogeographic factors: 1) the absence of continental montane/subalpine genera such as those of Podocarpaceae in Hawaii; and, 2) the poor representation of highland-adapted species among existent rain forest tree genera in Hawaii (compare the ranges of *Syzygium*, *Myrsine* and *Ilex* between the two mountains in Fig. 4.8).

Podocarps of the genera *Dacrydium*, *Dacrycarpus*, and *Podocarpus* are the preponderant elements in the subalpine zones on equatorial African mountains (Troll 1958; Livingstone 1967), Andean mountains (Troll 1958; Walter 1979), and Malesian mountains (Wade & McVean 1969; Johns 1982; Kitayama 1987). The absence of these elements in Hawaii is due to the islands' geographic isolation.

To elaborate on the second point, the only rain forest tree species which extends beyond the current forest line on Haleakalā, is *Metrosideros polymorpha*. A stunted, pubescent-leaved sclerophyllous variety of the species, variety *polymorpha*, occurs above the forest line, but is widely scattered and confined to topographic depressions. According to Aradhya (1992), this morpho-variety corresponds to the genetic entity which is relatively sharply demarcated from the other populations of the same species occurring below the forest line. This variety is probably one of a few examples of adaptation into the high-altitude environment among Hawaiian rain forest tree genera.

On the geologically younger mountain of Mauna Kea on the neighboring island of Hawaii, Sophora chrysophylla forms a monospecific forest or a mixed forest with Myoporum sandwicense in the subalpine zone, and its forest line ascends as high as 2800 m (Mueller-Dombois 1981b; Scowcroft & Giffin 1983). By contrast, Sophora is shorter in stature on Haleakalā, and forms only scrub vegetation. Effects of the past grazing by feral sheep and goats (Scowcroft 1983; Scowcroft & Giffin 1983; Loope & Scowcroft 1985) may be one explanation for stunted Sophora, and become a contributing factor for the forest-line depression. However, this explanation is only putative, because feral grazers have long been eradicated in the subalpine area.

Patterns of altitudinal reduction in alpha diversity

Figure 4.9 compares the altitudinal reduction in the alpha species diversity (1) for trees ≥2 m height on Haleakalā with those for trees ≥10 cm DBH on several mountains where such data are available: (2) Mt. Kinabalu, Borneo; (3) a stable tropical mountain in Costa Rica; (4) a tropical volcanic mountain, Mt. Kerinci, Sumatra; (5) a temperate volcanic mountain, Mt. Fuji, Japan; and, (6) an ultramafic tropical mountain, Mt. Silam, Borneo. Altitudinal linear reduction with increasing altitude in alpha diversity of tree species seems to be typical on these continental and continental-island mountains regardless of substrate. By contrast, on Haleakalā, the alpha index follows a distinct normal curve with a maximum value on the mid-slope at 1000 m a.s.l.

Along a latitudinal gradient, Fisher's alpha diversity of forest species decreases exponentially in East Asia (Itow 1979, 1990). The implication is that the habitat harshness of the forests increases along the equator-to-pole gradient. The exponential reduction in Fisher's alpha diversity on Kinabalu (Fig. 4.9) simulates this latitudinal reduction. This may suggest the importance of thermal factors limiting diversity because the temperature lapse is nearly linear independent of other factors along both latitudinal and altitudinal gradients.

The deviation of diversity from the exponential pattern seems unique to oceanic islands where the flora is initially limited in number, and disharmonic (Carlquist 1974). Adaptability of current native plant species to altitudinal climates may be predefined by the physiology intrinsic to their progenitors. Thus, the ecological amplitude of radiated sibling species, and the course of community development including species diversity are set probably by the initial flora. The normal curve on Haleakalā suggests the hypothesis that the majority of the tree species are preadapted to wet montane habitats.

Species representativeness and sympatric congeneric species

The species representativeness on Kinabalu follows a lognormal distribution pattern (near-sigmoid) at low altitudes and becomes a geometric series (linear) with increasing altitude (Fig. 4.7). That on Haleakalā conforms to a geometric series across all altitudes (Fig. 4.6). Two explanations can be derived from the results.

First, the allocation of space (i.e. resources) among species is not randomly determined on the two mountains. The obtained lognormal and geometric patterns depart from MacArthur's broken stick model which is based on the random niche boundary hypothesis (MacArthur 1957). This model predicts that the resource/space allocation among species is randomly determined. The lognormal distribution pattern is believed to be a consequence of several factors, among which competitive species preemption, and stochastic events are important (Whittaker & Woodwell 1969; Itow & Miyata 1977; Hubbell 1979). The geometric series is interpreted to suggest stronger space preemption by species competition than the lognormal curve (Whittaker 1972; Itow & Miyata 1977; Hubbell 1979).

Secondly, it seems that the number of sympatric congeneric species within a stand is proportionate to the number of dominant species and to the extent of deviation of the leading dominant species from regression lines in the stand (Figs. 4.6 and 4.7). Table 4.10 shows the number of congeners per genus, and the frequency of genera which contain sympatric congeners within each stand. On Kinabalu, the number of genera which have multiple sympatric congeners, and the highest number of congeners per genus decrease with increasing altitude. On the lower slope below 1800 m, there are several genera which have more than five sympatric congeneric species. One genus (Eugenia) has a total of 13 morpho-species at 1200 m. A high number of sympatric congeneric species is typical for the lowland rain forest in the western part of Malesia (Poore 1968; Ashton 1969). By contrast, the maximum number of sympatric congeneric taxa on Haleakalā is only two, and most of them are found on the midslope.

The fact that a higher number of sympatric congeners per stand is associated with a higher number of dominant species in the same stand appears contradictory. This is because congeneric species can be relatively similar in their overall architecture and morphology, thus the coexistence of multiple density-dependant congeneric species (cf. semi-species in MacArthur 1972) is theoretically expected to lead to strong competitive exclusion and a consequent population decline of "losing" species.

However, it is known that several sympatric congeneric taxa are highly divergent in autoecological characteristics and adaptive to different site-resources in Malesian Dipterocarpaceae (Ashton 1969, 1977) and Annonaceae (Rogstad 1990), and in Hawaiian Metrosideros (Stemmermann 1983). Several species of the family Dipterocarpaceae spatially and temporally utilize different parts of space and resources of the same site, thereby reducing competition among them. Habitat heterogeneity brought about by periodic micro- to meso-scale disturbances (Denslow 1987) is probably another mechanism for such congeners to coexist.

Most dominant species on Haleakalā have complementary relationship in upper synusia. For instance, a first leading species occurs in the canopy synusia, while a second dominant species in the subcanopy or shrub synusia. The only exception is the two conspecific varieties of Metrosideros polymorpha (i.e. glaberrima and incana), which occur in the same canopy layer at 1200 m with similar relative dominance values. It is not known whether one variety with a slight phenotypic difference in the leaf-pubescence is selectively favored over the other in this perhumid cloud-zone habitat.

The diminished species richness on Haleakalā despite its favorable climate is definitely a consequence of the geographic isolation of Hawaii. Another factor contributing to the low species richness and evenness (representativeness) per stand on Haleakalā (Fig 4.6 and Table 4.7) seems to be the less advanced differentiation of sympatric congeneric tree taxa.

Altitudinal vegetation zonation and parapatric occurrence of congeneric species

The results demonstrate a similar number of altitudinal vegetation zones on the two mountains (Fig. 4.8). This similarity exists despite the striking difference in species turnover along the slopes of the two mountains (beta diversity, Table 4.9). This apparent contradiction can be explained as follows:

The close agreement in the number of altitudinal floristic vegetation zones suggests that the two mountains support a similar number of altitudinal indicator groups of species. However, there are many species which extend from the lowland to the forest line over an extremely broad range on Haleakalā. Such wide-ranging species occur also on Kinabalu, but they are limited in number. Therefore, vegetation units on Haleakalā display a strong hierarchy, while those on Kinabalu express a very weak one (Fig. 4.8).

Interestingly, altitudinal floristic organization becomes similar on the two mountains when generic distributions are compared (Fig. 4.10). Figure 4.10 also shows the geographic distribution of each genus, cited from Mabberley (1987). On both mountains, tropical elements occur at low altitudes, while cosmopolitan, subtropical and warm-temperate elements stretch over a broad altitudinal range from low/mid to high altitude regions.

One important conclusion is that both Haleakalā and Kinabalu support a very similar altitudinal pattern of generic distributions. The two mountains differ in the fact that the altitudinal species differentiation of these wide-ranging genera is less advanced on Haleakalā but far more advanced on Kinabalu where the differentiation resulted in parapatric congeneric distribution patterns of distinct morpho-species. The account by Lee and Lowry (1980) indicates that the genus Leptospermum is one example, which has expanded into the postglacial summit area. Sibling species of this genus are morphologically and genetically distinct, and do not overlap in their altitudinal ranges.

Aradhya (1992) found that the wide-ranging dominant species on Haleakalā, Metrosideros polymorpha, has become genetically differentiated into three altitudinal entities, but the differentiation is incipient and intra-specific. Notably, the three genetic entities correspond to the three vegetation units, which are floristically differentiated in this study. The coincidence indicates that climatic factors are important driving forces for altitudinal species segregation.

CONCLUSIONS

Mode of altitudinal species/vegetation differentiation: a hypothesis based on the results

In the first chapter, Whittaker's concept on the species packing and diversion of species modes along an altitudinal gradient was schematically described. The concept of altitudinal gradient and species packing now needs to be modified in the light of the results from this study.

First, in a strict sense, an "altitudinal gradient" cannot be considered a "resource gradient" along which species become differentially adapted with Gaussian curves. In reality, the altitudinal gradient is merely the space concept of a directional axis along which multi-resource gradients form a continuum.

Secondly, there are stabilizing mechanisms (Arthur 1987) which may sympatrically preserve a newly arisen or introduced taxon which is genetically related to other congeners of the same habitat. One mechanism can be the differentiation in autoecological characteristics such as flowering period and root depth. This has been termed "niche differentiation" (Whittaker 1972; Chesson 1991).

Stochastic disturbances can be another mechanism to perpetuate mutually related competitors in the same site by creating temporal habitats.

In theoretical models, site-disturbance events have always been contrasted with the autecological niche differentiation of species (Denslow 1987; Chesson 1991) as to which mechanism is more important in allowing a stable multi-species coexistence. The former is described as "stochastic," the latter as "deterministic." However, the two mechanisms may be complementary in some plant communities where species or intraspecific varieties with divergent autecological characteristics have adapted to different disturbance regimes which create heterogeneity in their habitat.

To elaborate on the first remark, a given point along an altitudinal "gradient" consists of multiple environment/ resource gradients. Figure 4.11 schematically depicts such a multi-dimensional coordinate system along an altitudinal axis. There are many kinds of resources at one end of the altitudinal axis, among which light, temperature, water and nutrients will be four major gradients. These factors become four axes of a four-dimensional coordinate system as depicted here. The altitudinal axis is, in reality, the continuum of such four-dimensional coordinates (see diagram a). The intensity of each of the four resource gradients changes along the altitudinal axis; a few resource gradients (e.g. air temperature) change unidirectionally along the axis, while the rest (e.g. moisture) does not change unidirectionally. Thus, the total volume of the four-dimensional coordinate system changes along the altitudinal axis, although there is always the same number of resource gradients at any given point. This multi-dimensional coordinate system is similar in concept to the niche hyperspace of Hutchinson (1957-cited in Whittaker 1972). It may be conveniently considered a "habitat" at a given altitude. There are two scenarios which explain the results of this study.

1. Coexistence associated with sympatric congeneric taxa: The first scenario involves the stabilized coexistence of congeneric taxa, and proceeds from diagram (a) to (b). Initially four species are given along the altitudinal axis (a). They are divergent in the four resource gradients, and the interspecific competition is reduced among them. Their species dominance pattern varies from one altitude to another, because the absolute length of each of the resource gradients changes along the altitudinal axis, and subsequently also the biotic interactions among them change. Given a new allele or a new congeneric species whose ecological characteristics are slightly different from the rest, such an addition will increase competition. The competition is inter-genotypic in the former, and interspecific in the latter (Arthur 1987). Despite the

intergenotypic competition or the exclusion in the interspecific competition (Arthur 1987), the newly arisen taxon may be preserved by: 1) the adaptation to a different part of the resource coordinate system (=niche differentiation); 2) stochastic events; and, 3) the combination of both. According to Ashton (1977), among species of Shorea (Dipterocarpaceae), a shift of reproductive strategy becomes a cofactor for stabilizing sympatric congeners. These species are primarily density dependent in demography, and obligate outbreeders. Selection of a new form of a species will lead to a drastic decline of another form of the same species. The shift of sexual reproduction to apomixis is attributed to a counter-mechanism to save the declining obligate outbreeding species of Shorea.

This process will result in the coexistence of mutually related taxa. Consequently, the initial range of its progenitor will be maintained without being narrowed. In this scenario, alpha diversity increases from four to five species at one end of the altitudinal axis. Beta diversity changes little (from 0 to 0.17 based on Sørensen's coefficient of community assuming IA=100%, see diagram b).

2. Exclusion associated with parapatric congeneric taxa: The second scenario involves the exclusion of a competing taxon, and proceeds from diagram (a) to (c). Given a new allele or a new congeneric species which is very similar in resource demand and morphology to the rest; the

allele or species is selected at the expense of its competing form if the new taxon has a better fitness in the given multi-dimensional coordinate, and if the system is stable. Consequently, the distribution range of the ancestral entity becomes narrower. The new entity becomes discrete to its ancestor in altitudinal range. This form of speciation leads to an increase in beta diversity while alpha diversity remains unchanged. In diagram (c) beta diversity changes from the initial value of 0 to 0.42 based on Sørensen's CC assuming IA=100%.

Results of this study suggest both modes of altitudinal differentiation proceed probably simultaneously. However, it appears that the processes are much more advanced on Kinabalu than on Haleakalā. The evidence is the very low alpha and beta diversities on Haleakalā, and fewer examples of sympatric and parapatric congeners on Haleakalā than on Kinabalu. This difference is probably related to the initial floristic impoverishment.

Final remarks

It is inferred from the results of this study that the initial flora and floristic richness of the region is one important factor setting the subsequent pattern and extent of alpha and beta diversities along slopes. Geographic location and isolation chiefly determine the initial native flora and regional richness on oceanic islands, which in turn control spatial patterns of the subsequent species differentiation. Thus, the results do not entirely support Whittaker's hypothesis, at least on Haleakalā, that evolution is a self-augmenting process without an intrinsic limit on alpha and beta diversities. It seems that the initial disharmonic and impoverished flora on Haleakalā limits the increase in alpha and beta diversities of tree/shrub species in the rain forest community, hence limits its evolutionary community organization. This hypothesis applies primarily to the rain forest, not necessarily to all Hawaiian biomes.

In some of the other Hawaiian biomes, there are several examples of explosive adaptive radiation where a single progenitor has speciated into many morphologically and ecologically diverse sibling species ranging from one habitat extreme to another (e.g. Hawaiian Bidens and the silversword alliance, Carr 1987). However, their occurrence is often extremely localized and not sympatric. Therefore, adaptive radiation in Hawaii is definitely reflected in an increase of regional floristic richness (i.e. gamma diversity sensu Whittaker 1972) in the form of endemism, but this is not often witnessed at the level of individual sample stands or relevés.

The results of this study also do not entirely agree with Whittaker's conclusion that evolution results in random modes and limits of distribution curves for competing species along gradients driven by adaptation and competitive exclusion. The altitudinal vegetation zones, which are defined by groups of species with the same ranges, are distinct and discrete both on Haleakalā and Kinabalu. These are the species which converge to a zonal range of altitudinal climate through biological interactions in plant communities.

The altitudinal zones on the two mountains are a consequence of a number of factors. Among these, temperature and precipitation are most important. The discreteness and altitudinal limits of climatic zones probably determine the range, number and discreteness of vegetation zones. The importance of climatic factors, particularly of altitudinal temperature lapse, has been demonstrated by many authors including Grubb (1974, 1977), Sakai & Larcher (1987), and Ohsawa (1990).

It must be emphasized that categorizing vegetation on mountain slopes into zonal units is not necessarily a subjective or arbitrary process as criticized by some authors. It can be done by ecologically meaningful methods of abstraction from vegetation samples (relevés), which then becomes an optimal presentation of factual reality.

ACKNOWLEDGEMENTS

I thank Drs. D. Mueller-Dombois, G. D. Carr, C. W. Smith, H. Ikawa & T. W. Giambelluca at the University of Hawaii at Manoa for their critical comments on the manuscript. The Toyota Foundation, Tokyo, and the East-West Center, Honolulu, financially supported the project. My wife, Reiko Kitayama, and my brother, Yutaka Kitayama, are gratefully acknowledged for their excellent assistance in the field work and data analysis.

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Table 4.1. Comparison of some biogeographically important parameters of Mt. Haleakala and Mt. Kinabalu.

	Haleakala	Kinabalu
Latitude	20°45'N	06°05'N
Altitude	3055 m	4101 m
Geological age (million years)	Early Pleistocene (0.8 m.y.)	Folding of Tertiary sedimentary rock in the upper Miocence (7 to 9 m.y.), uplift of the summit granite in the early Pleistocene (1.5 m.y.)
Substrate & geology	Basaltic Volcanic	Tertiary sedimentary rock below 2700 m a.s.l., granite above Non-volcanic
Topography	Shield-shaped	Steep and rugged
Altitude/distance	(3055-450 m)/17 km	(4101-500 m)/17 km
Native vascular flora	Several hundred?[1] (c.f. 956 flowering plant spp. in Hawaii[3]) (c.f. 237 spp. on the leeward slope[4])	c. 4000 spp.[2]
Floristic affinity	Mostly Malesian with Australasian, North & South American, & boreal affinities	Malesian, east-Asiatic & Australasian
Mean annual air temp. at sea level	24.4°C (Honolulu Airport)	27.0°C (Sandakan, Sabah)
Month-to-month air temp. difference (warmest-coldest)	3 to 4°C	<1°C
Maximum mean annual rainfall	6500 mm on the mid-slope	>4000 mm on the mid-slope

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[1] No data available

[2] Beaman & Beaman (1990)

[3] Wagner et al. (1990)

[4] Medeiros et al. (1986)

Table 4.2. Similarity matrices among the sampled forest stands. Percentage similarity values based on Motyka's equation (see text).

Alt.x10 m

Haleakala

45	100								
60	53	100							
80	46	81	100						
100	41	77	81	100					
120	56	69	63	65	100				
140	56	56	53	59	74	100			
160	56	58	50	50	72	83	100		
180	56	56	48	48	69	81	93	100	
190	50	52	48	43	53	56	56	59	100
	45	60	80	100	120	140	160	180	190

Alt.x10 m

Kinabalu

60	100													
80	45	100												
100	21	13	100											
120	5	9	12	100										
140	1	2	6	24	100									
160	1	2	3	17	28	100								
180	0	0	2	5	15	27	100							
200	0	0	1	7	16	10	20	100						
235	0	0	0	1	2	3	4	8	100					
260	0	0	0	1	3	7	12	7	21	100				
280	0	0	0	0	2	6	15	1	1	12	100			
300	0	0	0	0	2	2	2	1	3	6	37	100		
320	0	0	0	0	2	6	7	1	2	9	30	59	100	
340	0	0	0	1	2	6	28	1	2	9	31	18	35	100
	60	80	100	120	140	160	180	200	235	260	280	300	320	340

Table 4.3. Number of tree taxa enumerated along the transects.

	Altitude transect	Number of plots (N)	Number of taxa (S)	Mean number of taxa per plot (S/N)
Haleakala	450-1900 m	9	34($\geq$2 m h)	3.8
Kinabalu	600-3400 m	14	425($\geq$10 cm DBH)	30.4

Table 4.4. Basic statistics characterizing the transects.

Haleakala (trees≥2 m height)

Alt. (m)	Quadrat (m^2)	Species number (per quadrat)		Total BA ($m^2 \cdot ha^{-1}$)		Density (trees·ha^{-1})	
		≥2m	≥5m	≥2m	≥5m	≥2m	≥5m
450	2500*	3	1	4.8	1.1	3450	8
600	400	7	2	9.5	2.3	1750	175
800	400	14	2	29.4	11.3	6350	1250
1000	400	19	10	60.4	37.4	5525	2075
1200	400	17	13	57.1	48.5	6950	2825
1400	400	20	14	69.3	64.5	8050	2250
1600	400	16	5	53.6	48.9	5950	1825
1800	400	8	7	86.9	84.4	2000	1500
1900	400	9	5	50.2	44.2	2675	850

* Sampled by a 50x50m quadrat

Kinabalu (trees≥10 cm DBH)

Alt. (m)	Area (m^2)	Sp.no. per plot	Sp.no. ($0.1ha^{-1}$)	Total BA ($m^2 \cdot ha^{-1}$)	Density (ha^{-1})
600	11 188	153	27	33.4	333
800	8063	102	27	29.8	372
1000	5636	93	24	27.5	369
1200	4027	79	33	34.0	447
1400	2477	70	39	46.6	759
1600	3707	58	29	33.2	572
1800	3441	41	24	39.0	593
2000	4907	50	24	36.7	497
2350	1439	26	25	59.5	778
2600	1700	13	13	49.2	659
2800	1034	16	17	26.4	1044
3000	574	17	17*	55.4	1950
3200	932	14	14*	57.4	1202
3400	542	11	11*	45.0	1844

* Extrapolated value from a plot smaller than 0.1ha

Table 4.5. Species diversity based on Fisher's alpha index.

Altitude (m)	Haleakala	Kinabalu
450	0.5	-
600	1.9	97.3
800	3.2	54.5
1000	5.0	64.6
1200	4.0	53.7
1400	4.7	40.5
1600	3.9	26.4
1800	2.2	15.5
1900	2.3	-
2000	-	19.0
2350	-	10.6
2600	-	3.8
2800	-	5.2
3000	-	5.6
3200	-	4.3
3400	-	3.2

Table 4.6. Space allocation ratios R (%) derived from log(1-R)=x coefficient.

Altitude (m)	Haleakala	Kinabalu
450	41.5	-
600	65.1	3.2
800	44.3	4.7
1000	38.5	5.1
1200	36.8	6.0
1400	35.3	6.2
1600	41.6	7.3
1800	55.1	12.2
1900	47.2	-
2000	48.2	11.2
2350	-	14.8
2600	-	32.1
2800	-	22.9
3000	-	15.8
3200	-	30.6
3400	-	28.1

Table 4.7.
Number of dominant species statistically differentiated using the dominance analysis (Ohsawa 1984), and results from the iteration of the analysis.
I, iteration; T, number of dominant species; x, expected relative dominance value of a dominant species (x=100/T). Indicated values in the matrix are deviation values. Minimum deviations are underlined.

Haleakala (trees ≥ 2 m height)

I&T	X	Altitude (m)								
		450	600	800	1000	1200	1400	1600	1800	1900
1	100	964	489	376	403	142	65	27	56	410
2	50	351	52	6	45	118	146	257	423	43
3	33.3	267	164	91	52	114				104
4						132				
Number of dominants		3	2	2	2	3	1	1	1	2

Kinabalu (trees ≥ 10 cm DBH)

I&T	X	Altitude (m)													
		600	800	1000	1200	1400	1600	1800	2000	2350	2600	2800	3000	3200	3400
1	100	52.59	65.21	84.86	89.44	92.79	68.35	136.3	161.9	204.3	219.8	371.2	296.3	317.9	567.5
2	50	21.05	26.41	34.34	35	33.68	32.83	43.42	62.59	85.28	122.9	136.1	97.64	98.68	126.9
3	33.33	11.16	15.58	19.58	19.37	20.64	25.17	24.85	31.87	50.82	113.9	69.39	55.49	66.84	56.09
4	25	6.33	11.04	12.78	13.99	14.65	22.21	20.36	17.77	36.91	110.2	44.98	48.2	55.65	49.01
5	20	4.83	8.46	9.39	10.85	11.83	20.74	18.02	12.31	29.83	108.7	32.62	47.4	54.53	
6	16.67	3.85	7.09	7.2	8.93	10.25	20.72	16.53	8.82	26.49	118.1	29.35	46.99	57.83	
7	14.29	3.18	6.2	5.91	7.74	9.22	20.87	15.8	6.87	25.05		27.33	47.28		
8	12.5	2.78	5.6	5	6.86	8.56	21	16.05	5.56	24.08		26.59			
9	11.11	2.45	5.18	4.33	6.27	8.09		16.42	5.21	23.68		27.85			
10	10	2.28	4.85	3.81	5.84	7.83			5.02	23.43					
11	9.09	2.16	4.59	3.4	5.51	7.62			4.91	24.41					
12	8.33	2.06	4.42	3.07	5.26	7.46			4.92						
13	7.69	2	4.28	2.86	5.08	7.35									
14	7.14	1.94	4.17	2.73	4.93	7.27									
15	6.67	1.91	4.09	2.63	4.81	7.21									
16	6.25	1.88	4.039	2.56	4.71	7.17									
17	5.88	1.87	4	2.511	4.64	7.15									
18	5.56	1.86	3.97	2.48	4.6	7.14									
19	5.26	1.855	3.95	2.45	4.56	7.13									
20	5	1.858	3.94	2.43	4.54	7.14									
21	4.76		3.927	2.417	4.53										
22	4.55		3.928	2.418	4.528										
23	4.35				4.526										
24	4.17				4.529										
Number of dominants		19	21	21	23	19	6	7	11	10	5	8	6	5	4

Table 4.8. Results of the linear least-square regression analysis in the computation of beta diversity.

	Haleakala (450-1900 m)	Kinabalu (600-3400 m)
Regression	$y=4.299-0.005584x$	$y=3.609-0.08196x$
r^2	0.314	0.566
N	32	63
F	13.8	79.4

Table 4.9. Internal association (IA), half-change (HC), turnover rate, and altitude required for IA to be reduced in half.

	Haleakala	Kinabalu
IA (%)	73.6	36.9
HC	0.81	11.83
Turnover rate ($\ln PS \cdot 100m^{-1}$)	0.0385	0.2927
Altitude (m) for 50 % reduction	1777	236

Table 4.10. Sympatric occurrence of congeneric taxa. Figures indicate the number of genera per number of congeneric taxa (S) ranging from monospecific (S=1) to multispecific (S=2,3,4----) genera among the enumerated species along the transects. For example, at 1900m on Haleakala, 7 genera are monospecific, 1 genus has 2 sympatric congeners in the same plot.

Haleakala (trees ≥2 m height)

Alt.	Number of congeneric taxa (S)		Total number	
(m)	1	2	sp.	genus
	(Number of genera)			
450	3	-	3	3
600	7	-	7	7
800	10	2	14	12
1000	11	4	19	15
1200	11	3	17	14
1400	12	4	20	16
1600	14	1	16	15
1800	8	-	8	8
1900	7	1	9	8

Kinabalu (trees ≥10 cm DBH)

Alt.	Number of congeneric taxa (S)													Total number	
(m)	1	2	3	4	5	6	7	8	9	10	11	12	13	sp.	genus
	(Number of genera)														
600	65	17	1	4	3	1	2	-	-	-	-	-	-	153	93
800	39	14	4	-	2	1	1	-	-	-	-	-	-	102	61
1000	49	6	3	3	-	-	-	-	-	-	1	-	-	93	62
1200	41	6	-	2	1	-	-	-	-	-	-	-	1	79	51
1400	42	5	1	-	1	-	-	-	-	1	-	-	-	70	50
1600	31	4	2	-	-	1	1	-	-	-	-	-	-	58	39
1800	25	3	-	1	-	1	-	-	-	-	-	-	-	41	30
2000	33	4	3	-	-	-	-	-	-	-	-	-	-	50	40
2350	20	3	-	-	-	-	-	-	-	-	-	-	-	26	23
2600	13	-	-	-	-	-	-	-	-	-	-	-	-	13	13
2800	10	3	-	-	-	-	-	-	-	-	-	-	-	16	13
3000	10	2	1	-	-	-	-	-	-	-	-	-	-	17	13
3200	14	-	-	-	-	-	-	-	-	-	-	-	-	14	14
3400	11	-	-	-	-	-	-	-	-	-	-	-	-	11	11

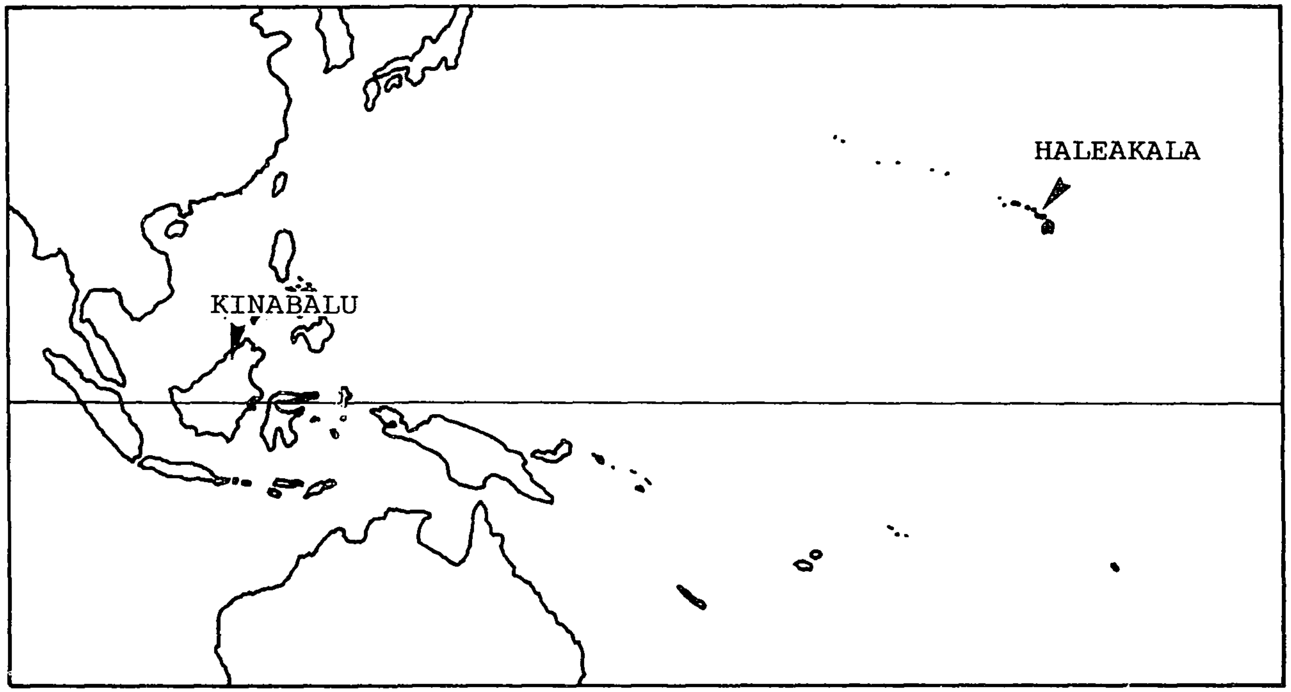


Fig. 4.1. Map showing the location of Mt. Haleakala and Mt. Kinabalu.

This figure demonstrates two different types of species representativeness using two hypothetical data sets each with 20 species. In each raw-data matrix (lower diagram), species are sequentially ordered from the top to the 20th species in the descending order of relative dominance values which total to 100. Straight lines, next to the relative dominance values, represent space K which is divided by the species proportionally according to their dominance values. Each of the upper diagrams depicts the species sequence-relative dominance relation of the given data set. The data set of (a) results in a sigmoid pattern, and the pattern has been termed as lognormal distribution curve; that of (b) results in a linear pattern which has been termed geometric series (Whittaker & Woodwell 1969; Whittaker 1972; Itow & Miyata 1977).

A sigmoid curve as termed the lognormal distribution (a) suggests that a few leading dominants occupy a relatively large fraction of the stand, and that mid-sequence species occupy mutually similar, modest to small fractions. Some of the least important species tail down sharply.

When the relationship shows a straight line (b), each species fills the same fraction of a remaining space following a geometric series: a first dominant species preempts a fraction (defined as R) of a given space (defined as K), a second dominant fills the same fraction R of the unfilled space K(1-R), a third dominant fills the same fraction R of the unfilled space $K(1-R)^2$, and i-th species fills the fraction R of the unfilled space $K(1-R)^{i-1}$. Thus, a linear relationship between the relative dominance (log) and the species sequence indicates the geometric series $K(1-R)^{i-1}$. Here, the term, space, can be substituted with an actually measurable parameter such as basal area. It should be noted that the species sequence by no means connotes a temporal sequence of species filling in a given stand. It is merely a result of multi-species interaction as well as stochastic effects in the stand seen at the time of field sampling.

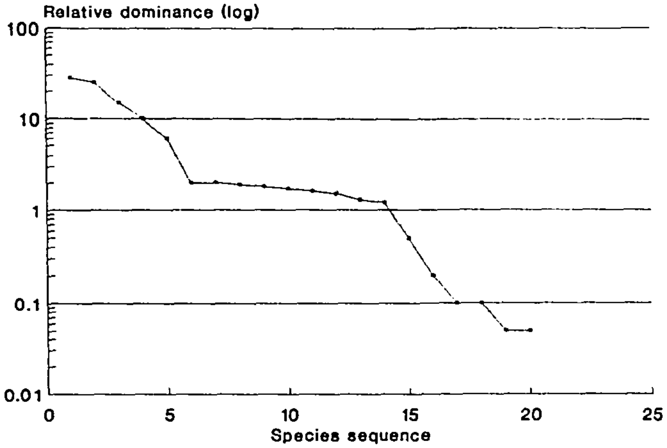
Inversely, if a geometric series is expressed, a linear regression y=a + bx will be given between the logarithmic relative dominance (y) and the species sequence (x). In this regression, the x coefficient, b, becomes equal to log(1-R).

Although the species sequence (x) and the relative dominance (y) are statistically dependent on each other, the regression analysis between these two parameters is a useful way of expressing an average inclination of the curvilinear relation. The inclination is indicated by b=log(1-R). The correlation coefficient r^2 indicates the degree of deviations of the actual species values from the geometric series.

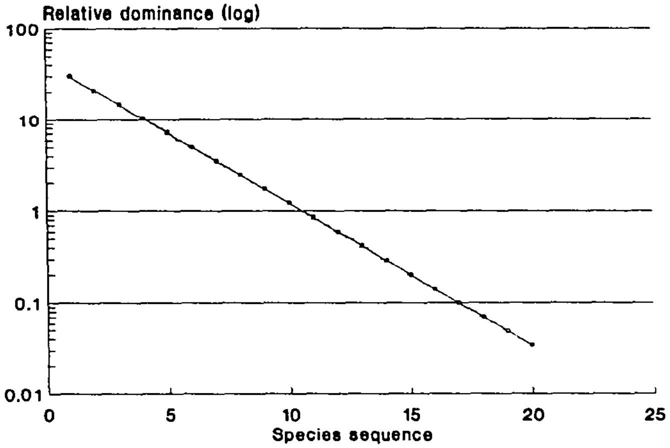
In the following, the fraction R obtainable from the regression analysis using log(1-R)=b is tentatively termed the "space allocation ratio." Thus, the ratio is an index of the space preemption by the i-th species in a stand expected from the average curvilinear inclination. It expresses how species are represented and packed within a stand.

Fig. 4.2. Theoretical explanation of the species sequence-relative dominance relationship, and definition of the "space allocation ratio," using hypothetical data sets.

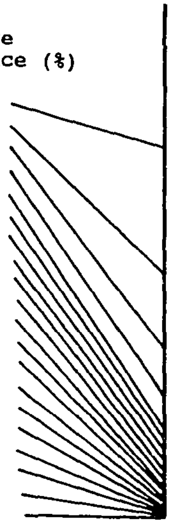
(a) Lognormal distribution curve



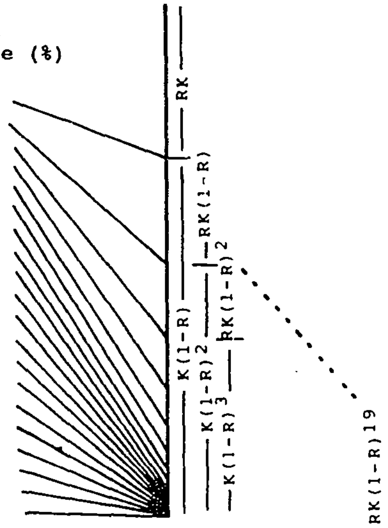
(b) Geometric series



Species sequence	Relative dominance (%)
1	28
2	25
3	15
4	10
5	6
6	2
7	2
8	1.9
9	1.8
10	1.7
11	1.6
12	1.5
13	1.3
14	1.2
15	0.5
16	0.2
17	0.1
18	0.1
19	0.05
20	0.05
Total	100



Species sequence	Relative dominance (%)
1	30
2	21
3	14.7
4	10.29
5	7.20
6	5.04
7	3.53
8	2.47
9	1.73
10	1.21
11	0.85
12	0.59
13	0.42
14	0.29
15	0.20
16	0.14
17	0.10
18	0.07
19	0.05
20	0.03
Total	100



HC is a measure of the gradient length where the community similarity between that point and the initial point of the gradient becomes one half of the internal similarity at the initial point. The HC value is the reciprocal of the obtained gradient length. In the top diagram, the x-axis is the gradient length, and scaled to 100; the y-axis is the community similarity between the sample of a given point and the sample at the initial point (x=0). The diagram depicts two lines with different turnover values. On line (a), community similarity becomes one half (50%) where gradient length is 75, hence HC is (1/75) x 100 =1.33. Similarly, on line (b), a half-change occurs at the length of 100, thus HC is (1/100) x 100 =1. The higher HC is, the more rapid turnover is. Thus, line (a) indicates a higher turnover than line (b) does.

In the above, the similarity index at the initial gradient point (internal similarity) was assumed to be 100%. However, when multiple replicate samples are placed side by side at the same gradient point, the reciprocally calculated similarity index among the replicates always results in a value <100%. This reciprocal similarity among replicates at the same gradient point is termed the "internal association (IA)" (Whittaker 1960). Such a low IA value is attributed to "sampling noise" (Whittaker 1975; Shmida & Wilson 1985). Nevertheless, no matter how carefully a field sampling is made, lower IA values <100% are inherent to actual vegetation. If vegetation is adequately sampled, the IA itself can be an index of the homogeneity of vegetation and of the species dispersion. Especially low IA values are believed to be typical in species-diverse and species-scattered lowland tropical rain forests (Hubbell & Foster 1986), when sampled by a conventional plot of a few hectares.

It is readily expected that a low IA value can erroneously result in higher altitudinal turnover if a correction is not made. As in the middle diagram, when a similarity index of 60% is obtained between two altitudinally separated replicate groups along a continuum of vegetation with IA of 50%, the result suggests that the true altitudinal turnover is null. This is because the altitudinal species change of 40% (=100-60) is less than the *in situ* variation of 50%.

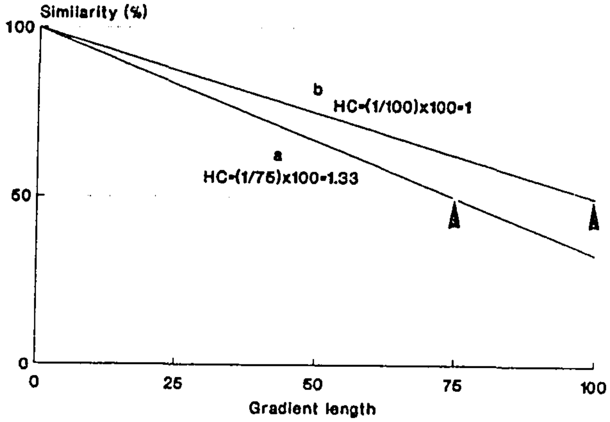
To correct the masking effects of internal variance (i.e. IA), the HC is now expressed as the ecological gradient length where similarity becomes one half of IA as in the lower diagram. In line with this diagram, Whittaker (1972) gave a fundamental equation to compute HC:

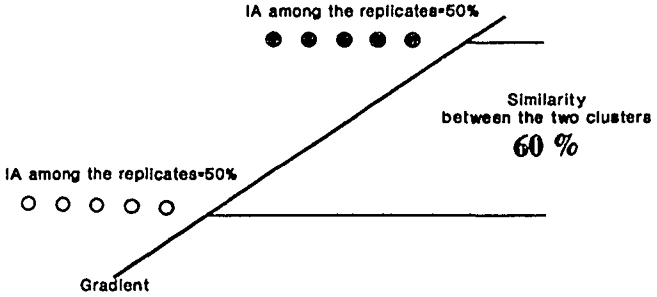
HC(a,b) = (log(IA) - log[S])/log2 (Whittaker 1972)

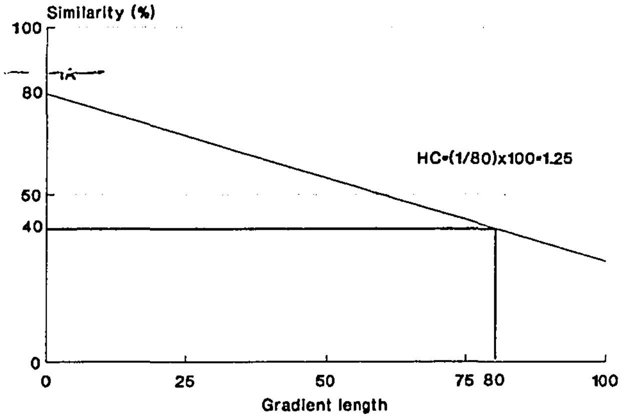
where HC(a,b) is the half-change between the samples a and b, and S is the similarity index value between a and b.

In this study, a modified equation by Wilson & Mohler (1986) is actually used for computing HC, as shown in the text. The IA value can be theoretically calculated following Wilson & Mohler (1986) and Itow (1990). It is the y value where the line of the lower diagram intercepts with.

Fig. 4.3. Theoretical consideration of the computation of the beta diversity index, HC.


Similarity (%)
100
50
0
b
HC=(1/100)x100=1
a
HC=(1/75)x100=1.33
0
25
50
75
100
Gradient length


IA among the replicates=50%
Similarity
between the two clusters
60 %
IA among the replicates=50%
Gradient


Similarity (%)
100
IA
80
HC=(1/80)x100=1.25
50
40
0
0
25
50
75
80
100
Gradient length

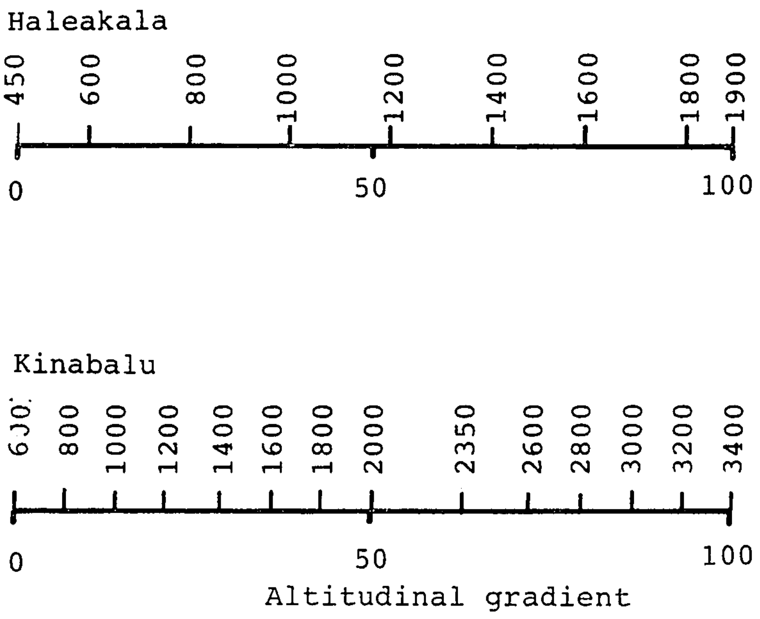


Fig. 4.4. Relative locations of the sampled stands along the altitudinal gradients scaled to 100.

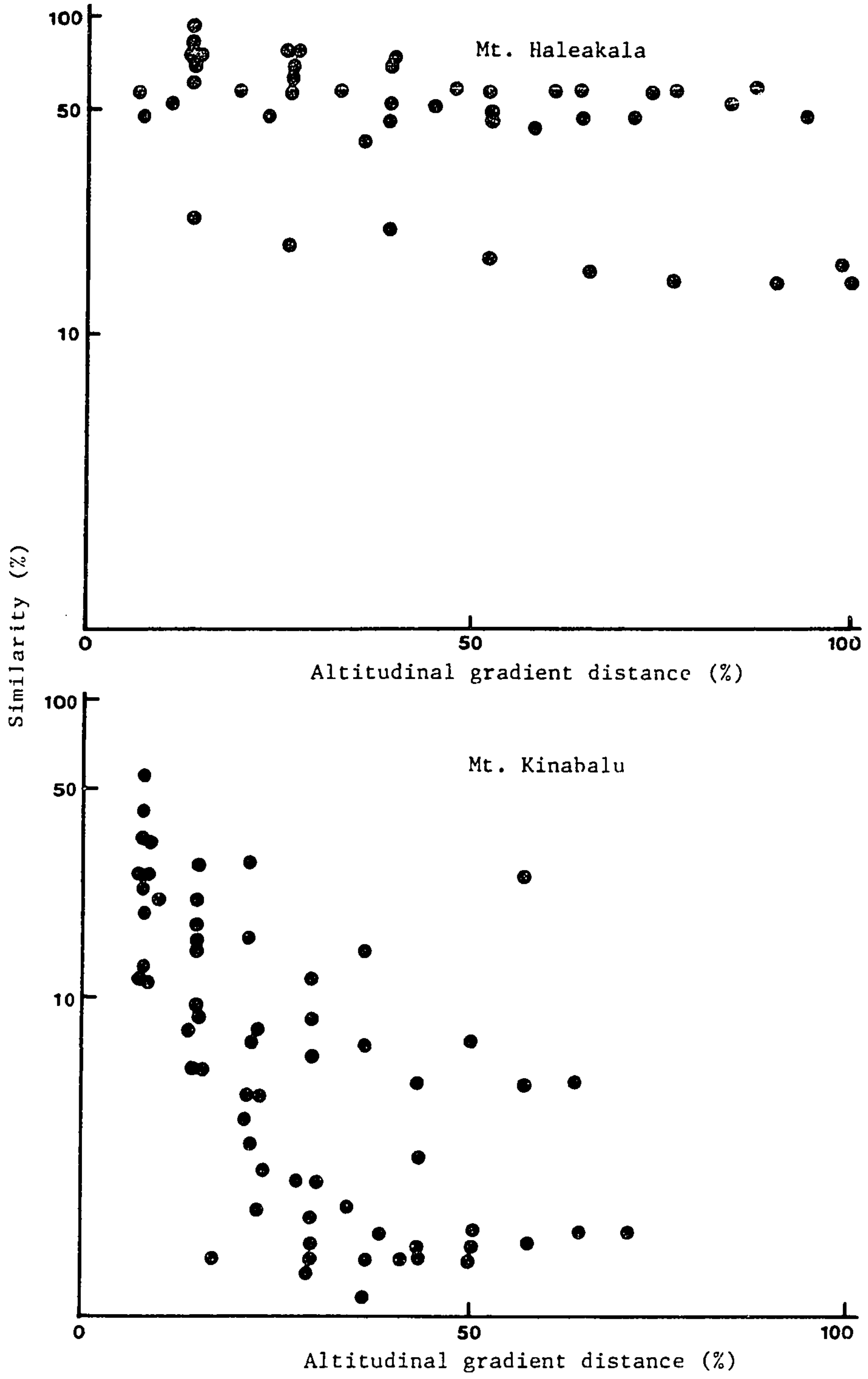
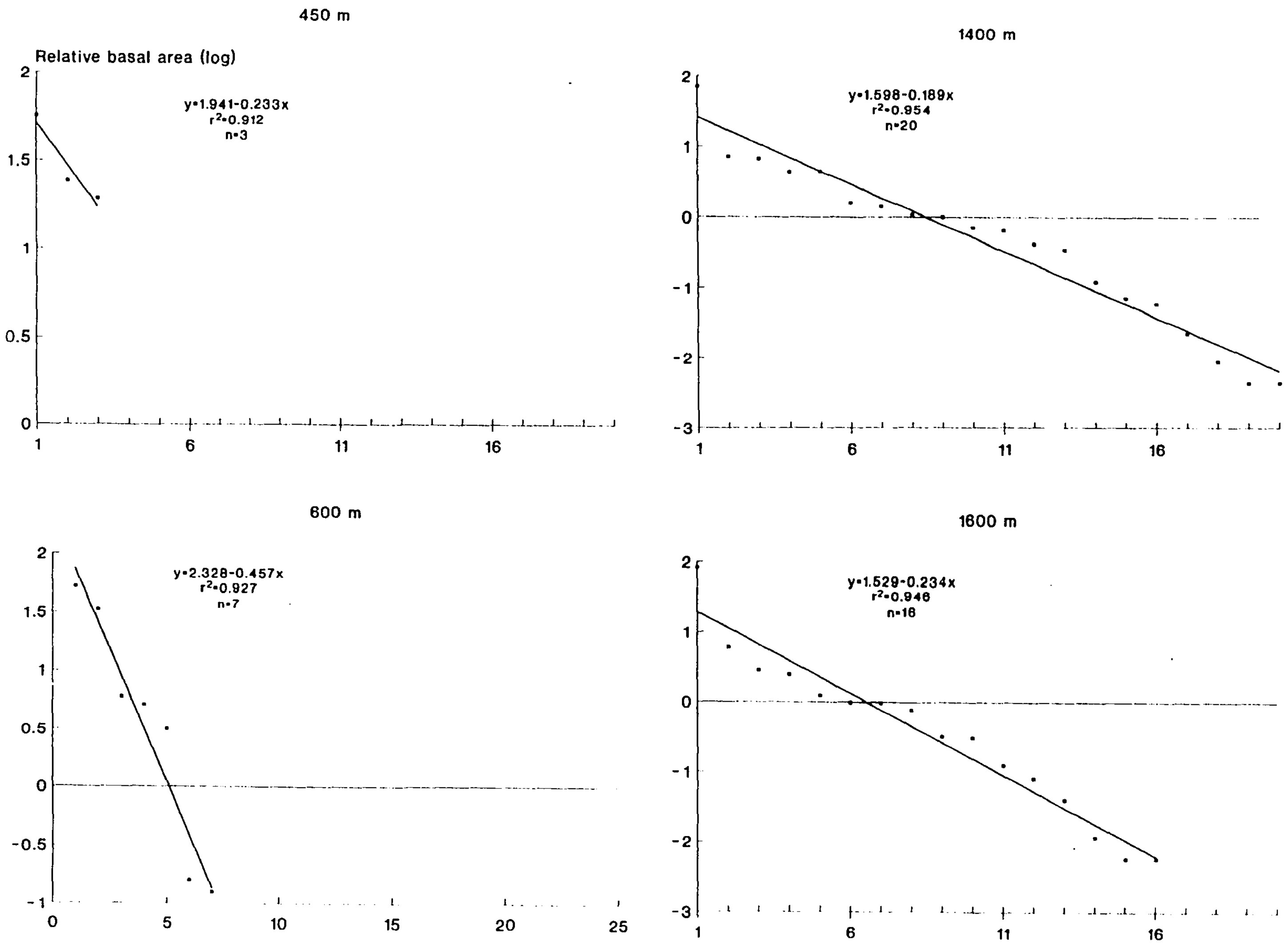
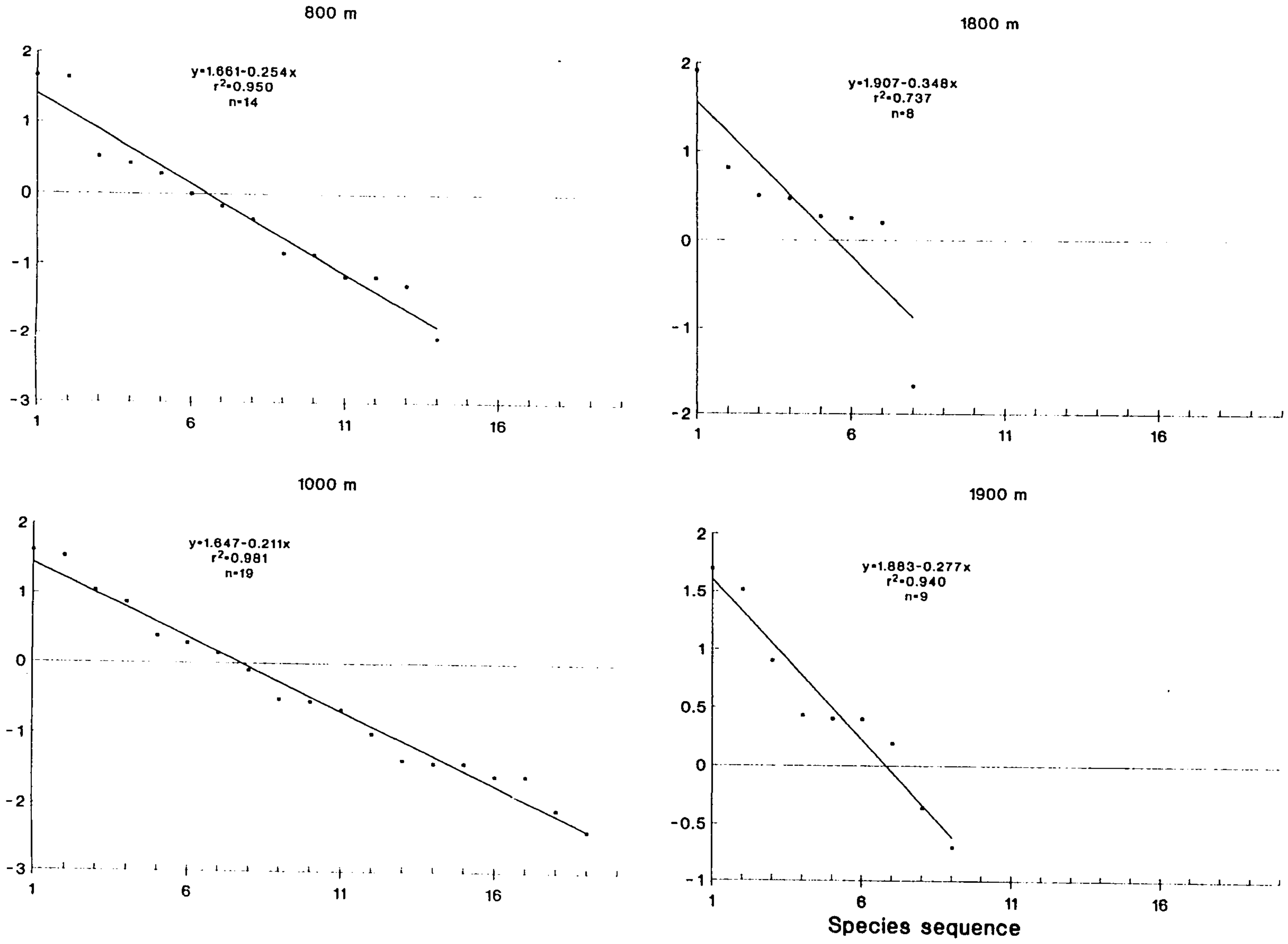


Fig. 4.5. Scatter diagrams showing the reduction of percentage similarities (log) (y-axis) with increasing ecological distance along the altitudinal gradient (x-axis).


450 m
Relative basal area (log)
2
1.5
1
0.5
0
1
6
11
16
y=1.941-0.233x
r²=0.912
n=3
1400 m
2
1
0
-1
-2
-3
1
6
11
16
y=1.598-0.189x
r²=0.954
n=20
600 m
2
1.5
1
0.5
0
-0.5
-1
0
5
10
15
20
25
y=2.328-0.457x
r²=0.927
n=7
1600 m
2
1
0
-1
-2
-3
1
6
11
16
y=1.529-0.234x
r²=0.946
n=16


800 m
y=1.661-0.254x
r^2=0.950
n=14
2
1
0
-1
-2
-3
1
6
11
16
1800 m
y=1.907-0.348x
r^2=0.737
n=8
2
1
0
-1
-2
1
6
11
16
1000 m
y=1.647-0.211x
r^2=0.981
n=19
2
1
0
-1
-2
-3
1
6
11
16
1900 m
y=1.883-0.277x
r^2=0.940
n=9
2
1.5
1
0.5
0
-0.5
-1
1
6
11
16
Species sequence

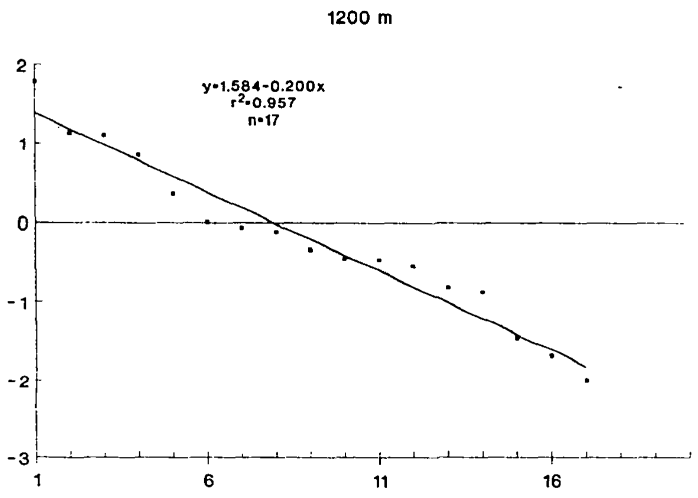
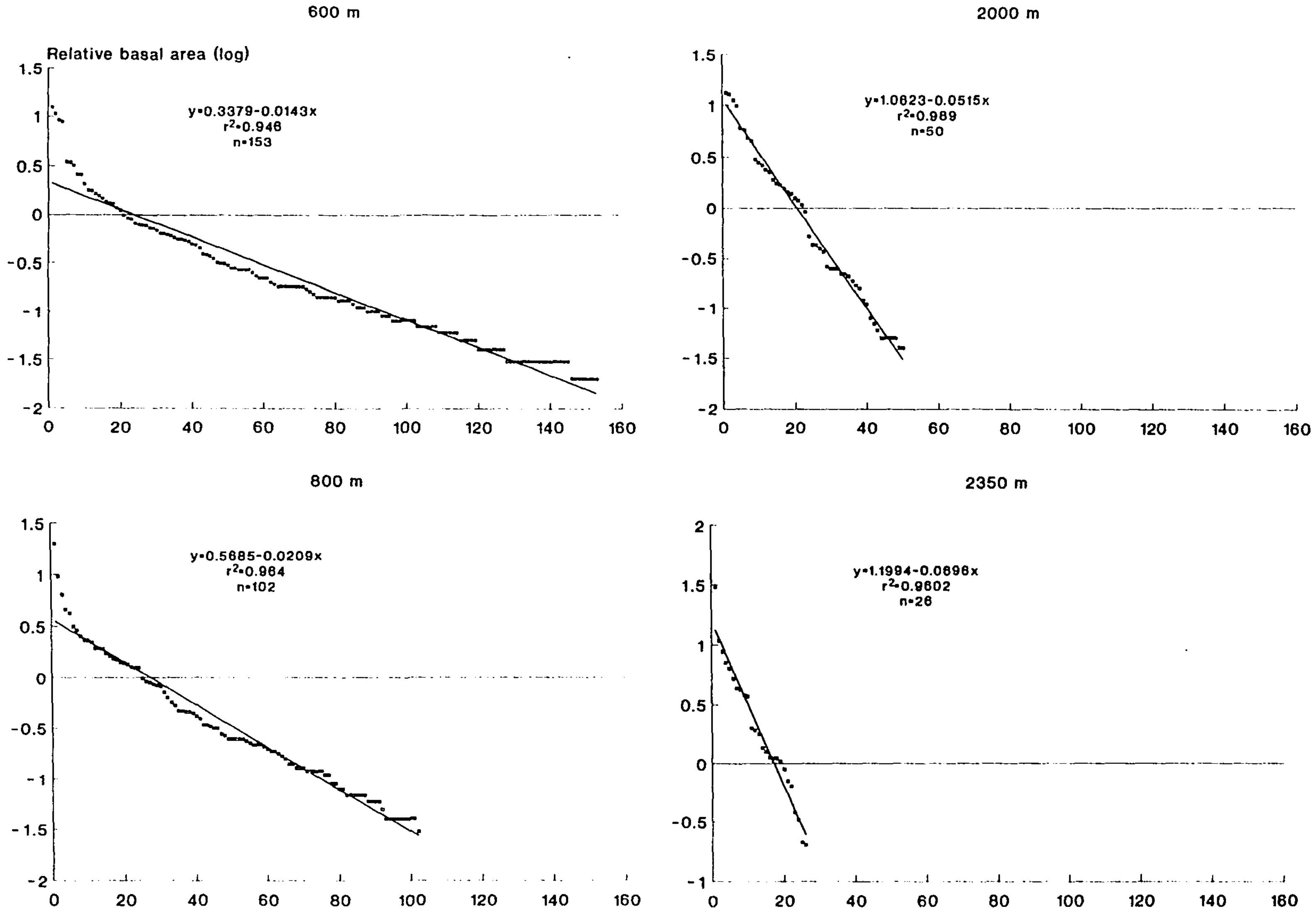
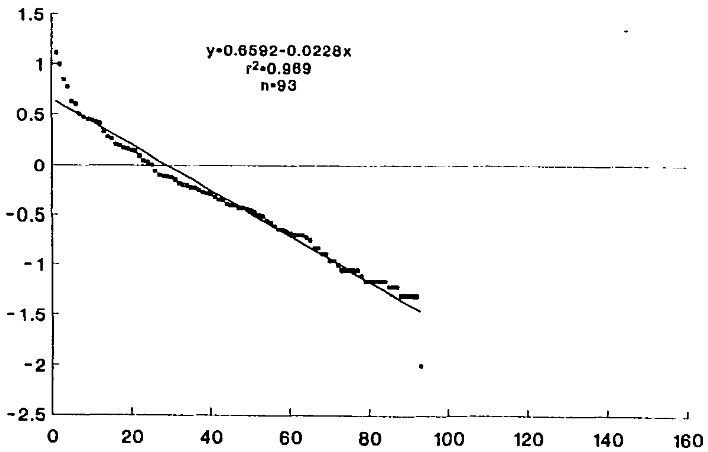


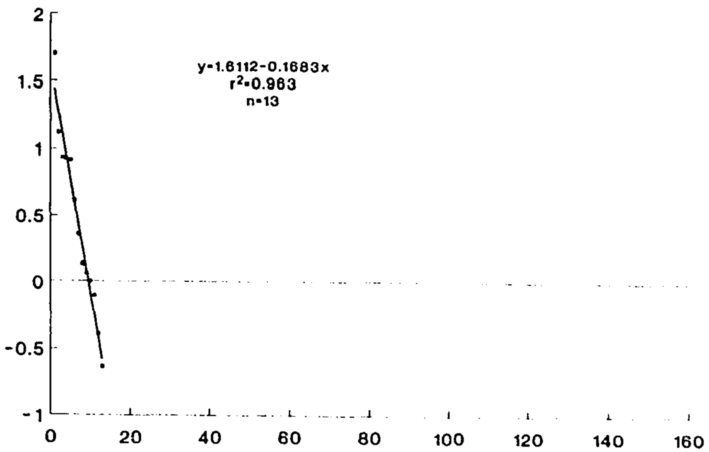
Fig. 4.6. Species sequence-relative dominance curves on Mt. Haleakala.


600 m
Relative basal area (log)
y=0.3379-0.0143x
r²=0.946
n=153
2000 m
y=1.0623-0.0515x
r²=0.989
n=50
800 m
y=0.5685-0.0209x
r²=0.964
n=102
2350 m
y=1.1994-0.0696x
r²=0.9602
n=26
1.5
1
0.5
0
-0.5
-1
-1.5
-2
2
0
20
40
60
80
100
120
140
160

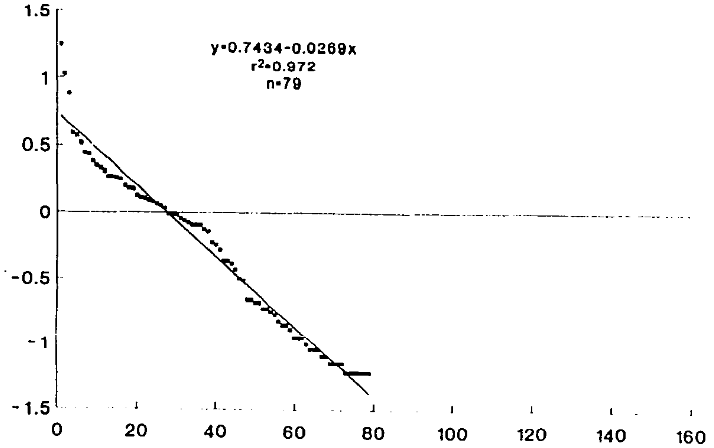
1000 m



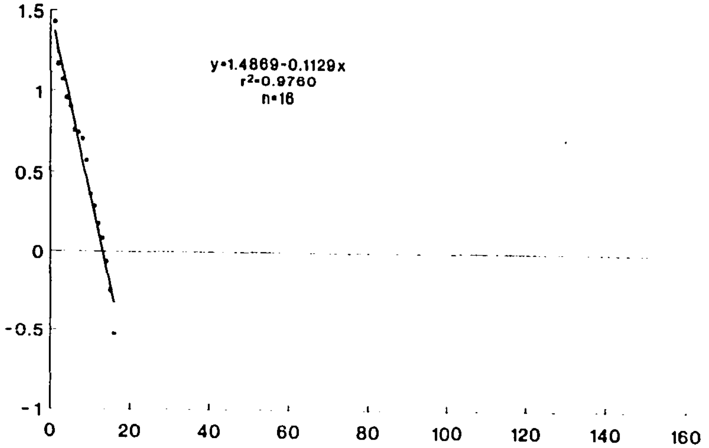
2600 m

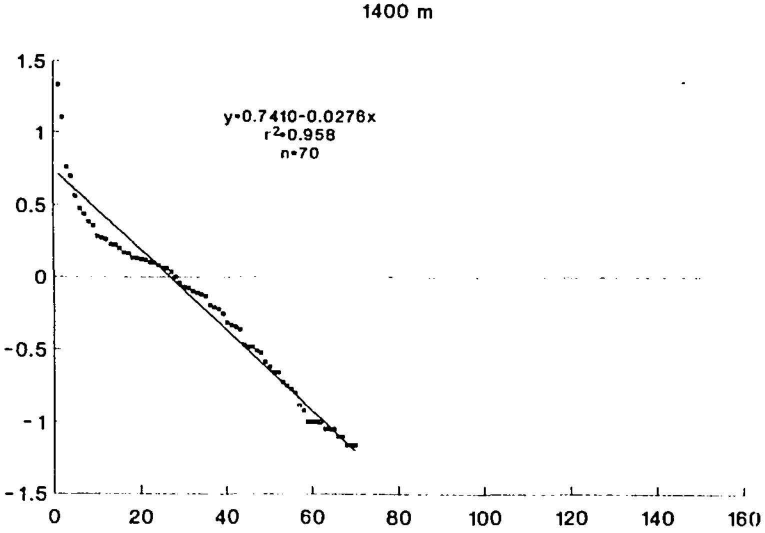


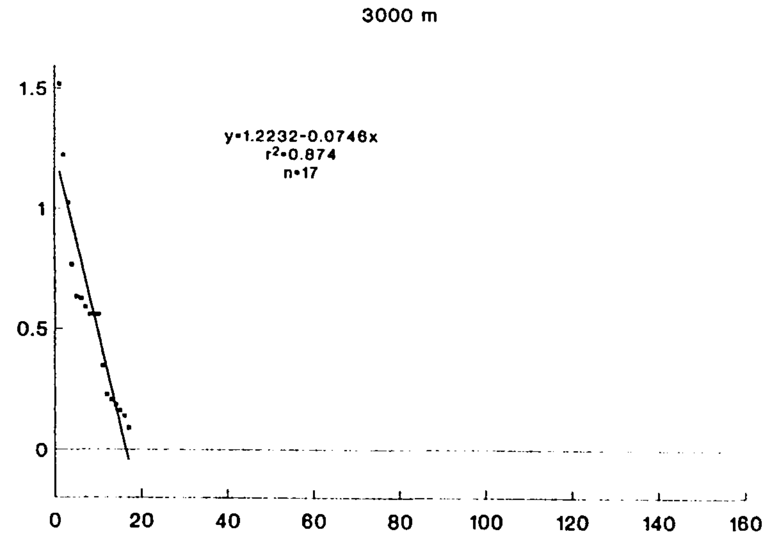
1200 m

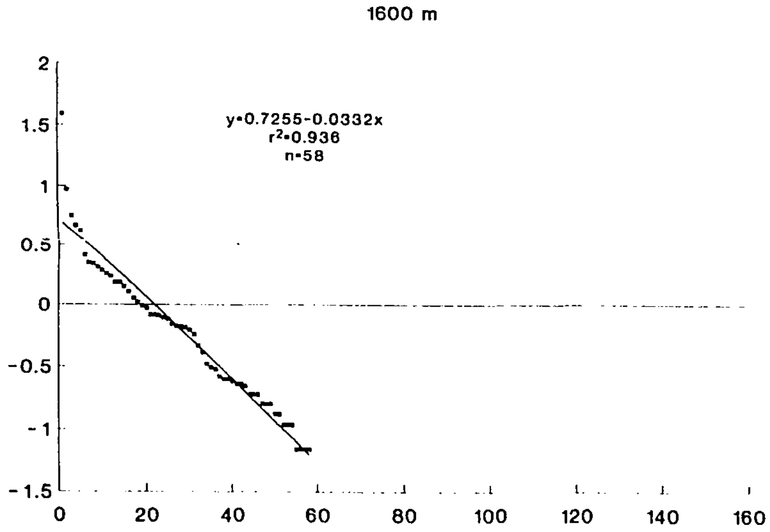


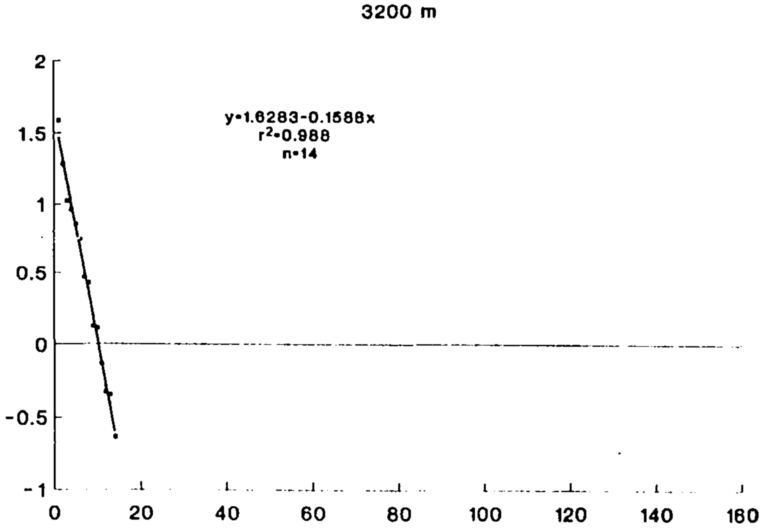
2800 m

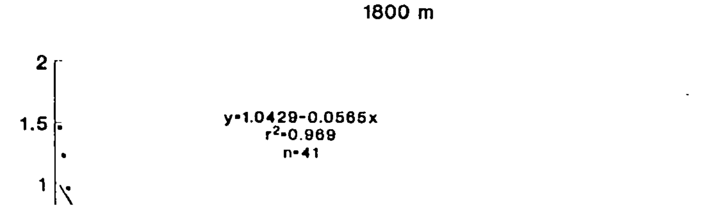


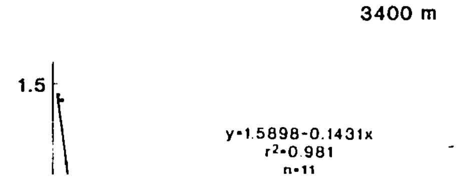

1400 m
y=0.7410-0.0276x
r²=0.958
n=70
1.5
1
0.5
0
-0.5
-1
-1.5
0
20
40
60
80
100
120
140
160


3000 m
y=1.2232-0.0746x
r²=0.874
n=17
1.5
1
0.5
0
0
20
40
60
80
100
120
140
160


1600 m
y=0.7255-0.0332x
r²=0.936
n=58
2
1.5
1
0.5
0
-0.5
-1
-1.5
0
20
40
60
80
100
120
140
160


3200 m
y=1.6283-0.1588x
r²=0.988
n=14
2
1.5
1
0.5
0
-0.5
-1
0
20
40
60
80
100
120
140
160


1800 m
y=1.0429-0.0565x
r²=0.969
n=41
2
1.5
1


3400 m
y=1.5898-0.1431x
r²=0.981
n=11
1.5

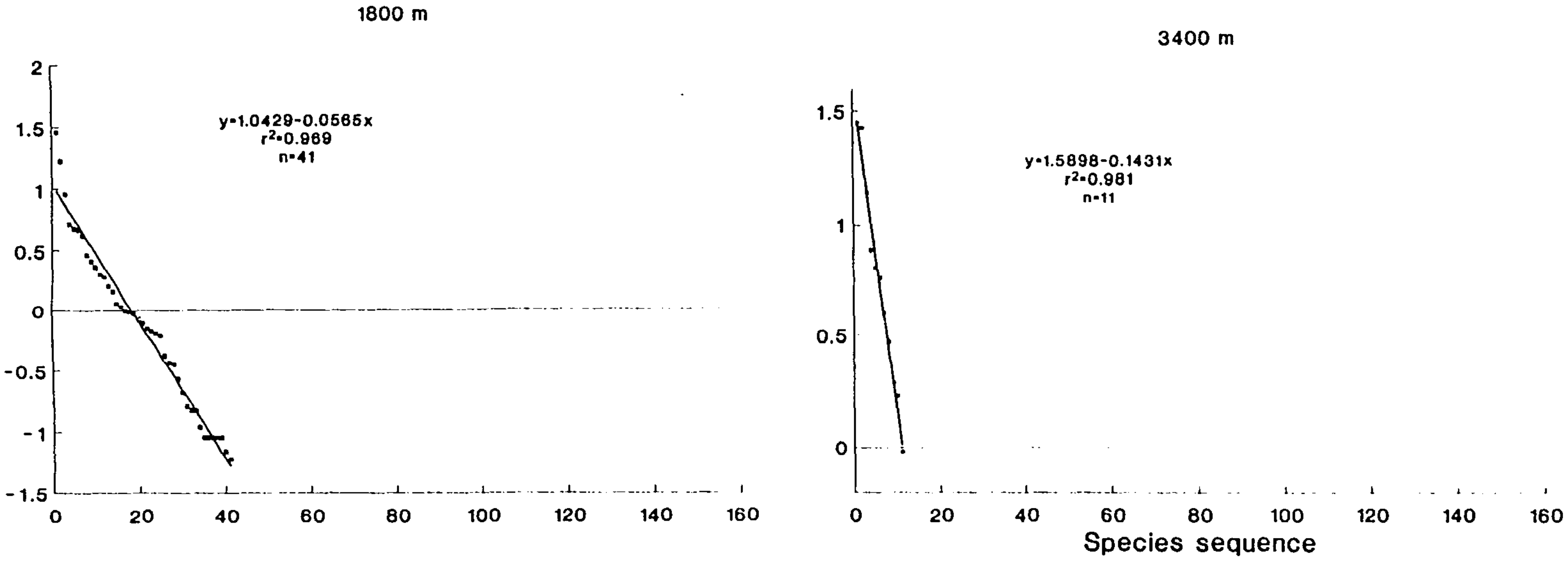


Fig. 4.7. Species sequence-relative dominance curves on Mt. Kinabalu.

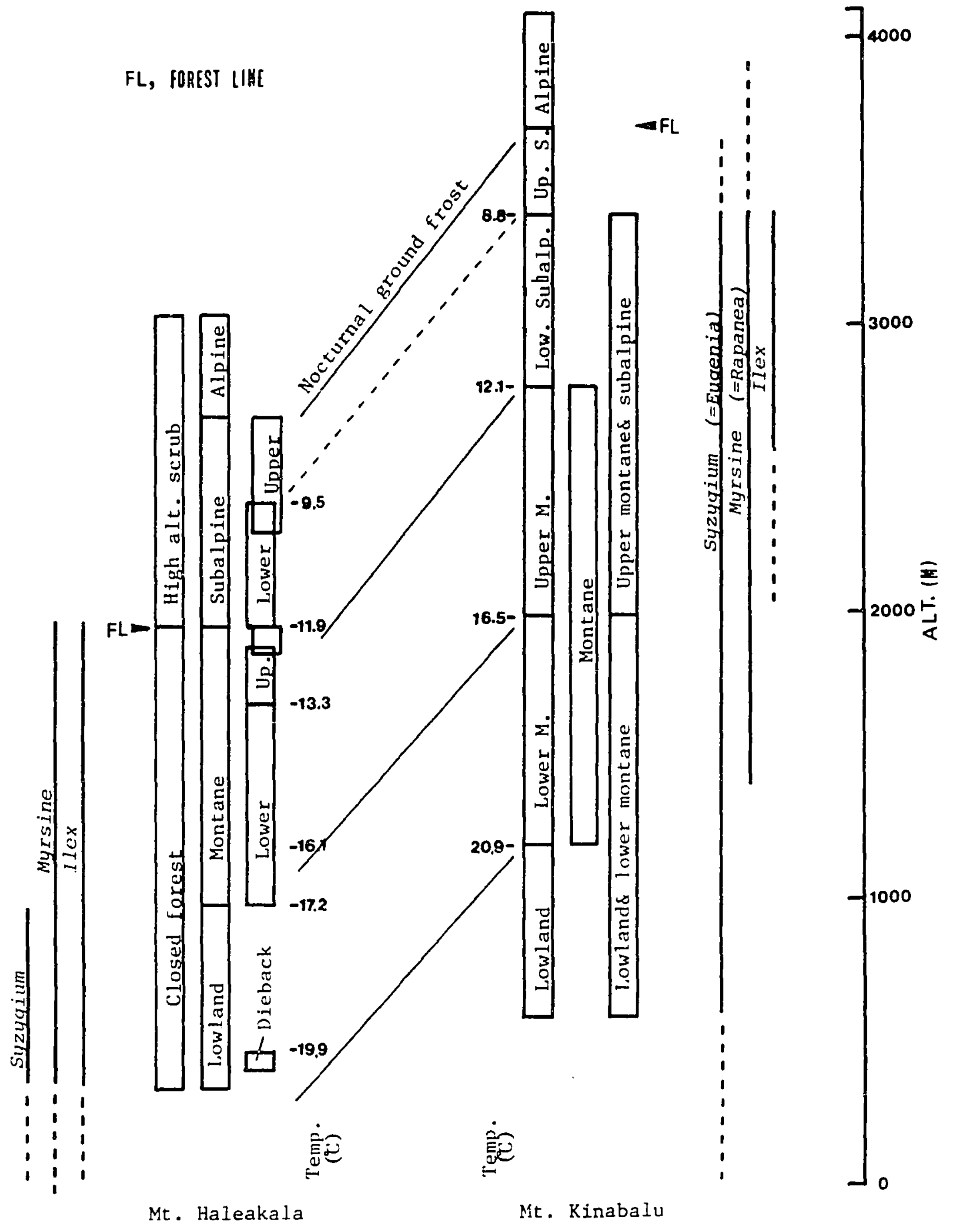


Fig. 4.8. Comparison of floristic vegetation zones between Mts. Kinabalu and Haleakala. The zones were based on mutually exclusive species groups obtained from the two-way table techniques. Estimated mean annual air temperatures are given at the boundaries of the differentiated zones.

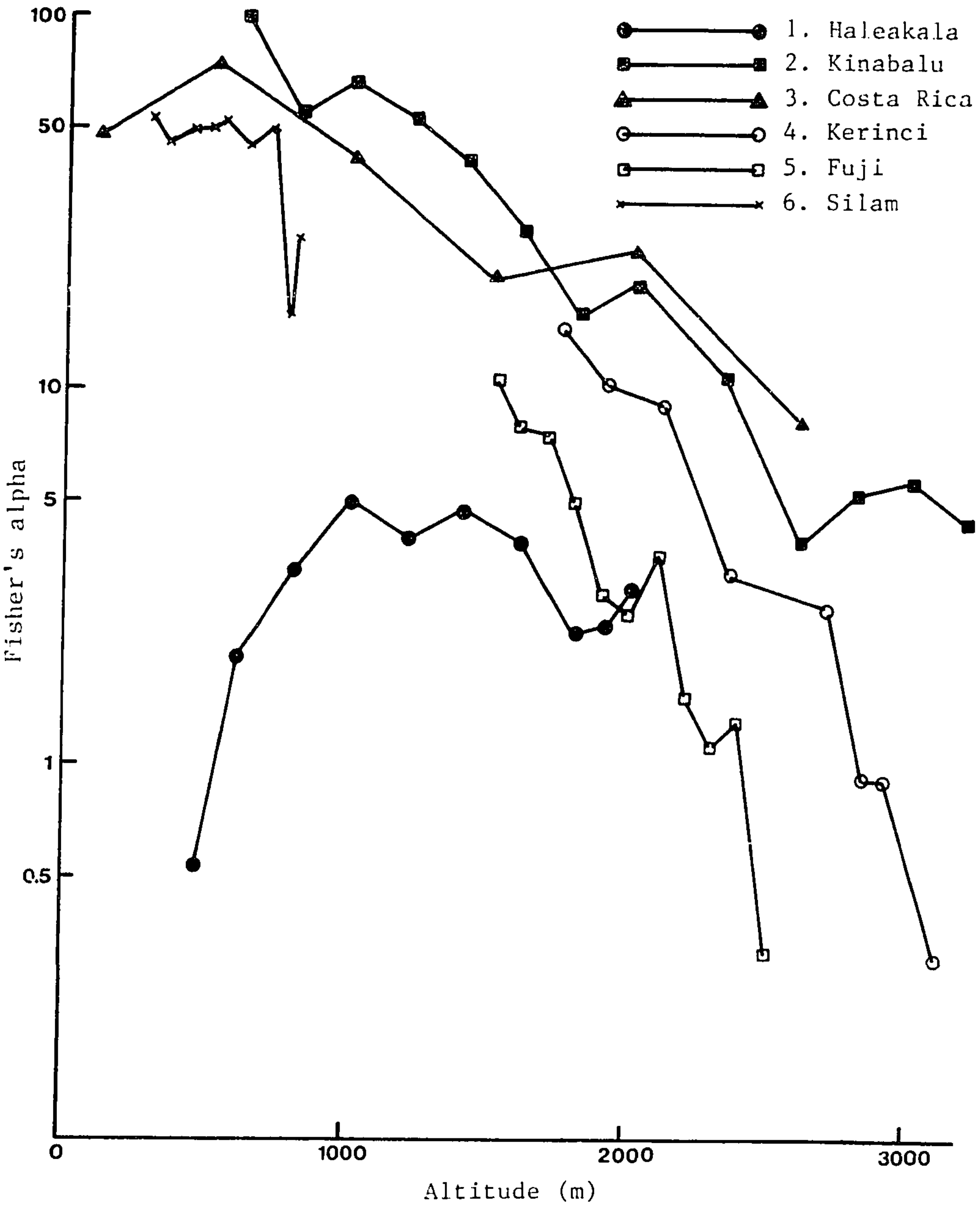
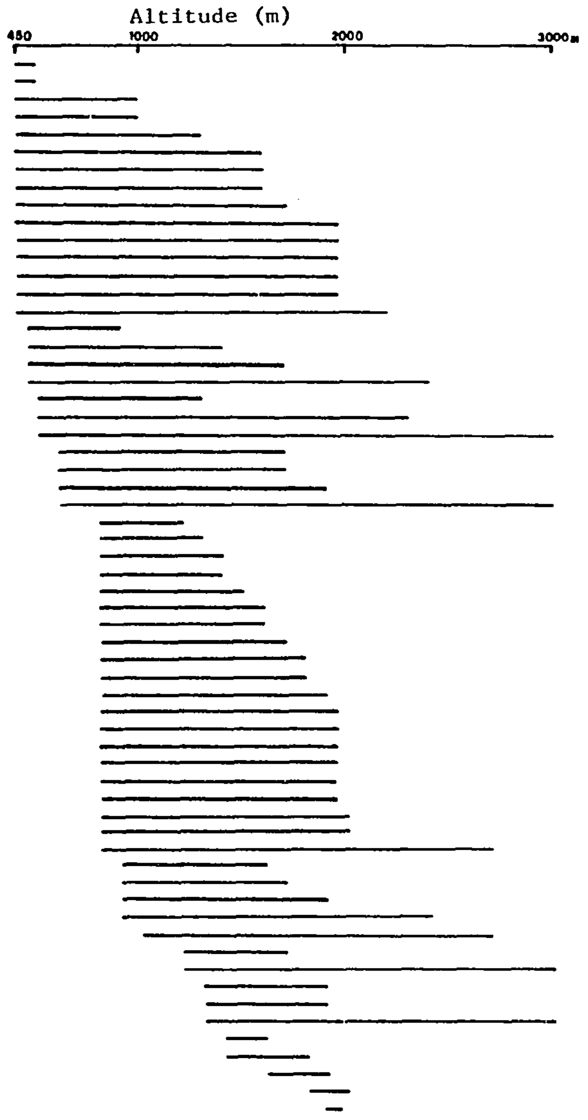


Fig. 4.9. Altitudinal reduction in alpha species diversity using Fisher's index on Mts. Kinabalu and Haleakala in comparison to some other selected mountains: 3) Heaney & Proctor (1990); 4) Ohsawa _et_ _al_. (1985); 5) Ohsawa (1984); 6) Proctor _et_ _al_. (1988).

(a)

Genus	Geogr. distri.
Ophioglossum	subcosmop.
Odontosoria	trop.Am.&Afr.
Syzygium	trop. OW
Nephrolepis	trop.&warm
Psilotum	trop.
Sphaerocionium	trop.
Dicranopteris	trop.
Mecodium	trop.&S.temp.
Cibotium	trop.As.Am.&Polynes.
Ilex	trop.&temp.As.&Am.
Adenophorus	Hawaii
Pleopeltis	trop.
Elaphoglossum	trop.&warm
Acacia	trop.&warm
Metrosideros	E.Mal.,Pacific&S.Afr.
Antidesma	trop.&warm OW
Huperzia	trop.&temp.
Grammitis	trop.&Aus.
Lycopodium	trop.&temp.
Tetraplasandra	Hawaii
Machaerina	trop.&warm
Asplenium	cosmop.
Clermontia	Hawaii
Psychotria	trop.
Peperomia	trop.&warm
Vaccinium	cosmop.
Freycinetia	S.Lank,N.Z.&Polynes.
Vandenboschia	cosmop.
Liparis	cosmop.
Wikstroemia	SE.AS.-Pacific
Diplopterygium	trop.&warmAs.-trop.Am.
Labordia	Hawaii
Alyxia	Indomal.-W.Pac.
Xiphopteris	trop.
Hedyotis	trop.&warm
Broussaisia	Hawaii
Pelea	Hawaii
Astelia	N.Guinea,Aus.,N.Z.&Polynes.
Polypodium	cosmop.
Athyrium	cosmop.
Myrsine	trop.&subtrop.
Smilax	trop.&temp.
Stenogyne	Hawaii
Cheirodendron	Hawaii&Marquesas
Sadleria	Hawaii
Coprosma	E.Mal.,Aus.&Pacific
Korthalsella	trop.Afr.-Himal.,Japan&N.Z.
Cyrtandra	Mal.&Pacific
Pittosporum	trop.&S.Afr.,N.Z.&Pacific
Dryopteris	cosmop.
Carex	cosmop.
Nertera	S.China,Java,Aus.,N.Z.&Hawaii
Styphelia	Java-Aus.
Uncinia	Mal.,Pacific,C.&S.Am.
Ctenitis	trop.
Dubautia	Hawaii
Thelypteris	subpantemp.
Coniogramme	trop.OW-Hawaii
Pteris	cosmop.
Rubus	cosmop.
Polystichum	cosmop.



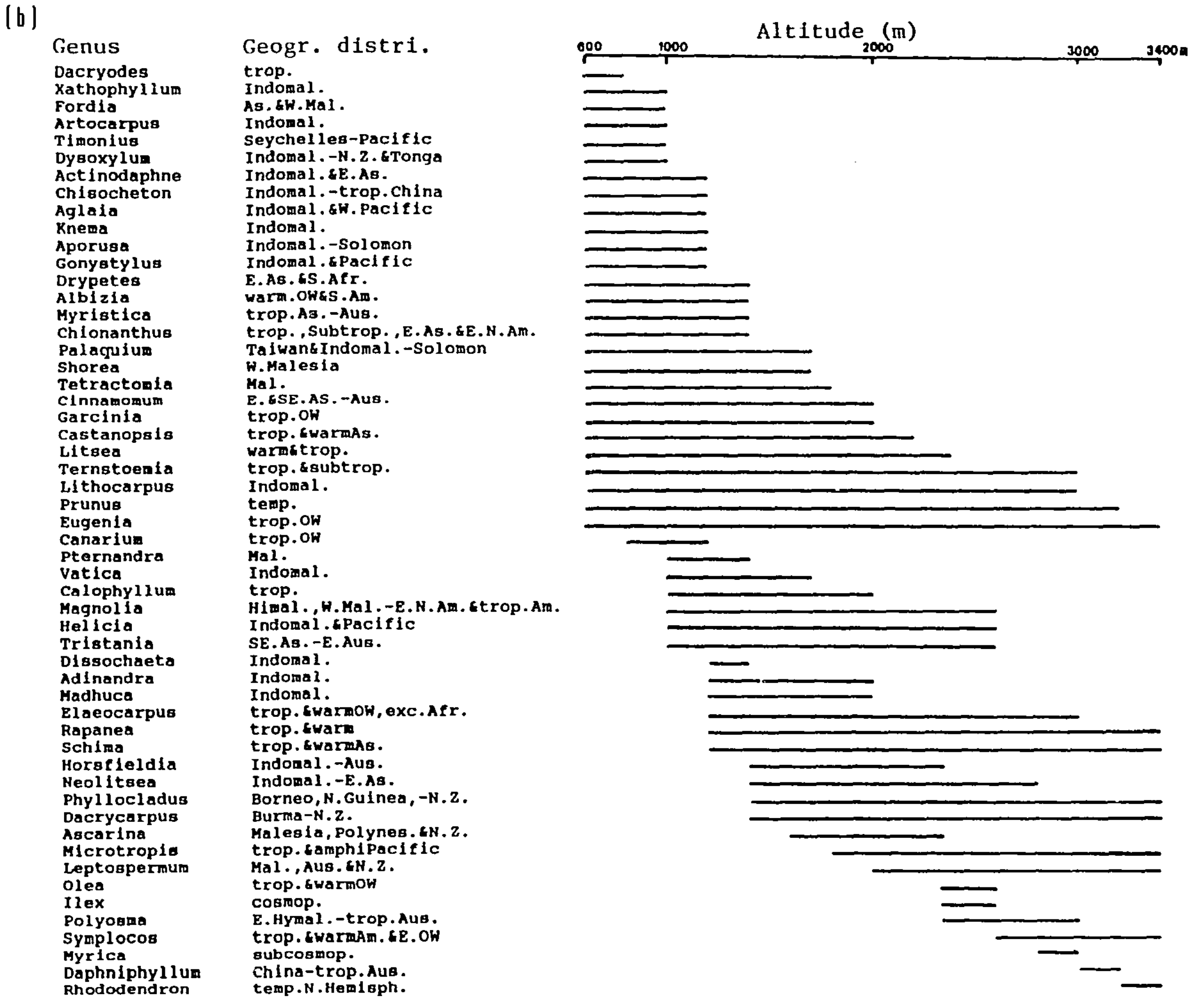


Fig. 4.10. Generic distributions along the altitudinal gradients based on the differential species of the forest vegetation: (a) Mt. Haleakala; (b) Mt. Kinabalu. The distributions of exotic species are excluded.

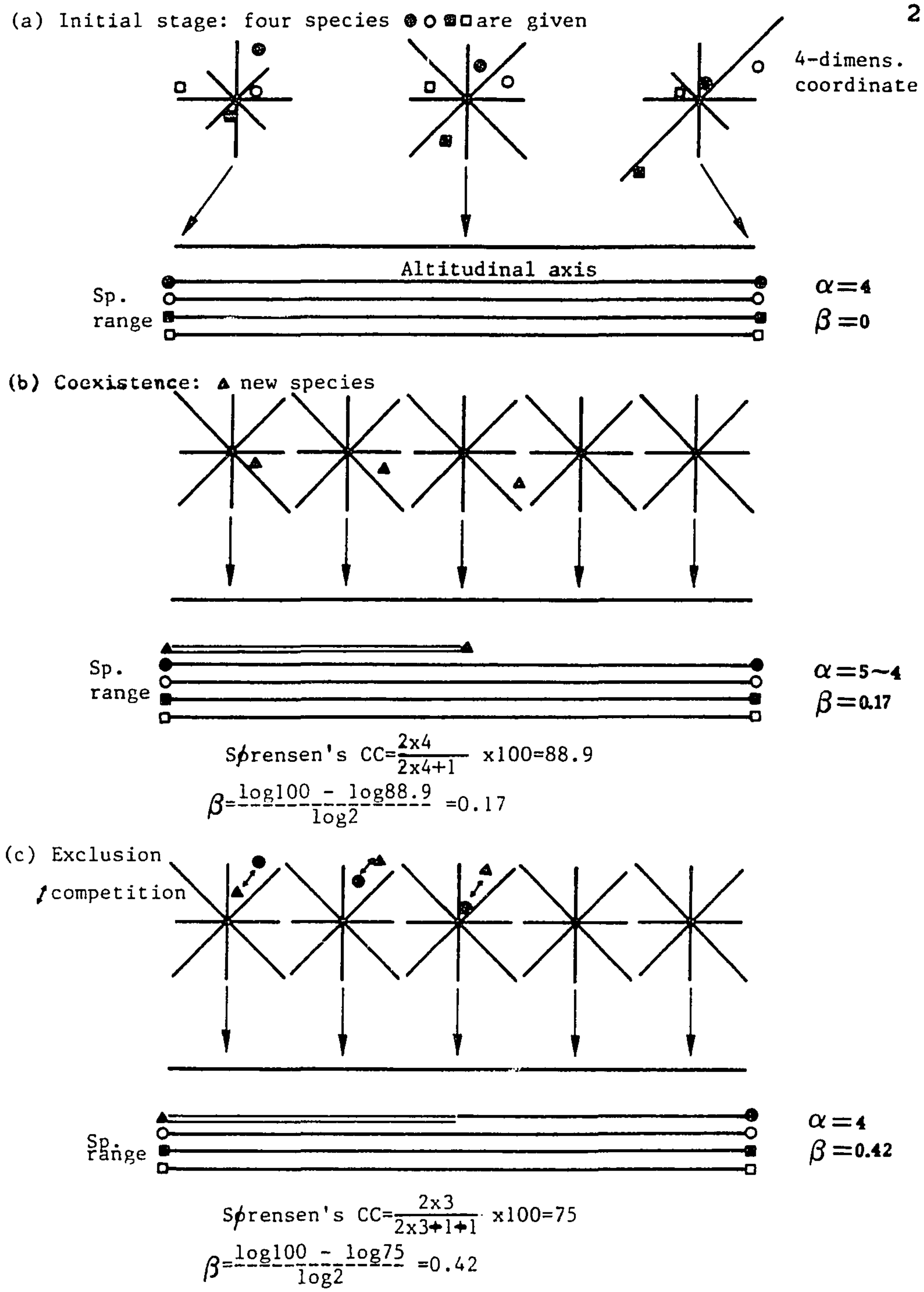


Fig. 4.11. Schematic presentation of the resource gradient coordinate system along an altitudinal axis. (a) Initial stage with four species divergent in the four-dimension coordinate system. (b) Stabilization of the coexistence of a newly added taxon with the four initial species; the process results in the increase of alpha and slight increase of beta. (c) Exclusion of a taxon which is competing with a newly added taxon; the process results in the increase in beta but in the unchanged alpha.

APPENDICES

Appendix 1.1. Species composition of the forest canopy (trees ≥10 cm DBH) at 600 m on Mt. Kinabalu.

Plot size: 1.12 ha
Number of species: 153
Density: 333 trees/ha, including dead standing trees
Total basal area: 333880 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
41090	12.31	9	585	Shorea leprosula
35290	10.57	6	716	Lithocarpus hallieri
30500	9.14	4	587	Shorea parvistipulata
29310	8.78	8	583	Shorea laevis
11440	3.43	1	942	Unknown
11290	3.38	2	795	Unknown
10590	3.17	11	568	Palaquium rostratum
8600	2.57	2	490	Alstonia angustiloba
8570	2.57	7	887	Eugenia elliptilimba
6880	2.06	1	808	Shorea
5970	1.79	1	695	Nephelium aculeatum
5950	1.78	5	895	Eugenia festigiatum
5540	1.66	3	714	Lithocarpus cf.nieuwenhuisii
5290	1.58	10	885	Eugenia caudatilimbum
4950	1.48	2	685	Nephelium lappaceum
4520	1.35	21	641	Aporusa accuminatissima
4330	1.3	19	727	Castanopsis
4270	1.28	2	875	Litsea
3850	1.15	2	747	Licania splendens
3690	1.1	3	686	Fordia coriacea
3270	0.98	4	537	Archidendron ellipticum
3030	0.91	2	500	Dacryodes
2960	0.89	1	501	Dacryodes
2670	0.8	6	863	Litsea cf. sarawakensis
2600	0.78	10	652	Aporusa lunata
2570	0.77	10	610	Xanthophyllum affine
2550	0.76	1	958	Koompasia excelsa
2410	0.72	1	675	Magnolia dolichogyne
2390	0.71	3	820	Dysoxylum macrocarpum
2280	0.68	3	559	Artocarpus
2100	0.63	7	507	Barringtonia lanceolata
2060	0.62	9	866	Beilschmiedia
2030	0.61	5	635	Macaranga hypoleuca
2000	0.6	4	735	Gonystylus consanguineus
1910	0.57	1	542	Albizia
1840	0.55	3	503	Gluta wallichii
1840	0.55	3	533	Eugenia
1810	0.54	3	495	Durio acutifolius

Appendix 1.1. -continued.

1720	0.52	2	847	Canarium
1650	0.49	2	923	ANNONACEAE
1600	0.48	1	889	Eugenia cf. festigiatum
1500	0.45	2	608	Diospyros
1300	0.39	2	880	Litsea brachystachya
1280	0.38	1	780	Fagraea elliptica
1220	0.37	1	813	Aphanamixis reticulosa
1160	0.35	1	842	Nauclea
1060	0.32	2	621	Horsfieldia subalpina
1040	0.31	2	513	Calophyllum venulosum
1020	0.31	1	476	Vernonia arborea
990	0.3	3	603	Diospyros piscicapa
930	0.28	1	573	SAPOTACEAE
920	0.28	3	645	Notaphoebe
920	0.27	1	570	Palaquium gutta
910	0.27	1	579	Shorea hopeifolia
910	0.27	2	715	Lithocarpus nieuwenhuisii
890	0.27	2	602	Austrobuxus nitidus
830	0.25	1	623	MYRISTICACEAE
780	0.23	2	722	Lithocarpus
740	0.22	1	564	Artocarpus integer
740	0.22	2	936	Unknown
740	0.22	3	837	Diplospora
670	0.2	4	823	Chisocheton
620	0.19	1	693	Dialium platysepalum
620	0.18	6	811	Dysoxylum rugulosum
610	0.18	1	697	Amoora
610	0.18	2	575	Parashorea malaanonan
610	0.18	2	613	Ochanostachys amentacea
610	0.18	3	616	Drypetes microphylla
600	0.18	2	835	Urophyllum hirsutum
600	0.18	4	611	Drypetes cf. crassipes
590	0.18	4	742	Scaphium macropodum
580	0.17	2	824	Aglaia
550	0.16	1	622	Myristica iners
490	0.15	1	683	OLEACEAE
480	0.14	2	510	Calophyllum cf. depresinerv.
480	0.14	2	865	Dehaasia
480	0.14	4	750	Garcinia cf. parrifolia
470	0.14	1	538	Aglaia
470	0.14	2	937	Unknown
470	0.14	3	876	Litsea
450	0.13	1	870	Litsea castanea
440	0.13	4	679	Chionanthus pluriflorus
440	0.13	1	689	Lithocarpus gracilis
420	0.13	3	639	Baccaurea racemosa
400	0.12	2	699	Ardisia macrophylla
370	0.11	1	940	Unknown
360	0.11	3	833	Timonius flavescens
360	0.11	1	598	Sterculia membraucea
330	0.1	1	858	LAURACEAE

Appendix 1.1. -continued.

330	0.1	1	706	Lithocarpus cf. leptogyne
330	0.1	1	729	Lithocarpus cf. beccarianus
320	0.1	2	665	Prunus arborea
300	0.09	1	938	Unknown
290	0.09	2	763	Colubrina anomala
290	0.09	1	680	Chionanthus cf. cuspidatus
280	0.08	2	534	Microcos cf. elmeri
280	0.08	1	869	Actinodaphne
280	0.08	1	619	Horsfieldia
270	0.08	1	846	Dacryodes costata
260	0.08	1	901	Eugenia cf. valdevenosa
260	0.08	1	848	Canarium
260	0.08	1	612	Xanthophyllum gracile
250	0.07	1	505	Gluta sabahana
230	0.07	1	600	ELAEOCARPACEAE
230	0.07	2	601	Diospyros sumatrana
220	0.07	1	618	Knema
220	0.07	2	643	Aporusa
220	0.07	2	592	Aporusa nigropunctata
220	0.06	1	724	Castanopsis clemensii
210	0.06	2	687	Nephelium ramboutan-ake
190	0.06	1	746	Helicia artocarpioides
190	0.06	1	929	Unknown
190	0.06	1	765	Mallotus
190	0.06	1	825	Aglaia
180	0.05	1	638	Croton oblongifolius
180	0.05	1	658	Ternstroemia cf. magnifica
170	0.05	1	815	Walsura
150	0.05	1	890	Eugenia
150	0.05	1	521	Garcinia cf. caudculata
150	0.04	1	822	Chisochetin beccarianus
140	0.04	1	789	Cleistanthus
140	0.04	1	778	Gonystylus borneensis
130	0.04	1	779	Garcinia caudiculate
130	0.04	1	917	Ardisia
130	0.04	1	541	Spatholobus
120	0.04	1	528	Pternandra cf. crassicalyx
120	0.04	1	407	Cinnamomum griffithii
120	0.03	1	574	Dipterocarpus kunstleri
120	0.03	1	554	Unknown
110	0.03	1	628	Knema palleus
110	0.03	1	755	Hydnocarpus cf. woodii
110	0.03	1	696	Nephelium cuspidatum
110	0.03	1	566	Payena gigas
110	0.03	1	646	Unknown
110	0.03	1	916	Cyathea
100	0.03	1	626	Knema kinabaluensis
100	0.03	1	691	Aglaia
100	0.03	1	841	Timonius
90	0.03	1	821	Aglaia
90	0.03	1	627	Knema

Appendix 1.1. -continued.

90	0.03	1	637	Macaranga triloba
90	0.03	1	625	Knema cinerea
90	0.03	1	0.1	Unknown
90	0.03	1	952	Unknown
80	0.03	1	351	Tetractomia tetrandrum
80	0.02	1	828	Polyalthia
80	0.02	1	520	Garcinia tetragonus
80	0.02	1	751	Memecylon
70	0.02	1	877	Litsea
70	0.02	1	776	Diospyros
70	0.02	1	694	Guioa pterorhachis
70	0.02	1	562	Ficus schwartzii
70	0.02	1	773	Archidendron havilandii

Appendix 1.2. Species composition of the forest canopy (trees ≥10 cm DBH) at 800 m on Mt. Kinabalu.

Plot size: 0.8036 ha
Number of species: 102
Density: 372 trees/ha, including standing dead trees
Total basal area: 297760 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
59600	20.01	7	585	Shorea leprosula
28530	9.58	14	583	Shorea laevis
18970	6.37	9	587	Shorea parvistipulata
13650	4.58	5	544	Vitex cf. quinate
12560	4.22	2	716	Lithocarpus hallieri
9360	3.14	4	846	Dacryodes costata
8500	2.85	1	959	Shorea argentifolia
7470	2.51	19	533	Eugenia
6930	2.33	25	610	Xanthophyllum affine
6920	2.32	6	844	Canarium littorale
6680	2.24	5	735	Gonystylus consanguineus
5800	1.95	12	495	Durio acutifolius
5780	1.94	7	843	Canarium megalanttum
5710	1.92	9	766	Xanthophyllum palembanicum
5120	1.72	1	553	Scaphium
4790	1.61	16	641	Aporusa accuminatissima
4550	1.53	2	503	Gluta wallichii
4480	1.5	5	586	Gonystylus
4230	1.42	7	613	Ochanostachys amentacea
4170	1.4	1	588	Adiandra collina
4040	1.36	1	699	Ardisia macrophylla

Appendix 1.2. -continued.

3830	1.29	1	956	Unknown
3770	1.26	2	542	Albizia
3760	1.26	7	895	Eugenia festigiatum
2890	0.97	2	695	Nephelium aculeatum
2700	0.91	5	570	Palaquium gutta
2660	0.89	5	621	Horsfieldia subalpina
2550	0.86	4	689	Lithocarpus gracilis
2490	0.84	5	0.1	Unknown
2430	0.82	2	887	Eugenia elliptilimba
2130	0.72	1	931	Unknown
1870	0.63	7	507	Barringtonia lanceolata
1700	0.57	6	510	Calophyllum cf. depresinerv.
1590	0.53	1	612	Xanthophyllum grocile
1410	0.47	6	889	Eugenia cf. festigiatum
1400	0.47	5	818	Dysoxylum
1380	0.46	2	924	Unknown
1370	0.46	5	622	Myristica iners
1330	0.45	5	724	Castanopsis clemensii
1260	0.42	2	885	Eugenia caudatilimbum
1180	0.4	4	826	Aglaia
1020	0.34	1	497	Lophopetalum cf. beccarianum
1000	0.34	2	704	Lithocarpus cf. sericobalan.
980	0.33	2	864	Litsea cf. angulata
960	0.32	4	869	Actinodaphne
960	0.32	2	568	Palaquium rostratum
820	0.28	4	625	Knema cinerea
790	0.27	2	761	Sterculia stipulata
750	0.25	1	717	Lithocarpus conocarpus
750	0.25	1	557	Artocarpus
740	0.25	4	825	Aglaia
740	0.25	1	608	Diospyros
730	0.25	1	543	Dialium cf. indum
720	0.24	1	496	Durio zibethianus
690	0.23	1	904	Engelhardia serrata
660	0.22	2	520	Garcinia tetragonus
660	0.22	1	565	Payena cf. gigas
640	0.22	5	645	Notaphoebe
630	0.21	1	577	Hopea pentanervia
600	0.2	4	616	Drypetes microphylla
560	0.19	1	635	Macaranga hypoleuca
560	0.19	1	534	Microcos cf. elmeri
530	0.18	1	686	Fordia coriaceae
520	0.17	5	838	Nauclea subdita
490	0.16	1	576	Shorea fallax
430	0.14	1	847	Canarium
410	0.14	1	742	Scaphium macropodum
390	0.13	4	605	Diospyros ferrugenescens
380	0.13	1	779	Garcinia caudiculate
370	0.13	2	558	Artocarpus elasticus
370	0.12	2	855	Beilschmiedia tawaensis
350	0.12	1	650	Aporusa maingayi

Appendix 1.2. -continued.

350	0.12	2	833	Timonius flavescesns
350	0.12	1	567	Madhuca elmeri
340	0.12	1	773	Archidendron havilandii
320	0.11	2	870	Litsea castanea
320	0.11	4	530	Memecylon borneensis
270	0.09	2	578	Hopea dyeri
260	0.09	2	888	Eugenia filiformis
250	0.08	2	639	Baccaurea racemosa
240	0.08	2	944	Unknown
220	0.07	2	878	Litsea
220	0.07	1	884	Endiandra
220	0.07	1	928	Unknown
200	0.07	1	744	Elaeocarpus angustipes
200	0.07	2	609	Xanthophyllum scorteehinii
200	0.07	1	862	Cryptocarya
190	0.06	1	938	Unknown
190	0.06	1	727	Castanopsis
180	0.06	1	685	Nephelium lappaceum
180	0.06	1	559	Artocarpus
150	0.05	1	0.5	Unknown
130	0.04	1	537	Archidendron ellipticum
120	0.04	1	893	Memecylon
120	0.04	1	649	Aporusa frutescens
120	0.04	1	810	shorea cf. faguetiana
120	0.04	1	566	Payena gigas
120	0.04	1	676	Magnolia
120	0.04	1	886	Eugenia
110	0.04	1	615	Xanthophyllum velutinum
110	0.04	1	811	Dysoxylum rugulosum
100	0.03	1	729	Lithocarpus cf. beccarianus

Appendix 1.3. Species composition of the forest canopy (trees ≥10 cm DBH) at 1000 m on Mt. Kinabalu.

Plot size: 0.5636 ha
Number of species: 93
Density: 369 trees/ha, including standing dead trees.
Total basal area: 275020 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
35450	12.89	4	494	Durio cf. graveolens
27160	9.87	7	716	Lithocarpus hallieri
19170	6.97	2	512	Calophyllum teysmannii
16190	5.89	9	685	Nephelium lappaceum

Appendix 1.3. -continued.

11820	4.3	7	585	Shorea leprosula
11250	4.09	4	560	Ficus sumatrana
8830	3.21	18	525	Unknown
8200	2.98	7	728	Castanopsis
7780	2.83	21	894	Eugenia cf. accuminatissima
7550	2.75	5	708	Lithocarpus cf. cantleyanus
7360	2.68	9	351	Tetractomia tetrandrum
7130	2.59	5	498	Dacryodes cf. incurvata
5940	2.16	4	569	Helicia fusco-tomentosa
5220	1.9	2	589	Shorea
5020	1.82	2	950	Unknown
4360	1.59	7	864	Litsea cf. angulata
4240	1.54	4	558	Artocarpus elasticus
4000	1.46	5	686	Fordia coriacea
3950	1.44	7	658	Ternstroemia cf. magnifica
3810	1.39	2	581	Shorea platyclados
3740	1.36	2	502	Gluta oba
3400	1.24	4	889	Eugenia cf. festigiatum
3080	1.12	5	552	Sterculia cf. spectabilis
3000	1.09	5	704	Lithocarpus cf. sericobalan.
2830	1.03	2	960	Artocarpus odoratissima
2400	0.87	2	501	Dacryodes
2180	0.79	11	750	Garcinia cf. parrifolia
2130	0.77	4	727	Castanopsis
2090	0.76	5	888	Eugenia filiformis
2080	0.75	2	565	Payena cf. gigas
1950	0.71	11	430	Eugenia
1820	0.66	7	529	Pternandra coerulescens
1750	0.64	11	724	Castanopsis clemensii
1740	0.63	4	432	Calophyllum blancoi
1660	0.6	4	622	Myristica iners
1630	0.59	2	892	Eugenia
1560	0.57	4	843	Canarium megalanttum
1470	0.54	5	614	Vatica dulitensis
1450	0.53	2	951	Unknown
1390	0.51	2	726	Castanopsis
1310	0.48	2	671	Eugenia
1250	0.45	2	955	Unknown
1210	0.44	4	824	Aglaia
1090	0.4	2	559	Artocarpus
1080	0.39	2	612	Xanthophyllum grocile
1060	0.39	5	407	Cinnamomum griffithii
1030	0.37	5	0.5	Unknown
1020	0.37	2	896	Eugnia cf. confertum
980	0.36	9	615	Xanthophyllum velutinum
970	0.35	4	886	Eugenia
950	0.34	7	890	Eugenia
870	0.32	2	810	Shorea cf. faguetiana
850	0.31	7	838	Nauclea subdita
760	0.28	4	692	Dacryodes
740	0.27	2	819	Dysoxylum

Appendix 1.3. -continued.

670	0.25	2	849	Santiria apiculata
630	0.23	2	765	Mallotus
630	0.23	2	770	Tristania obovata
600	0.22	5	823	Chisocheton
570	0.21	4	651	Aporusa benthamiana
560	0.2	2	542	Albizia
560	0.2	2	664	Casearia hosei
550	0.2	2	825	Aglaia
510	0.19	5	916	Cyathea
510	0.18	4	545	Vitex parviflora
420	0.15	2	611	Drypetes cf. crassipes
410	0.15	2	354	Magnolia carsonii
370	0.13	4	857	Neolitsea
350	0.13	2	555	Ashtonia excelsa
310	0.11	2	563	Ficus treubii
310	0.11	2	539	Archidendron
280	0.1	4	609	Xanthophyllum scorteehinii
260	0.09	2	929	Unknown
250	0.09	2	705	Lithocarpus lampadarius
250	0.09	2	802	Glochidion
250	0.09	2	731	Symplocos cf. goodeniacea
240	0.09	2	930	Unknown
220	0.08	2	749	Garcinia
200	0.07	2	861	Alseodaphne oblanceolata
200	0.07	2	814	Azadirachta integrifolia
200	0.07	2	934	Unknown
190	0.07	2	903	Eugenia
180	0.07	2	915	Dracaena
180	0.07	2	872	Litsea
170	0.06	2	922	RUBIACEAE
170	0.06	2	680	Chionanthus cf. cuspidatus
150	0.06	2	835	Urophyllum hirsutum
140	0.05	2	833	Timonius flavescens
140	0.05	2	551	Baccaurea cf. bracteata
140	0.05	2	901	Eugenia cf. valdevenosa
140	0.05	2	0.1	Unknown
140	0.05	2	829	ANNONACEAE
20	0.01	2	811	Dysoxylum rugulosum

Appendix 1.4. Species composition of the forest canopy (trees ≥10 cm DBH) at 1200 m on Mt. Kinabalu.

Plot size: 0.4027 ha
Number of species: 79
Density: 447 trees/ha, including dead standing trees
Total basal area: 339940 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
60150	17.69	32	777	Madhuca glabrescens
36390	10.7	12	570	Palaquium gutta
26200	7.71	10	770	Tristania obovata
13170	3.87	35	614	Vatica dulitensis
12550	3.69	30	351	Tetractomia tetrandrum
11230	3.3	22	888	Eugenia filiformis
9490	2.79	12	889	Eugenia cf. festigiatum
9230	2.71	7	572	Ganua
8170	2.4	5	713	Lithocarpus cf. lucidus
7610	2.24	10	531	Dissochaeta
7260	2.14	5	854	Litsea
6930	2.04	7	654	Adiandra clemensiae
6270	1.84	2	735	Gonystylus consanguineus
6260	1.84	15	887	Eugenia elliptilimba
6190	1.82	10	817	Dysoxylum grande
6020	1.77	5	533	Eugenia
5380	1.58	2	512	Calophyllum teysmannii
5170	1.52	2	778	Gonystylus borneensis
5090	1.5	2	872	Litsea
4580	1.35	5	901	Eugenia cf. valdevenosa
4420	1.3	2	653	Schima wallichii
4340	1.28	12	529	Pternandra cf. coerulescens
4200	1.24	2	844	Canarium littorale
4130	1.21	2	590	Bruinsmia styracoides
3980	1.17	5	355	Magnolia
3840	1.13	2	910	Garcinia
3670	1.08	2	491	Alstonia macrophylla
3310	0.97	5	823	Chisocheton
3310	0.97	2	631	Diplycosia punctulata
3280	0.96	2	894	Eugenia cf. accuminatissima
3040	0.9	7	58	Rapanea affinis
2950	0.87	2	710	Lithocarpus cf. elegans
2860	0.84	5	891	Eugenia cf. eurpea
2760	0.81	7	546	LAURACEAE
2760	0.81	10	749	Garcinia
2760	0.81	2	874	Litsea odorifera
2540	0.75	2	671	Eugenia
2440	0.72	10	819	Dysoxylum
2020	0.59	5	900	Eugenia cf. caudatilimbum
1940	0.57	5	517	CLUSIACEAE

Appendix 1.4. -continued.

1780	0.52	2	926	Unknown
1470	0.43	7	724	Castanopsis clemensii
1460	0.43	5	850	Canarium
1390	0.41	2	430	Eugenia
1240	0.37	5	825	Aglaia
1100	0.32	2	641	Aporusa accuminatissima
1040	0.31	5	753	Teijsmanniodendron halophy.
730	0.22	2	896	Eugenia cf. confertum
730	0.22	2	354	Magnolia carsonii
730	0.21	2	605	Diospyros ferrugenescens
700	0.21	2	569	Helicia fusco-tomentosa
650	0.19	5	658	Ternstroemia cf. magnifica
640	0.19	2	948	Unknown
620	0.18	2	345	Garcinia ramiflora
580	0.17	2	680	Chionanthus cf. cuspidatus
510	0.15	2	280	Lithocarpus havilandii
490	0.14	2	706	Lithocarpus cf. leptogyne
480	0.14	2	869	Actinodaphne
440	0.13	2	886	Eugenia
370	0.11	2	860	Litsea
370	0.11	2	903	Eugenia
360	0.11	2	651	Aporusa benthamiana
320	0.1	2	617	Horsfieldia
300	0.09	2	616	Drypetes microphylla
300	0.09	2	812	Aphanamixis pedicellata
300	0.09	2	0.5	Unknown
270	0.08	2	515	Garcinia trianii
260	0.08	2	623	MYRISTICACEAE
250	0.07	2	625	Knema cinerea
240	0.07	2	708	Lithocarpus cantleyanus
240	0.07	2	857	Neolitsea
220	0.07	2	840	Timonius
220	0.06	2	935	Unknown
220	0.06	2	550	Symplocos cf. ferruginea
220	0.06	2	595	Elaeocarpus cf. fulvo-tom.
210	0.06	2	553	Scaphium
200	0.06	2	622	Myristica iners
200	0.06	2	849	Santiria apiculata
200	0.06	2	599	ELAEOCARPACEAE

Appendix 1.5. Species composition of the forest canopy (trees ≥10 cm DBH) at 1400 m on Mt. Kinabalu.

Plot size: 0.2477 ha
Number of species: 70
Density: 759 trees/ha, including standing dead trees
Total basal area: 465600 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
99310	21.33	16	702	Lithocarpus ewyckii
59190	12.71	32	570	Palaquium gutta
26520	5.7	16	710	Lithocarpus cf. elegans
23120	4.97	4	707	Lithocarpus cf. confragosus
16840	3.62	40	896	Eugenia cf. confertum
13980	3	4	927	Unknown
12750	2.74	16	768	Tristania cf. whiteana
11260	2.42	44	654	Adinandra clemensiae
10590	2.27	4	901	Eugenia cf. valdevenosa
8860	1.9	24	903	Eugenia
8650	1.86	12	964	Weinmannia
8460	1.82	8	571	Palaquium
7800	1.68	4	913	Phyllocladus hypophyllus
7740	1.66	12	725	Castanopsis
7340	1.58	24	853	LAURACEAE
6850	1.47	28	749	Garcinia
6770	1.45	4	914	Podocarpus
6300	1.35	8	961	Agathis dammara
6250	1.34	4	622	Myristica iners
6080	1.31	4	511	Calophyllum garcinioides
6050	1.3	40	900	Eugenia cf. caudatilimbum
5840	1.25	16	354	Magnolia carsonii
5760	1.24	8	888	Eugenia filiformis
5590	1.2	12	591	Unknown
5340	1.15	24	620	Horsfieldia glabra
5330	1.14	16	430	Eugenia
5040	1.08	8	951	Unknown
4680	1	12	546	LAURACEAE
4240	0.91	8	709	Lithocarpus pusillus
3960	0.85	16	531	Dissochaeta
3910	0.84	4	889	Eugenia cf. festigiatum
3710	0.8	12	529	Pternandra coerulescens
3640	0.78	8	504	Dacryodes
3540	0.76	8	483	Dacrycarpus imbricatus
3450	0.74	12	770	Tristania obovata
2980	0.64	12	850	Canarium
2890	0.62	20	680	Chionanthus cf. cuspidatus
2790	0.6	20	595	Elaeocarpus cf. fulvo-tom.
2590	0.56	4	705	Lithocarpus lampadarius
2230	0.48	8	522	Garcinia coriacea

Appendix 1.5. -continued.

2160	0.46	4	432	Calophyllum blancoi
2110	0.45	8	854	Litsea
2020	0.43	16	730	Polyosma
1560	0.34	4	624	Knema
1540	0.33	8	257	Eugenia subdecussata
1530	0.33	8	502	Gluta oba
1450	0.31	4	734	Gonystylus forbesii
1400	0.3	4	963	Eugenia cf. subdecussata
1220	0.26	8	366	Pruns arborea
1130	0.24	8	868	LAURACEAE
1000	0.22	4	856	Neolitsea
1000	0.22	4	514	CLUSIACEAE
860	0.19	8	834	Timonius mutabile
830	0.18	4	630	Diplycosia cf. punctulata
800	0.17	4	724	Castanopsis clemensii
760	0.16	4	421	PITTOSPORACEAE
600	0.13	4	518	Garcinia brianii
580	0.12	4	629	Vaccinium bancanum
460	0.1	4	882	Litsea
460	0.1	4	653	Schima wallichii
450	0.1	4	947	Unknown
450	0.1	4	772	Cinnamomum kinabaluensis
430	0.09	4	58	Rapanea affinis
420	0.09	4	616	Drypetes microphylla
400	0.09	4	754	Lophopetalum beccarianum
390	0.08	4	658	Ternstroemia cf. magnifica
360	0.08	4	478	Dacrydium falciforme
340	0.07	4	932	Unknown
340	0.07	4	886	Eugenia
330	0.07	4	248	Helicia

Appendix 1.6. Species composition of the forest canopy (trees ≥10 cm DBH) at 1600 m on Mt. Kinabalu.

Plot size: 0.3706 ha
Number of species: 58
Density: 572 trees/ha, including standing dead trees.
Total basal area: 332220 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
128580	38.71	78	570	Palaquium gutta
30910	9.31	67	963	Eugenia cf. subdecussata
18840	5.67	16	913	Phyllocladus hypophyllus
15500	4.67	11	511	Calophyllum garcinioides
14030	4.22	32	654	Adinandra clemensiae
8510	2.56	5	720	Lithocarpus
7380	2.22	19	283	Lithocarpus bullatus
7220	2.17	19	662	Adinandra dumosa
6740	2.03	3	906	Vaccinium
6310	1.9	13	257	Eugenia subdecussata
5940	1.79	8	852	Notaphoebe
5660	1.7	5	711	Lithocarpus hatsusimae
5030	1.51	16	351	Tetractomia tetrandrum
5000	1.51	5	478	Dacrydium falciforme
4680	1.41	27	354	Magnolia carsonii
4220	1.27	8	483	Dacrycarpus imbricatus
3760	1.13	11	870	Litsea castanea
3500	1.05	11	345	Garcinia ramiflora
3220	0.97	3	707	Lithocarpus cf. confragosus
3100	0.93	19	903	Eugenia
2730	0.82	13	595	Elaeocarpus cf. fulvo-tom.
2720	0.82	3	542	Albizia
2690	0.81	8	896	Eugenia cf. confertum
2590	0.78	5	355	Magnolia
2540	0.76	11	659	Ternstroemia cf. coriacea
2290	0.69	8	964	Weinmannia
2220	0.67	3	589	Shorea
2190	0.66	11	634	Macaranga
2160	0.65	3	899	Eugenia
2070	0.62	11	853	LAURACEAE
1890	0.57	5	582	Shorea monticola
1540	0.46	8	702	Lithocarpus ewyckii
1370	0.41	3	770	Tristania obovata
1100	0.33	3	620	Horsfieldia glabra
1020	0.31	3	941	Unknown
990	0.3	5	933	Unknown
870	0.26	3	366	Prunus arborea
840	0.25	3	817	Dysoxylum grande
820	0.25	5	546	LAURACEAE
800	0.24	3	905	Gynotroches axillasrisris

Appendix 1.6. -continued.

780	0.23	8	347	Elaeocarpus
780	0.23	5	709	Lithocarpus pusillus
730	0.22	5	779	Garcinia caudiculate
640	0.19	3	681	OLEACEAE
640	0.19	3	492	Madhuca endertii
630	0.19	3	892	Eugenia
540	0.16	3	856	Neolitsea
530	0.16	3	669	RUTACEAE
520	0.16	3	509	Ascarina philippinensis
440	0.13	3	248	Helicia
420	0.13	3	522	Garcinia coriacea
370	0.11	3	730	Polyosma
370	0.11	3	653	Schima wallichii
360	0.11	3	881	Litsea orocola
230	0.07	3	700	Ardisia lancifolia
230	0.07	3	593	ELAEOCARPACEAE
220	0.07	3	431	Eugenia
220	0.07	3	827	Aglaia squamulosa

Appendix 1.7. Species composition of the forest canopy (trees ≥10 cm DBH) at 1800 m on Mt. Kinabalu.

Plot size: 0.3441 ha
Number of species: 41
Density: 593 trees/ha, including standing dead trees.
Total basal area: 389650 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
111440	28.6	81	913	Phyllocladus hypophyllus
64990	16.68	32	511	Calophyllum garcinioides
35290	9.06	12	710	Lithocarpus cf. elegans
19980	5.13	81	963	Eugenia cf. subdecussata
18570	4.77	23	257	Eugenia subdecussata
18250	4.68	23	522	Garcinia coriacea
16420	4.21	15	711	Lithocarpus hatsusimae
11230	2.88	6	790	Quercus valdinervosa
10020	2.57	32	659	Ternstroemia cf.coriacea
8970	2.3	15	620	Horsfieldia glabra
7750	1.99	29	354	Magnolia carsonii
7400	1.9	17	653	Schima wallichii
6170	1.58	6	284	Dacrydium cf. beccarii
5670	1.45	9	769	Tristania grandifolia
4490	1.15	17	896	Eugenia cf. confertum
4210	1.08	20	654	Adiandra clemensiae

Appendix 1.7. -continued.

3860	0.99	12	351	Tetractomia tetrandrum
3730	0.96	12	899	Eugenia
3630	0.93	3	953	Unknown
3260	0.84	20	606	Diospyros cf. mindanaensis
3060	0.78	3	50	Microtropis walllichiana
2760	0.71	12	832	Horsfieldia
2660	0.68	12	366	Prunus arborea
2540	0.65	20	856	Neolitsea
2420	0.62	9	347	Elaeocarpus
1630	0.42	6	283	Lithocarpus bullatus
1450	0.37	9	519	Garcinia bancana
1390	0.36	6	669	RUTACEAE
1060	0.27	6	492	Madhuca endertii
820	0.21	3	58	Rapanea affinis
630	0.16	3	870	Litsea castanea
590	0.15	3	903	Eugenia
570	0.15	3	431	Eugenia
410	0.11	3	772	Cinnamomum kinabaluensis
370	0.09	3	356	Arthrophyllum diversifolium
370	0.09	3	265	Actinodaphne
360	0.09	3	754	Lophopetalum beccarianum
360	0.09	3	943	Unknown
350	0.09	3	720	Lithocarpus
280	0.07	3	949	Unknown
240	0.06	3	593	ELAEOCARPACEAE

Appendix 1.8. Species composition of the forest canopy (trees ≥10 cm DBH) at 2000 m on Mt. Kinabalu.

Plot size: 0.4907 ha
Number of species: 50
Density: 497 trees/ha, including standing dead trees.
Total basal area: 367060 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
48220	13.14	6	710	Lithocarpus cf. elegans
46890	12.77	45	431	Eugenia
40330	10.99	33	902	Eugenia valdevenosa
35750	9.74	31	703	Lithocarpus confertus
21990	5.99	14	354	Magnolia carsonii
21170	5.77	39	659	Ternstroemia cf. coriacea
17640	4.8	37	854	Litsea
16560	4.51	4	767	Tristania cf. clementis
11020	3	71	407	Cinnamomum griffithii

Appendix 1.8. -continued.

10220	2.78	6	654	Adiandra clemensiae
9660	2.63	20	492	Madhuca endertii
8660	2.36	10	677	Magnolia
8260	2.25	8	945	Unknown
7010	1.91	26	903	Eugenia
6440	1.75	8	853	LAURACEAE
6240	1.7	6	859	Endiandra cf. kugiana
5730	1.56	6	653	Schima wallichii
5250	1.43	10	719	Castanopsis
5020	1.37	2	913	Phyllocladus hypophyllus
4560	1.24	10	832	Horsfieldia
4350	1.18	14	523	Garcinia multinervia
3950	1.08	12	604	Diospyros cf. sumatrana
3340	0.91	4	437	Calophyllum
1910	0.52	10	836	Timonius
1590	0.43	4	657	Ternstroemia cf. microcalyx
1580	0.43	2	595	Elaeocarpus cf. fulvo-tom.
1460	0.4	2	522	Garcinia coriacea
1370	0.37	2	933	Unknown
960	0.26	2	905	Gynotroches axillaris
930	0.25	6	420	Helicia
910	0.25	8	678	Magnolia uvariifolia
910	0.25	4	593	ELAEOCARPACEAE
820	0.22	2	925	Unknown
800	0.22	4	737	Rapanea cf. avenis
780	0.21	4	860	Litsea
700	0.19	6	624	Knema
620	0.17	2	366	Prunus arborea
580	0.16	2	363	Ficus
450	0.12	4	350	Evodia subunifoliolata
410	0.11	2	705	Lithocarpus lampadarius
290	0.08	2	946	Unknown
260	0.07	2	546	LAURACEAE
210	0.06	2	406	Actinodaphne
200	0.05	2	594	Flacortia kinabaluensis
190	0.05	2	698	Ardisia colorata
190	0.05	2	736	Lepisanthes cf. fruticosa
180	0.05	2	732	Saurauia hoterosepala
180	0.05	2	547	Clerodendrum
160	0.04	2	839	Lasianthus
160	0.04	2	483	Dacrycarpus imbricatus

Appendix 1.9. Species composition of the forest canopy (trees ≥10 cm DBH) at 2350 m on Mt. Kinabalu.

Plot size: 0.1439 ha
Number of species: 26
Density: 778 trees/ha, including standing dead trees.
Total basal area: 595480 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
177960	29.88	63	354	Magnolia carsonii
64510	10.83	132	509	Ascarina philippinensis
52360	8.79	69	663	Unknown
42070	7.07	14	832	Horsfieldia
37210	6.25	56	287	Eugenia punctilimba
30780	5.17	21	347	Elaeocarpus
25650	4.31	14	467	Lithocarpus turbinatus
24940	4.19	104	143	Clethra pachyphylla
22450	3.77	35	739	Diplycosia
22010	3.7	21	526	LAURACEAE
11860	1.99	14	198	Cyathea havilandii
11350	1.91	21	20	Eurya trichocarpa
10680	1.79	7	151	Prunus mirabilis
8100	1.36	7	205	Polyosma
7520	1.26	14	911	Notaphoebe
6750	1.13	49	66	Olea rubrovenia
6530	1.1	49	248	Helicia
6530	1.1	14	58	Rapanea affinis
6210	1.04	7	5	Ilex zygophylla
5320	0.89	21	26	Eugenia houttuynii
4210	0.71	14	315	Cyathea
3830	0.64	14	913	Phyllocladus hypophyllus
2270	0.38	7	860	Litsea
1990	0.33	7	660	THEACEAE
1220	0.21	7	939	Unknown
1170	0.2	7	280	Lithocarpus havilandii

Appendix 1.10. Species composition of the forest canopy (trees ≥10 cm DBH) at 2600 m on Mt. Kinabalu.

Plot size: 0.17 ha
Number of species: 13
Density: 659 trees/ha, including standing dead trees.
Total basal area: 492360 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
248690	50.51	235	287	Eugenia punctilimba
64520	13.1	53	5	Ilex zygophylla
42140	8.56	47	913	Phyllocladus hypophyllus
41160	8.36	88	354	Magnolia carsonii
40050	8.13	141	66	Olea rubrovenia
20020	4.07	18	205	Polyosma
11330	2.3	29	280	Lithocarpus havilandii
6750	1.37	12	347	Elaeocarpus
5690	1.16	12	2	Symplocos pendula
4920	1	24	145	Prunus arborea v. stipulacea
3960	0.8	18	143	Clethra pachyphylla
2020	0.41	12	50	Microtropis wallichiana
1110	0.23	6	58	Rapanea affinis

Appendix 1.11. Species composition of the forest canopy (trees ≥10 cm DBH) at 2800 m on Mt. Kinabalu.

Plot size: 0.1034 ha
Number of species: 16
Density: 1044 trees/ha, including standing dead trees
Total basal area: 264110 $sqcm^2$/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
71630	27.12	203	280	Lithocarpus havilandii
38920	14.74	213	913	Phyllocladus hypophyllus
31510	11.93	145	962	Dacrycarpus kinabaluensis
23980	9.08	87	252	Leptospermum recurvum
21560	8.16	106	256	Eugenia kinabaluensis
15270	5.78	77	147	Schima wallichii ssp. brevi.
14800	5.6	19	27	Tristania elliptica
13470	5.1	58	536	Myrica javanica
9970	3.78	77	3	Polyosma hookeri
6100	2.31	58	2	Symplocos pendula

Appendix 1.11. -continued.

5110	1.93	39	1	Ilex havilandii
3960	1.5	29	13	Vaccinium pachydermum
3220	1.22	19	8	Vaccinium stapfianum
2280	0.87	19	297	Podocarpus brevifolius
1540	0.58	19	26	Eugenia houttuynii
790	0.3	10	18	Symplocos buxifolia

Appendix 1.12. Species composition of the forest canopy (trees ≥10 cm DBH) at 3000 m on Mt. Kinabalu.

Plot size: 0.0574 ha
Number of species: 17
Density: 1950 trees/ha, including standing dead trees
Total basal area: 553960 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
181970	32.85	540	962	Dacrycarpus kinabaluensis
92080	16.62	261	147	Schima wallichii ssp. brevi.
58050	10.48	174	256	Eugenia kinabaluensis
32140	5.8	226	3	Polyosma hookeri
23720	4.28	105	52	Eurya obovata
23350	4.22	87	56	Talauma rigida
21420	3.87	157	337	Daphniphyllum glaucescens
19970	3.6	157	4	Ternstroemia lowii
19950	3.6	35	205	Polyosma
19950	3.6	105	26	Eugenia houttuynii
12250	2.21	17	536	Myrica javanica
9290	1.68	70	18	Symplocos buxifolia
8870	1.6	35	913	Phyllocladus hypophyllus
8510	1.54	52	25	Eugenia steenisii
8010	1.45	17	252	Leptospermum recurvum
7600	1.37	35	146	Adinandra impressa
6830	1.23	35	2	Symplocos pendula

Appendix 1.13. Species composition of the forest canopy (trees ≥10 cm DBH) at 3200 m on Mt. Kinabalu.

Plot size: 0.0932 ha
Number of species: 14
Density: 1202 trees/ha, including standing dead trees.
Total basal area: 573660 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
220600	38.45	397	962	Dacrycarpus kinabaluensis
109820	19.14	172	147	Schima wallichii ssp. brev.
60120	10.48	86	151	Prunus mirabilis
52570	9.16	21	22	Eugenia ampullaria
41290	7.2	182	913	Phyllocladus hypophyllus
31570	5.5	129	2	Symplocos pendula
16690	2.91	118	337	Daphniphyllum glaucescens
15300	2.67	32	252	Leptospermum recurvum
7580	1.32	43	338	Rhododendron buxifolium
7380	1.29	11	56	Talauma rigida
4180	0.73	11	52	Eurya obovata
2680	0.47	11	297	Podocarpus brevifolius
2580	0.45	11	149	Photinia davidiana
1300	0.23	11	50	Microtropis wallichiana

Appendix 1.14. Species composition of the forest canopy (trees ≥10 cm DBH) at 3400 m on Mt. Kinabalu.

Plot size: 0.0542 ha
Number of species: 11
Density: 1844 trees/ha, including standing dead trees
Total basal area: 450060 cm^2/ha

Basal area cm^2/ha	Rel. domi. %	Stem /ha	Sp. no.	Species
126190	28.04	535	22	Eugenia ampullaria
119300	26.51	701	913	Phyllocladus hypophyllus
62780	13.95	517	338	Rhododendron buxifolium
34780	7.73	185	147	Schima wallichii ssp. brev.
28810	6.4	129	18	Symplocos buxifolia
26140	5.81	111	962	Dacrycarpus kinabaluensis
18190	4.04	111	149	Photinia davidiana
13230	2.94	92	252	Leptospermum recurvum
8740	1.94	37	8	Vaccinium stapfianum
7620	1.69	74	58	Rapanea affinis
4280	0.95	18	50	Microtropis wallichiana

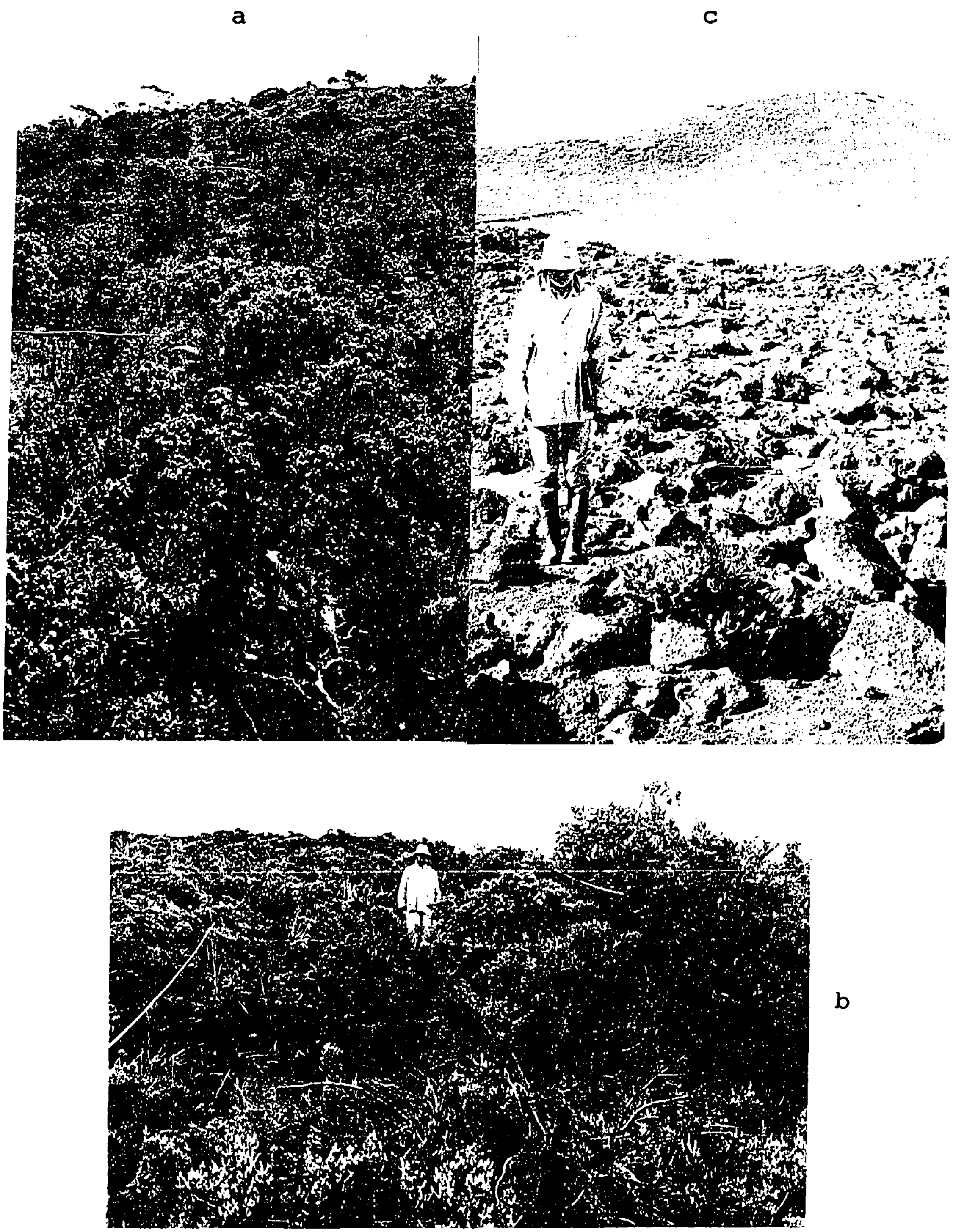
Appendix 2. Relative dominance values of species >2m height along the transect on Mt. Haleakala.
The dominance values (%) are based on species basal areas per 20x20 m quadrat.

Plot no.	HK128	HK042	HK117	HK036	HK025	HK010	HK039	HK005	HK107	HK133	HK060	HK050
Alt. (m)	450	600	800	1000	1200	1400	1600	1800	1900	2000	2200	2400
Acacia koa	.	.	.	.	.	.	.	.	32.6	19.8	.	.
Alyxia olivaeformis	.	.	.	+	+	+	+	.	.	.	.	.
Antidesma platyphyllum	.	6	0.7	.	.	.	.	.	.	.	.	.
Broussaisia arguta	.	.	.	0.1	0.3	0.7	0.3	.	.	.	.	.
Cheirodendron trigynum	.	3.1	1.9	10.9	6.9	7.1	6.1	6.4	2.5	.	.	.
Cibotium chamissoi	.	33.1	43.8	33.5	13.5	.	2.5	.	.	.	.	.
Cibotium glaucum	.	.	3.3	7.3	.	6.7	.	.	.	.	.	.
Clermontia arborescens ssp. waihiae	.	.	0.1	+	.	0.4	0.3	.	.	.	.	.
Coprosma ochracea	.	.	.	.	.	.	0.1	1.6	1.5	33.9	.	.
Cyrtandra platyphylla	.	.	.	.	.	+	.	.	.	.	.	.
Freycinetia arborea	.	.	.	+	+	.	.	.	.	.	.	.
Gouldia terminalis	.	0.2	.	.	+	+	+	.	.	.	.	.
Ilex anomala	.	.	.	.	0.1	0.1	+	.	2.7	1.1	.	.
Melaleuca quinquenervia	24.6	.	.	.	.	.	.	.	.	.	.	.
Metrosideros polymorpha v. glaberrima	56.2	52.5	45.7	40.6	60.1	70	83.8	82.1	49.6	13	.	.
Metrosideros polymorpha v. incana	.	.	.	0.2	12.7	1.6	.	.	.	.	.	.
Metrosideros polymorpha v. polymorpha	.	.	.	.	.	.	.	.	.	0.2	.	.
Myrsine lessertiana	.	0.1	.	1.4	2.3	1.4	1	1.8	.	8.9	.	.
Myrsine sandwicensis	.	.	0.4	0.8	0.9	0.6	.	.	.	.	.	.
Pelea clusiifolia	.	.	.	.	.	.	0.8	3.2	.	.	.	.
Pelea haleakalae	.	.	1	2.4	0.8	4.4	.	.	.	.	.	.
Pelea orbicularis	.	.	0.1	0.3	0.3	0.1	.	.	.	.	.	.
Phychotria mariniana	.	.	.	1.9	.	.	.	.	.	.	.	.
Pritchardia arecina	.	.	2.7	.	.	.	.	.	.	.	.	.
Psidium cattleianum	19.2	.	+	.	.	.	.	.	.	.	.	.
Psychotria hawaiiensis	.	.	.	.	1	1	1	.	.	.	.	.
Rubus hawaiensis	.	.	.	.	.	.	.	+	0.4	0.4	.	.
Smilax sandwicensis	.	.	.	+	.	+	+	.	.	.	.	.
Sophora chrysophylla	.	.	.	.	.	.	.	.	.	.	100	100
Stenogyne kamehamehae	.	.	.	+	.	.	.	.	.	.	.	.
Styphelia tameiameiae	.	.	.	.	0.2	4.4	2.9	1.9	2.5	3.7	.	.
Tetraplasandra oahuensis	.	5	0.1	0.3	.	.	.	.	.	.	.	.
Vaccinium calycinum	.	.	.	.	0.5	1.1	1.2	3	7.9	19.2	.	.
Vaccinium dentatum	.	.	0.1	+	.	0.1	0.1	.	0.2	.	.	.
Wikstroemia monticola	.	.	0.1	+	0.4	0.4	.	.	.	.	.	.
Total species no.	3	7	14	19	17	20	16	8	9	9	1	1

Appendix 3. South face of Mt. Kinabalu (4101 m) viewed from 1700 m a.s.l.

Appendix 4. East slope of Mt. Haleakalā (3055 m) viewed from 500 m a.s.l.

Appendix 5. Views of the lower transect communities on Mt. Haleakalā. a: Lowland dieback community at 450 m. b: Lowland intact forest at 800 m. c: Lower montane forest at 1500 m.



Appendix 6. Views of the upper transect communities on Mt. Haleakalā. a: Forest line at 1950 m. b: Lower subalpine scrub at 2200 m. c: Alpine desert near the summit.

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Table 3.4. Summarized differential table of the vegetation on the windward slope of Mt. Haleakala, Maui, Hawaii.

[illegible]

Table 3.4. Summarized differential table of the vegetation on the windward slope of Mt. Haleakala, Maui, Hawaii. Figures are constancy values (%) per vegetation unit.

** alien species, * indigenous species, 'unmarked' endemic species

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Forest Vegetation
A. Elaphoglossum crassifolium unit
- A1. M. polymorpha v. glaberrima-O. chinensis community
- A2. M. polymorpha v. glaberrima-A. pinnatifidus community

B. Vaccinium calycinum unit
- B1. M. polymorpha v. glaberrima-N. granadensis community
- B2. M. polymorpha v. glaberrima-P. clusiifolia community
- B3. M. polymorpha v. glaberrima-S. cyatheoides community

Treeless Vegetation
C. Dubautia menziesii unit
- C1. Sophora chrysophylla community
  - C1a. Prunella vulgaris subunit
  - C1b. Trisetum glomeratum subunit
- C2. Tetramolopium humile community

Plant Community Code	A1	A2	B1	B2	B3	C1a	C1b	C2
Number of Relevés	8	19	23	9	12	16	13	11
Differential species of the forest vegetation								
Metrosideros polymorpha v. glaberrima	100	100	100	100	75	0	0	0
Cheirodendron trigynum	0	95	100	100	75	0	0	0
Vaccinium dentatum	0	95	100	67	17	0	0	0
Myrsine lessertiana	0	58	96	78	50	0	0	0
Elaphoglossum hirtum*	13	53	91	100	33	0	0	0
Broussaisia arguta	0	79	100	33	0	0	0	0
Athyrium microphyllum	0	26	100	44	58	0	0	0
Hedyotis (Gouldia) terminalis	0	74	87	11	0	0	0	0
Astelia menziesiana	0	47	100	11	8	0	0	0
Sadleria pallida	0	53	87	22	17	0	0	0
Carex alligata	0	5	70	56	67	6	0	0
Polypodium pellucidum	0	26	87	44	17	0	0	0
Asplenium polyodon*	13	32	57	89	17	0	0	0
Myrsine sandwicensis	0	63	70	22	0	0	0	0
Athyrium sandwichianum	0	42	44	100	17	0	0	0
Ilex anomala*	13	47	52	22	25	0	0	0
Pleopeltis thunbergiana*	38	16	39	78	33	0	0	0
Smilax sandwicensis	0	58	44	11	8	0	0	0
Asplenium lobulatum*	0	37	44	33	0	0	0	0
Rubus argutus**	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[illegible]	13	32	57	89	17	0	0	0
Myrsine sandwicensis	0	63	70	22	0	0	0	0
Athyrium sandwichianum	0	42	44	100	17	0	0	0
Ilex anomala*	13	47	52	22	25	0	0	0
Pleopeltis thunbergiana*	38	16	39	78	33	0	0	0
Smilax sandwicensis	0	58	44	11	8	0	0	0
Asplenium lobulatum*	0	37	44	33	0	0	0	0
Rubus argutus**	0	47	4	11	75	0	0	0
Differential species of C								
Dubautia menziesii	0	0	0	0	0	50	100	100
Differential species of A								
Elaphoglossum crassifolium	88	95	0	0	0	0	0	0
Paspalum conjugatum**	100	68	0	0	0	0	0	0
Adenophorus hymenophylloides	63	58	13	0	0	0	0	0
Psilotum complanatum*	38	68	4	0	0	0	0	0
Antidesma platyphyllum	63	47	0	0	0	0	0	0
Tetraplasandra oahuensis	13	58	9	0	0	0	0	0
Cyperus halpan**	50	47	0	0	0	0	0	0
Huperzia phyllanthum*	63	42	0	0	0	0	0	0
Nephrolepis cordifolia*	25	58	0	0	0	0	0	0
Rubus rosifolius**	25	47	9	0	0	0	0	0
Psilotum nudum*	38	32	0	0	0	0	0	0
Setaria palmifolia**	13	42	0	0	0	0	0	0
Differential species of B								
Vaccinium calycinum	0	0	96	100	83	0	0	0
Dryopteris wallichiana*	0	0	91	89	83	25	0	0
Elaphoglossum wawrae	0	0	100	100	50	0	0	0
Dryopteris glabra	0	0	61	89	58	0	0	0
Coprosma ochracea	0	0	39	100	83	0	0	0
Rubus hawaiensis	0	0	30	89	83	0	0	0
Uncinia uncinata*	0	0	61	78	33	0	0	0
Ctenitis rubiginosa	0	0	44	100	17	0	0	0
Dryopteris subbipinnata	0	0	4	78	42	0	0	0
Adenophorus tripinnatifidus	0	0	26	44	8	0	0	0
Differential species of A1								
Odontosoria (Sphenomeris) chinensis*	100	11	0	0	0	0	0	0
Andropogon virginicus**	88	16	0	0	0	0	0	0
Psidium cattleianum**	88	5	0	0	0	0	0	0
Centella asiatica**	75	5	0	0	0	0	0	0

Uncinia uncinata*	0	0	61	78	33	0	0	0
Ctenitis rubiginosa	0	0	44	100	17	0	0	0
Dryopteris subbipinnata	0	0	4	78	42	0	0	0
Adenophorus tripinnatifidus	0	0	26	44	8	0	0	0
Differential species of A1								
Odontosoria (Sphenomeris) chinensis*	100	11	0	0	0	0	0	0
Andropogon virginicus**	88	16	0	0	0	0	0	0
Psidium cattleianum**	88	5	0	0	0	0	0	0
Centella asiatica**	75	5	0	0	0	0	0	0
Sacciolepis indica**	50	16	0	0	0	0	0	0
Tibouchina herbacea**	75	0	0	0	0	0	0	0
Clidemia hirta**	50	5	0	0	0	0	0	0
Machaerina mariscoides ssp. meyenii*	25	0	0	0	0	0	0	0
Differential species of A2								
Adenophorus pinnatifidus	0	84	4	0	0	0	0	0
Freycinetia arborea*	0	63	13	0	0	0	0	0
Psychotria mariniana	0	68	0	0	0	0	0	0
Peperomia obovatilimba	0	63	4	0	0	0	0	0
Syzygium sandwicensis	0	58	0	0	0	0	0	0
Peperomia hirtipetiola	0	42	13	0	0	0	0	0
Diplopterygium pinnatum*	0	42	17	0	0	0	0	0
Labordia hedyosmifolia	0	26	0	0	0	0	0	0
Differential species of B1								
Nertera granadensis*	0	0	100	11	0	0	0	0
Peperomia expallescens	0	0	91	11	0	0	0	0
Metrosideros polymorpha v. incana	0	16	78	0	0	0	0	0
Peperomia macraeana	0	16	74	0	0	0	0	0
Xiphopteris saffordii	0	11	74	0	0	0	0	0
Grammitis hookeri*	0	0	78	0	0	0	0	0
Cyrtandra hashimotoi	0	11	65	0	0	0	0	0
Labordia venosa	0	0	74	0	0	0	0	0
Adenophorus montanus	0	0	65	0	0	0	0	0
Psychotria hawaiiensis	0	0	65	0	0	0	0	0
Cyrtandra platyphylla	0	11	52	0	0	0	0	0
Korthalsella complanata*	0	16	44	0	0	0	0	0
Thelypteris sandwicensis	0	0	39	0	0	0	0	0
Dryopteris acutidens	0	0	30	0	0	0	0	0
Differential species of B2								
Pelea clusiifolia	0	0	22	78	0	0	0	0
Asplenium normale*	0	0	4	56	8	0	0	0
Peperomia membranacea	0	0	4	56	8	0	0	0

Differential species of B3								
Sadleria cyatheoides	0	0	0	33	100	0	0	0
Metrosideros polymorpha v. polymorpha	0	0	0	0	83	13	0	0
Oreobolus furcatus	0	0	0	0	42	0	0	0
Polystichum bonseyi	0	0	0	0	33	0	0	0
Differential species of A2 and/or B1								
Cibotium chamissoi	38	100	91	0	0	0	0	0
Mecodium recurvum	75	90	65	0	0	0	0	0
Adenophorus tamariscinus	88	90	61	0	0	0	0	0
Grammitis tenella	88	79	48	0	0	0	0	0
Cibotium glaucum	75	100	96	0	0	0	0	0
Dicranopteris linearis*	100	79	61	0	0	0	0	0
Lycopodium cernuum*	100	68	22	0	0	0	0	0
Dryopteris tetrapinnata	0	5	22	0	0	0	0	0
Liparis hawaiensis	0	16	26	0	0	0	0	0
Dryopteris nuda	0	16	35	0	0	0	0	0
Pelea haleakalae	0	84	87	0	0	0	0	0
Sphaerocionium lanceolatum	0	84	70	0	0	0	0	0
Clermontia arborescens ssp. waihiae	0	84	65	0	0	0	0	0
Elaphoglossum alatum	0	74	44	0	0	0	0	0
Alyxia oliviformis	0	58	57	0	0	0	0	0
Pelea orbicularis	0	47	52	0	8	0	0	0
Juncus planifolius**	0	47	22	0	0	0	0	0
Stenogyne rotundifolia	0	21	22	11	8	0	0	0
Wikstroemia monticola	0	37	30	0	0	0	0	0
Vandenboschia cyrtotheca	0	21	9	0	0	0	0	0
Machaerina angustifolia*	0	26	4	0	0	0	0	0
Hedyotis (Gouldia) hillebrandii	0	21	9	11	0	0	0	0
Coprosma pubens	0	32	9	0	0	0	0	0
Differential species of C1								
Sophora chrysophylla	0	0	0	0	0	94	100	0
Coprosma montana	0	0	0	0	0	81	100	0
Geranium cuneatum ssp. tridens	0	0	0	0	0	88	62	0
Carex wahuensis	0	0	0	0	0	63	39	0
Differential species of C2								
Tetramolopium humile ssp. haleakalae	0	0	0	0	0	0	0	100
Argyroxiphium sand. ssp. macrocephalum	0	0	0	0	0	0	0	64
Differential species of C1b								
Trisetum glomeratum	0	0	0	0	0	0	92	82
Rumex acetosella**	0	0	0	11	33	38	92	0
Pellaea ternifolia*	0	0	0	0	0	0	62	9
Asplenium adiantum-nigrum*	0	0	0	0	0	0	46	36
Asplenium trichomanes*	0	0	0	0	0	0	31	46
Dodonaea viscosa*	0	0	0	0	0	0	23	0

Differential species of C1b								
Trisetum glomeratum	0	0	0	0	0	0	92	82
Rumex acetosella**	0	0	0	11	33	38	92	0
Pellaea ternifolia*	0	0	0	0	0	0	62	9
Asplenium adiantum-nigrum*	0	0	0	0	0	0	46	36
Asplenium trichomanes*	0	0	0	0	0	0	31	46
Dodonaea viscosa*	0	0	0	0	0	0	23	0
Differential species of C1a and/or B3								
Epilobium billardierianum ssp. cinereum	0	0	0	0	17	50	0	0
Prunella vulgaris**	0	0	0	0	58	69	0	0
Coprosma ernodeoides	0	0	0	0	58	50	0	9
Hypochoeris radicata**	0	0	0	0	83	100	100	91
Deschampsia nubigena	0	0	9	0	67	81	100	82
Vaccinium reticulatum	0	0	0	0	83	100	92	18
Anthoxanthum odoratum**	0	0	4	22	83	100	62	0
Pteridium aquilinum v. decompositum*	0	0	0	0	42	100	100	0
Holcus lanatus**	0	0	4	0	58	100	54	0
Luzula hawaiiensis	0	0	0	0	33	44	85	18
Lycopodium venustulum	0	11	4	0	33	6	0	0
Unclassified species								
Styphelia tameiameiae*	0	0	100	89	92	100	100	46
Peperomia eekana	0	5	26	22	0	0	0	0
Erechtites valerianifolia**	13	32	4	0	0	0	0	0
Acacia koa	13	0	0	33	25	0	0	0
Lapsana communis**	0	0	0	11	25	0	23	0
Stenogyne kamehamehae	0	11	13	11	0	0	0	0
Dryopteris unidentata	0	11	4	22	0	0	0	0
Ageratina adenophora**	13	16	4	0	0	0	0	0
Pteris excelsa*	0	0	4	22	17	0	0	0
Sphaerocionium obtusum	13	21	0	0	0	0	0	0
Asplenium acuminatum	0	0	13	11	0	0	0	0
Commelina diffusa**	0	16	4	0	0	0	0	0
Coniogramme pilosa	0	0	13	11	0	0	0	0
Marattia douglasii	0	0	17	0	0	0	0	0
Nephrolepis multiflora**	38	5	0	0	0	0	0	0
Cyanea kunthiana	0	0	13	0	0	0	0	0
Digitaria sp**	0	16	0	0	0	0	0	0
Elaphoglossum pellucidum	0	16	0	0	0	0	0	0
Huperzia serratum*	0	11	4	0	0	0	0	0
Gahnia gahniiformis*	0	0	0	0	0	13	[illegible]	0
Paspalum urvillei**	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Stenogyne kamehamehae	0	11	13	11	0	0	0	0
Dryopteris unidentata	0	11	4	22	0	0	0	0
Ageratina adenophora**	13	16	4	0	0	0	0	0
Pteris excelsa*	0	0	4	22	17	0	0	0
Sphaerocionium obtusum	13	21	0	0	0	0	0	0
Asplenium acuminatum	0	0	13	11	0	0	0	0
Commelina diffusa**	0	16	4	0	0	0	0	0
Coniogramme pilosa	0	0	13	11	0	0	0	0
Marattia douglasii	0	0	17	0	0	0	0	0
Nephrolepis multiflora**	38	5	0	0	0	0	0	0
Cyanea kunthiana	0	0	13	0	0	0	0	0
Digitaria sp**	0	16	0	0	0	0	0	0
Elaphoglossum pellucidum	0	16	0	0	0	0	0	0
Huperzia serratum*	0	11	4	0	0	0	0	0
Gahnia gahniiformis*	0	0	0	0	0	13	8	0
Paspalum urvillei**	13	11	0	0	0	0	0	0
Scaevola chamissoniana	0	16	0	0	0	0	0	0
Cerastium fontanum ssp. triviale**	0	0	0	0	0	6	8	0
Clermontia kakeana	0	11	0	0	0	0	0	0
Dactylis glomerata**	0	0	0	0	0	13	0	0
Dryopteris fusco-atra	0	0	9	0	0	0	0	0
Dubautia reticulata	0	0	0	0	17	0	0	0
Fragaria chiloensis ssp. sandwicensis	0	0	0	0	8	6	0	0
Lythrum maritimum*	0	0	0	0	17	0	0	0
Melaleuca quinquenervia**	25	0	0	0	0	0	0	0
Ophioglossum pendulum*	13	5	0	0	0	0	0	0
Pinus radiata**	0	0	0	0	0	13	0	0
Pittosporum glabrum	0	5	4	0	0	0	0	0
Plantago lanceolata**	0	0	0	0	0	6	8	0
Psidium guajava**	13	5	0	0	0	0	0	0
Pteris cretica*	0	0	0	0	17	0	0	0
Setaria gracilis**	13	5	0	0	0	0	0	0
Silene struthioloides	0	0	0	0	0	0	15	0
Agrostis sandwicensis	0	0	0	0	0	0	8	0
Asplenium fragile*	0	0	0	11	0	0	0	0
Carex sp**	0	5	0	0	0	0	0	0
Clermontia grandiflora ssp. grandiflora	0	0	4	0	0	0	0	0
Ctenitis latifrons	0	0	0	11	0	0	0	0
Cuphea carthagenensis**	13	0	0	0	0	0	0	0
Cyanea sp	0	0	4	0	0	0	0	0
Kyllinga brevifolia**	13	0	0	0	0	0	0	0
Dryopteris insularis*	0	0	4	0	0	0	0	0
Dryopteris hawaiiensis	0	0	0	11	0	0	0	0
Conyza bonariensis**	0	0	0	0	0	0	0	9

[illegible]	0	0	0	11	0	0	0	0
Carex sp**	0	5	0	0	0	0	0	0
Clermontia grandiflora ssp. grandiflora	0	0	4	0	0	0	0	0
Ctenitis latifrons	0	0	0	11	0	0	0	0
Cuphea carthagenensis**	13	0	0	0	0	0	0	0
Cyanea sp	0	0	4	0	0	0	0	0
Kyllinga brevifolia**	13	0	0	0	0	0	0	0
Dryopteris insularis*	0	0	4	0	0	0	0	0
Dryopteris hawaiiensis	0	0	0	11	0	0	0	0
Conyza bonariensis**	0	0	0	0	0	0	0	9
Eucalyptus sp**	13	0	0	0	0	0	0	0
Juncus effusus**	0	5	0	0	0	0	0	0
Ludwigia octovalvis**	13	0	0	0	0	0	0	0
Paspalum scrobiculatum**	13	0	0	0	0	0	0	0
Peperomia cookiana	0	0	4	0	0	0	0	0
Perrottetia sandwicensis	0	5	0	0	0	0	0	0
Phymatosorus scolopendria**	0	5	0	0	0	0	0	0
Pittosporum confertiflorum	0	0	0	0	8	0	0	0
Pritchardia arecina	0	5	0	0	0	0	0	0
Rubus macraei	0	0	0	0	8	0	0	0
Sadleria squarrosa	0	0	4	0	0	0	0	0
Trifolium repens**	0	0	0	0	0	6	0	0
unidentified	0	5	0	0	0	0	0	0
unidentified	0	0	0	0	0	0	8	0
Total Species Number	47	100	103	52	56	28	26	14