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Altitudinal zonation of evergreen broad-leaved forest on Mount Lopei, Taiwan

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Abstract. Evergreen broad-leaved forest was studied in a transect on the northwestern slope of Mount Lopei in order to reveal altitudinal zonation in structure and floristic composition and the decisive environmental factors. 20 plots of 20 m × 20 m at altitudes from 540 m to 1320 m were analysed. 144 woody species were found. The results of a DCA ordination clearly pointed to a single dominant altitudinal gradient. Nevertheless, wind-exposure associated topography was found to account for additional variation for a given altitudinal range. Along the altitudinal gradient, four dominance-based forest types were recognized. Tree density, species diversity and evenness of the four types differed significantly but total basal area and tree volume were not significantly different. The 95 % turnover range for woody species as measured by the Community Coefficient was calculated as 1030 m, and the 50 % turnover range as 238 m. For the understorey, the change in species composition with altitude was less obvious. Species population structures of 57 sufficiently abundant species revealed four characteristic patterns, but most species showed a good fit to the negatively exponential or power function distribution and thus appeared to have good reproduction and regular recruitment. Both ANOVA and Redundancy Analysis (RDA) showed that significant differences among forest types were found for most soil variables. Organic C, exchangeable Na and K tended to increase with altitude, while pH and available N showed a reverse trend. There was little evidence that the differences in soil pH and available N were responsible for the variation in forest growth.

Keywords: Floristics; Forest type; Gradient analysis; Population structure; Species diversity; Soil.

Nomenclature: Li et al. (1975-1979); Huang et al. (1996).

Introduction

The evergreen broad-leaved forests of eastern and southeastern Asia extend from Okinawa through Taiwan and southern China to the northern half of Vietnam (Kira 1991). These forests have been referred to as 'lauro-fagaceous association' in Taiwan (Kudo & Sasaki 1931), and are known as laurel forests in Japan. Floristically they are characterized by evergreen broad-leaved species of the *Fagaceae*, *Lauraceae*, *Theaceae* and *Symplocaceae*. In the mountain regions of Taiwan, evergreen broad-leaved forests show a clear zonation pattern due to the overlap of tropical and temperate zonation types (Ohsawa 1993). Although Taiwan is one of the most diversified areas of evergreen broad-leaved forest in eastern Asia, only few studies are available (Liu 1968; Su 1984).

This study was conducted on Mount Lopei in northern Taiwan where a large continuous tract of the original forest still can be found. Few studies have been made of forests in northern Taiwan (Liu & Su 1976; Su & Wang 1988; Chen 1993). No attempt has been made to relate the forest types to edaphic features at a range of altitudes. The main objectives of the present study are: (1) to elucidate floristic and structural variation accounted for by the altitudinal gradient; (2) to investigate species turnover and diversity patterns along the altitudinal gradient; and (3) to relate species composition gradient to other environmental variables.

Study area

The study area is situated on the northwestern slope of Mount Lopei (121° 27' 50" N, 24° 48' 42" E, 1553 m high), ca. 20 km south of Taipei City in northern Taiwan. Elevation ranges from 540 m to 1320 m. The Lopei main ridge extends in a northeast to southwest direction with the highest peak rising to 1907 m in the south. This region has a highly dissected topography with narrow ridges and steep side slopes. The area has since long been protected as national forest land and forms an important source of water for Taipei City.

Mean monthly temperature ranges from 11.1 - 27.3 °C at 600 m to 8.1 - 23.3 °C at 1300 m, and mean annual temperature is 19.7 °C at 600 m and 16.2 °C at 1300 m (estimated from three nearby weather stations). Mean annual precipitation varies from 3000 to 3500 mm. High-intensity rainfall commonly accompanies typhoons and thunderstorms during the period June - September. However, rainfall is evenly distributed throughout the year. Occasional snow occurs in January above 1000 m.

Strong northeasterly monsoon winds occur frequently from November to April. Forests above 800 m are cloud-affected.

The whole area is underlain by Oligocene bedrock, consisting mainly of massive siltstone or dark gray shale (Teng et al. 1988). Soil depth ranges from 20 to 40 cm. Soil profiles are classified as Inceptisols with a clay content of usually more than 40 % and a silt content of 30 - 50 % (Hsieh & Chen 1989). Soils are poorly developed. A cambic horizon and an ochric epipedon are usually present. The soil surface on the upper slopes is generally wet and slippery.

Evergreen broad-leaved forest covers most of the area, but patches of *Cryptomeria japonica* (Japanese cedar) plantation exist on the lower and middle slopes. In addition, almost pure stands of *Fagus hayatae* (Taiwan beech) occur along the ridge tops. For additional information on the beech forest see Hsieh (1989a).

Material and Methods

Five sites were selected along a trail on the northern slope of Mount Lopei at ca. 650 m, 850 m, 1070 m, 1180 m and 1300 m elevation. At each site four 20 m × 20 m plots were established and analysed between September 1988 and July 1989. Within each plot, all free-standing woody plants (including trees, shrubs and lianas) with a stem diameter at breast height (DBH) of ≥ 1 cm were identified, and their DBH and height measured. Percentage cover of herbs and ferns was estimated visually. In addition, altitude, aspect, slope and land form were recorded.

Soil samples were collected in 1991 and 1992. Within each plot, two randomly located soil pits were dug. In addition, four pits were dug under beech forest on ridge tops. In each pit, the soil was sampled at 0 - 10 cm and 10 - 20 cm depth. Procedures followed for soil chemical properties were according to USDA-SCS (Anon. 1984):

- Soil pH was measured with combined electrodes in a 1:1 soil/water suspension;
- Organic C was determined by a modified Walkley-Black procedure;
- Exchangeable K, Na, Ca and Mg were extracted using 1 M ammonium acetate (pH 7.0);
- Exchangeable Al and H were exchanged with 1 M KCl;
- Concentrations of K, Na, Ca, Mg and Al were measured by atomic absorption spectroscopy (Hitachi, 180-30 type);
- Available-N concentration of soils, after incubation at 40 °C for two weeks, was extracted with 2 M KCl and then determined by the Kjeldahl distillation method;
- Available P was measured by the Bray No. 1 procedure, and available K by the Mehlich method;

The chemical analyses were carried out in duplicate.

Relative basal area, density and volume were calculated for each woody species. Tree volume was estimated as height × basal area × 0.5 (Whitmore 1984). A primary matrix (144 species × 20 plots) with relative basal area values was subjected to Detrended Correspondence Analysis (DCA) using the DECORANA package (Hill 1979a). In order to obtain a display of the soil-landscape and soil-vegetation relationships, redundancy analysis, RDA (ter Braak 1990) was applied to the soil data with topographic properties and vegetation types as external variables. For the RDA ordination, a forward selection of variables was used to determine the relative importance of environmental (external) variables. Monte Carlo permutation tests were used to test the significance of the first two RDA axes.

Species diversity (Hill 1973) was measured using species richness (number of species per plot), the Shannon-Wiener index, and Hill's diversity numbers $N1$ and $N2$. Evenness was calculated as the modified Hill's ratio $E5$, which approaches zero as a single species becomes dominant. Beta diversity (Whittaker 1972) along the whole altitudinal gradient was calculated by plotting the log values of the Community Coefficient against altitudinal difference for each pair of plots and calculating the regression equation. The Community Coefficient for pairs of plots (expressed as %) follows from:

$$\mathrm{CC} = 200\ \mathrm{S}_{\mathrm{ab}}/(\mathrm{S}_{\mathrm{a}} + \mathrm{S}_{\mathrm{b}}) \qquad (1)$$

where S_{ab} = is the number of species shared by plots A and B; S_{a} = the number in plot A; and S_{b} = the number in plot B.

Five beta diversity parameters (Itow 1991) were derived: (1) the expected similarity value of replicate samples (internal association, IA); (2) the slope of the regression line (indicating the average turnover rate of species per 1 m altitudinal difference); (3) half-change value (HC), expressed in gradient length units; and (4) altitudinal range over which the floristic turnover is 50 % and 95 % respectively.

Size-class analysis of each vegetation type and for selected species was conducted. Only species with at least 20 individuals in each vegetation type were included. The number of classes was determined as: $M = \mathrm{INT}\,(6 \times \log_{10} N)$, where M is the number of classes, INT is the integer, and N is the population size. DBH class width was then obtained by dividing the DBH range by the number of classes.

Differences in soil properties, species diversity, and forest structure among vegetation types were tested by ANOVA and Duncan's test (Anon. 1988).

Results

Floristic composition

243 vascular species in 162 genera and 89 families were recorded in the 20 plots. They included 96 trees, 22 shrubs, 26 lianas, 40 herbs and 59 pteridophytes. Species numbers in plots of 0.04 ha varied from 32 to 70 (mean = 52), free-standing woody species from 24 to 55 (mean = 39). In total 6226 individuals of woody species were encountered. The number of individuals per plot varied from 108 to 822 (mean = 311), and total basal area ranged from 1.00 to 1.84 m^2 (mean = 1.52 m^2). The canopy reached a height of 6 - 12 m. 6.9 % of all individuals with a DBH ≤ 1 cm, (15.2% of the species) were deciduous, while 4.9% (6.1% of the species) had compound leaves.

As to trees, the most important families, in terms of species number and total basal area, were:

Lauraceae	12 species	*Lauraceae*	10.2 m^2/ha
Theaceae	11	*Fagaceae*	9.3
Rosaceae	10	*Ebenaceae*	1.8
Rubiaceae	10	*Illiciaceae*	1.8
Fagaceae	7	*Theaceae*	1.6
Symplocaceae	7	*Aceraceae*	1.5

The most important species as to basal area were:

Trees:

Machilus (Persea) thunbergii	5.98 m^2/ha
Cyclobalanopsis (Quercus) longinux	4.11
Cyclobalanopsis (Quercus) sessilifolia	2.46
Machilus (Persea) japonica var. *kusanoi*	1.79
Diospyros morrisiana	1.77

Shrubs:

Hydrangea angustipetala
Blastus cochinchinensis
Eurya loquaiana
Antidesma japonicum

Lianas:

Erycibe henryi
Morinda umbellata
Ampelopsis cantoniensis
Ecdysanthera utilis

Herbs and ferns:

Selaginella doederleinii
Pellionia radicans
Diplazium dilatatum
Monachosorum henryi.

Gradient analysis and forest types

The first four DCA axes (Fig. 1) had eigenvalues 0.83, 0.31, 0.18 and 0.11, and the corresponding gradient lengths were: 5.16, 2.70, 1.90 and 1.31, respectively. The first axis explained 49.73% of the total variance in the species data and was, by far, the dominant compositional gradient. As expected, plot scores on DCA axis 1 were significantly correlated with altitude (Spearman rank correlation coefficient $r = -0.97$, $p < 0.001$). This is also clear from the sequence of the plots on the first axis. Four forest types, labelled I, II, III and IV, can be recognized along the gradient from higher to lower altitudes.

Tree density was highest in Type III and lowest in Type IV. Although tree density varied greatly, total basal area and tree volume were not significantly different among the forest types.

In contrast, the herb and fern composition was similar; only Type IV was different. According to Spearman correlation analysis, altitude was surpassed by terrain features (topographic position: $r = -0.82$, $p < 0.001$; aspect: $r = 0.63$, $p < 0.01$) in accounting for most of the species distribution patterns.

As shown in Table 1, marked distribution patterns are evident for several species.

Type I: Machilus thunbergii-Cyclobalanopsis longinux-Litsea acuminata

Type I is represented by four plots between 1280 and 1320 m. Trees of 20-35 (up to 50) cm DBH and 10 - 12 m tall formed a closed canopy. 96 species were recorded, of which 38 were trees and 11 were shrubs. The most important trees are included in the name of the type. The epiphytic flora was luxuriant. Trunks were frequently covered with bryophytes. Lianas were uncommon and all thin (< 5 cm DBH). The understorey and substrate were permanently damp. The shrub layer was dominated by *Hydrangea angustipetala*. The herb layer covered 37% and was the richest (41 species) among the four types. *Monachosorum henryi* and *Pellionia radicans* were the principal species.

Type II: Cyclobalanopsis longinux-Machilus thunbergii-Cyclobalanopsis sessilifolia

This type is represented by eight plots on wide, slightly inclined ridges between 1050 and 1210 m. Trees attained DBH values of 25 - 44 (60) cm and were 9 - 15 m tall. Wind-throw of whole trees was common in some plots. 59 tree species and 13 shrub species attained a DBH ≥ 1 cm. The three dominant species contributed 44.5 % of the basal area. *Diospyros morrisiana* is a shade-intolerant canopy tree which can reach the upper canopy after the colonization of small treefall and limbfall gaps. There were occasional trees of a larger girth (*Trochodendron aralioides* up to 60 cm DBH, and *Castanopsis cuspidata* var. *carlesii* fo. *sessilis* > 45 cm DBH). In the subcanopy *Illicium arborescens* was very abundant (1547 stems/ha). Lianas were not prominent, probably due to the cloudy conditions. *Eurya loquaiana* was the dominant shrub. Herb cover was 46 %.

Type III: Myrsine seguinii-Castanopsis cuspidata var. carlesii fo. sessilis-Cinnamomum camphora

This type was confined to a wind-exposed and narrow side ridge. The four plots of this type were located on the southwestern slopes at 870 - 885 m, but some of them extended upward to the ridge crest. Tree density

Table 1. Species with their relative basal area in each of four forest types on Mount Lopei. Species order according to score along DCA-axis 1. (Only species with basal area ≥ 0.04 m^2/ha are included.)

Species	Forest type			
	I	II	III	IV
Illicium anisatum	0.53	0.00	0.00	0.00
Litsea elongata var. *mushaensis*	1.09	0.00	0.00	0.00
Acer kawakamii	4.13	0.01	0.07	0.00
Neolitsea aciculata	3.77	0.12	0.00	0.00
Hydrangea angustipetala	1.30	0.05	0.00	0.00
Osmanthus matsumuranus	0.72	0.07	0.02	0.00
Ilex rotunda	1.52	0.89	0.02	0.00
Prunus phaeosticta	2.32	0.85	0.00	0.00
Litsea acuminata	9.80	2.24	0.27	0.00
Trochodendron aralioides	3.44	2.26	0.00	0.00
Pourthiaea beauverdiana	0.14	0.33	0.00	0.00
Machilus thunbergii	41.18	16.62	2.76	0.08
Cyclobalanopsis sessilifolia	8.65	11.12	0.00	0.00
Ligustrum japonicum	0.05	0.31	0.00	0.00
Dendropanax dentiger	0.50	0.28	0.12	0.00
Symplocos sumuntia	0.00	1.34	0.04	0.00
Rhododendron ellipticum	0.00	0.60	0.09	0.00
Prunus campanulata	1.04	0.74	0.03	0.00
Symplocos lucida	0.22	1.00	0.07	0.00
Meliosma squamulata	0.00	2.57	0.55	0.00
Ternstroemia gymnanthera	0.14	0.46	0.24	0.00
Eurya loquaiana	0.00	0.39	0.20	0.83
Illicium arborescens	0.29	8.81	3.33	0.34
Cyclobalanopsis longinux	10.20	16.71	6.88	2.08
Cinnamomum subavenium	0.00	0.63	0.28	0.00
Pyrenaria shinkoensis	0.00	2.63	1.84	0.00
Diospyros morrisiana	0.00	8.12	6.50	0.00
Adinandra formosana	0.36	0.87	2.05	0.00
Syzygium buxifolium	0.00	1.72	2.89	0.00
Elaeocarpus japonicus	2.38	0.88	5.66	0.00
Ilex formosana	0.00	0.44	0.13	0.04
Michelia compressa	0.05	2.26	3.65	0.00
Symplocos wikstroemifolia	0.01	0.74	3.52	0.00
Itea parviflora	4.19	3.19	0.94	0.83
Ilex goshiensis	0.07	0.02	1.12	0.00
Gordonia axillaris	0.00	0.00	3.81	0.00
Euonymus laxiflorus	0.00	0.02	0.36	0.00
Myrsine seguinii	0.00	0.49	9.77	0.00
Tricalysia dubia	0.00	0.29	0.07	0.11
Daphniphyllum glaucescens ssp. *oldhamii*	0.38	0.81	1.54	0.36
Symplocos cochinchinensis ssp. *laurina*	0.26	0.05	0.84	0.02
Fraxinus formosana	0.00	0.00	1.09	0.00
Randia cochinchinensis	0.00	0.00	0.55	0.01
Cinnamomum camphora	0.00	0.14	8.14	0.00
Styrax suberifolia	0.00	0.00	3.31	0.16
Castanopsis cuspidata var. *carlesii* f. *sessilis*	0.00	4.26	8.35	3.98
Engelhardtia roxburghiana	0.00	0.00	6.66	1.67
Myrica rubra	0.03	0.35	2.06	0.70
Pasania harlandii	0.00	1.96	4.01	2.70
Cleyera japonica	0.21	0.29	0.82	1.76
Wendlandia formosana	0.00	0.00	0.01	0.49
Pasania kawakamii	0.00	0.00	0.00	0.89
Cyclobalanopsis glauca	0.00	0.00	0.28	0.77
Meliosma rhoifolia	0.00	0.00	0.20	1.42
Schefflera octophylla	0.00	0.11	2.33	10.65
Helicia formosana	0.00	0.10	0.00	1.37
Ardisia sieboldii	0.00	0.00	0.13	4.34
Acer serrulatum	0.14	0.35	0.44	13.29
Turpinia formosana	0.00	0.01	0.00	3.17
Cyathea lepifera	0.00	0.00	0.00	7.00
Lindera communis	0.00	0.00	0.00	1.79
Glochidion rubrum	0.00	0.00	0.00	1.08
Pasania hancei var. *ternaticupula*	0.00	0.00	0.24	2.95
Machilus japonica var. *kusanoi*	0.00	0.00	0.00	25.19
Lagerstroemia subcostata	0.00	0.00	0.00	5.36
Saurauja tristyla var. *oldhamii*	0.00	0.00	0.00	0.64
Oreocnide pedunculata	0.00	0.00	0.00	0.86
Beilschmiedia erythrophloia	0.00	0.00	0.00	1.13

was very high (11 388 stems/ha). The canopy was 9 - 12 m tall on leeward slopes, but only 6-8 m on windswept ridges. It was more diverse than in types I and II; 70 trees and 14 shrubs were encountered in the plots. The species included in the name are important components of the canopy, but *Myrsine seguinii* is more pronounced on exposed sites. *Illicium arborescens* was again abundant below the upper canopy. The understorey was much denser (8425 stems/ha, 1-5 cm DBH) than in other forest types. This was chiefly due to the abundance of *Euonymus laxiflorus* and saplings of *Syzygium buxifolium*, *Myrsine seguinii* and *Illicium arborescens*. Shrubs and lianas were rare. The herb stratum was generally poorly developed.

Type IV: Machilus japonica var. kusanoi-Acer serrulatum-Schefflera octophylla

Type IV was restricted to the foot of the steep ledge, where the substrate consisted mainly of rock debris and talus deposits. The four plots of this forest type were situated between 540 and 640 m, on slopes adjoining the valley bottom. This forest type differs from the others in having a lower density in all strata and the smallest number of woody species per plot. The height of the canopy ranged from 10 to 13 m, with trees attaining 35 - 50 cm DBH. The major canopy trees (see type name) are accompanied by *Ardisia sieboldii* and *Turpinia formosana* as main subcanopy trees. Tree ferns were common; individuals of *Cyathea lepifera* regularly reached trunk diameters of 20 - 25 cm, and heights of 9 - 10 m. The widespread gap colonist *Diospyros morrisiana*, common in the upper slope forests, was completely absent here. Woody lianas were more frequent than in other forest types, representing about 1% of the total basal area. *Erycibe henryi* and *Ampelopsis cantoniensis* were two major species, which often attained a DBH of 5-6 cm. The shrub layer was strongly dominated by *Blastus cochinchinensis*. Herb cover was high (60 %) and had a patchy structure.

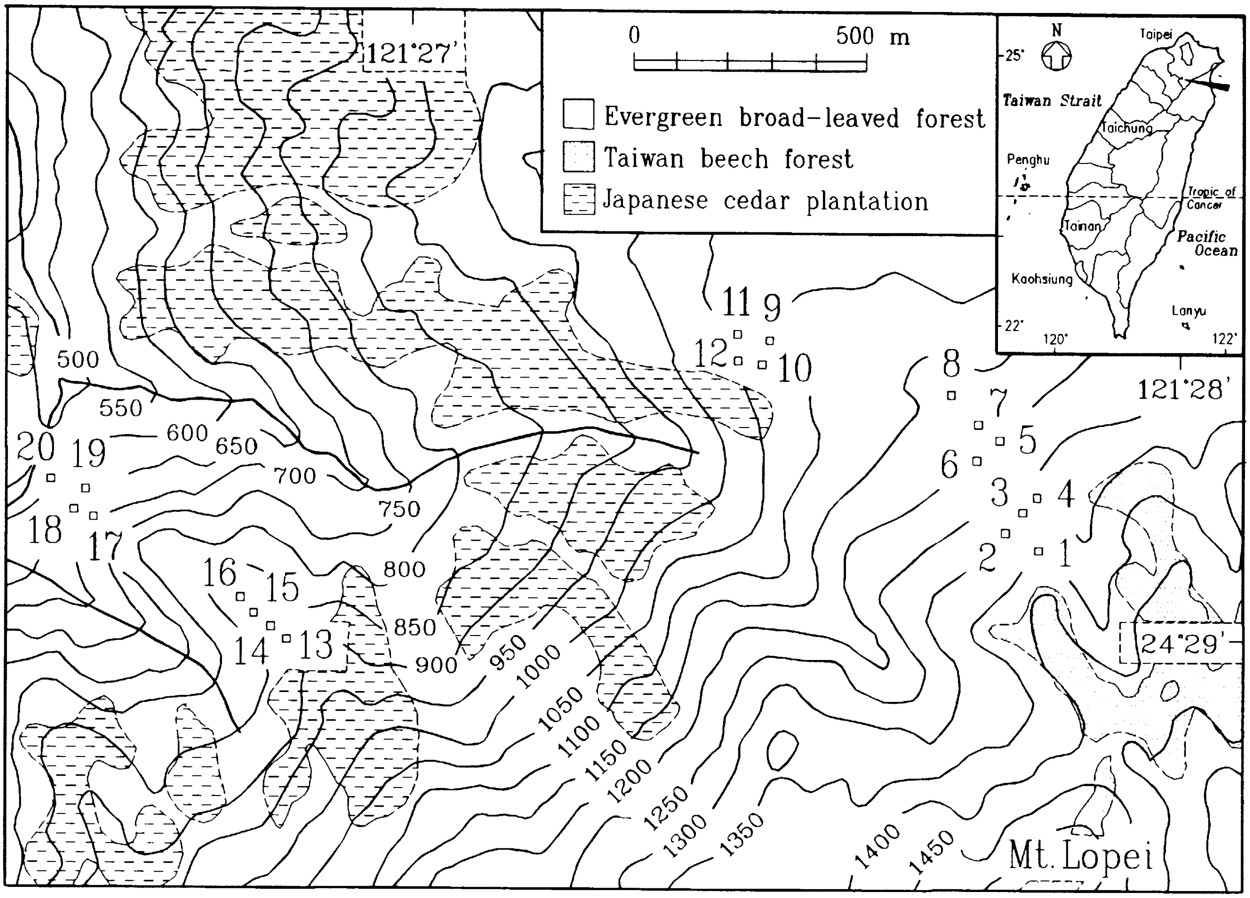

Fig. 1. Diagram (axes 1 and 2) of the Detrended Correspondence Analysis of the Lopei forest data. For species names seeTable 1. Four forest types were separated along axis 1, following decreasing altitude.

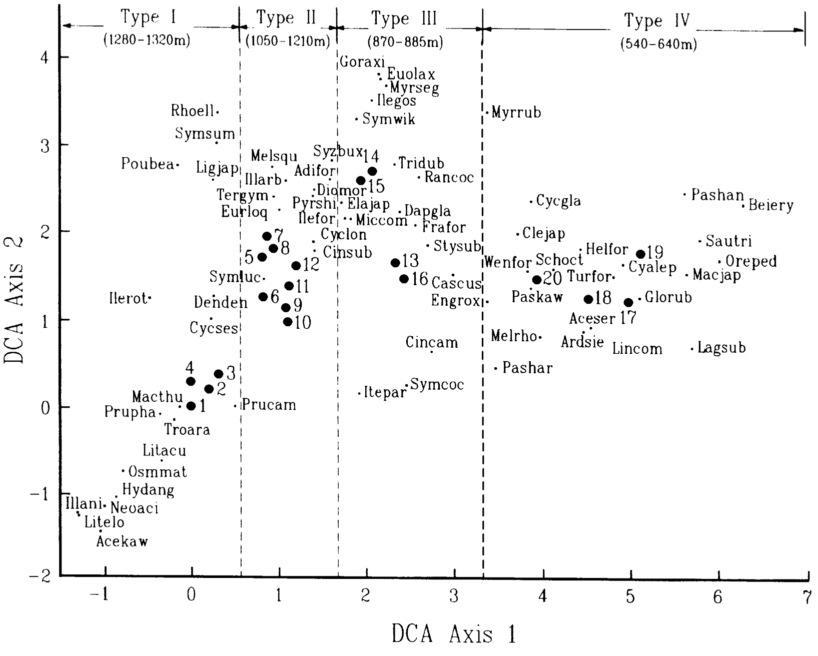

Fig. 2. Relationship between values for the Community Coefficient for pairs of plots and their altitudinal differences.

Table 2. Diversity measures and structural characteristics (mean ± S.D. per plot) for the four forest types on Mount Lopei. Only trees and shrubs with a DBH ≥ 1 cm were included in the calculations. Values in parentheses are the taxon numbers for all vascular plants. Significantly different values ($p < 0.05$) are indicated by different superscripts. H'= Shannon-Wiener index; $N1$ = Hill' diversity number $N1$; $N2$ = Hill' diversity number $N2$; $E5$ = Hill' $E5$ evenness index.

Forest type	I	II	III	IV
No. of plots / area (ha)	4 / 0.16	8 / 0.32	4 / 0.16	4 / 0.16
Altitudinal range (m)	1280 - 1320	1050 - 1210	870 - 885	540 - 640
No. of species	26.50 ± 4.65^{a}	37.88 ± 6.06^{b}	41.75 ± 8.10^{b}	23.75 ± 8.85^{a}
H'	2.43 ± 0.08^{a}	2.89 ± 0.10^{bc}	3.10 ± 0.14^{c}	2.66 ± 0.34^{ab}
$N1$	11.35 ± 0.91^{a}	18.00 ± 1.75^{b}	22.40 ± 3.22^{c}	14.87 ± 5.18^{ab}
$N2$	7.84 ± 0.89^{a}	13.75 ± 1.92^{b}	19.54 ± 5.03^{c}	12.54 ± 4.69^{b}
$E5$	0.66 ± 0.08^{a}	0.75 ± 0.07^{ab}	0.86 ± 0.13^{b}	0.82 ± 0.05^{b}
Tree height (m)	9.98 ± 1.00^{a}	9.65 ± 1.87^{a}	8.32 ± 1.98^{b}	9.95 ± 1.67^{a}
Basal area (m^2/ha)	36.93 ± 3.56^{a}	40.95 ± 4.30^{a}	34.22 ± 6.67^{a}	36.26 ± 8.00^{a}
Volume (m^3/ha)	162.70 ± 29.20^{a}	162.90 ± 44.20^{a}	139.50 ± 56.30^{a}	172.90 ± 33.40^{a}
Density (stems/ha)	5325 ± 1127^{a}	8562 ± 2347^{ab}	11387 ± 7827^{b}	3100 ± 859^{a}
Total families	22 (56)	30 (71)	33 (66)	29 (56)
Total genera	32 (85)	50 (120)	50 (97)	40 (86)

Diversity

Species richness, diversity and evenness indices differed significantly among the four forest types ($p < 0.001$ for all indices), and largely paralleled the density pattern (Table 2). The forest at the highest altitude had the lowest species diversity. Values for $N1$, $N2$ and $E5$ reflected a higher degree of dominance concentration in this forest relative to the forests at lower altitudes. There was a consistent decrease of species richness from lower to upper forest layers. The average number of woody species was 24 ± 11, 21 ± 7 and 16 ± 4 for stems ≤ 3 cm, 3 - 8 cm and > 8 cm DBH, respectively.

Since the herbaceous species did not follow the trend in compositional change along the altitudinal gradient, only woody species (118) were included in the measurement of beta diversity. Fig. 2 shows the trend of community similarity which decreases with separation along the altitudinal gradient. The gradient length corresponding to a half-change in floristic composition was 3.27 (Table 3). The altitudinal ranges for 50 % and 95 % turnover were 238 m and 1030 m, respectively. The turnover rate of the understorey (DBH ≤ 3 cm) was comparable to that of the overstorey (DBH > 10 cm).

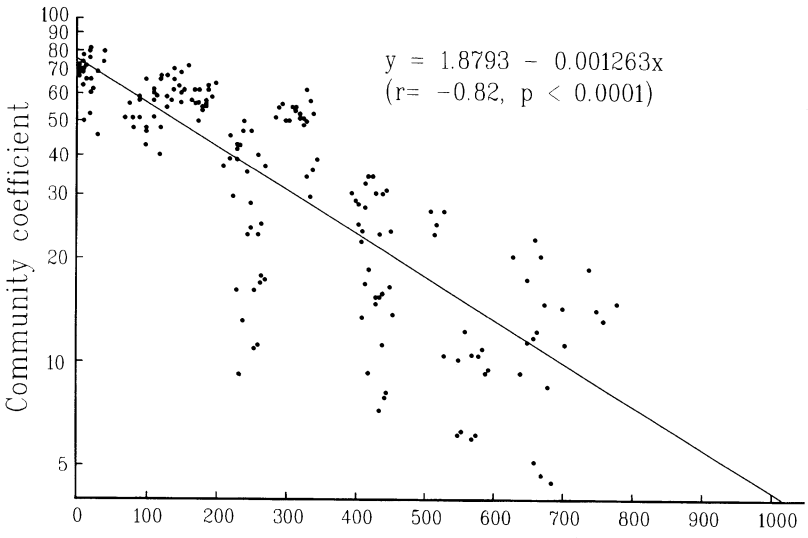

Fig. 3. Frequency distributions of DBH of the four representative species.

Table 3. Beta diversity parameters on the basis of Community Coefficient.

	DBH ≤ 3 cm	DBH > 3 cm	DBH > 10 cm	Woody species
Internal Association (%)	71.4	72.7	72.9	79.3
Turnover rate	- 0.0019	- 0.0013	- 0.0018	- 0.0013
Altitudinal range (m) / 50% change	156	229	151	238
Altitudinal range (m) / 95% change	673	989	652	1030
Gradient length (HC)	5.01	3.41	5.17	3.27

Size-class structure

The size-class structure of each forest type approximated that expected for uneven-aged forests. Both the negative exponential and negative power functions showed good fits ($r > 0.99$) to diameter distributions for each of the forest types. However, the population structures of sufficiently abundant species varied apparently. Four general patterns, suggesting different population dynamics, could be distinguished (Fig. 3). Group 1 (40 species) showed a good fit to the negative exponential or negative power function (Fig. 3a). Typical examples were: *Cyclobalanopsis sessilifolia*, *Schefflera octophylla* and *Myrsine seguinii*. The seven species of group 2 had essentially a negative exponential distribution, but were slightly underrepresented in the smaller size classes (Fig. 3b). Examples are *Cyclobalanopsis loginux* and *Litsea acuminata*. Group 3 (8 species) showed scattered peaks (Fig. 3c). Examples are *Ardisia sieboldii* and *Ilex formosana*. The two species of group 4 were characterized by a normal distribution of size-classes, e.g. *Acer serrulatum* at the footslope site (Fig. 3d).

For most widespread species, a similar population structure was shown at all sites in which they occurred. A notable exception was *Machilus thunbergii*, which had a normal distribution in the Type I forest, but a negative exponential distribution in other forests. This indicated that even for the most abundant canopy species different recurring patterns might exist.

Soil-vegetation relationships

Since soil data for the 0 - 10 cm and 10 - 20 cm depths were correlated, soil-vegetation relationships are shown for the surface layer only. Fig. 4 shows the position of 44 soil samples, 11 soil variables and one nominal variable (topographic position). The ordination axes included accounted for 43 % of the variance. The first axis indicated significant ($p < 0.01$) differences in soils among sites. The position of the soil samples relative to each other was somewhat similar to that of the vegetation plots in the DCA ordination (Fig. 1). Five groups (including soil data for the beech forest) were distinguished. Altitude was the major determinant of axis 1.

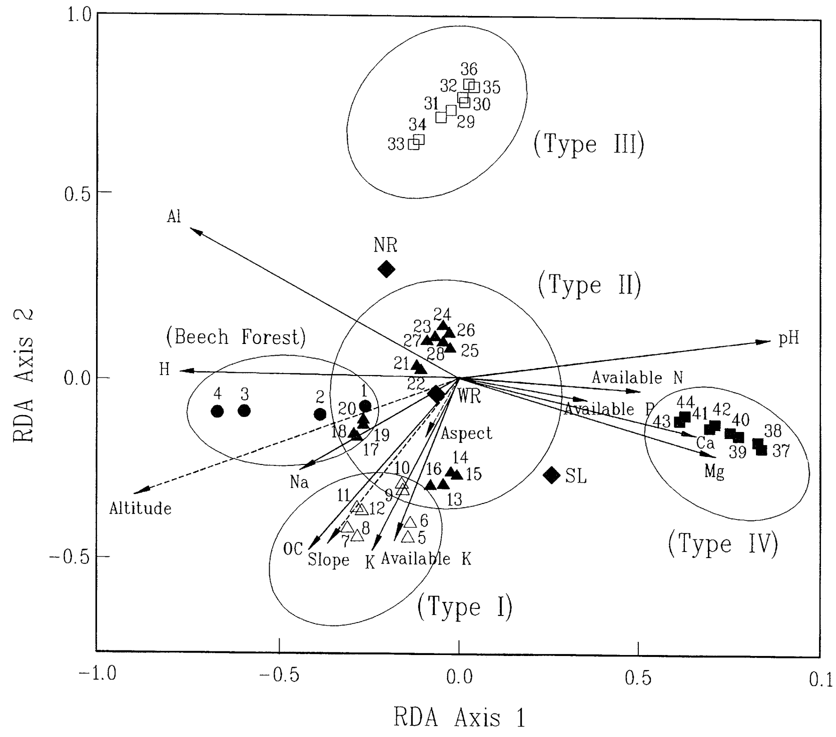

Fig. 4. Redundancy Analysis (RDA) triplot with soil variables (arrows), soil samples (numbers) and external variables (dashed lines).
◆ = centroids of land forms;
● = soil samples of the beech forest;
Δ = soil samples of Type I forest;
▲ = soil samples of Type II forest;
□ = soil samples of Type III forest;
■ = soil samples of Type IV forest;
NR = narrow ridge;
WR = wide ridge;
SL = slope;
OC = organic C;
K, Na, Ca, Mg, Al, H = elements in exchangeable form
($\lambda_1 = 0.337$, $\lambda_2 = 0.089$).

The ANOVA results (Table 4) revealed that most soil properties differed significantly ($p < 0.05$) among vegetation types, including pH, organic C and exchangeable Ca. These variables are represented by longer arrows in Fig. 4. Organic C, exchangeable Na and K tended to decrease in a downslope direction, while pH and available N decreased with increasing altitude. Levels for exchangeable Ca and Mg were highest in the footslope soils, for exchangeable Al on the ridge (beech forest, Type III forest). Spearman rank correlation values generally showed similar relations between soil properties, vegetation types and topographic variables as ANOVA did.

Discussion

Gradient analysis and forest types

Ordination of the sample data by DCA produced a species and plot distribution pattern which accounted for a significant proportion of the total variance along the first two axes. Our results were checked for not suffering from the problems of instability in ordination results produced by subprograms in the packages DECORANA and CANOCO (Oksanen & Minchin 1997). The relative magnitude of the various correlations suggested that altitude played a dominant role in determining the distribution of species. This reflects the traditional view of the importance of altitude for the differentiation of montane rain forests in Taiwan (Liu 1968). On the other hand, for a given altitudinal range, topographic exposure was still a significant factor for vegetation variation. This is illustrated by the second DCA axis (accounting for 18.71% of the variation) which contrasts forests developed on more exposed narrow ridges (in the upper part of Fig. 1) from those developed on more or less sheltered slopes in the lower part. A remarkable difference between windward and leeward forests was shown by the distribution of *Myrsine seguinii* and some other species which were restricted mainly to the windward sites at 800-1200 m, while *Castanopsis cuspidata* var. *carlesii* fo. *sessilis* and other taxa which occurred predominantly on the leeward slopes. Similar results were reported by Fernández-Palacios et al. (1995) in a study of vegetation on the trade-wind affected island Tenerife where altitude and, to a lesser extent, exposure to wind were the major determinants of vegetation variation.

Su (1984) divided the evergreen broad-leaved forests of central Taiwan – in upward sequence – into four major zones: *Ficus-Machilus* zone (0 - 500 m, tropical climatic zone), *Machilus-Castanopsis* zone (500 - 1400 m, subtropical), Lower *Quercus* (1400 - 1800 m, warm-temperate) and Upper *Quercus* zone (1800-2400 m, temperate). In order to clarify the altitudinal zonation of the Lopei forests, existing data from 759 plots collected over the full altitudinal range of the evergreen broad-leaved forest vegetation in Taiwan (Hsieh et al. 1997) were combined with the Lopei plots to generate a data matrix of 779 plots with 569 species. These data were subjected to a TWINSPAN classification (Hill 1979b) and complementary DCA analysis, and the results compared with the classification scheme of Su (1984). The four lower plots of the present study belong to the *Machilus-Castanopsis* forest zone, and the uppermost plot just marked the Upper *Quercus* zone. The other plots in between were all included in the Lower *Quercus* zone. The lower limit of the Lower *Quercus* forest zone in the study area appears to be at ca. 800 m, and there is a gradual transition from the Lower *Quercus* forest zone at 1300 m to the Upper *Quercus* zone. In comparison with the forests in central Taiwan, the altitudes of floristically similar stands were 500 - 600 m lower in the study area in the north of Taiwan, probably due to the decline in latitude. In Taiwan, the zone of cloud forests generally coincides with the *Quercus* forests (Su 1984). No long-term systematic records have been made of the cloud cover on Mount Lopei, but limited observations suggested that the base of the monsoon wind-driven cloud

Table 4. Mean values (S.D.) for soil chemical properties in plots within each of the four forest types of Mount Lopei. Values for Taiwan beech forest are also shown. Means with different superscripts are significantly different at $p < 0.05$. Organic C in g/kg; available N, P and K in mg/kg; exchangeable K, Na, Ca, Mg, Al and H in cmol(+)/kg.

Soil parameter	Beech forest	Type I	Type II	Type III	Type IV
pH	3.20 ± 0.12^{a}	3.40 ± 0.18^{a}	3.39 ± 0.21^{a}	3.81 ± 0.15^{b}	4.65 ± 0.57^{c}
Organic C	135.50 ± 7.23^{a}	156.38 ± 27.74^{a}	122.13 ± 38.26^{a}	80.50 ± 26.84^{b}	85.38 ± 40.67^{b}
Available N	104.50 ± 16.90^{a}	145.13 ± 42.11^{a}	162.69 ± 60.00^{ab}	165.50 ± 46.69^{ab}	216.88 ± 76.12^{b}
Available P	6.53 ± 5.08^{a}	7.46 ± 2.83^{a}	7.23 ± 5.92^{a}	7.76 ± 2.90^{a}	11.78 ± 3.66^{a}
Available K	128.50 ± 51.16^{a}	128.38 ± 28.84^{a}	111.94 ± 29.35^{ab}	76.13 ± 30.42^{b}	104.38 ± 45.14^{ab}
Exchangeable K	0.54 ± 0.22^{a}	0.53 ± 0.12^{a}	0.47 ± 0.12^{a}	0.31 ± 0.13^{b}	0.42 ± 0.16^{ab}
Exchangeable Na	0.09 ± 0.02^{a}	0.10 ± 0.03^{a}	0.08 ± 0.03^{ab}	0.07 ± 0.03^{ab}	0.05 ± 0.02^{b}
Exchangeable Ca	0.30 ± 0.22^{a}	0.35 ± 0.28^{a}	0.54 ± 0.37^{a}	0.11 ± 0.14^{a}	10.78 ± 11.54^{b}
Exchangeable Mg	0.69 ± 0.15^{a}	0.66 ± 0.15^{a}	0.52 ± 0.16^{a}	0.40 ± 0.08^{a}	3.23 ± 2.29^{b}
Exchangeable Al	10.18 ± 0.77^{a}	6.38 ± 1.00^{b}	6.04 ± 1.01^{b}	9.07 ± 2.19^{a}	1.74 ± 1.73^{c}
Exchangeable H	2.21 ± 0.50^{a}	1.30 ± 0.52^{b}	1.14 ± 0.41^{b}	1.19 ± 0.37^{b}	0.26 ± 0.22^{c}

zone appeared to be at about 800 m, and the band of dense cloud cover was found above 1300 m. According to the data compiled from the equipment installed on the main Lopei ridge, there were only 46 hours of cloud-free conditions during the 92 days of the study from November 1987 to January 1988, and there were only 24 clear days out of the 217 days of our observations (from July 1987 to January 1988).

Locally, the classification largely agrees with earlier forest studies in northern Taiwan. Forest type II, III and Type IV are comparable to the *Cyclobalanopsis sessilifolia-C. longinux*, *Randia cochinchinensis-Castanopsis cuspidata* var. *carlesii* f. *sessilis* and *Lagerstroemia subcostata* forest types of Liu & Su (1976) and Chen (1993). However, the extensive dominance of *Limlia* (*Castanopsis*) *uraiana* in the *Randia cochinchinensis-Castanopsis cuspidata* var. *carlesii* fo. *sessilis* forest is not represented here.

Vegetation characteristics

The environment of the evergreen broad-leaved forests in Taiwan differs from that of temperate forests and tropical rain forests in many ways. One of the most striking differences is the persistence of northeasterly monsoon winds in the winter season. Monsoon winds do not cause massive damage to the forests, but the chronic stress can have profound effects on the structural and floristic features of the forests (Sun et al. 1996; Chen et al. 1997). In many parts of the most exposed windward slopes and ridges in southeastern Taiwan, winds usually reduce the canopy height of the forests to 3 - 5 m. The forests studied lie on the northwestern slope of Mount Lopei, and some plots (e.g. 7, 8, 14, 15) on side-ridges were constantly exposed to strong winds usually at a peak speed of 8 - 10 m/s (measured by a 3-cup anemometer during January and February 1997). This is one of the reasons that may cause the stunting of forests on the ridges. Typhoons are also common during the period from July to September in the western Pacific region. As the typhoons first approach northern Taiwan, the strong northeasterly winds reflect the normal monsoon winds direction. They can be very destructive. However, most of the damage was concentrated on the side-ridge plots, and this was reflected by the occurrence of many small gaps created by single treefall or limbfall. In the steep mountain terrain of the study area there were relatively large areas with little wind damage. Nevertheless, treefall gaps of various sizes still could be observed in these areas. Possible reasons that could explain frequent treefalls included: steep slope, unstable substrate, erosion accompanying heavy rains, shallow soil and high soil moisture. These factors, together with monsoon winds and typhoons, may play a very important role in maintaining floristic diversity in the Lopei forests, generating on-going dynamics of vegetation structure and composition. A combination of these factors may also lead to the reduced stature of the forests along the entire transect. A lower stature (< 15 m) of canopy trees is commonly observed in the lower montane forests elsewhere in Taiwan (Hsieh et al. 1990; Chen 1993; Sun et al. 1996), and also in the Caribbean region (Howard 1968; Lawton & Dryer 1980; Sugden 1986). In contrast, the best-developed evergreen broad-leaved forests can be found in sheltered sites at middle altitudes (1800 -2400 m), where the canopy may attain heights of 30 - 40 m tall (Song 1996).

The basal areas of the forests studied are within the range of 33 - 40 m^2/ha (DBH ≥ 1 cm). These are comparable to values obtained from a variety of lowland rain forests in southernmost Taiwan (Yang 1994; Sun et al. 1996). A relatively higher value of basal area (53-80 m^2/ha) has been reported for the *Machilus-Castanopsis* and *Quercus* forests at middle altitudes (Hsieh 1989b; Song 1996), where the forests were relatively protected from the strong monsoon winds and typhoons because of their sheltered topographic positions. Stem density throughout all plots was unrelated to altitude, but showed a significant change with land form ($r = 0.827$, $p < 0.001$). The highest density was recorded on narrower and more exposed ridges (plots 7, 8, 14 and 15) with an average of 14 450 stems/ha. Henceforth, species density can be used as the measure of exposure in the Lopei forests. It is clear from Table 2 that there are no trends of basal area and tree volume in relation to elevation and land forms, i.e. no correlation of species density with basal area or tree volume has been found.

Diversity

The relative species poverty of the footslope forest near the valley bottom is due to the talus deposits being filled with patches of rock rubble and the occurrence of fewer individuals per unit area. The species-area curve for this forest suggested that more species would be found if more plots were enumerated. Apart from this forest type, there was a strong tendency for both species richness and diversity indices to be lower at higher altitudes (Table 2). A similar result was obtained for evenness index $E5$.

The comparison of beta diversity along the Lopei altitudinal gradient with that of other mountains in Taiwan is not possible due to the lack of relevant data. Similar turnover rates have been reported for an evergreen broad-leaved forest on Tsushima (southern Japan) (Itow 1991), where the altitudinal range for 95 % change is 1160 m for woody species and 617 m for trees > 10 cm DBH. In the present study area, the *Machilus-Castanopsis* and Lower *Quercus* forest zones are prevalent between 300 - 1300 m, the calculated 95 % turnover fits well to this altitudinal range. Although Itow (1991) found that the turnover rate of the herbaceous understorey along an altitudinal gradient was higher than that of the overstorey, no such pattern was apparent in this study. The change of the herbaceous understorey with altitude was distorted by topographic features. Within a certain altitudinal range, topographic associated factors such as canopy structure, soil moisture and nutrients may have been responsible for the greater segregation of the herbaceous species there.

Size-class distribution

Fire and large-scale geomorphic disturbance such as landslides are important determinants of forest composition in the central mountains of Taiwan (Chen et al. 1986; Hsieh et al. 1989). However, in the very humid climate and relatively stable land forms of the Lopei forests their roles are very minor. There was no indication from the DCA results that any of the first two axes reflected such kinds of disturbances. The size-class structure for all forest types also suggested that there had been no large-scale anthropogenic disturbance. Like many other tropical lowland rain forests (Bongers et al. 1988; Lawton & Putz 1988; Uhl et al. 1988), single-treefall and limbfalls appear to be the prevalent modes of disturbance in the Lopei forests. Canopy closure will thus occur mainly by lateral growth of existing individuals, or due to the growth of the primary forest species.

As to individual species, the present results support the superiority of the negative exponential function for describing population structure. These species appeared to have a good reproduction and regular recruitment in the study area. The markedly normal size-class distribution of *Machilus thunbergii* in Type I forest probably reflected its massive establishment after a local disturbance many years ago, followed by a period of relative stability. Owing to its relative shade-intolerance as compared with other species such as *Itea parviflora* and *Litsea acuminata*, the abundance of seedlings has diminished greatly beneath closed canopies. In contrast, there were many saplings and small trees on the exposed ridge sites. This is probably due to the more open canopies of the forests.

Soil-vegetation relationship

Variation in soil properties along the altitudinal gradient has long been known (Whittaker et al. 1968; Marrs et al. 1988; Grieve et al. 1990). Grieve et al. (1990) mentioned that the most consistent altitudinal trends in wet tropical montane forests were increases in soil organic C and soil acidity. This is the case in the Lopei forests. The present result which points to a nitrogen trend is also congruent with the data of Heaney & Proctor (1989) for Volcán Barva of Costa Rica, where available nitrogen in soils diminished with altitude.

The soil change is not smooth throughout the entire altitudinal gradient. With the exception of exchangeable Al and H, there is rather little change in the upper three forest types (Table 4, beech, Type I and II forests). However, it seems clear that there are marked changes in pH ($p < 0.0001$), organic C ($p < 0.0001$), available N ($p < 0.028$), exchangeable K ($p < 0.005$), Na ($p < 0.004$) and H ($p < 0.001$) between the soils of the *Quercus* forest zone (cloud forest) and *Machilus-Castanopsis* forest zone. The high content of exchangeable Ca and Mg observed on the footslope presumably reflects local variation in parent material. These differences together with the highest values of pH and N-content cause the distinctiveness of the footslope soils. Significant differences between the *Fagus* and *Quercus* forests are limited to pH and exchangeable Al-content. The higher level of exchangeable Al and lower pH value on the beech forest floor is probably correlated with the increasingly cool and moist aerial environment. It is also, in part, due to excessive leaching of the soils on the flat ridge tops.

It has been suggested that extreme soil acidity seems likely to account for the low stature of tropical upper montane rain forests (Grubb 1977; Tanner 1977). There is also some evidence that nitrogen supply may be a contributory factor controlling growth and structure of the montane forests (Marrs et al. 1988; Heaney & Proctor 1989; Bruijnzeel et al. 1993). In the case of the Lopei forests, soil acidity decreased and available nitrogen increased monotonically downslope. However, no consistent altitudinal trend was observed for canopy height, total basal area or tree volume, suggesting that neither soil acidity nor available nitrogen is likely to be a major constraint on tree growth. The results of this study is generally consistent with those from the montane forests of Margarita (Sugden 1986) in suggesting that winds may outweigh edaphic factors in restricting forest growth on the exposed slopes and ridge crests.

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References

Anon. 1984. *Procedures for collecting soil samples and methods of analysis for soil survey.* USDA-SCS Soil Survey Investigation Rep. no. 1. U.S. Government Printing Office, Washington, DC.

Anon. 1988. *SAS/STAT user's guide.* SAS Institute, Inc., Cary, NC.

Bongers, F., Popma, J., Meave del Castillo, J. & Carabias, J. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55-80.

Bruijnzeel, L.A., Waterloo, M.J., Proctor, J., Kuiters, A.T. & Kotterink, B. 1993. Hydrological observations in montane rain forests on Gunung Silam, Sabah, Malaysia, with special reference to the 'Massenerhebung' effect. *J. Ecol.* 81: 145-167.

Chen, M.Y., Liu, Y.C., Lu, K.C. & Lin, C.Y. 1986. The succession of Taiwan red pine forest at Mt. Tong-mao in the first post-fire year. *Quart. J. Chin. For.* 19 (2): 1-15. (In Chinese.)

Chen, T.I. 1993. Vegetation analysis on the broad-leaved forests of *Machilus-Castanopsis* forest zone in Northern Taiwan. *Quart. J. Exp. For. Natl. Taiwan Univ.* 7(3): 127-146. (In Chinese.)

Chen, Z.S., Hsieh, C.F., Jiang, F.Y., Hsieh, T.H. & Sun, I.F. 1997. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. *Plant Ecol.* 132: 229-241.

Fernández-Palacios, J.M. & de Nicolás, J.P. 1995. Altitudinal pattern of vegetation variation on Tenerife. *J. Veg. Sci.* 6: 183-190.

Grieve, I.C., Proctor, J. & Cousins, S.A. 1990. Soil variation with altitude on Volcán Barva, Costa Rica. *Catena* 17: 525-534.

Grubb, P.J. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annu. Rev. Ecol.* Syst. 8: 83-107.

Heaney, A. & Proctor, J. 1989. Chemical elements in litter in forests on Volcán Barva, Costa Rica. In: Proctor, J. (ed.) *Mineral nutrients in tropical forest and savanna ecosystems*, pp. 255-271. Blackwell Scientific Publ., Oxford.

Hill, M.O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427-249.

Hill, M.O. 1979a. *DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Ecology and Systematics, Cornell University, Ithaca, NY.

Hill, M.O. 1979b. *TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Ecology and Systematics, Cornell University, Ithaca, NY.

Howard, R.A. 1968. The ecology of an elfin forest in Puerto Rico, 1. Introduction and composition studies. *J. Arnold. Arbor.* 49: 381-418.

Hsieh, C.F. 1989a. Structure and floristic composition of the beech forest in Taiwan. *Taiwania* 34: 28-44.

Hsieh, C.F. 1989b. Structure and floristic composition of the warm-temperate rain forest of the Kaoling area. *J. Taiwan Mus.* 42 (2): 31-42.

Hsieh, C.F. & Chen, Z.S. 1989. *Developing an ecological data system for nature preserves*, pp. 58-59. Technical Report, No. 22. Council of Agriculture, ROC. Taipei.

Hsieh, C.F., Chao, W.C., Liao, C.C., Yang, K.C. & Hsieh, T. H. 1997. Floristic composition of the evergreen broad-leaved forests of Taiwan. In: Hara, M. & Yonebayashi, C. (eds.) *Lucidophyllous forests in southwestern Japan and Taiwan*, pp. 1-16. Natural History Research, Special Issue, No. 4. Natural History Museum and Institute, Chiba.

Hsieh, C.F., Hsieh, T.H. & Lin, S.M. 1989. Structure and succession of the warm-temperate forest at Techi Reservoir. *J. Taiwan Mus.* 42 (2): 77-90.

Hsieh, C.F., Huang, T.C., Hsieh, T.H., Yang, K.C. & Huang, S.F. 1990. Structure and composition of the windward and leeward forests in the Wushipi Nature Preserve, northern Taiwan. *J. Taiwan Mus.* 43 (2): 157-166.

Huang, T.C., Boufford, D.E., Hsieh, C.F., Ohashi, H. & Yang, Y.P. (eds.) 1996. *Flora of Taiwan,* 2nd ed. Vol. 2. Department of Botany, National Taiwan University, Taipei.

Itow, S. 1991. Species turnover and diversity patterns along an evergreen broad-leaved forest coenocline. *J. Veg. Sci.* 2: 477-484.

Kira, T. 1991. Forest ecosystems of east and southeast Asia in a global perspective. *Ecol. Res.* 6: 185-200.

Kudo, Y. & Sasaki, S. 1931. An ecological survey of the vegetation of the border of Lake Jitsugetsutan. *Ann. Rep. Taihoku Bot. Gard.* 1: 1-50.

Lawton, R.O. & Dryer, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101-116.

Lawton, R.O. & Putz, F.E. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69: 764-777.

Li, H.L., Liu, T.S., Huang, T.C., Koyama, T. & DeVol, C.E. (eds.) 1975-1979. *Flora of Taiwan,* Vols. 1-6. Epoch Publ. Co., Taipei.

Liu, T. 1968. Studies on the classification of the climax vegetation communities of Taiwan, I. Classification of the climax formations of the vegetation of Taiwan. *Bull. Taiwan For. Res. Inst.* No. 166. (In Chinese with English summary.)

Liu, T.S. & Su, H.J. 1976. Synecological studies on the hardwood forests of a small watershed at Wulai in northern Taiwan (I). *Bull. Exp. For. Natl. Taiwan Univ.* 118: 183-199. (In Chinese.)

Marrs, R.H., Proctor, J., Heaney, A. & Mountford, M.D. 1988. Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *J. Ecol.* 76: 466-482.

Ohsawa, M. 1993. Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. *J. Veg. Sci.* 4: 13-18.

Oksanen, J. & Minchin, P.R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. *J. Veg. Sci.* 8: 447-454.

Song, G.Z. 1996. *Species composition and distribution patterns of the temperate evergreen broad-leaved forest of Mt. Peitungyen, central Taiwan. M.Sc. Thesis,* National Taiwan University, Taipei. (In Chinese with English summary.)

Su, H.J. 1984. Studies on the climate and vegetation types of the natural forests in Taiwan II. Altitudinal vegetation zones in relation to temperature gradient. *Quart. J. Chin. For.* 17 (4): 57-73.

Su, H.J. & Wang, L.J. 1988. Forest vegetation in the upper Nanshihchi watershed of northern Taiwan. *Quart. J. Exp. For. Natl. Taiwan Univ.* 2 (4): 89-100. (In Chinese.)

Sugden, A.M. 1986. The montane vegetation and flora of Margarita Island, Venezuela. *J. Arnold Arbor.* 67: 187-232.

Sun, I.F., Hsieh, C.F. & Hubbell, S.P. 1996. The structure and species composition of a subtropical monsoon forest in southern Taiwan on a steep wind-stress gradient. In: Turner, I.M., Diong, C.H., Lim, S.S.L. & Ng, P.K.L. (eds.) *Biodiversity and the dynamics of ecosystems.* DIWPA Series, Vol. 1, pp. 147-169. The International Network for DIVERSITAS in Western Pacific and Asia (DIWPA). Center for Ecological Research, Kyoto University, Kyoto.

Tanner, E.V.J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J. Ecol.* 65: 883-918.

Teng, L.S., Huang, C.Y. & Lee, C.T. 1988. On the stratigraphy of the Wulai group in the Wulai-Pinglin area, northern Hsuehshan Terrain, Taiwan. *Proc. Geol. Soc. China* 31: 93-100.

ter Braak, C.J.F. 1990. *CANOCO version 3.10.* Agricultural Mathematics Group, Wageningen.

Uhl, C., Clark, K., Dezzeo, N. & Maquirino, P. 1988. Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69: 751-763.

Whitmore, T.C. 1984. *Tropical rain forests of the Far East.* Clarendon Press, Oxford.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.

Whittaker, R.H., Buol, S.W., Niering, W.A. & Havens, Y.H. 1968. A soil and vegetation pattern in the Santa Catalina Mountains, Arizona. *Soil Sci.* 105: 440-450.

Yang, J.J. 1994. *Woody floristic composition, structure and distribution pattern of a para-tropical rain forest in Nanjenshan area.* M.Sc. Thesis, National Taiwan University. (In Chinese with English summary.)

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