Malaysian Journal of Science **17A**: 25-35 (1996)

Altitudinal zonation of tropical rain forest at the Danum Valley Research Centre, Sabah, Malaysia

Jumaat H. Adam and Ferdinand L. Enning
Fakulti Sains Sumber Alam, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor Darul Ehsan

ABSTRACT Clustering analysis of forest community types at the Danum Valley Tropical Rain Forest Research Centre, Sabah, Malaysia using complete linkage method and average linkage method has been carried out. The analysis resulted in the identification of four forest types/zones. To determine the dominant and codominant species within each forest zone, the highest and second highest importance values (I_v) of all tree species were calculated. In forest zone 1 (FZ1), at 150-250 m a.s.l., the dominant and codominant species are respectively, *Shorea pauciflora* and *Shorea fallax*; in forest zone 2 (FZ2), at 350-500 m altitude, *Shorea leprosula* and *Vatica dulitensis*; in forest zone 3 (FZ3), at 600-700 m, *Shorea pauciflora* and *Vatica dulitensis*; and in forest zone 4 (FZ4) or summit zone, at 820 m, are *Schima wallichii* and *Ternstroemia aneura*. Forest zones 1 and 2 share many common attributes: both zones comprise three tree-canopy layers, i.e. emergent, main canopy and lower storey; both the dominant and codominant species belong to the family Dipterocarpaceae; both containing a high number of families and species; in terms of species richness, the two dominant families are the Euphorbiaceae and the Dipterocarpaceae; more than 70% of the families with a dbh of >3 cm contributed less than 10 stems each. Forest zone 3 (FZ3), occurring at higher altitude, differs from FZ1 and FZ2 in its two tree-storeys (main canopy and lower storey) and the Myrtaceae being the second dominant family in terms of species richness and density. The summit zone (FZ4) differs markedly from FZ1, FZ2 and FZ3 in having one tree-layer, comprising of trees of lower height and small diameter; the dominant and codominant species being *Schima wallichii* and *Ternstroemia aneura* of the Theaceae instead of Dipterocarpaceae; and the number of species and families and species diversity value are lower. In physiognomy, forest zone 4 is similar to that of the typical high altitude montane mossy forest in Sabah, thus demonstrating the Massenerhebung effect. There is a decrease in species and family richness, species diversity, tree height and diameter, above ground biomass, basal area, and stratification with increasing altitude. Conversely, tree density and frequency of small sized trees increase with increasing altitude.

ABSTRAK Analisis pengklusteran jenis komuniti hutan di Pusat Penyelidikan Hutan Hujan Tropika Danum, Sabah, Malaysia berdasarkan kaedah Rangkaian Lengkap dan kaedah Rangkaian Purata telah dilakukan. Analisis tersebut telah mengenalpasti empat jenis/zon hutan. Pengiraan nilai indeks kemustahakan (I_v) dilakukan pada setiap zon tersebut untuk menentukan spesies yang dominan dengan I_v tertinggi dan spesies kodominan dengan I_v kedua tertinggi. Zon hutan 1 (FZ1) berada pada 150-250 m dari aras laut dikuasai oleh *Shorea pauciflora* dan *Shorea fallax* sebagai spesies yang dominan dan kodominan masing-masing; zon hutan 2 (FZ2), terletak pada 350-500 m altitud dikuasai oleh *Shorea leprosula* dan *Vatica dulitensis*; zon hutan 3 (FZ3), terletak pada 600-700 m altitud dikuasai oleh *Shorea pauciflora* dan *Vatica dulitensis*; zon hutan 4 (FZ4) atau zon puncak (820 m), dikuasai oleh *Schima wallichii* dan *Ternstroemia aneura*. Zon hutan 1 dan 2 berkongsi banyak atribut sepunya: hutan dua zon tersebut mempunyai tiga lapisan kanopi pokok iaitu lapisan menjulang, lapisan kanopi selanjar dan lapisan subkanopi; spesies yang dominan dan kodominan dikuasai oleh dua spesies yang tergolong dalam famili Dipterocarpaceae; kedua-dua zon tersebut mempunyai kekayaan famili, spesies yang tinggi; dua famili yang mempunyai bilangan spesies dan kelimpahan individu tertinggi dan kedua tertinggi diwakili oleh famili Euphorbiaceae dan Dipterocarpaceae masing-masing; lebih daripada 70% daripada famili mengandungi kurang daripada 10 pokok dengan dbh lebih daripada 3 cm. Zon hutan 3 (FZ3) berada pada altitud yang lebih tinggi menunjukkan perbezaan ciri dengan zon hutan 1 (FZ1) dan zon hutan 2 (FZ2) iaitu hutannya mempunyai dua lapisan pokok (kanopi selanjar dan subkanopi) dan Myrtaceae adalah famili kedua dominan dari segi bilangan spesies dan kepadatan. Zon puncak (FZ4) jelas berbeza daripada FZ1, FZ2, dan FZ3, dan hutannya terdiri daripada satu lapisan pokok dan terdiri daripada pokok dengan ketinggian dan saiz diameter pokok yang kecil; spesies dominan dan kodominan diwakili oleh dua spesies yang tergolong dalam famili Theaceae iaitu *Schima wallichii* dan *Ternstroemia aneura*; dan bilangan spesies, famili dan nilai kepelbagaian spesies yang rendah. Dari segi ciri fisiognomi, zon hutan 4 (FZ4) mempunyai persamaan dengan hutan lumut pergunungan tinggi yang tipikal di Sabah, dan ini menggambarkan kesan Massenerhebung. Kekayaan spesies dan famili, nilai indeks kepelbagaian spesies, ketinggian dan diameter pokok, biomas dan penstratuman hutan menurun dengan peningkatan altitud. Disebaliknya, kepadatan pokok dan kekerapan bersaiz kecil bertambah dengan peningkatan altitud.

(altidudinal zonation, tropical rain forest)

INTRODUCTION

The change in forest structure and physiognomy with increasing altitude is often very conspicuous in tropical rain forest. As a forested tropical mountain is ascended, the physiognomy of the dominant species and the structure of the forest change [1]. Altitudinal increment accompanied by the appearance of distinct plant communities on tropical mountains is determined by a complex of environmental factors [2]. The presence, on separate continents, of tropical montane plant communities with similar physiognomic characters but distinct in floristic differences lead to the conclusion that they are affected by a common set of environmental factors [3].

Ewusie [4] suggested that montane vegetation is affected by changes in the climate prevailing at different altitudes but the relation of climate to altitude is by no means simple [1]. The mean temperature decreases by about 0.4-0.7 °C per 100 m increase in altitude. Beside temperature, other climatic factors influencing plant growth which also change with altitude are rainfall, atmospheric humidity, wind velocity and sunshine. These factors as a rule do not vary uniformly with change in altitude. The rate of change of climate with altitude varies from place to place depending on topography and other factors. Consequently, the actual limits of vegetation zones are different on different mountain ranges and on different parts of the same mountain. On coastal mountains and isolated peaks and ridges, the limits of zonation are lower than that on more extensive inland mountains and on mountain ranges. The lowering of the upper limits of lowland and montane tropical rain forest zones is known as the Massenerhebung effect [1,5,6,7]. The altitudinal zonation of forest vegetation in Malesian region (Malaysia, Indonesia, Brunei, Philippines, New Guinea, and the Solomon Island) was comprehensively reviewed by van Steenis [8], who recognised five different forest zones with the critical altitudinal limits at 1000 m, 2400 m, 4000 m and 4500 m, eventhough due to various local factors, including the Massenerhebung effect, the limits may vary greatly in different places [1,5,8]. In Sarawak, for example, the low isolated Mt. Santubong near Kuching, the transition from lowland forest to mossy montane forest occurs at 750 m, while on Mt. Mulu it takes place at 2300 m. Similar variation is also observed in Sabah, for instance, on Mt. Silam on the coast of Lahad Datu the transition occurs at 700 m, on Bukit Tawai at 900 m, on Pig Hill at 2300 m, on Mt. Kinabalu at 1980-2900 m; and in Peninsular Malaysia: on Mt. Blumut Johor at 840 m.

Studies on altitudinal zonation of tropical rain forests in S.E. Asia have been carried out by researchers such as Ohsawa *et al.* [10], Soepadmo [11], Edwards *et al.* [12], Adam and Ismail [13], Mahmud *et al.* [14] and Kochummen [15].

MATERIAL AND METHODS

Eight plots were established at 150 m, 250 m, 350 m, 500 m, 600 m, and 820 m altitude in the UKMS Danum Valley Research Centre, in Sabah, Malaysia (5° 05' N, 117° 48' E). At 150 m altitude, two plots, each measuring 50 m x 50 m, were established, and subdivided into 25 subplots of 10 m x 10 m each. One of the plots is located on a flat river bank, which is temporarily inundated during heavy rain. The other plot is set on the foothill, about 50 m away from the river bank. Plots at 250 m, 350 m, 500 m, 600 m, and 700 m, each measuring 40 m x 40 m were established and each plot was subdivided into 16 subplots each measuring 10 m x 10 m; and plot at 820 m was 20 m x 40 m and subdivided into eight subplots each measuring 10 m x 10 m. In these plots an inventory of all tree species with a diameter at breast height (dbh) > 3 cm was made. Voucher specimens were collected and identified at the Herbarium, Jabatan Biologi, Universiti Kebangsaan Malaysia Kampus Sabah (UKMS) and Herbarium, Forest Department Sandakan (SAN) at Sepilok, Sandakan, Sabah.

Floristic affinity of tree species between plots has been assessed by average linkage and complete linkage methods using SAS statistical package in FSSA, UKMS computer. The forest vegetation at different altitude were subjected to Sorenson's index of similarity (CC). Dissimilarity values were calculated by 100-CC and computed in SAS software for clustering analysis.

The sum of relative frequency (R_f), relative density (R_d) and relative dominance (R_D) constitute the importance values of all tree species (I_v) enumerated in each forest zone, which can range from 0-300. R_f, R_d, R_D were calculated using formulas proposed by Curtis and McIntosh [16] and Mueller-Dombois & Ellenberg [17].

Species diversity index for each forest zone was calculated using Shannon's diversity index [18] as follow:

$$H' = -\sum_{i=1}^{s} \{(ni/n) \ln (ni/n)\}$$

where, ni = number of individuals belonging to the ith of S species

n = total number of individuals of all species

Basal area, tree height and above ground biomass of all trees enumerated in the plots were calculated using the regression equations introduced by Kato *et al.* [19].

RESULTS

Clustering analyses using mean linkage and complete linkage methods have shown that four distinct forest zones can be recognised at the study site. These are: the *Shorea pauciflora-Shorea fallax* forest zone (FZ1), *Shorea leprosula-Vatica dulitensis* forest zone (FZ2), *Shorea parvifolia-Vatica dulitensis* forest zone (FZ3), and the *Schima wallichii-Ternstroemia aneura* forest zone (FZ4) (Fig. 1).

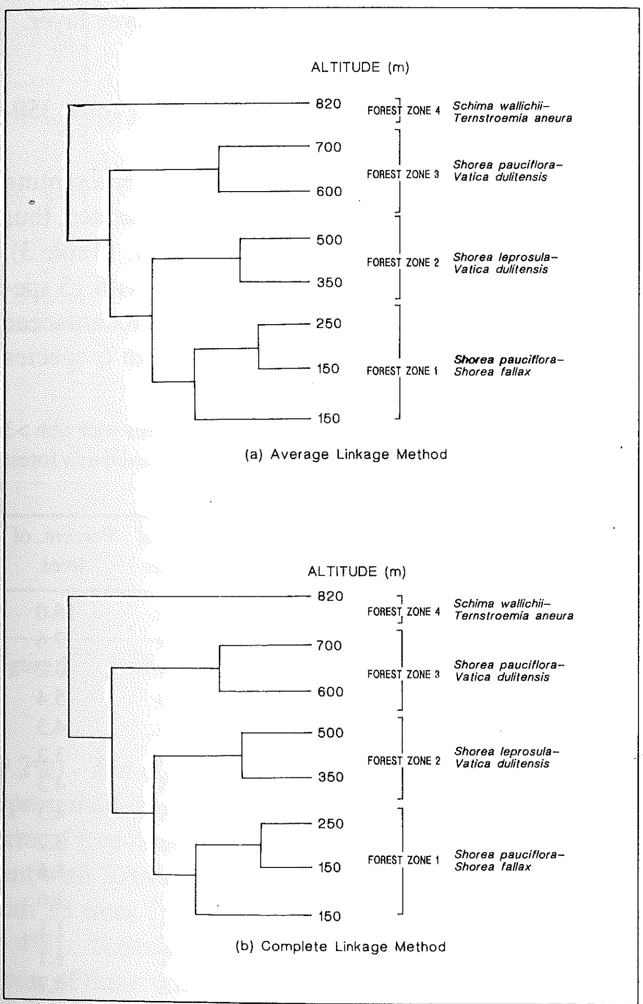

Figure 1. Dendrogram showing floristic affinities between plots.

1. *Shorea pauciflora-Shorea fallax* forest zone, 150-250 m above sea level (Plots 1, 2, 3)

A total of 390 trees (estimated density of 590 trees ha^{-1}) with a dbh of over 3 cm representing 32 families and 106 species have been identified (Table 1). Euphorbiaceae is the most diverse family comprising 20 species (18.9%), followed by Dipterocarpaceae with 12 species (11.3%). A total of 15 families (47%) were each represented by one species. However, in terms of tree density, Dipterocarpaceae is the most dominant family with 103 trees (27.1%), followed by Euphorbiaceae with 85 trees (22.4%). The 24 other families were each represented by less than 10 trees.

Table 1. Number and percentage of species and trees with dbh >3 cm of each family in Forest Zone 1 (FZ1): *Shorea pauciflora-Shorea fallax* forest zone at 150-250 m.

Family	No. of Species	Percent. of Species	No. of trees	Percent. of trees
Euphorbiaceae	20	18.9	85	22.1
Dipterocarpaceae	12	11.3	103	27.8
Meliaceae	9	8.5	18	4.7
Annonaceae	8	7.5	29	7.6
Sapindaceae	7	6.6	23	6.0
Lauraceae	5	4.7	13	3.4
Ebenaceae	4	3.8	4	1.0
Myrtaceae	3	2.8	29	7.5
Polygalaceae	3	2.8	8	2.1
Flacourtiaceae	3	2.8	6	1.6
Rubiaceae	3	2.8	6	1.6
Tiliaceae	3	2.8	6	1.6
Anacardiaceae	3	2.8	3	0.8
Lecythidaceae	2	1.8	5	1.3
Dilleniaceae	2	1.8	8	2.1
Rhamnaceae	2	1.8	3	0.8
Myristicaceae	2	1.8	2	0.5
Vitaceae	1	0.9	13	3.4
Burseraceae	1	0.9	6	1.5
Leguminosae	1	0.9	5	1.3
Sterculiaceae	1	0.9	3	0.8
Rhizophoraceae	1	0.9	2	0.5
Loganiaceae	1	0.9	1	0.3
Alangiaceae	1	0.9	1	0.3
Bombacaceae	1	0.9	1	0.3
Convolvulaceae	1	0.9	1	0.3
Fagaceae	1	0.9	1	0.3
Myrsinaceae	1	0.9	1	0.3
Oleaceae	1	0.9	1	0.3
Rutaceae	1	0.9	1	0.3
Saurauriaceae	1	0.9	1	0.3
Ulmaceae	1	0.9	1	0.3
Total	106	100	390	100

The importance values of 11 species, excluding 95 species with I_v below 6%, are tabulated in Table 2. The dominant and codominant species were *Shorea pauciflora* (I_v = 47.18%) and *S. fallax* (32.57%) respectively. These are followed distantly by *Parashorea malaanonan* (I_v = 15.79%). The study also shows that 72% of the tree species enumerated have I_v

less than 2.5%. Other notable species with I_v of between 7-10% are *Eugenia elopurae, Dipterocarpus caudiferus* and *S. agami*. The I_v of all dipterocarps combined is 134.9%, making the family the most important of all trees encountered in this zone. This value represents about 45% of the total I_v (300) possible for all trees. The Shannon's index of diversity (H') of tree species recorded in this zone is 4.33.

Table 2. Relative frequency (R_f), relative density (R_d), relative dominance (R_D) and importance values (I_v) of tree species with a dbh of >3cm in FZ1.

Species	R_f	R_d	R_D	I_v
Shorea pauciflora	3.67	3.84	39.67	47.18
Shorea fallax	1.63	1.54	9.40	32.57
Parashorea malaanonan	5.51	6.41	3.87	15.79
Eugenia elopurae	3.06	3.33	3.36	9.70
Dipterocarpus caudiferus	2.86	5.12	1.08	9.06
Shorea agami	0.61	0.51	6.00	7.12
Aporusa acuminatissima	3.06	3.58	0.22	6.86
Phaenthus crassipetalus	3.06	3.08	0.52	6.66
Leea indica	3.06	3.33	0.20	6.59
Eugenia chrysantha	3.06	3.33	0.16	6.55
Mallotus wrayi	2.44	3.08	0.48	6.00

I_v: <1% - 52 species (49%); 1-1.7% - 24 species (23%); 2-3% - 7 species (7%); 3-5% - 6 species (6%); 4.5 - 5.7% - 6 species (6%)

To facilitate comparison, the dbh of trees enumerated in the plots has been classified into five different size classes, i.e. Class 1 = 3-10 cm, Class 2 = 10.1-20 cm, Class 3 = 20.1-30 cm, Class 4 = 30.1-40 cm and Class 5 = >40 cm. Of the 390 trees enumerated, 79% falls into class 1, 13% into class 2, 4% into class 3, 8% into class 4 and 2% into class 5. The total basal area of all trees recorded from this zone is 136,265 cm^2, giving an estimate of 207,123 cm^2 ha^{-1}. The estimated total above-ground biomass of enumerated trees is about 219 tonnes or 333 tonnes ha^{-1}.

The forest of this zone has three tree-canopy layers, i.e. the emergent layer, main canopy layer and under-storey layer (Fig. 2). The emergent layer is made up of trees reaching a height of 30-50 m. These emergent trees rise well above the main canopy layer, randomly distributed, and their crowns are far apart thus forming a discontinuous layer. The emergent layer comprises mainly of dipterocarp species such as *Shorea pauciflora, S. fallax* and *Parashorea malaanonan*. The main canopy layer is composed of trees which rise to a height of 15-30 m. The tree-crowns are more or less contiguous and tending to form a continuous canopy layer, interrupted only by gaps formed by dead or fallen trees. The species constituting this canopy layer include *Eugenia elapurae, Macaranga brevipetiolata, Aporusa acuminatissima* and young trees of species from the emergent layer. The under-storey, which is 8-10 m high, is heterogeneous in species composition. Among the commonest species are *Dillenia excelsa, Mallotus wrayi, Leea indica, Eugenia chrysantha* and *Blumeodendron tokbrai*. In addition, most species of the main canopy layer and emergent layers were also represented by young trees in the under-storey layer.

2. *Shorea leprosula-Vatica dulitensis* forest zone, 350-500 m a.s.l. (Plots 4, 5)

A total of 186 trees with a dbh of > 3 cm representing 23 families and 65 species have been enumerated, thus giving an estimated density of 578 trees ha^{-1} (Table 3). Euphorbiaceae is the most diverse family with 13 species (20%), followed very closely by Dipterocarpaceae with 11 species (17%) and Lauraceae with 6 species

Table 3. Number and percentage of species and trees with dbh >3 cm of each family in FZ2: *Shorea leprosula-vatica dulitensis* forest Zone at 300-500 m above sea level.

Family	No. of Species	Percent. of Species	No. of trees	Percent. of trees
Euphorbiaceae	13	20.0	33	18.0
Dipterocarpaceae	11	17.0	70	37.6
Lauraceae	6	9.2	6	3.2
Myrtaceae	4	6.2	10	5.4
Annonaceae	4	6.2	8	4.3
Tiliaceae	3	4.6	6	3.2
Dilleniaceae	2	3.1	8	4.3
Meliaceae	2	3.1	8	4.3
Sapindaceae	2	3.1	6	3.2
Ebenaceae	2	3.1	3	1.6
Moraceae	2	3.1	3	1.6
Anacardiaceae	2	3.1	2	1.1
Sapotaceae	2	3.1	2	1.1
Burseraceae	1	1.6	8	4.3
Leguminosae	1	1.6	2	1.1
Polygalaceae	1	1.6	2	1.1
Saurauiaceae	1	1.6	2	1.1
Bombacaceae	1	1.6	1	0.5
Magnoliaceae	1	1.6	1	0.5
Myrsinaceae	1	1.6	1	0.5
Verbenaceae	1	1.6	1	0.5
Violaceae	1	1.6	1	0.5
Vitaceae	1	1.6	1	0.5
Total	65	100	186	100

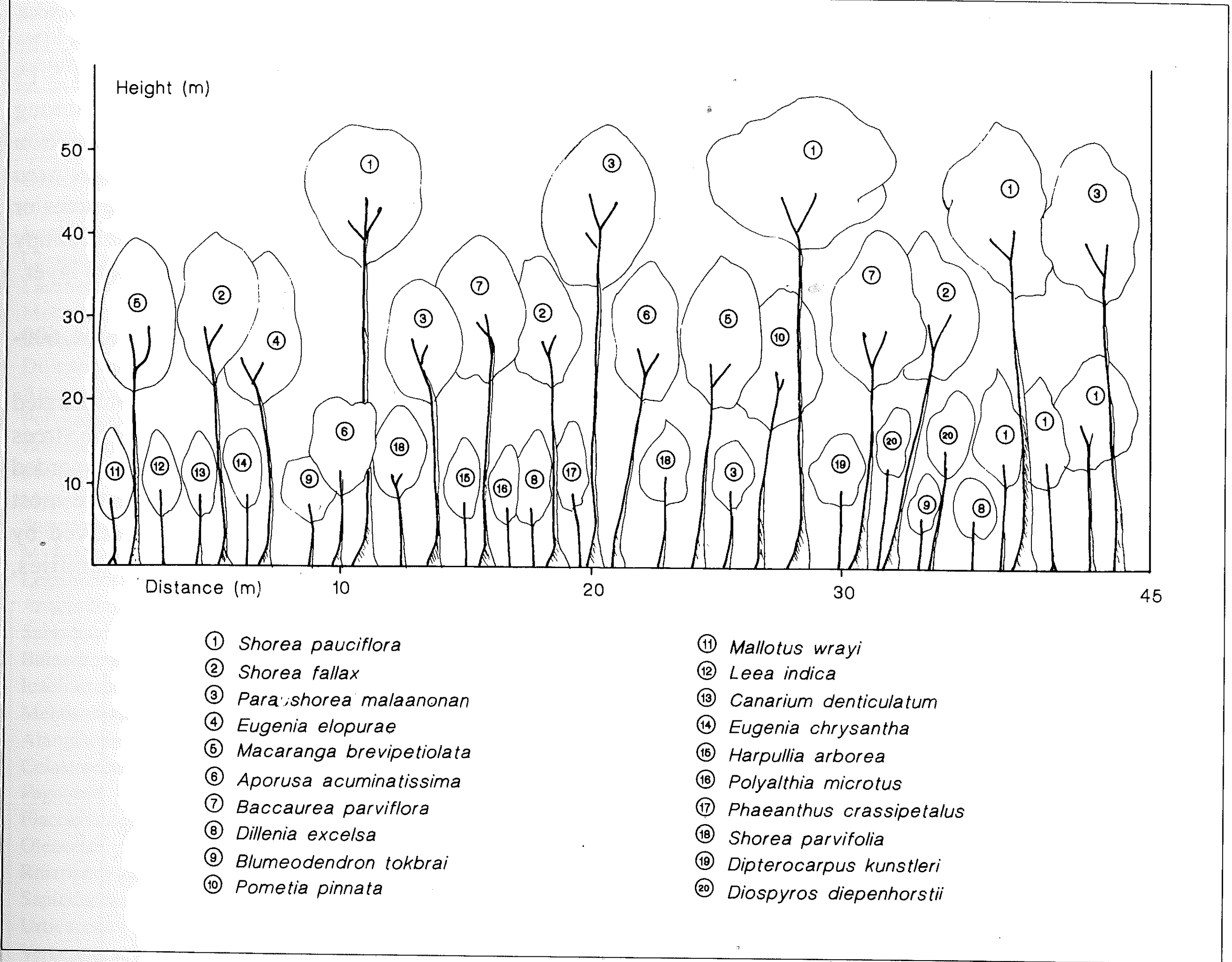

Figure 2. Profile diagram of *Shorea pauciflora – Shorea fallax* forest zone (FZ1) and represents a forest strip of 10 m x 45 m.

(9.2%). Ten other families (43.5%) were very poorly represented, each comprising of one species only. In term of tree density, the Dipterocarpaceae is predominant with 70 trees (37.8%), followed by Euphorbiaceae with 33 trees (17.8%), and Annonaceae with 10 trees (5.4%). Ninteen families (82.6%) have less than 10 trees, of these 6 families (26%) have one tree each.

Table 4 shows the importance values of 16 tree species with I_v greater than 6%. *Shorea leprosula* with the highest I_v (24.51%) and *Vatica dulitensis* (23.21%) with the second highest I_v were, respectively, the dominant and codominant species. Five species have I_v over 10%, i.e. *Parashorea malaanonan* (21.31%), *Dipterocarpus kunstleri* (16.01%), *Shorea agami* (13.62%), *Dillenia excelsa* (12.28%) and *Canarium denticulatum* (11.76%). Importance values were also computed for all species, but the relative ranking of those with lower values is rather insignifcant. This study shows that 44.7% of tree species have I_v values less than 2.1%. The Shannon's index of diversity of tree species in this zone is 3.75.

All trees enumerated were distributed randomly among the five dbh size classes, i.e. 38.2% falls into class 1, 35.4% class 2, 11.2% class 3, 5.1% class 4 and 10.1% class 5. The calculated total basal area of all trees recorded is 208,218 cm^2 or approximately equal to 650, 681 cm^2 ha^{-1}; and the total above-ground biomass of enumerated trees is 103 tonnes or 322 tonnes ha^{-1}.

The forest consists of three tree-canopy layers (Fig. 3). The emergent is composed of dipterocarp species such as *S. leprosula* and *Vatica dulitensis*, attaining a height of 30-40 m. The main canopy layer comprising trees with a height of 15-25 m, is represented by other

Table 4. R_f, R_d, R_D and I_v of all trees with a dbh of 3 cm in FZ2.

Species	R_f	R_d	R_D	I_v
Shorea leprosula	3.71	4.30	16.50	24.51
Vatica dulitensis	2.08	15.05	6.08	23.21
Parashorea malaanonan	6.50	5.38	9.43	21.31
Dipterocarpus kunstleri	3.71	3.22	9.08	16.01
Shorea agami	2.78	2.15	8.69	13.62
Dillenia excelsa	4.18	3.78	4.34	12.28
Canarium denticulatum	5.80	4.30	1.66	11.76
Mallotus brevipetiolata	4.18	4.30	0.28	8.76
Shorea pauciflora	2.08	1.61	4.96	8.65
Cynometra inaequifolia	1.39	1.08	6.06	8.53
Aporusa benthamiana	2.78	3.76	1.66	8.20
Eugenia chrysantha	3.71	2.68	0.56	6.95
Shorea acuminatissima	0.70	0.54	5.56	6.80
Shorea parvifolia	1.39	1.08	4.30	6.78
Dryobalanops lanceolata	2.08	2.15	2.54	6.77
Ardisia artemata	0.70	0.54	4.84	6.08

I_v: 1-2% - 29 species (44.7%); 2.1-3% - 8 species (12.3%); 3.1-4% - 3 species (4.6%); 4.1-6% - 7 species (10.8%)

dipterocarp species such as *Parashorea malaanonan, S. agami, S. leprosula* and *Dipterocarpus kunstleri*. The under-storey, consisting of trees with a height of 5-15 m, is heterogeneous in species composition. Among the tree species encountered were *Canarium denticulatum, Cynometra inaequifolia, Aporusa benthamiana* and *Aporusa frutescens*. Young trees or sapling of species from the emergent and main canopy layers were also represented in this understorey layer.

3. *Shorea parvifolia-Vatica dulitensis* forest zone, 600-700 m a.s.l. (Plots 6, 7)

A total of 212 trees with a dbh of >3 cm was enumerated from this zone, giving an estimated density of 663 trees ha^{-1}. A total of 31 families and 72 species were recorded in this zone (Table 5). Dipterocarpaceae is the most diverse family with 12 species (17%), followed by Myrtaceae with 9 species (13%). Five families,

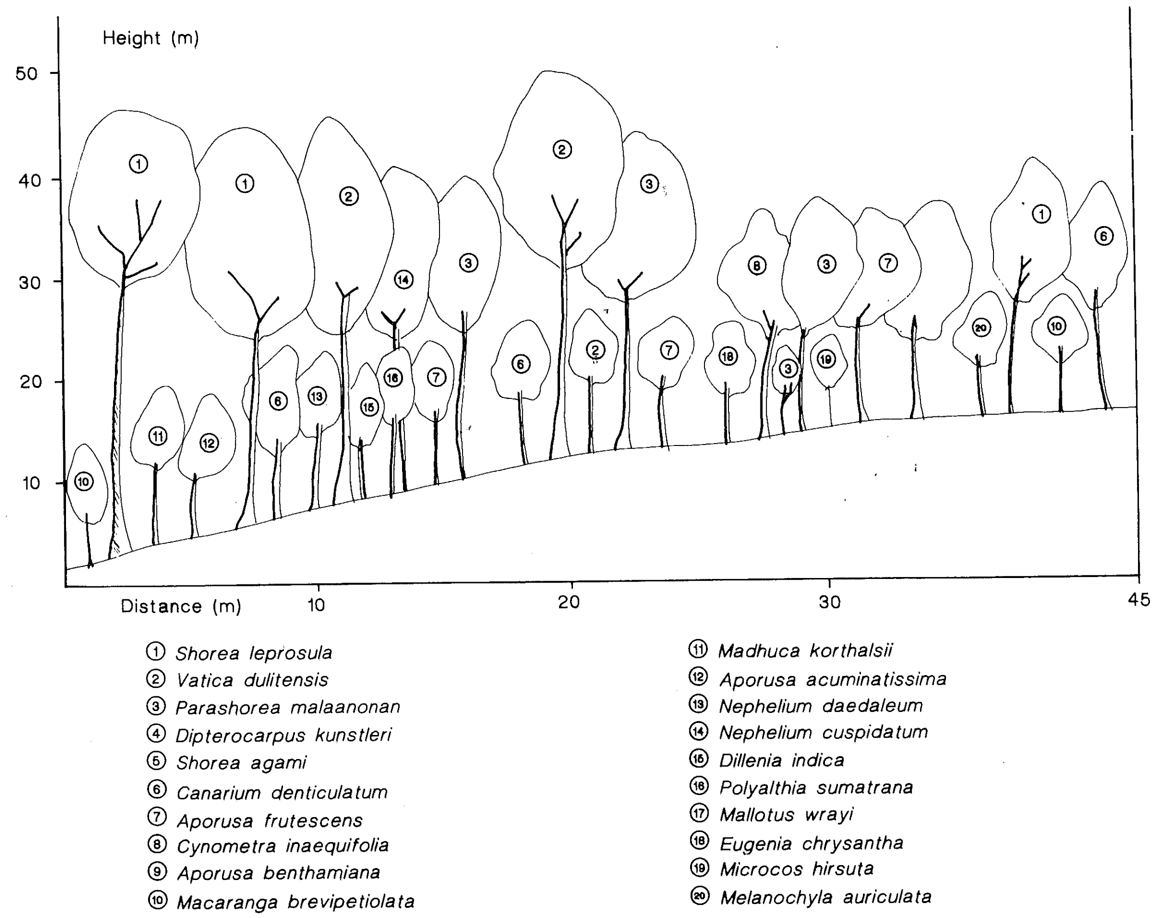

Figure 3. Profile diagram of *Shorea leprosula – Vatica dulitensis* forest zone (FZ2) and represents a forest strip of 10 m x 45 m.

Table 5. Number and percentage of species and trees with dbh > 3 cm of each family in FZ3: *Shorea parvifolia-Vatica dulitensis* forest zone at 600-700 m above sea level.

Family	No. of Species	Percent. of Species	No. of trees	Percent. of trees
Dipterocarpaceae	12	17.0	86	40.0
Myrtaceae	9	13.0	23	11.5
Euphorbiaceae	4	5.6	13	6.5
Clusiaceae	4	5.6	11	5.9
Lauraceae	4	5.6	8	4.0
Moraceae	4	5.6	6	3.0
Ebenaceae	4	5.6	5	2.5
Dilleniaceae	2	2.8	12	5.7
Annonaceae	2	2.8	6	3.0
Polygalaceae	2	2.8	4	2.0
Bombacaceae	2	2.8	3	1.5
Meliaceae	2	2.8	3	1.5
Myristicaceae	2	2.8	2	1.0
Sapotaceae	2	2.8	2	1.0
Myrsinaceae	1	1.4	6	3.0
Leguminosae	1	1.4	3	1.5
Anacardiaceae	1	1.4	2	1.0
Sabiaceae	1	1.4	2	1.0
Burseraceae	1	1.4	2	1.0
Icacinaceae	1	1.4	2	1.0
Melastomataceae	1	1.4	2	1.0
Alangiaceae	1	1.4	1	0.5
Celastraceae	1	1.4	1	0.5
Fagaceae	1	1.4	1	0.5
Flacourtiaceae	1	1.4	1	0.5
Oleaceae	1	1.4	1	0.5
Rhizophoraceae	1	1.4	1	0.5
Sapindaceae	1	1.4	1	0.5
Urticaceae	1	1.4	1	0.5
Verbenaceae	1	1.4	1	0.5
Violaceae	1	1.4	1	0.5
Total	72	100	212	100

Euphorbiaceae, Clusiaceae, Lauraceae, Moraceae and Ebenaceae, were each represented by four species. Twenty four other families (75%) were poorly represented with one to two species each. In terms of density, the Dipterocarpaceae is the most dominant family with 86 trees (40%), followed distantly by Myrtaceae (23, 11.5%), Euphorbiaceae (13, 6.5%), Dilleniaceae (12, 5.7%), and Clusiaceae (11, 5.9%). Twenty six families (83.9%) were each represented by less than 10 trees.

The dominant and codominant species of this forest zone were *Shorea parvifolia* (I_v =54.93%) and *Vatica dulitensis* (I_v= 29.09%) (Table 6). These are followed by *Dipterocarpus kunstleri* (I_v=20.88%), *Shorea agami* (I_v=10.79%) and *Eugenia clavatum* (I_v=10.55%). Approximately 47.3% of tree species recorded have I_v below 2.1%. The Shannon's index of diversity of tree species of this forest zone is 3.69.

Table 6. R_f, R_d, R_D and I_v of tree species with a dbh of more >3 cm in FZ3.

Species	R_f	R_d	R_D	I_v
Shorea parvifolia	7.32	8.49	39.12	54.93
Vatica dulitensis	8.86	11.79	8.44	29.09
Dipterocarpus kunstleri	7.32	8.96	4.60	20.88
Shorea agami	3.46	3.77	3.56	10.79
Eugenia clavatum	3.08	2.83	4.64	10.55
Garcinia mangostana	3.66	3.30	2.84	9.80
Phoebe macrophylla	1.73	2.36	5.55	9.64
Xanthophyllum amoenum	0.58	0.47	7.67	8.67
Dillenia indica	3.08	2.83	1.06	6.97
Eugenia cerasiformis	1.73	2.36	2.21	6.30
Dillenia excelsa	3.08	0.94	1.70	5.72
Ardisia colorata	1.73	2.83	0.61	5.17
Shorea seminis	2.31	2.36	0.42	5.09

I_v: 1-2% - 34 species (47.3%); 2.1-3 % - 17 species (23.6%); 3.1-5% - 8 species (11.12%)

The dbh class distribution of all trees in this forest zone is as follows: 69% belongs to class 1, 24% class 2, 8% class 3, 1% class 4 and 2% class 5. All trees enumerated contributed a total basal area of 28,3384 cm^2 or approximately 85,531 cm^2 ha^{-1}. The estimated above-ground biomass of enumerated trees is 37 tonnes or 115 tonnes ha^{-1}.

Forest stratification of this zone is reduced to two tree-canopy layers, i.e. main canopy and understorey layers (Fig. 4). The main canopy layer reaches a height of 30-40 m and comprises dipterocarp species such as *Vatica dulitensis, Dipterocarpus kunstleri* and *Shorea pauciflora*. The understorey layer, reaching a height of 5-20 m, is composed of non-dipterocarp species such as *Eugenia claviflora, Xanthophyllum affine, Garcinia mangostana, Garcinia minimiflora, Ardisia colorata* and *Phoebe macrophylla*.

4. *Schima wallichii-Ternstroemia aneura* forest zone, 820 m a.s.l. (Plot 8)

A total of 108 trees or approximately 1350 trees ha^{-1}, representing 17 families and 30 species were enumerated from this zone (Table 7). The most diverse family is Myrtaceae with 5 species, followed by Anacardiaceae (4), Theaceae (3), Sapotaceae (3), Dipterocarpaceae (2) and Rubiaceae (2). Eleven families (65%) are each represented by one species. In terms of density, the Theaceae is the most dominant family with 37 trees (34%), followed by Dipterocarpaceae (12%) and Myrtaceae (11.1%). Fourteen families (82%) were each represented by less than 10 trees, and of these four families have a single tree each.

In terms of I_v (Table 8), the most dominant and codominant species were *Schima wallichii* (I_v = 39.85%) and *Ternstroemia aneura* (38.46%), followed closely by *Shorea carapae* (27.40%) and *S. parvistipulata* (24.65%). The Shannon's index of diversity of tree species of this forest zone is 2.85.

The dbh class distribution of all trees enumerated is as follows: 77.8% class 1, 20.4% class 2, and 1.9% class 3. The calculated total basal area contribution of enumerated trees was 6,708 cm^2 or about 83,850 ha^{-1}, and the estimated above-ground biomass contribution was 4.8 tonnes or approximately 59 tonnes ha^{-1}. This forest zone is composed of small-sized trees, attaining a height of 5-10 m (Fig. 5). It is codominated by *Schima wallichii* and *Ternstroemia aneura*. However, three trees of *Shorea carapae* reached a maximum height of about 30 m.

DISCUSSION

On tropical mountains, forest zonation is generally associated with altitude. In most cases, typical lowland rain forest with three tree-canopy layers is found at the base of the mountain, followed by a forest type with two tree-canopy layers, and by low-statured forest comprising of one tree-canopy layer toward the peak. Ewusie [4] attributed this zonation to changing temperatures at different altitudes, since an increase of 100 m results in the decrease of temperature of about 0.4-0.7 °C. However, because the rate of change of climatic factors with altitude varies from area to area,

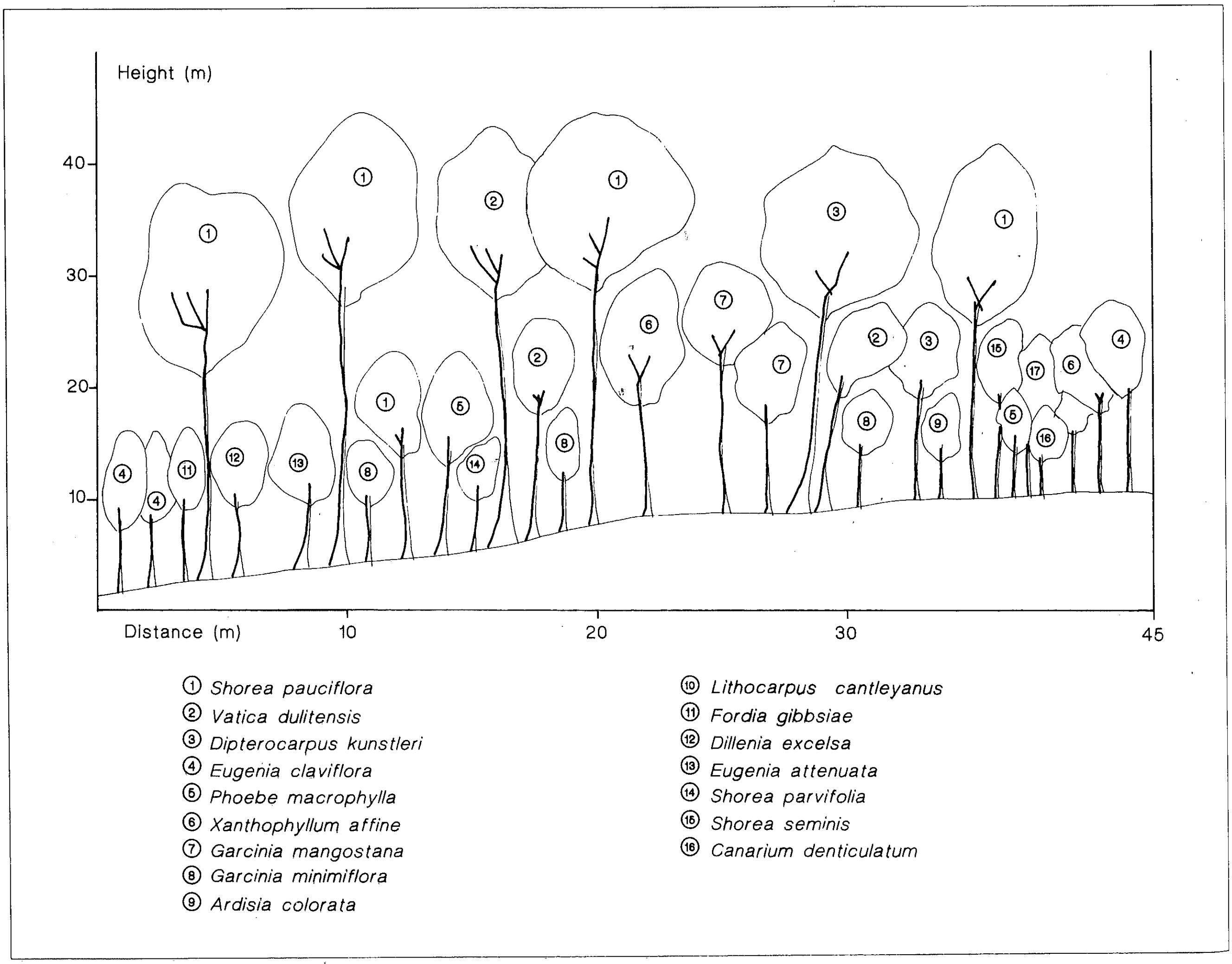

Figure 4. Profile diagram of *Shorea pauciflora – Vatica dulitensis* forest zone (FZ3) and represents a forest strip of 10 m x 45 m.

Table 7. Number and percentage of species and trees with dbh > 3 cm of each family in FZ4: *Schima wallichii-Ternstroemia aneura* forest zone at 820 m above sea level.

Family	No. of Species	Percent. of Species	No. of trees	Percent. of trees
Myrtaceae	5	16.7	12	11.1
Anacardiaceae	4	13.3	5	4.6
Theaceae	3	10.0	37	34.3
Sapotaceae	3	10.0	6	5.6
Dipterocarpaceae	2	6.6	13	12.0
Rubiaceae	2	6.6	6	5.6
Araliaceae	1	3.3	5	4.6
Clusiaceae	1	3.3	5	4.6
Juglandaceae	1	3.3	5	4.6
Clethraceae	1	3.3	4	3.7
Rutaceae	1	3.3	3	2.8
Lauraceae	1	3.3	2	1.9
Celastraceae	1	3.3	1	0.9
Euphorbiaceae	1	3.3	1	0.9
Leguminosae	1	3.3	1	0.9
Rosaceae	1	3.3	1	0.9
Ulmaceae	1	3.3	1	0.9
Total	30	100	108	100

Table 8. R_f, R_d, R_D and I_v of all tree species with a dbh of > 3cm in FZ4.

Species	R_f	R_d	R_D	I_v
Schima wallichii	11.06	14.81	13.98	39.85
Ternstroemia aneura	9.42	15.74	13.30	38.46
Shorea carapae	1.50	3.70	22.20	27.40
Shorea parvistipulata	6.28	8.33	10.04	24.65
Aralidium pinnatifidum	6.28	4.62	7.12	18.02
Engelhardtia serrata	4.77	4.62	3.44	12.83
Tristinia grandifolia	3.14	4.62	4.52	12.28
Adinandra sp 1	4.77	3.70	3.62	12.09
Calophyllum canum	4.77	4.62	2.36	11.75
Chasalia curviflora	4.77	4.62	1.88	11.27
Eugenia attenuata	4.77	3.70	1.88	10.35
Ganua motleyana	4.77	2.78	2.58	10.13
Clethra canescens	3.14	3.70	3.07	9.91
Madhuca korthalsii	3.14	1.85	2.17	7.16
Maclurodendron pubescens	3.14	2.78	1.00	6.92

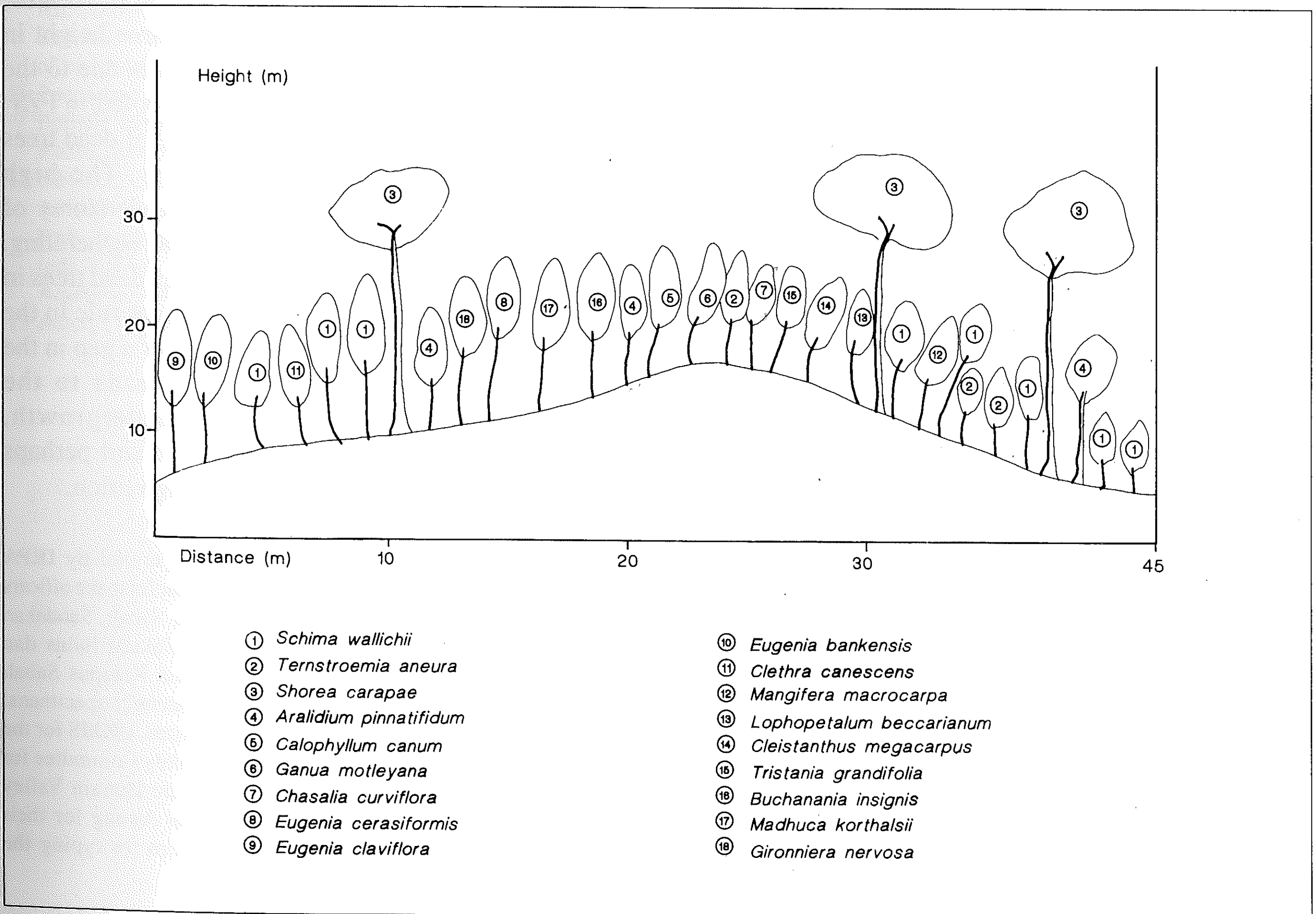

Figure 5. Profile diagram of *Schima wallichii – Ternstroemia aneura* forest zone (FZ4) and represents a forest strip of 10 m x 45 m.

the actual altitudinal limits of forest zones are also different on different mountain ranges and on different parts of the same mountain [1]. On low isolated peaks and ridges, the upper limits of forest zonation are generally lower than on more extensive mountain ranges [1]. These limits also tend to be lower on coastal mountains such as Mt. Silam in Lahad Datu, Sabah, and Mt. Santubong in Sarawak than those further inland. Such a phenomena is known as Massenerhebung effect.

In the present study, clustering analyses using complete and average linkage methods have demonstrated that the forest of the study area can be divided into four different forest zones. The results also show that forest zonation of the forest is directly correlated with altitude, i.e. forest zone 1 (FZ1) occurs at 150-250 m, forest zone 2 (FZ2) at 350-500 m, forest zone 3 (FZ3) at 600-700 m and forest zone 4 (FZ4) at 820 m.

The dominant and codominant species of each forest zone have been quantified using the highest and second highest I_v, respectively. There is no single species dominant in these four forest zones. In FZ1, *Shorea pauciflora* is dominant, and it is replaced by *S. leprosula* and *S. parvifolia* in FZ2 and FZ3. The results also show that *Vatica dulitensis* is the codominant species in FZ2 and FZ3. FZ1 and FZ2 zones share most of the common attributes: both zones having three tree-canopy layers, rich in families and species representation, high species diversity value, high percentage of large-sized tree, high percentage of trees with buttresses as compared to FZ4 at the uppermost zone. In terms of tree density, the Euphorbiaceae and Dipterocarpaceae are the most dominant and second most dominant families, respectively. The influence of altitude on the physiognomy of the forest is apparent at higher altitude, i.e at zone FZ3 (600-700 m) and particularly distinct at zone FZ4 on the summit (820 m). The FZ3 zone has two tree-canopy layers and without emergents. In forest zone 4 only one tree-canopy layer is found; the trees are smaller in stature (with a dbh mostly below 20 cm and are shorter in height); the number of species decreased but the density increased; species diversity value (2.97) is the lowest; and dipterocarps became rare as compared to the other three forest zones below 700 m. There is also very drastic change in the dominant and codominant species as well as tree density, from species of Dipterocarpaceae to those of Theaceae. In structure and physiognomy, forest zone 4 at 820 m altitude is similar to that of typical montane mossy forest found on other mountains at higher altitude in Sabah and elsewhere, thus demonstrating the influence of Massenerhebung effect. In this forest the ground, tree trunks and branches were densely covered with mosses.

In terms of structure, physiognomy and above ground biomass, the four forest zones recognised in the study area, show the following general trends: the percentage of small-sized trees (dbh class 1) increases with increasing altitude; conversely the percentage of large-sized trees (dbh class 4 and 5) decreases with increasing altitude; the mean dbh, mean basal area, mean above-ground biomass per tree, percentage of trees with buttresses decreased with increasing altitude; the mean dbh ha^{-1}, basal area ha^{-1}, and above-ground biomass ha^{-1} decreases with increasing altitude. These findings conform with the results obtained by a number of ecologists working on tropical rain forests, e.g. Ohsawa *et al.* [10], Soepadmo [11], Mahmud *et al.* [14], Adam & Affandi [20], Yamada [21, 22], Martin [23] and Proctor *et al.* [24]. The similarity of high percentage of trees in dbh class 1, low mean dbh, mean basal area, mean above-ground biomass and mean tree height in FZ1 (150-250 m) and FZ2 (350-500 m) is due to the high percentage (20%) of dead trees recorded in FZ1. In forest zones 2, 3 and 4, the percentage of dead trees is 15%, 10%, and 10% respectively. The high percentage of small-sized trees in the understorey of forest zone FZ1 indicates that the forest is regenerating. Richards [1] reported that gaps created by dead trees in tropical rain forest played a very important role in the process of regeneration. The formation of a gap in the emergent and main canopy layers leads to the development of a dense patch of undergrowth, stimulated by the increased illumination and perhaps also by the locally diminishing root competition.

Acknowledgments This research has been funded by IRPA (UKM) 4-07-03-042 and 4-07-03-054. We are grateful to the officers in charge of the Herbarium, Forest Department Sabah, Sandakan (SAN), and the Herbarium Jabatan Biologi, Fakulti Sains dan Sumber Alam, Universiti Kebangsaan Malaysia Kampus Sabah (UKMS) for their permission to examine and identify specimens; to Jabatan Biologi, Fakulti Sains dan Sumber Alam, UKMS for the laboratory and transport facilities; to Danum Valley Committee for the permission to carry out the research in the Danum Valley Conservation Area; to Sukup Akin and Zainal Awang for their assistance in the field; and Mrs. Aspah Hashim for typing the manuscripts.

REFERENCES

1 Richards P.W. (1964) *The tropical rain forest. An ecological study*. Cambridge University Press. 2nd edition.

2 Grubb P.J. (1977) Control of the growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Ann. Rev. Ecol. & Syst.* **8**:83-107.

3 Lee D.W. and Lowry J.B. (1980) Plant Speciation on tropical mountains: *Leptospermum* (Myrtaceae) on Mount Kinabalu, Borneo. *Bot. J. Linn. Soc.* **80**:223-242

4 Ewusie J.Y. (1980) Elements of Tropical Ecology. Heinemann Educational Books Inc., New Hampshire USA and London.

5 Van Steenis C.G.G. (1984) Florisitic altitudinal zones in Malaysia. *Bot. J. Linn. Soc.* **89**:289-292.

6 Whitmore T.C. (1984) *Tropical rain forests of the Far East.* Clarendon Press, Oxford. 2nd edition.

7 Proctor J., Lee Y.F., Langley A.M., Munro W.R.C and Nelson T. (1988) Ecological studies on Gunung Silam: A small ultrabasic mountain in Sabah, Malaysia. *J. Ecol.* **76**:320-340.

8 Steenis C.G.G. Van (1935) On the origin of the Malaysian mountian flora. Part II. Altitudinal zones, general consideration and renewed statement of the problem. *Bull. Jard. Bot. Buitenz.* **(Ser. 3) 13**:289-417.

9 Richards P.W. (1936) Ecological observations on the rain forest of Mt. Dulit, Sarawak. *J. Ecol.* **24(2)**:340-360.

10 Ohsawa M., Nainggolan P.H.J., Tanaka N. and Anwar C. (1985) Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. *J. Ecol.* **1**:193-216.

11 Soepadmo E. (1987) Structure, above ground biomass and floristic composition of forests at Gunung Janing Barat, Ulu Endau, Johore, Malaysia. *Malay. Nat. J.* **41**:275-290.

12 Edwards I.D., Payton R.W., Proctor J. and Riswan S. (1990) Altitudinal zonation of the rain forests in the Manusela National Park, Seram, Maluku, Indonesia. In: *Plant Diversity of Malesia* (eds. P. Baas, K. Kalkman and R. Geesink) pp. 161-175. Kluwer Academic Publishers. Dordrecht, The Netherlands.

13 Adam J.H. and Ismail H.M.K.A (1993) Kajian ke atas kandungan dan analisis kuantitatif flora pokok angiosperma di Gunung Kinabalu. *Prosiding Simposium Sumber Alam Pertama*, FSSA, UKM Kampus Sabah **I**:102-112.

14 Mahmud T., Adam J.H. and Affandi N.M. (1992) Analisis pengklusteran Hutan Bukit Tawai, Sabah. *Persidangan Ekologi Malaysia* **I**: 25-30. Persatuan Ekologi Malaysia.

15 Kochummen K.M. (1982) Effects of elevation on vegetation on Gunung Jerai, Kedah. *FRI-Research Pamphlet* **87**:1-28.

16 Curtis J.T. and McIntosh R.P. (1950) The inter-relations of certain analytic and synthetic phytosociological characters. *Ecology* **13**:435-455.

17 Mueller-Dombois D. and Ellenberg H. (1974) *Aims and Methods of Vegetation Ecology.* John Wiley & Sons.

18 Ludwig J.A. and Reynolds J.F. (1988) *Statistical Ecology. A Primer on Methods and Computing*. A Wiley-Publication. John Wiley & Sons.

19 Kato R., Tadaki Y., and Ogawa H. (1978) Plant biomass and growth increment studies in Pasoh forest. *Malay. Nat. J.* **30 (2)**:211-224

20 Adam J.H. and Affandi N.H. (1993) Hutan Ultrabasik di Sabah khususnya di Bukit Tawai, Telupid, Sabah. *Penerbitan Tak Berkala* **8**:1-21. Fakulti Sains dan Sumber Alam, UKM Kampus Sabah.

21 Yamada I. (1975) Forest ecological studies of montane forest of Mt. Pangrango, West Java. I. Stratification and floristic composition of the montane forest near Cibodas. *Tonan Ajia Kenkyu* **13**: 402-426.

22 Yamada I. (1976) Forest ecological studies of the montane forest of Mt. Pangrango, West Java. II. Stratification and florisitic composition of forest vegetation of the higher part of Mt. Pangrango. *Tonan Ajia Kenkyu* **13**:513-534.

23 Martin P.J. (1977) The altitudinal zonation of forests along the west ridge of Gunung Mulu. Forest Department Sarawak. pp. 1-77.

24 Proctor J., Anderson J.M., Chai P., Vallack H.W. (1983) Ecological studies in four contrasting lowland forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *J. Ecol.* **71**:237-260.