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Floristic Composition and Stand Structure of Three Evergreen Broad-leaved Forests in Taiwan, with Special Reference to the Relationship between Micro-landform and Vegetation Pattern

Masatoshi Hara[1], Kazuhiro Hirata[1], Michirou Fujihara[1], Keiichi Oono[1] and Chang-Fu Hsieh[2]

[1] Natural History Museum and Institute, Chiba
955–2 Aoba-cho, Chuo-ku, Chiba 260, Japan
[2] Department of Botany, National Taiwan University
Taipei 106, Taiwan

Abstract The floristic composition and stand structure of evergreen broad-leaved forests in Taiwan are described on the basis of data from three plots which were established on slopes from ridges to the valley bottom, one plot (Nanjenshan Plot) in South Taiwan and two plots (Pinglin Plot and Lopeishan Plot) in North Taiwan. In each plot, the plot area was divided into several micro-landform units based on the form of the land surface and the distribution of micro-landform elements. These units were grouped into upper and lower slopes, and their tree distributions and vegetation structure were compared. Floristic richness for tree and shrub species at family, genus and species level was highest in Nanjenshan Plot, but lower and similar in the other two plots. The total basal area of a plot and the density of trunks taller than 2.0 m were 41.0–46.7 m^2ha^{-1} and 61.6–84.1/100 m^2, respectively. Within each plot, the lower slope was characterized by the lower values for basal area and trunk density than the upper slope, and far more species showed a distribution bias to the upper slope (Group A) than to the lower slope (Group B). Although there was a considerable overlap of floristic composition between the upper and lower slopes, the amounts of many of the component species differed considerably between the slopes. Fagaceae, including *Castanopsis* and *Quercus*, was the most important dominant taxon of the upper slope, whereas Lauraceae such as *Machilus* were more conspicuous on the lower slope, although there was a considerable variation among plots. The floristic richness for tree and shrub species at stand level was similar to those obtained from the same type forests in the Ryukyu Islands, although the species diversity of the canopy layer was considerably higher in Taiwan. The strong effect of wind by the winter monsoon and typhoons to the forest structure in Taiwan is discussed.

Key words: Taiwan, evergreen broad-leaved forests, micro-landform, stand structure, floristic composition, Ryukyu Islands.

Taiwan is located between the southernmost part (Ryukyu Islands) of the Japanese Archipelago and the Asian Continent, and thus is important for understanding the biogeography of Japan in relation to the Asian Continent. According to the classification system of forest ecosystems of East and Southeast Asia by Kira (1991), Taiwan belongs to the same forest formations as the Ryukyu Islands and South China: the subtropical forest formations. In terms of flora, Taiwan and Japan (particularly the Ryukyu Islands) have many species in common (Hatusima, 1975), but elements common to South China are richer in Taiwan.

Evergreen broad-leaved forests dominated mainly by evergreen oaks with associated rich evergreen tree species cover a wide altitudinal range from 500 to 2500 m asl in Taiwan (Su, 1984). This type of forest in particular contains many species that are the same or closely related to those in the same forest type in Japan (Suzuki, 1952; Hsieh *et al.*, 1994), and thus for this type of forest, the comparative study between the two areas is essential from the viewpoint of vegetation ecology. Some earlier vegetation ecologists (e.g., Suzuki, 1938, 1941a, b, 1952, 1953, 1954, 1963; Hosokawa, 1958) studied the evergreen broad-leaved forests of Taiwan in comparison with the same forest types in Japan. In particular, Suzuki (1952) studied the forests of Taiwan and Japan comprehensively from a phytosociological viewpoint. There are many later works on the evergreen broad-leaved forests of Japan focusing on phytosociological classification of vegetation (e.g., Suzuki, 1979; Fujiwara, 1981), and forest structure and dynamics (e.g., Naka, 1982; Yamamoto, 1992; Tanouchi and Yamamoto, 1995). There are also later works on the natural, evergreen broad-leaved forests of Taiwan (e.g., Liu and Su, 1976; Su and Lin, 1979; Su, 1977, 1984, 1985; Su and Su, 1988; Hsieh, 1989b; Hsieh *et al.*, 1989, 1990a, 1990b; Sun *et al.*, 1996). A classification system of forest formations in East and Southeast Asia was proposed by Kira (1977, 1991). Another scheme of altitudinal and latitudinal vegetation zonation in East Asia has been proposed by Ohsawa (1990, 1993), in which particular attention is paid to the distribution limit of evergreen broad-leaved forest. The distribution of lucidophyllous forests, i.e. the evergreen broad-leaved forest dominated by Fagaceae and Lauraceae, in Asia and other areas has been reviewed by Tagawa (1995). However, in spite of these many studies related to the evergreen broad-leaved forests of Taiwan and Japan, no recent work has directly compared the evergreen broad-leaved forests in the two areas based on the same research method, and thus the similarities and differences in these forests have remained unclear.

From the viewpoint of biogeography, there is a remarkable discontinuity of flora and fauna in southwestern Japan, between Amami Ohshima Island and Yakushima Island, the boundary of which is known as Watase's line. Many plant species which are common to Taiwan and the Ryukyu Islands (the term used in this paper for the islands from Amami Ohshima to Yaeyama) are absent on Yakushima and on mainland Japan (Hatusima, 1975). From the viewpoint of community classification by the phytosociological method, evergreen broad-leaved forests of the Ryukyu Islands are classified into a different type (alliance) from those of mainland Japan, because of their species composition including many of the southern elements common to Taiwan and elements endemic to the Ryukyu Islands (Suzuki, 1979; Fujiwara, 1981). On the other hand, it has also been pointed out that the dominant species of the forest are more closely related to the species of mainland Japan than the species of the southern area (Kira, 1989). However, no study has directly compared the forests of Taiwan with those of the Ryukyu Islands at the forest stand level.

We have studied the stand structure of evergreen broad-leaved forests in the Ryukyu Islands; Amami Ohshima Island (Hara *et al.*, 1996b), Tokunoshima Island (unpublished data), Okinawa Island (Hara *et al.*, 1996a) and Iriomote Island (unpublished data), particularly in relation to microlandform. In this paper, we describe the stand structure of three evergreen broad-leaved forests in Taiwan, which were investigated using the same method as that for our earlier studies of the Ryukyu Islands. Because all of our plots were chosen in order to cover the slopes from ridges to the valley bottom, on almost the same spatial scale, we were able to compare how species were packed on the slopes in relation to the topographical conditions among these areas.

The nomenclature enployed basically follows that of the Wild Flowers of Japan, Woody Plants (Satake *et al.*, 1989) and Flora of Taiwan, first edition (Editorial Committee of the Flora of Taiwan, 1975–1979) and second edition (Editorial Committee of the Flora of Taiwan, Second Edition, 1994–1996).

Study Area

We selected three plots in Taiwan: two (Pinglin Plot and Lopeishan Plot) in the north and one (Nanjenshan Plot) in the south (Fig. 1). Pinglin Plot (470 m asl) was located at the foot of low mountains in northeastern Taiwan, where the terrain is deeply dissected, but is generally lower than 1000 m above sea level. Nanjenshan Plot (320 m asl) was also located on a hill (300–500 m asl) on the Hengchun Peninsula, the southern tip of

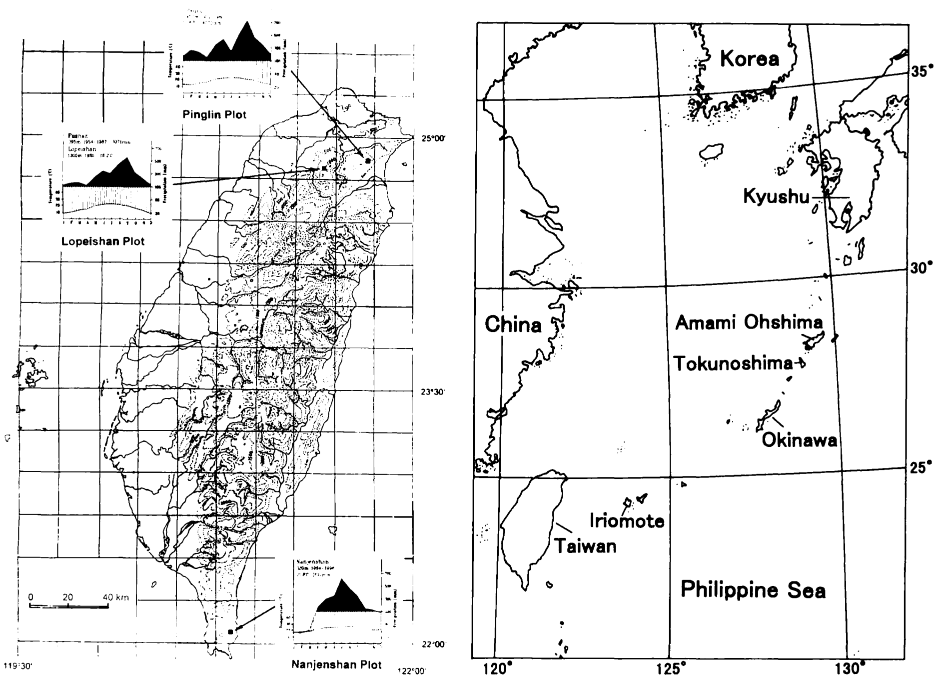

Fig. 1. Geographical locations of Taiwan and the Ryukyu Islands (right) and those of the study sites in Taiwan (left). Climatic diagrams of the nearest weather stations to each plot are also shown in the map of Taiwan.

Table 1. Location and climate of the study sites. Rainfall data are 1), based on Nanjenshan weather station (1994–1996); 2) based on Ssutu weather station (1971–1980), 450 m asl, 1.5 km east of the plot; 3), annual rainfall based on Fushan weather station, 395 m asl, 5.5 km southwest of the plot. Temperature data are estimated from the nearest weather stations. AM, annual mean temperature; Min MM, minimum monthly mean temperature; Max MM, maximum monthly mean temperature; WI, Warmth Index (Kira, 1948); AR, annual rainfall.

	Nanjenshan	Pinglin	Lopeishan
Latitude	22°03'N	24°52'N	24°50'N
Longitude	120°51'N	121°44'E	121°28'E
Altitude (m)	320	470	1150
Plot areas (m^2)	975	677	933
Slope direction	N52°W	S25°E	S82°W
AM (℃)	21.8	18.5	16.7
Min MM (℃)	18.8	11.9	8.2
Max MM (℃)	24.2	24.5	24.4
WI (℃·month)	218	175	135
AR (mm)	2691[1)]	4070[2)]	3071[3)]

Taiwan. On the other hand, Lopeishan Plot (1150 m asl) was located on a small ridge of higher mountains where the main ridges are about 1500–2100 m above sea level. The terrain of the area is rugged with steep slopes, but the plot was located on a gentle slope near the head of a small valley.

The annual mean temperature is highest at Nanjenshan and lowest at Lopeishan (Table 1). The monthly mean temperature in the coldest month does not fall below 18.0°at Nanjenshan but is near 8.0° at Lopeishan. According to the division of altitudinal vegetation zones in Taiwan by Su (1984), Nanjenshan Plot is located near the lower margin of the *Machilus-Castanopsis* Zone (WI=144–

216℃·month), Pinglin Plot in the middle part of the same zone, and Lopeishan Plot in the lower *Quercus* Zone (WI=108–144℃·month).

The annual rainfall exceeds 2500 mm at every study site, and reaches about 4000 mm at Pinglin. The seasonal distribution of precipitation differs among the study sites (Fig. 1). The northeastern part of Taiwan where Pinglin and Lopeishan are located has the highest rainfall and cloud frequency in Taiwan, and there is no dry period. The ridges and summits near Lopeishan are always wrapped with cloud even on rainless days (Hsieh, 1989a). On the other hand, at Hengchun Peninsula where Nanjenshan is located, rainfall is more seasonal; 70–80% of the total annual precipitation falls between May and September.

Strong monsoon winds blow continuously across Taiwan from the northeast in winter. Based on data from the Central Weather Bureau for 1981–1990, the mean number of days with strong winds (≧10 m/s) in the winter months from October to February reaches 8.5–14.3 at Hengchun (near the southern tip of Taiwan) and 3.4–5.1 at Chilung (near the northern tip). The maximum wind velocity in the winter months usually exceeds 10 m/s and sometimes reaches more than 20 m/s. Cold and wet monsoon winds over the East China Sea bring cold weather and much rainfall to the northeastern part of Taiwan in winter.

In addition, typhoons frequently sweep Taiwan in summer from July to September. These bring much rainfall and strong winds, which often cause flooding, landslides and uprooting of trees.

Methods

1. Field survey

At every study site, a plot 20 m in width was selected to cover the whole slope from the ridge to the valley bottom. The lengths of the plots were between 50 m and 60 m. Species name, trunk diameter at 1.3 m above the ground (DBH), tree height and location were recorded for all trees larger than 2.0 m high. When one plant had multiple trunks taller than 2.0 m, trunks of the second or lower size rank were recorded as a "sprouting trunks".

Changes in slope inclination were surveyed along five lines parallel to the longer side of the plot, and were drawn at intervals of 5 m. At break points of inclination along the lines, the slope angles from the adjacent points were measured with a hand level. Along each line, 14 to 25 points were measured and the distances among the adjacent points ranged mostly from 1.0 to 4.0 m, and rarely exceeded 5.0 m. Based on these data, topographical profiles and a contour map were drawn. The distribution of micro-landform elements such as small cliffs was also recorded in the field.

2. Landform classification

The whole area of the plot was divided into several micro-landform units, based on the form of the land surface and the distribution of micro-landform elements, in accordance with the micro-landform classification system of Tamura (1969, 1974, 1987). These microlandform units were further grouped into two landform units on the semimicro scale; the upper and lower slopes. A more detailed description of the micro-landform classification method is given in our previous paper (Hara *et al.*, 1996b). The upper slope is an intact slope whose land surface is relatively stable without active surface soil movement, whereas the land surface of the lower slope is more unstable with frequent landslides or small-scale slope failures and with temporal accumulation and flushing away of debris (Kikuchi and Miura, 1993; Hara *et al.*, 1996b).

3. Analysis of vegetation data

The occurrences of the various species on the upper vs. lower slopes were compared statistically using the binomial test. The expected numbers of each species on the upper or lower slopes were calculated as the total number of individuals of each species in the plot multiplied by the proportion of the area of the upper or lower slopes relative to the total area of the plot, and these were compared with the actual numbers of the plants occurring on the slopes. Species showing significantly higher density on the upper slope were termed Group A, those with higher density on the lower slope Group B;

those whose density did not differ significantly between the upper and lower slopes were termed Group C.

The dominant species were determined by the method of Ohsawa (1984) from the following equation:

$$d = 1/N\left\{\sum_{i\in T}(x_i - x)^2 + \sum_{j\in U} x_j^2\right\},$$

where x_i is the relative basal area (%) of the top species (T), x is the ideal percentage share of dominant species, determined from the number of the dominant species, and x_j is the percentage share of the remaining species (U). N is the total number of species. In a community dominated by a single species, the ideal percentage share of the dominant species is 100%. If there are two dominants, their ideal percentage share is 50%, and if there are three dominants, the ideal percentage share is 33.3%, and so on. The number of dominant species in the actual community is given as one, which shows the least deviation (d) in the above equation.

The similarity of vegetation between the upper and lower slopes was calculated for each plot. Three indices calculated were CC, the index of floristic similarity (Sørensen, 1948); PS(N), the percentage similarity (Whittaker, 1952) calculated from the relative number of trunks of each species, and PS (BA), the percentage similarity calculated from the relative value of the basal area.

Two indices of species diversity, H' and J' (Pielou, 1969) were calculated as follows for each plot:

$$H' = -\sum_{i=1}^{S} p_i \operatorname{Log}_2 p_i$$

$$J' = H'/H\max' = H'/\operatorname{Log}_2 S$$

where p_i is the relative quantity of species i, and S is the total number of species. The relative value of basal area (RBA) was used as the relative quantity of each species in this study.

Results

1. Nanjenshan plot

1.1. Micro-landform.

The topographical profile of Nanjenshan

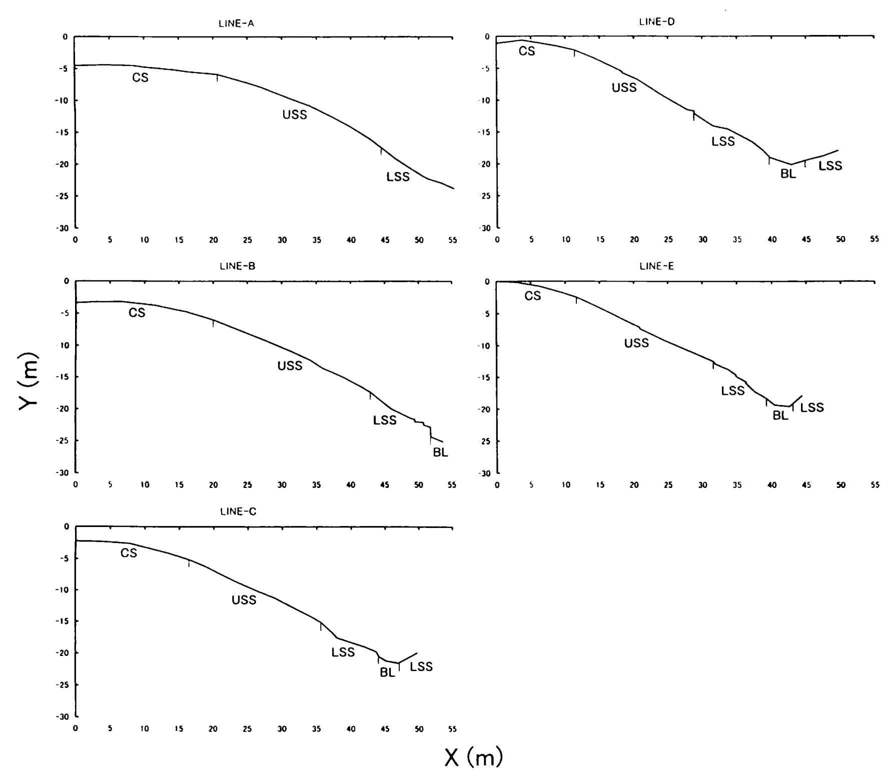

Fig. 2. Geomorphic profiles with divisions of landform units in Nanjenshan Plot. For the horizontal location of each profile, see Fig. 3a. For abbreviations of landform units, see text and Fig. 3c.

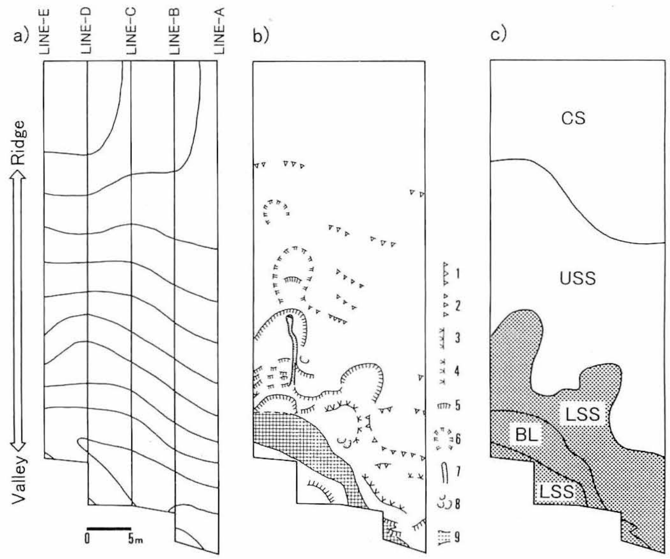

Fig. 3. Contour map (a), geomorphological explanations (b) and arrangement of landform units (c) in Nanjenshan Plot. Contours in (a) are drawn at 2-m intervals. Symbols of micro-landfrom elements in (b) are, 1, sharp convex break of slope; 2, gradual convex break of slope; 3, sharp concave break of slope; 4, gradual concave break of slope; 5, small cliff; 6, shallow depression; 7, channel; 8, bare rocks; 9, valley floor. Abbreviations of micro-landform units in (c) are, CS, crest slope; USS, upper side slope; LSS, lower side slope; BL, bottomland. In (c), the open area shows the upper slope and the shaded area the lower slope.

Plot was characterized by a broad ridge in the uppermost part and a long, gentle downward slope, as shown clearly in Lines A, B and C (Fig. 2). The steepest parts, whose inclinations exceeded 35°, occurred only in the lowest part of the lines near the valley bottom.

Few cliffs and channels were found in the upper half of the plot, except for a small cliff and shallow depressions between the Lines D and E (Fig. 3b). The intact slope of the upper side was fringed with small cliffs at its lowest margin.

Based on the topographical profile and distribution of microlandform elements, the land surface in the plot was divided into four micro-landform units (Fig. 3c). Among the six micro-landform units recognized by Tamura (1987), the head hollow and the foot slope were absent here. Among the four micro-landform units recognized in the plot, the crest slope (CS) and the upper side slope (USS) were grouped into the upper slope, and the lower side slope (LSS) and the bottomland (BL) were grouped into the lower slope.

1.2. Floristic composition.

Sixty-eight species occurred in the plot, as individuals taller than 2.0 m, except for lianas and epiphytes (Table 2). They comprised 29 families and 49 genera. The largest number of species was represented by Lauraceae (9 species, 6 genera), followed by Rubiaceae (7 species, 5 genera) and Fagaceae (5 species, 3 genera). Thirteen genera had two or more species. Two canopy individuals of a tree fern, *Cyathea lepifera* (J. Sm. ex Hook.) Copel., were included.

At species level, the basal area was shared with many species and there was no distinct dominant species. No species shared more than 10% of the total basal area. On the other hand, at family level, Fagaceae shared the largest portion (31.7%) of the total basal area, followed by Melastomataceae (10.0%) and Lauraceae (9.0%).

In terms of the number of trunks, the most abundant species was *Ilex cochinchinensis* (Lour.) Loes. (79 trunks), followed by *Antidesma hiiranense* Hayata (59 trunks), *Psychotria rubra* (Lour.) Poir. (57 trunks) and *Illicium arborescens* Hayata (42 trunks). In addition,

Table 2. Frequency distributions of trunks in DBH class in Nanjenshan Plot. The relative basal area (RBA) of each species is also shown on the right hand side of the table. *, dominant species determined by the method of Ohsawa (1984) based on RBA for each species.

Species	DBH Class (cm)										Total	RBA (%)
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50		
* *Ilex cochinchinensis*	63	13	1		1	1					79	3.96
Antidesma hiiranense	59										59	0.54
Psychotria rubra	56	1									57	0.67
* *Illicium arborescens*	19	16	5	2							42	4.41
* *Castanopsis carlesii*	19	5		2	4	1	1				32	8.32
Litsea acutivena	26	5									31	0.38
Neolitsea hiiranensis	24	5									29	0.65
* *Daphniphyllum teijsmannii*	19	4	4		2						29	3.43
* *Diospyros eriantha*	18	8	3								29	1.65
* *Ilex liukiuensis*	20	3	1				1				25	2.31
Prunus phaeosticta	19	3	3								25	1.22
Helicia formosana	20	3									23	0.65
Tricalysia dubia	11	7	1								19	0.99
* *Astronia formosana*	2	4	5	2	5				1		19	9.99
* *Quercus longinux*	12	1	2	1	1					1	18	5.78
* *Syzygium euphlebium*	6	5	4			1	1		1		18	7.66
* *Schefflera octophylla*	11	2	4			1					18	2.33
Microtropis japonica	11	4	1								16	0.75
Syzygium kusukusense	13		1			1					15	1.52
* *Beilshmiedia tsangii*	7	3	3	1							14	1.78
* *Beilshmiedia erythrophloia*	6	4	3		1						14	2.04
Wendlandia formosana	9	3	1								13	0.65
* *Castanopsis fabri*	9	1	2						1		13	3.69
* *Quercus pachyloma*	7	1	1	1	1				1		12	4.85
Engelhardtia roxburghiana	10	1									11	0.22
Osmanthus marginatus	10		1								11	0.43
Ilex lonicerifolia var. *matsudai*	7	2	1								10	0.67
Garcinia multiflora	7	1		1							9	0.78
Aucuba chinensis	9										9	0.07
Machilus thunbergii	5	1	1	1							8	0.82
* *Adinandra formosana*	2	4				1	1				8	3.73
Glochidion zeylanicum	3	2		1							6	0.90
Callicarpa remotiserrulata	6										6	0.03
Tarenna gracilipes	6										6	0.03
Cryptocarya chinensis	1	3		1							5	0.93
Symplocos theophrastiifolia	2	1	1	1							5	1.02
Turpinia ternata	4										4	0.04
Glochidion lanceolatum	3			1							4	0.46
* *Michelia compressa*	2				1	1					4	2.03
Euonymus tashiroi	4										4	0.02
Ternstroemia gymnanthera	2	1									3	0.08
Machilus obovatifolia	2		1								3	0.24
Magnolia kachirachirai	3										3	0.06
* *Lithocarpus amygdalifolius*								1	1	1	3	9.09
Ficus bengutensis	2		1								3	0.21
Eurya chinensis	3										3	0.03
Bridelia balansae	2	1									3	0.12
Podocarpus fasciculus	3										3	0.08

Table 2. (continued).

Species	DBH Class (cm)										Total	RBA (%)
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50		
Ardisia quinquegona	3										3	0.02
Sloanea formosana	2					1					3	1.26
Cyathea lepifera				1	1						2	1.43
* *Machilus kusanoi*					1	1					2	2.18
* *Elaeocarpus sylvestris*	1							1			2	2.24
Melastoma candidum	2										2	0.03
Glycosmis citrifolia	2										2	0.02
Eurya nitida var. *nanjenshanensis*	2										2	0.01
Ardisia cornudentata	2										2	0.01
Decaspermum gracilentum	2										2	0.00
Callicarpa remotiflora	2										2	0.00
Ficus ruficaulis	1										1	0.04
Cinnamomum brevipedunulatum	1										1	0.01
Symplocos shilnensis	1										1	0.01
Syzygium densinervium var. *insulare*	1										1	0.01
Ficus variegata			1								1	0.33
Lasianthus chinensis	1										1	0.00
Lasianthus cyanocarpus	1										1	0.00
Lasianthus obliquinervis	1										1	0.00
Podocarpus nagi	1										1	0.02
Total	590	118	52	16	18	9	4	2	5	2	816	100.0

two palms, *Calamus formosanus* Beccari and *Daemonorops margaritae* (Hance) Beccari, were relatively common on the forest floor, although they were not included in the data.

1.3. Species distribution pattern.

Among 25 species which had more than eight individuals in the plot, 13 species (Group A) showed densities significantly higher on the upper slope at the 1.0% level, and two (Group B) on the lower slope (Table 3). No species with total number of eight or fewer individuals in the plot showed a density that differed significantly between the two slopes.

Most of the Group A species showed a scattered distribution of individuals on both the crest slope (CS) and the upper side slope (USS, Fig. 4). The distribution of their individuals within the upper slope appeared to be random or only weakly contagious, and was not biased to either CS or USS. Only *Syzygium euphlebium* (Hayata) Mori appeared to show a somewhat contagious distribution, and only *Engelhardtia roxburghiana* Wall. showed a distribution biased to the crest slope.

Of the two Group B species, *Astronia formosana* Kanehira showed a distribution strongly aggregated on the lower slope, although individuals of *Schefflera octophylla* (Lour.) Harms occurred throughout the plot, not only on the lower slope but also in the upper slope (Fig. 4). In addition, although statistically insignificant, individuals of some Group C species appear to be aggregated to the lower slope: these included *Wendlandia formosana* Cowan, *Syzygium kusukusense* (Hayata) Mori, *Turpinia ternata* Nakai, *Cyathea lepifera, Machilus kusanoi* Hayata and *Ficus* spp.

Many of the Group A species had successor trees in the understorey, as indicated by the abundant representation of trunks in the smallest size class (Table 2). On the other hand, one of the Group B species, *Astronia ferruginera,* showed a DBH distribution in which fewer trunks were seen only in the smallest size class as compared with the

Table 3. Binomial tests for the distribution of trees between the upper (US) and lower (LS) slopes in Nanjenshan Plot. Only species with more than eight individuals are shown. For each species groups (Group A, B and C) and test procedures, see text. **, significant difference at the 0.5% level; *, significant difference at the 1.0% level. Note that N in the table is not the number of trunks but the number of individuals for which sprouting trunks were neglected.

Species	Relative number of trees		N	Species group
	US	LS		
Ilex cochinchinensis	93.9	6.1	66	A**
Antidesma hiiranense	91.5	8.5	59	A**
Psychotria rubra	88.7	11.3	53	A**
Illicium arborescens	100.0	0.0	42	A**
Litsea acutivena	87.1	12.9	31	A*
Daphniphyllum teijsmannii	100.0	0.0	28	A**
Ilex liukiuensis	72.0	28.0	25	C
Prunus phaeosticta	82.6	17.4	23	C
Astronia formosana	27.8	72.2	18	B**
Helicia formosana	61.1	38.9	18	C
Schefflera octophylla	50.0	50.0	18	B*
Syzygium euphlebium	100.0	0.0	17	A**
Tricalysia dubia	94.1	5.9	17	A*
Quercus longinux	87.5	12.5	16	C
Beilshmiedia tsangii	93.8	6.3	16	A*
Neolitsea hiiranensis	100.0	0.0	15	A**
Beilshmiedia erythrophloia	92.9	7.1	14	C
Microtropis japonica	92.9	7.1	14	C
Wendlandia formosana	54.4	45.5	11	C
Castanopsis carlesii	100.0	0.0	10	A**
Quercus pachyloma	77.8	22.2	9	C
Osmanthus marginatus	77.8	22.2	9	C
Syzygium kusukusense	44.4	55.6	9	C
Engelhardtia roxburghiana	100.0	0.0	9	A*
Garcinia multiflora	100.0	0.0	9	A*
Area (%)	71.3	28.7	—	—

larger classes.

1.4. Vegetation on the upper and lower slopes.

Among the 68 species in the plot, 29 occurred on both the upper and lower slopes, and the index of floristic similarity (CC) was relatively high (59.2%). However, there were considerable differences in the quantities of the various species between the two slopes, and as a consequence, the similarity indices based on the relative abundance of each species, PS(N) and PS(BA), were much lower: 22.4% and 11.4% respectively.

In terms of basal area and the number of trunks, there were no distinct dominant species on the upper slope. As shown in Table 4, species which shared more than 5% of the total basal area on the upper slope were *Lithocarpus amygdalifolius* (Skan ex Forbes et Hemsl.) Hayata (11.0%), *Castanopsis carlesii* (Hemsl.) Hayata (10.0%), *Syzygium euphlebium* (9.2%), *Quercus longinux* Hayata (6.6%) and *Illicium arborescens* (5.3%). In terms of the number of trunks also, no species shared more than 10.1% (the highest value shown by *Ilex cochinchinensis*) of the total number.

On the other hand, there were several species with a larger share of the total basal area on the lower slope (Table 4), such as *Astronia formosana* (36.7%), *Quercus pachyloma* O. Seem. (20.3%) and *Machilus kusanoi* (12.0%). Although *Quercus pachyloma* was one of the dominant species of the lower slope, many individuals were scattered on the upper slope (Fig. 4). Two individuals of the tree fern *Cyathea lepifera* taller than 8 m were also

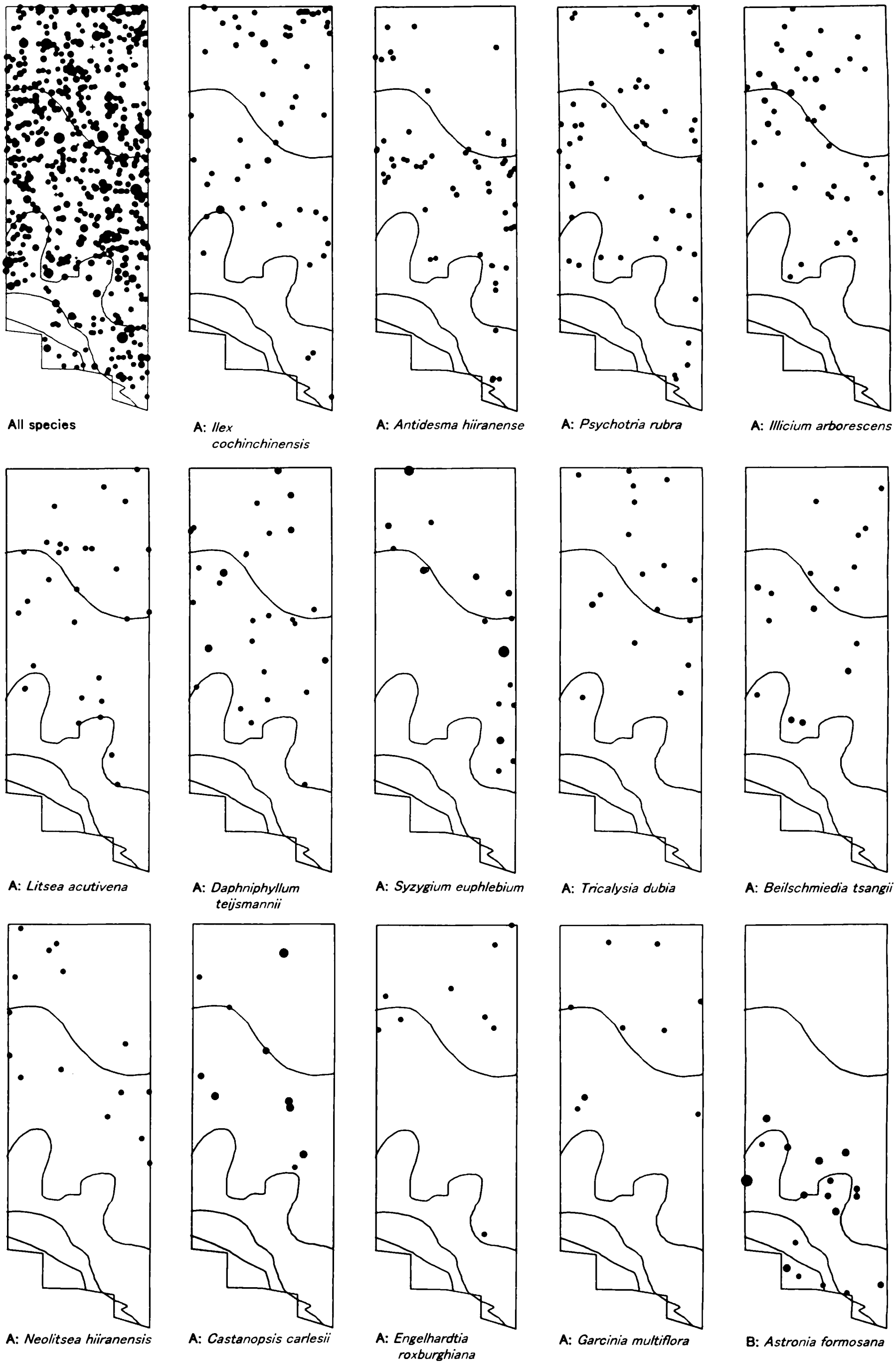

Fig. 4. Examples of tree distributions in Nanjenshan Plot. Abbreviations of species groups; A, B and C, are also presented just before each species name. For distinction of species groups (Group A, B and C), see text and Table 3. Boundaries among micro-landform units are also shown. Living and dead trunks are represented as circles and crosses, respectively, and their sizes correspond to the trunk diameters.

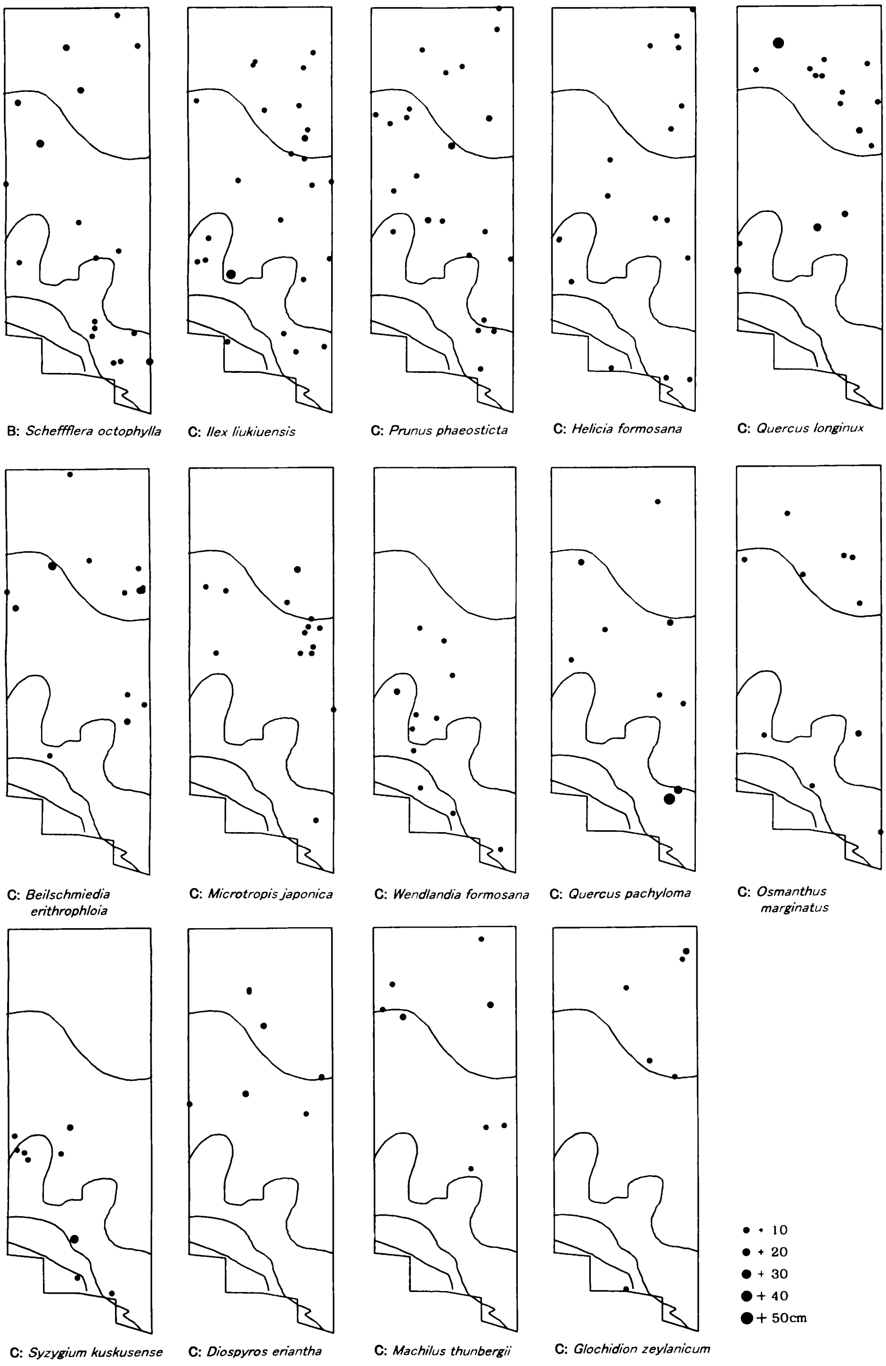

Fig. 4. (continued).

seen there.

2. Pinglin plot

2.1. Micro-landform.

The topographical profile of Pinglin Plot was characterized by a narrow ridge in the uppermost part, and a long, steep downward slope (Fig. 5, Fig. 6a). The gentle part of the ridge was only about 5 m wide and a steep slope exceeding 35° in inclination continued

Table 4. Dominant species on the upper and lower solpes of Nanjenshan Plot. Dominant species in each slope was determined by the method of Ohsawa (1984) based on the relative basal areas (RBA) of each species.

Dominant species	RBA (%)	No. of trunks
Upper slope		
Lithocarpus amygdalifolius	11.0	3
Castanopsis carlesii	10.0	32
Syzygium euphlebium	9.2	18
Quercus longinux	6.6	16
Illicium arborescens	5.3	42
Castanopsis fabri	4.5	13
Adinandra formosana	4.5	8
Ilex cochinchinensis	4.4	71
Daphniphyllum teijsmannii	4.2	29
Astronia formosana	4.1	6
Ilex liukiuensis	2.8	18
Elaecocarpus sylvestris	2.7	2
Beilshmiedia tsangii	2.5	15
Michelia compressa	2.5	4
Beilshmiedia erythrophloia	2.4	13
Schefflera octophylla	2.3	9
Diospyros eriantha	2.0	29
Lower slope		
Astronia formosana	36.7	13
Quercus pachyloma	20.3	3
Machilus kusanoi	12.0	2
Cyathea lepifera	7.9	2

to the valley bottom. The inclination of the steepest part in the profile of Lines A–E reached 51°–66°. There was a short but very steep segment occurring at the lowest part of the slope along the valley bottom.

The dense distribution of small cliffs and debris (Fig. 6b), which covered more than half of the plot area, indicated that small-scale landslides had occurred frequently on the slope. The rugged form of the profile, which was particularly clear in Lines B and D (Fig. 5), was caused by these landslides. The only remaining intact land surface was located in the uppermost part of the plot area.

Based on the above topographical profile and the distribution of micro-landform elements, the land surface in the plot was divided into four micro-landform units (Fig. 6c). Small cliffs (Fig. 6b) indicating the occurrence of small-scale landslides were scattered not only on the lower side slope (LSS) but also on a part of the upper side slope (USS). LSS was further subdivided into the upper part (LSS1) and the lower, steepest part (LSS 2). The head hollow and foot slope among the micro-landform units recognized by Tamura (1987) were also absent in this plot. As in Nanjenshan Plot, CS and USS were grouped into the upper slope, and LSS (LSS1 and LSS2) and BL into the lower slope.

2.2. Floristic composition.

Fifty-two species occurred in the plot as individuals taller than 2.0 m, except for lianas and epiphytes (Table 5). They comprised 25 families and 37 genera. The families with four species, which had the largest representation in the plot, were Aquifoliaceae (*Ilex*), Euphorbiaceae (*Antidesma*, *Glochidion* and *Mallotus*), Lauraceae (*Cryptocarya*, *Machilus* and *Neolitsea*), Rubiaceae (*Lasianthus*, *Psychotria*, *Randia* and *Wendlandia*) and Theaceae (*Adinandra*, *Eurya*, *Gordonia* and *Pyrenaria*). Nine genera had two or more species. One tree fern, *Cyathea podophylla* (Hook.) Copel., was included.

At species level, the relative basal area was largest for *Castanopsis carlesii* (Hemsl.) Hayata var. *sessilis* (Nakai) (20.6%), followed by *Cryptocarya chinensis* (Hance) Hemsl. (10.4%), *Schefflera octophylla* (9.8%) and *Machilus kusanoi* (8.3%). At family level, Fagaceae and Lauraceae accounted for the largest portion, 29.4% and 21.7% of the total basal area respectively. The most abundant species in terms of trunk number were *Ardisia quiquegona* Blume (42 trunks), *Myrsine seguinii* Lév. (40 trunks) and *Blastus cochinchinensis* Lour. (38 trunks).

2.3. Species distribution pattern.

Binomial tests revealed that the distributions of 11 species (Group A species) were significantly biased to the upper slope at the 1.0% level (Table 6). For a few of the Group A species such as *Castanopsis carlesii* var. *sessilis*, the distribution appeared to be restricted to the crest slope (CS), but the remaining species of Group A did not show any clear differences in density between the two micro-landform units (the crest slope and the upper side slope; USS) within the upper slope (Fig. 7).

On the other hand, the Group B species comprised only two species, *Blastus cochinchinensis* and *Turpinia formosana* Nakai.

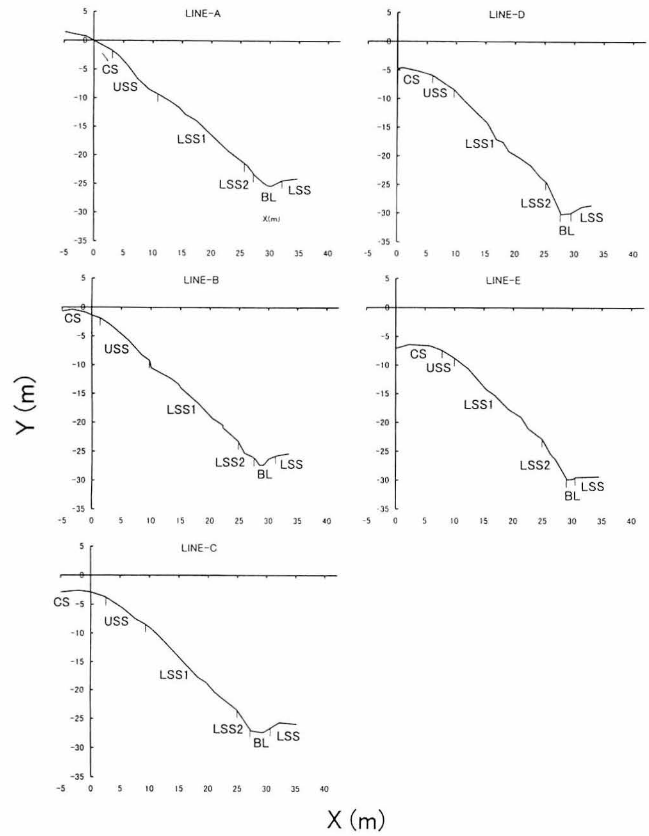

Fig. 5. Geomorphic profiles with divisions of landform units in Pinglin Plot. For horizontal location of each profile, see Fig. 6a. For abbreviations of landform units, see text and Fig. 6c.

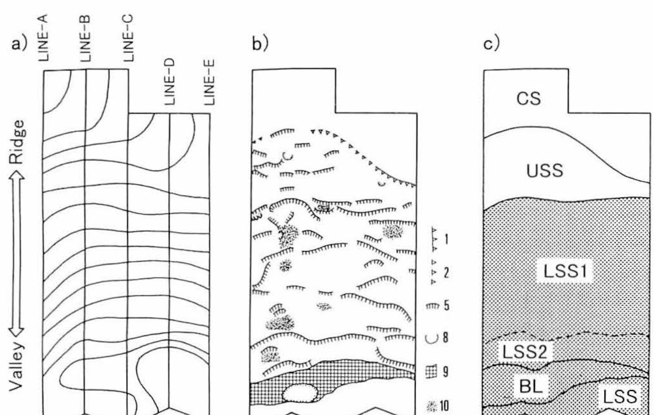

Fig. 6. Contour map (a), geomorphological explanations (b) and arrangement of landform units (c) in Pinglin Plot. Contours in (a) are drawn at 2-m intervals. Symbols of micro-landfrom elements in (b) are as follows: 1, 2, 5, 8, 9, the same as in Fig. 3b; 10, debris. For abbreviations of landform units in (c), see Fig. 3 and text. In (c), the open area shows the upper slope and the shaded area the lower slope.

Table 5. Frequency distributions of trunks in DBH class in Pinglin Plot. The relative basal area (RBA) of each species is also presented on the right-hand side of the table. *, dominant species determined by the method of Ohsawa (1984) based on RBA for each species.

Species	DBH Class (cm)												Total	RBA (%)
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60		
Ardisia quinquegona	42												42	0.35
Myrsine seguinii	34	5	1										40	1.32
Blastus cochinchinensis	38												38	0.33
* *Castanopsis carlesii* var. *sessilis*	12		1			3		2				1	19	20.63
* *Schefflera octophylla*	2	4	4	3	1	1	1						16	9.77
Helicia formosana	14	2											16	0.56
Turpinia formosana	13	2											15	0.25
* *Engelhardtia roxburghiana*	10	2	1	1					1				15	6.00
Randia cochinchinensis	11	2											13	0.40
* *Quercus longinux*	6	3	1	1	1		1						13	4.37
Meliosma squamulata	5	6	1										12	1.50
* *Ardisia sieboldii*		7	4	1									12	2.65
Ilex pubescense	12												12	0.11
Diospyros morrisiana	7	1	1		1								10	2.11
Adinandra formosana	5	1	1	1									8	1.44
Psychotria rubra	8												8	0.07
Eurya loquaiana	7	1											8	0.23
Antidesma japonicum var. *densiflorum*	7												7	0.12
Machilus thunbergii	4	2		1									7	0.97
Ilex ficoidea	5		1										6	0.44
Diospyros eriantha	4	1	1										6	0.49
Ilex liukiuensis	4	1											5	0.17
* *Michelia compressa*	1	2		1			1						5	3.32
Meliosma rigida	5												5	0.19
* *Quercus gilva*	1		1		2	1							5	4.43
* *Machilus kusanoi*	1				2	1		1					5	8.30
Neolitsea sp.	2	1	1		1								5	1.94
Syzygium buxifolium	3	1											4	0.21
Daphniphyllum teijsmannii	3	1											4	0.14
Wendlandia formosana	2	2											4	0.41
* *Pyrenaria shinkoensis*		1	2			1							4	2.59
* *Cryptocarya chinensis*	2								1	1			4	10.44
Elaeocarpus japonicus		2				1							3	1.84
Ficus nervosa	1	1	1										3	0.39
Symplocos glauca	3												3	0.01
Sauraia tristyla		2											2	0.51
* *Glochidion acuminatum*				1			1						2	2.78
Ilex formosana			1	1									2	0.92
Sloanea formosana		1		1									2	1.32
Symplocos theophrastiifolia	2												2	0.00
Trochodendron aralioides		1											1	0.21
Mallotus paniculatus				1									1	0.72
Cyathea podophlla				1									1	0.59
Lagerstroemia subcostata				1									1	0.56
Styrax suberifolia						1							1	1.81
Symplocos caudata		1											1	0.24
Gordonia axillaris	1												1	0.01

Table 5. (continued).

Species	DBH Class (cm)												Total	RBA (%)
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55–60		
Ficus bengutensis					1								1	1.30
Glochidion rubrum	1												1	0.00
Elaeocarpus sylvestris	1												1	0.00
Lasiantus sp.	1												1	0.00
Unknown			1										1	0.54
Total	280	56	24	15	9	9	4	3	2	1	0	1	404	100.0

Table 6. Binomial tests for the distribution of trees between the upper (US) and lower (LS) slopes in Pinglin Plot. Species with less than three individuals are not presented. For each species groups (Group, A, B and C) and test procedures, see text. **, significant difference at the level of 0.5% level; *, significant difference at the 1.0% level. Note that N in the table is not the number of trunks but the number of individuals for which sproting trunks were neglected.

Species	Relative number of trees		N	Species group
	US	LS		
Myrsine seguinii	89.2	10.8	37	A**
Blastus cochinchinensis	2.9	97.1	35	B**
Ardisia quinquegona	79.3	20.7	29	A**
Engelhardtia roxburghiana	92.3	7.7	13	A**
Randia cochinchinehsis	76.9	23.1	13	A**
Schefflera octophylla	41.7	58.3	12	C
Turpinia formosana	0.0	100.0	11	B**
Castanopsis carlesii var. *sessilis*	81.8	18.2	11	A**
Ilex pubescense	60.0	40.0	10	C
Diospyros morrisiana	100.0	0.0	10	A**
Helicia formosana	10.0	90.0	10	C
Meliosma squamulata	33.3	66.7	9	C
Ardisia sieboldii	25.0	75.0	8	C
Psychotria rubra	62.5	37.5	8	C
Antidesma japonicum var. *densiflorum*	85.7	14.3	7	A**
Machilus thunbergii	100.0	0.0	6	A**
Ilex ficoidea	83.3	16.7	6	A*
Eurya loquaiana	33.3	66.7	6	C
Ilex liukiuensis	80.0	20.0	5	A*
Adinandra formosana	60.0	40.0	5	C
Micheia compressa	40.0	60.0	5	C
Daphniphyllum teijsmannii	75.0	25.0	4	C
Wendlandia formosana	50.0	50.0	4	C
Pyrenaria shinkoensis	75.0	25.0	4	C
Cryptocarya chinensis	50.0	50.0	4	C
Machilus kusanoi	0.0	100.0	4	C
Meliosma rigida	33.3	66.7	3	C
Ficus nervosa	0.0	100.0	3	C
Quercus gilva	100.0	0.0	3	A*
Symplocos glauca	0.0	100.0	3	C
Diospyros eriantha	33.3	66.7	3	C
Area (%)	30.4	69.6	—	—

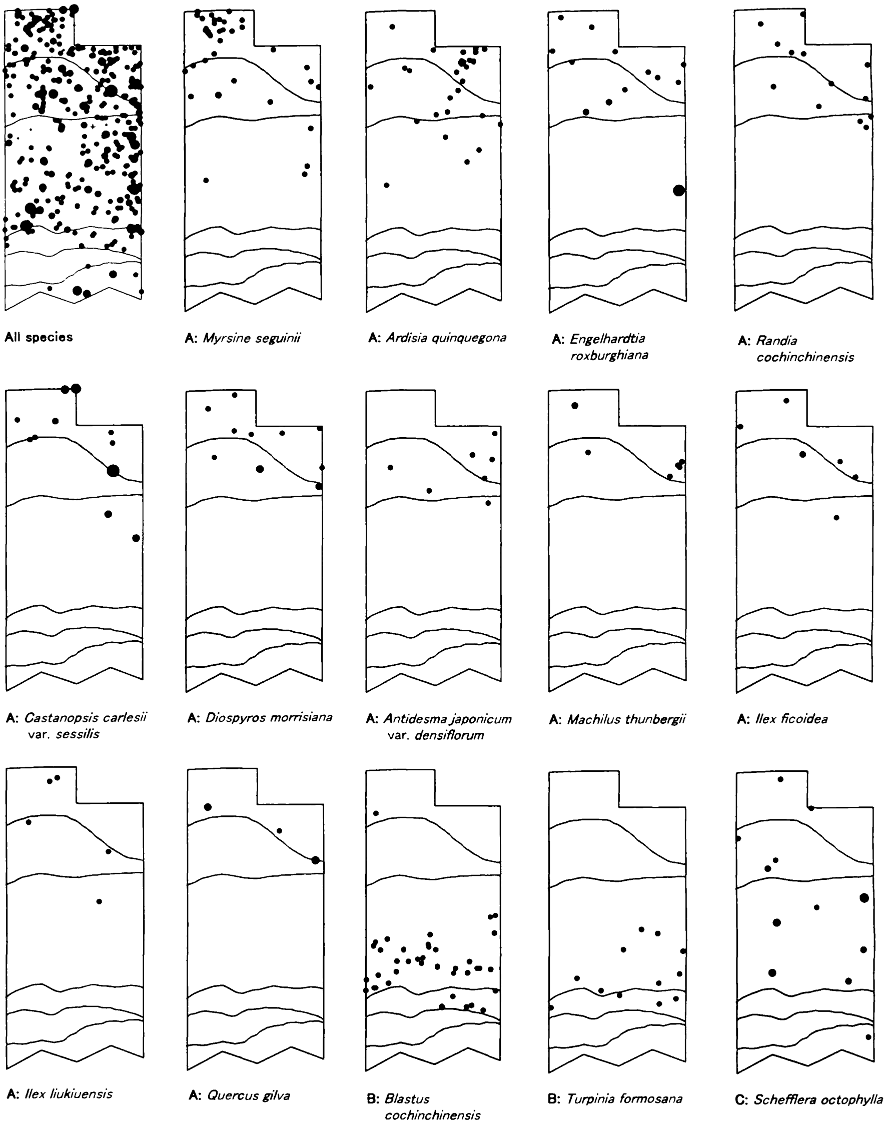

Fig. 7. Examples of tree distributions in Pinglin Plot. Abbreviations of species groups; A, B and C, are also presented just before the species name. For the distinction of species groups (Group A, B and C), see text and Table 3. Boundaries among micro-landform units are also shown. Living and dead trunks are represented as circles and crosses, respectively, and their sizes correspond to the trunk diameters.

However, two of the three Group C species, *Helicia formosana* Hemsl. and *Machilus kusanoi*, also showed a distribution that was highly biased to the lower slope, although this was no statistically significant. On the steepest part (LSS2) of the lower slope, there were almost no trees, but individuals of *Blastus cochinchinensis* and *Turpinia formosana* were found (Fig. 7).

Also in this plot, many of the Group A species showed the most abundant representation of trunks in the smallest size class (Table 5), suggesting that these species had many successor trees in the understorey. On the other hand, the Group B species, *Blastus cochinchinensis* and *Turpinia formosana,* had many trunks in the smallest size class but no or few trunks in the larger size class, indicating that the two species are shrubs which cannot reach a larger size.

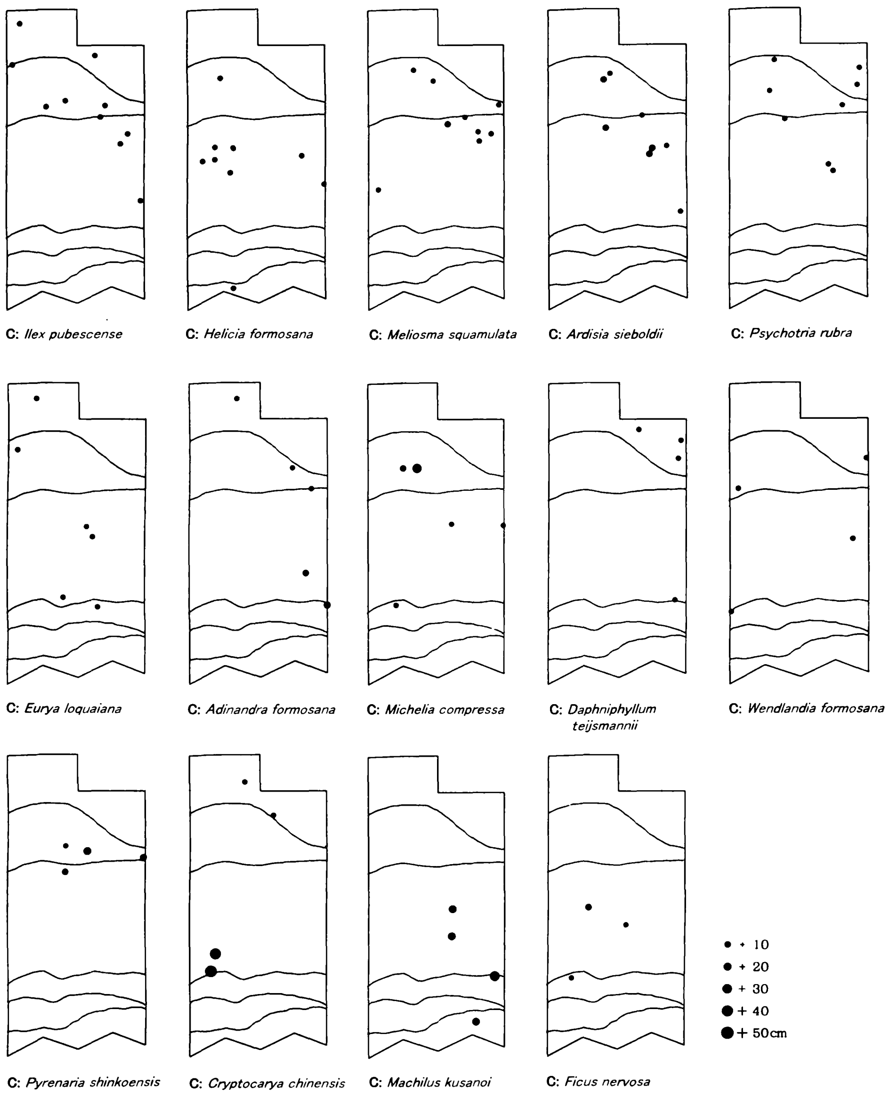

Fig. 7. (continued).

2.4. Vegetation on the upper and lower slopes.

The floristic similarity of vegetation between the upper and lower slopes was relatively high (CC=62.3%). In contrast, there were large differences in the quantities of each species, as indicated by lower values of PS(N) and PS(BA) between the slopes, 34.6% and 21.3% respectively.

The most dominant species on the upper slope, in terms of basal area, was *Castanopsis carlesii* var. *sessilis*, which occupied 39.8% of the total basal area, followed by *Quercus gilva* Blume (10.6%) and *Michelia compressa* (Maxim.) Sargent (7.0%), as shown in Table 7. Among the total of 203 trunks, *Myrsine seguinii* (n=36) and *Ardisia quiquegona* (n=28) were the most abundant.

On the other hand, on the lower slope, no species had a larger share comparble to that of *Castanopsis carlesii* var. *sessilis* on the upper slope, but three species (*Cryptocarya chinensis*, *Schefflera octophylla* and *Machilus kusanoi*) had the largest share, 17.4%, 15.0% and 13.9%, of the total basal area respectively (Table 7). In terms of the number of

Table 7. Dominant species on the upper and lower slopes of Pinglin Plot. Dominant species on each slope were determined by the method of Ohsawa (1984) based on the relative basal area (RBA) for each species.

Dominant species	RBA (%)	No. of trunks
Upper slope		
Castanopsis carlesii var. *sessilis*	39.8	15
Quercus gilva	10.6	5
Michelia compressa	7.0	2
Pyrenaria shinkoensis	5.4	3
Diospyros morrisiana	5.1	10
Elaeocarpus japonicus	4.4	3
Styrax suberifolia	4.3	1
Lower slope		
Cryptocarya chinensis	17.4	2
Schefflera octopylla	15.0	11
Machilus kusanoi	13.9	5
Engelhardtia roxburghiana	7.9	2
Quercus longinux	7.5	12
Castanopsis carlesii var. *sessilis*	6.3	4
Glochidion acuminatum	4.8	2
Neolitsea sp.	3.3	5

trunks, *Blastus cochinchinensis* (38 trunks), *Turpinia formosana* (15 trunks) and *Helicia formosana* (15 trunks) were the most abundant.

3. Lopeishan plot

3.1. Micro-landform.

The topography of Lopeishan Plot was characterized by slope gentleness (Fig. 8, Fig. 9a). The mean inclination of the slope from the ridge to the valley bottom was lowest among the three study plots. In the lines A, C and D, the gentle slope of the upper part gradually increased in inclination and extended into the valley bottom without any steeper segment intervening.

A shallow but long gully extended into the upper part of the slope from the valley bottom (Fig. 9b). The distribution of fresh debris and the rugged profile near the gully in Lines B, C and D indicated that erosion had occurred there. Although only a few small cliffs and bare rocks were seen in the plot, their distribution were concentrated in the middle part of the slope. Several small cliffs had been created by tree uprooting.

Because of the gentleness of the slope, it was difficult to distinguish the micro-scale landform units in this plot, and therefore only semi-micro scale landform units (upper and lower slopes) were distinguished. Based on the topographical profile and distribution of micro-landform elements, the plot area was divided into two parts, the upper and lower slopes (Fig. 9c). The land surface of the upper slope was relatively intact, although some mounds created by tree uprooting were found. On the other hand, the land surface of the lower slope appeared to be more disturbed.

3.2. Floristic composition.

Fifty-three species occurred in the plot, as individuals taller than 2.0 m, except for lianas and epiphytes (Table 8). They comprised 25 families and 40 genera. The largest number of species was represented by Theaceae (6 species, 6 genera) and Aquifoliaceae (6 species, one genus; *Ilex*), followed by Lauraceae (5 species, 4 genera) and Symplocaceae (4 species, one genus; *Symplocos*).

Dominant species in terms of basal area were *Quercus longinux* (26.3%), *Machilus thunbergii* Sieb. et Zucc. (18.5%), *Diospyros morrisiana* Hance (9.5%), *Quercus sessilifolia* (Blume) Schott. (8.3%) and *Illicium arborescens* (6.7%). At family level, Fagaceae and Lauraceae accounted for the largest portion, 36.1% and 23.1% of the total basal area, respectively. The most abundant species in terms of trunk number were *Illicium arborescens* (113 trunks) and *Quercus longinux* (103 trunks).

3.3. Species distribution pattern.

Twelve species (Group A) showed densities significantly higher on the upper slope and two (Group B) on the lower slope by binomial tests (Table 9). However, the distribution of many of Group A species was not strictly restricted to the upper slope, and a considerable number of trees were seen also on the lower slope. Five dominant species in terms of basal area (*Quercus longinux, Q. sessilifolia, Machilus thunbergii, Diospyros morrisiana* and *Illicium arborescens*) all showed a scattered distribution, covering both slopes widely with a high degree of mutual overlapping (Fig. 10). In addition to the two Group B

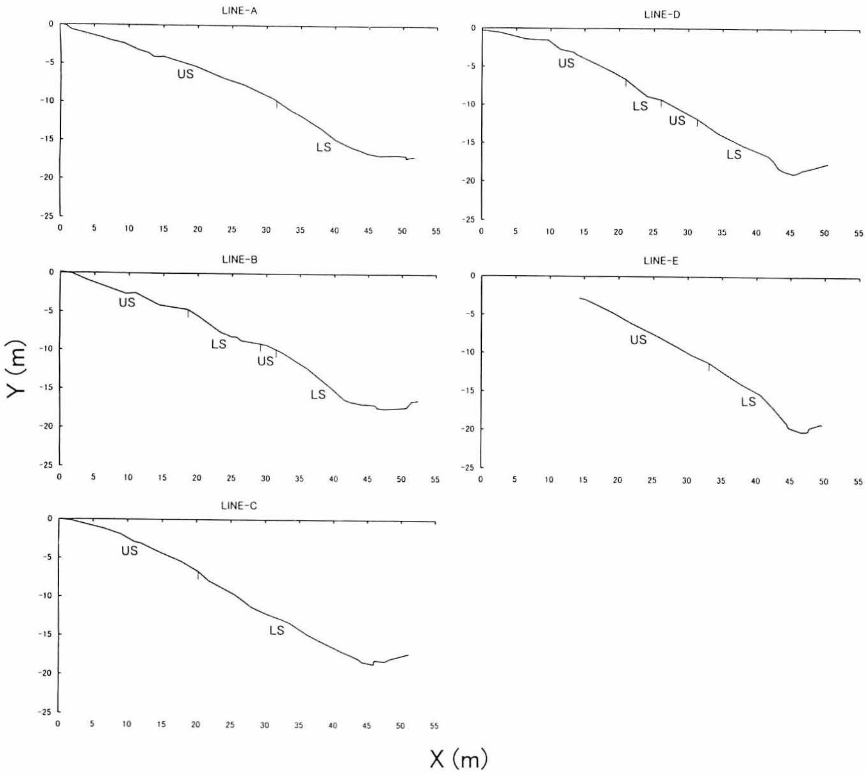

Fig. 8. Geomorphic profiles with divisions of landform units in Lopeishan Plot. For horizontal location of each profile, see Fig. 9a. For abbreviations of landform units, see text and Fig. 9c.

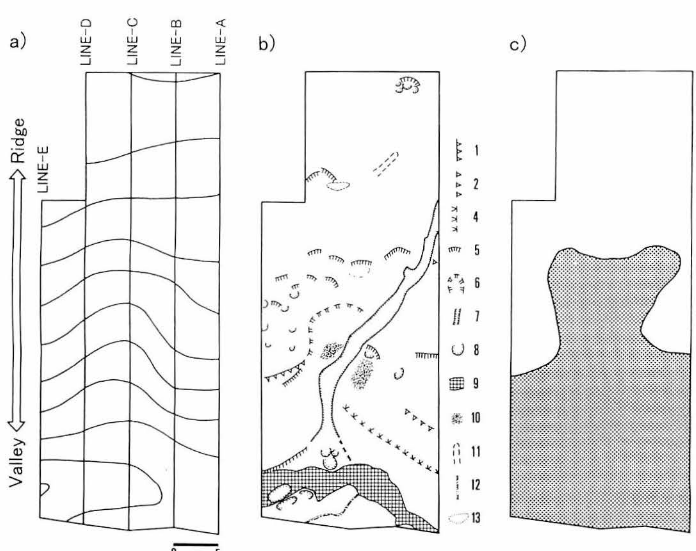

Fig. 9. Contour map (a), geomorphological explanations (b) and arrangement of landform units (c) in Lopeishan Plot. Contours in (a) are drawn at 2-m intervals. Symbols of micro-landform elements in (b) are as follows: 1–9, same as in Fig. 3b; 10, same as in Fig. 6; 11, shallow channel; 12, difference in level; 13, soil mound created by uprooting. In (c), the open area shows the upper slope and the shaded area the lower slope.

Table 8. Frequency distribution of trunks in DBH class in Lopeishan Plot. The relative basal area (RBA) for each species is also presentd on the right-hand side of the table. *, dominant species determined by the method of Ohsawa (1984) based on RBA for each species.

Species	DBH Class (cm)							Total	RBA (%)
	0–5	5–10	10–15	15–20	20–25	25–30	30–35		
* *Illicium arborescens*	78	27	7	1				113	6.66
* *Quercus longinux*	27	38	17	16	2	2	1	103	26.34
* *Machilus thunbergii*	6	32	16	12	2	1		69	18.50
* *Quercus sessilifolia*	24	11	6	4	1	1		47	8.30
Itea parviflora	26	17	2	1				46	3.22
* *Diospyros morrisiana*	23	3	9	8		1		44	9.50
Hydrangea angustipetala	28							28	0.29
Pyrenaria shinkoensis	7	11	3					21	2.03
Litsea acuminata	5	13	1					19	1.88
Michelia compressa	7	6	3	1	1			18	3.66
Tricalysia dubia	15	1						16	0.23
Ilex formosana	9	4	1					14	0.92
Prunus phaeosticta	3	2	6		1			12	3.12
Ternstroemia gymnanthera	7	1	1					9	0.53
Myrsine seguinii	7	1						8	0.21
Syzygium buxifolium	8							8	0.10
Adinandra formosana	3		3					6	0.71
Elaeocarpus japonicus	3	1	1			1		6	1.76
Fatsia polycarpa	6							6	0.13
Cinnamomum subavenium	2		2	2				6	2.11
Ilex rotunda	3	2						5	0.25
Daphniphyllum teijsmannii		3	2					5	1.14
Dendropanax dentiger	2	2	1					5	0.52
Neolitsea aciculata var. *variabillima*	4	1						5	0.16
Machilus zuihoensis	2	3						5	0.47
Trochodendron aralioides	2	2	1					5	0.68
Meliosma squamulata	3	1						4	0.11
Cleyera japonica var. *morii*	4							4	0.07
Symplocos glauca	2	2						4	0.27
Ficus erecta var. *beecheyana*	1	2						3	0.20
Osmanthus heterophyllus	2	1						3	0.10
Ilex ficoidea		2	1					3	0.46
Ilex goshiensis			1	1				2	0.78
Ligustrum sp.	2							2	0.06
Camelia brevistyla	1	1						2	0.15
Symplocos confusa	1	1						2	0.14
Symplocos caudata				1				1	0.68
Pourthiaea beauverdiana var. *notabilis*				1				1	0.77
Castanopsis carlesii var. *sessilis*						1		1	1.44
Osmanthus matsumuranus		1						1	0.10
Benthamidia japonica var. *chinensis*			1					1	0.25
Diospyros eriantha			1					1	0.37
Acer serrulatum			1					1	0.29

Table 8. (continued).

Species	DBH Class (cm) 0–5	5–10	10–15	15–20	20–25	25–30	30–35	Total	RBA (%)
Malus doumeri			1					1	0.29
Myrica rubra		1						1	0.05
Symplocos wirkstroemifolia	1							1	0.05
Prunus campanulata		1						1	0.18
Ardisia quinquegona	1							1	0.02
Ilex tanakae	1							1	0.01
Euonymus carnosus	1							1	0.01
Eurya chinensis	1							1	0.00
Rhododendron latoucheae	1							1	0.00
Ilex lonicelifolia	1							1	0.00
Total	329	195	88	48	7	7	1	675	100.0

Table 9. Binomial tests for the distribution of trees between the upper (US) and lower (LS) slopes in Lopeishan Plot. Species with less than four individuals are not presented. For each of the species groups (Group A, B and C) and test procedures, see text. **, significant difference at the 0.5% level; *, significant difference at the 1.0% level. Note that N in the table is not the number of trunks but the number of individuals for wihch sprouting trunks were neglected.

Species	Relative number of trees US	LS	N	Sopecies group
Illicium arborescens	70.7	29.3	92	A**
Quercus longinux	77.8	22.2	81	A**
Itea parviflora	27.3	72.7	44	B**
Machilus thunbergii	40.5	59.5	42	C
Diospyros morrisiana	73.7	26.3	38	A**
Quercus sessilifolia	66.7	33.3	33	A*
Hydrangea angustipetala	26.1	73.9	23	B*
Pyrenaria shinkoensis	73.7	26.3	19	A*
Michelia compressa	88.2	11.8	17	A**
Litsea acuminata	46.7	53.3	15	C
Prunus phaeosticta	25.0	75.0	12	C
Tricalysia dubia	75.0	25.0	12	A*
Ilex formosana	40.0	60.0	10	C
Syzygium buxifolium	71.4	28.6	7	C
Myrsine seguinii	57.1	42.9	7	C
Elaeocarpus japonicus	100.0	0.0	6	A*
Adinandra formosana	100.0	0.0	6	A*
Cinnamomum subavenium	80.0	20.0	5	C
Dendropanax dentiger	20.0	80.0	5	C
Ternstroemia gymnanthera	80.0	20.0	5	C
Trochodendron aralioides	60.0	40.0	5	C
Dqphniphyllum teijsmannii	80.0	20.0	5	C
Neolitsea aciculata var. *variabillima*	50.0	50.0	4	C
Cleyera japonica var. *morii*	100.0	0.0	4	A*
Ilex rotunda	100.0	0.0	4	A*
Machilus zuihoensis	100.0	0.0	4	A*
Fatsia polycarpa	25.0	75.0	4	C
Area (%)	46.7	53.3	—	—

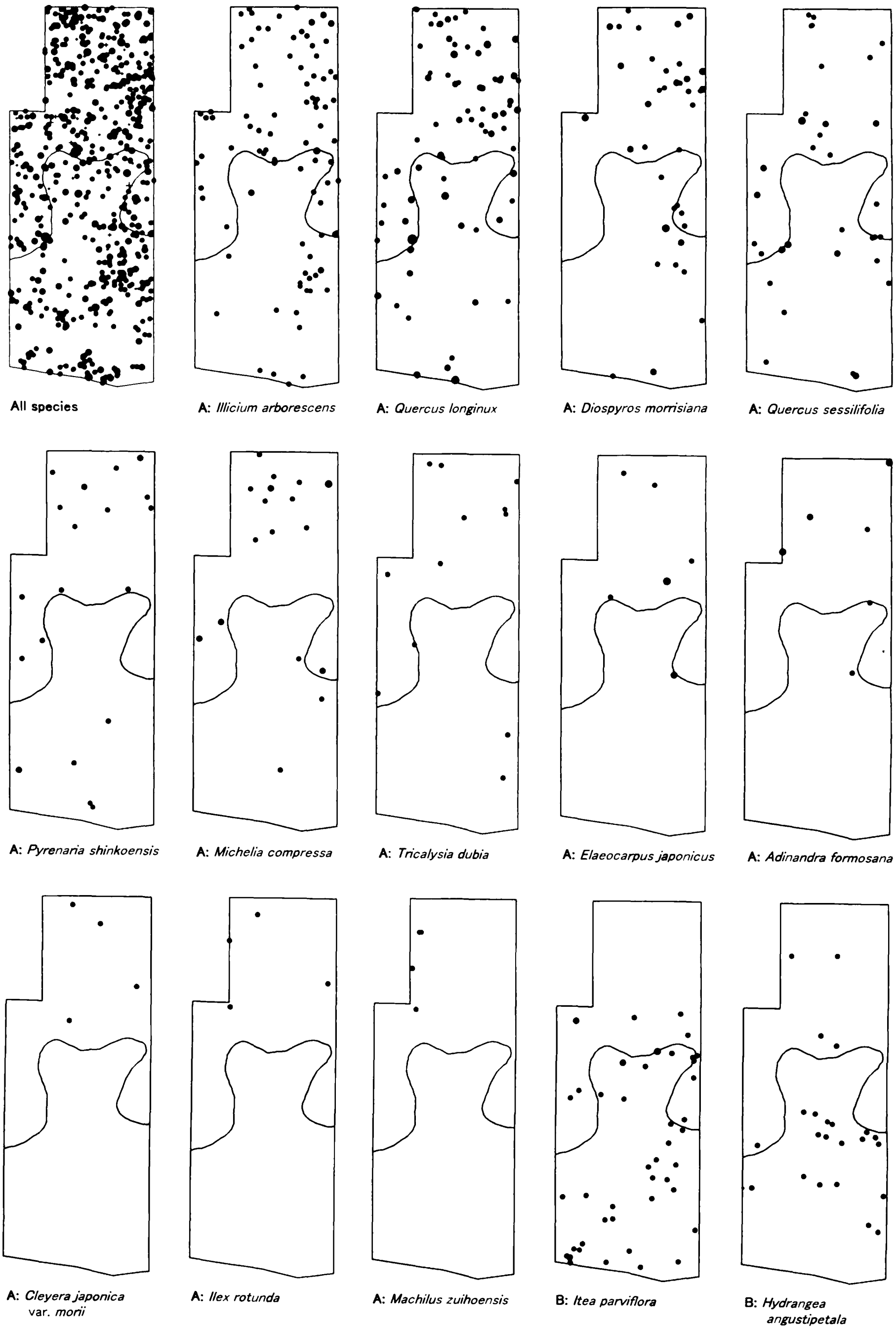

Fig. 10. Examples of tree distribution in Lopeishan Plot. Abbreviations of species groups; A, B and C, are also represented just before the species name. For the distinction of species groups (Group A, B and C), see text and Table 3. Boundaries among micro-landform units are also shown. Living and dead trunks are represented as circles and crosses, respectively, and their sizes correspond to the trunk diameters.

species (*Itea parvifolia* Hemsl. and *Hydrangea angustipetala* Hayata), the distribution of *Prunus phaeosticta* (Hance) Maxim. was also biased to the lower slope, although this was not statistically significant.

Some of the Group A species such as *Illic-*

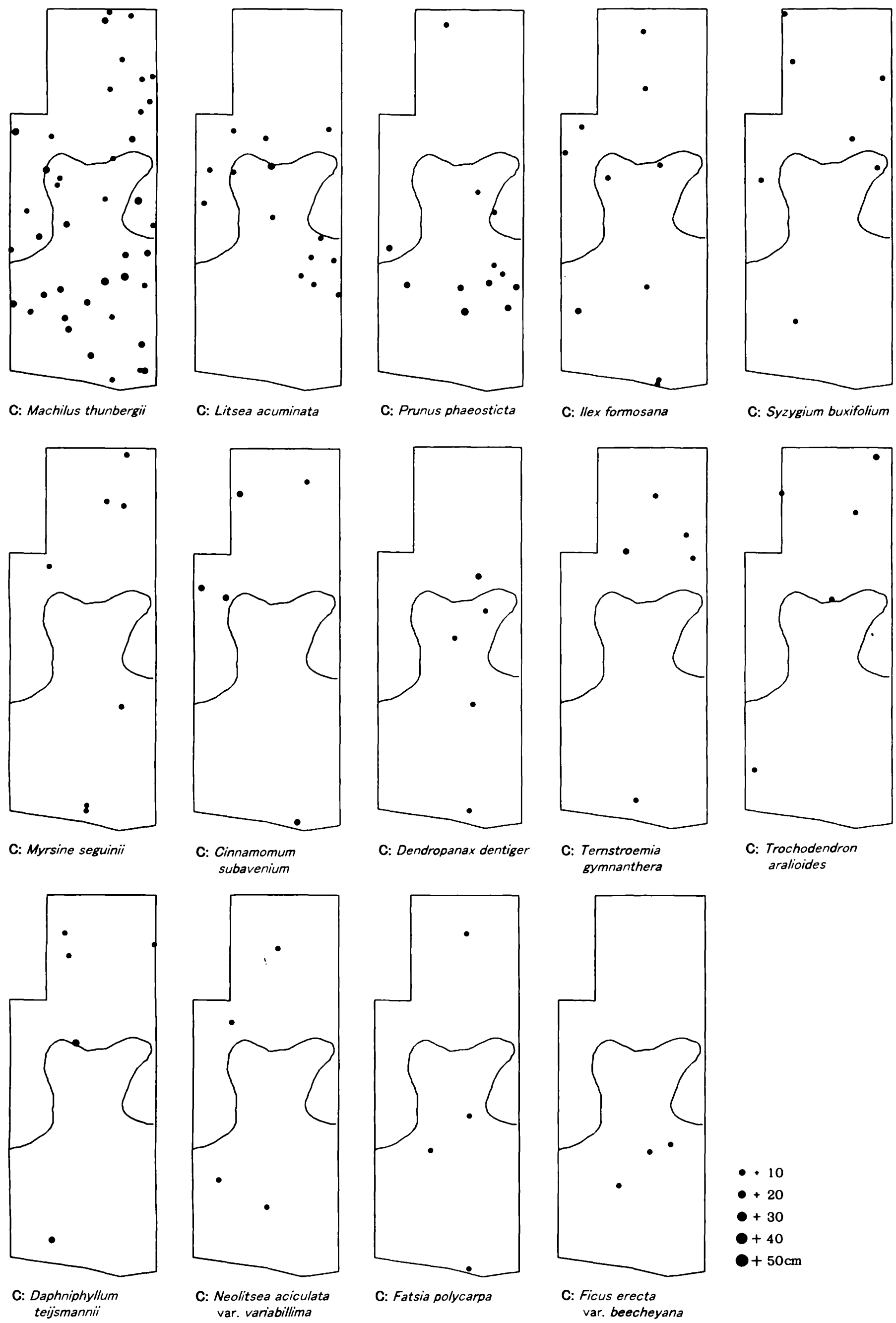

Fig. 10. (continued).

ium arborescens and *Diospyros morrisiana* showed the most abundant representation of trunks in the smallest size class, but others, such as *Quercus longinux* and *Machilus thunbergii*, did not (Table 8). On the other hand, among the Group B species, *Itea parvifolia* also showed the most abundant representation of trunks in the smallest size class. On the other hand, *Hydrangea angustipetala* had no trunks larger than 5.0 cm in DBH, indicating that this species is a shrub.

Table 10. Dominant species on the upper and lower slopes of Lopeishan Plot. Dominant species on each slope were detrmined by the method of Ohsawa (1984) based on the relative basal area (RBA) for each species.

Dominant species	RBA (%)	No. of trunks
Upper slope		
Quercus longinux	31.5	80
Diospyros morrisiana	10.2	32
Quercus sessilifolia	9.1	31
Machilus thunbergii	9.1	25
Illicium arborescens	8.6	81
Michelia compressa	6.1	16
Lower slope		
Machilus thunbergii	32.4	44
Quercus longinux	18.4	23
Diospyros morrisiana	8.4	12
Quercus sessilifolia	7.0	16
Prunus phaeosticta	6.7	9
Itea parviflora	6.6	34

3.4. Vegetation on the upper and lower slopes.

Not only in terms of floristic composition but also the relative abundance (RN and RBA) of each species, the similarity of vegetation between the upper and lower slopes was higher in Lopeishan Plot than in the Nanjenshan and Pinglin plots. The similarity indices, CC, PS(N) and PS(BA), were 83.6%, 49.6% and 54.8%, respectively, between the two slopes. The most dominant species in terms of basal area differed between the slopes: *Quercus longinux* (RBA = 31.5%) on the upper slope and *Machilus thunbergii* (RBA = 32.4%) on the lower one. However, as shown in Table 10, four species which were common to both slopes (*Quercus longinux, Q. sessilifolia, Machilus thunbergii* and *Diospyros morrisiana*) shared the largest portions (1st to 4th) of the basal area in both plots, although the order was different. The total relative basal area shared by these four species reached 59.9% on the upper slope and 66.2% on the lower slope. In addition to the RBA for these four species, *Illicium arborescens* was quite abundant on both slopes, in terms of the number of trunks.

4. Comparison of stand structure among the three plots

The values of richness for families, genera and species were all highest in Nanjenshan Plot, and were similar between the Pinglin and Lopeishan plots (Table 11). The values of H' and J' were also highest in Nanjenshan Plot and lowest in Lopeishan Plot. The number of dominant species determined by the method of Ohsawa (1984) reached nineteen in Nanjenshan Plot and eleven in Pinglin Plot, indicating that there were no distinct dominant species. The number was lowest in Lopeishan Plot, but even there, no species shared more than 30% of the total basal area (Table 8) or more than 20% of the total number of trunks. In every plot, the rank-abundance curve drawn on the basis of RBA for each species was characterized by a scarceness of superior species having a RBA of more than 10.0%, and an abundance of intermediate species having a RBA of 0.1%–10.0% (Fig. 11).

In all plots, values of basal area and trunk density were higher on the upper than on the lower slope (Table 11). The total basal area values for the whole plot were similar among the three plots. Differences among plots were larger for trunk density, being highest in Nanjenshan and lowest in Pinglin. This was mainly because the upper slope, where the density was higher, comprised the largest portion (71.3%) in Nanjenshan Plot and the smallest (30.4%) in Pinglin Plot.

The DBH of the largest trunk (maximum DBH) was not so large in every plot (Table 11), and in Lopeishan it was only 34.0 cm. The maxima of tree heights were also restricted to only 16 m in the Nanjenshan and Lopeishan plots.

Discussion

1. Floristic diversity

We have already investigated the floristic composition of evergreen broad-leaved forests on four (Amami Ohshima, Tokunoshima, Okinawa and Iriomote) of the Ryukyu Islands using the same method as that in this study (Hara *et al.*, 1996a, b and unpublished data). Therefore, we were able to compare the richness of tree and shrub species between the three plots in Taiwan and the four

Table 11. Comparison of species diversity and stand structures among the Nanjenshan, Pinglin and Lopeishan plots. *, Dominant species on each slope were determined by the method of Ohsawa (1984) based on the relative basal area (RBA) for each species.

	Nanjenshan	Pinglin	Lopeishan
Richness of taxa			
Family	29	25	25
Genus	49	37	40
Species	68	52	53
H'	4.84	4.35	3.77
J'	2.63	2.51	2.17
No. of dominant spp.*	19	11	5
Basal area (m^2/ha)			
in the upper slope	51.3	59.1	52.7
in the lower slope	29.8	40.7	30.8
in the whole plot	45.4	46.7	41.0
Trunk density (/100 m^2)			
in the upper slope	99.9	91.1	94.7
in the lower slope	42.6	47.0	52.7
in the whole polt	84.1	61.6	72.3
Mean DBH (cm)	5.1	5.8	6.7
Maximum DBH (cm)	46.0	55.0	34.0
Maximum tree heigh (m)	16	22	16
Area (m^2)			
Upper slope	695	206	436
Lower slope	280	472	497
Total	975	678	933

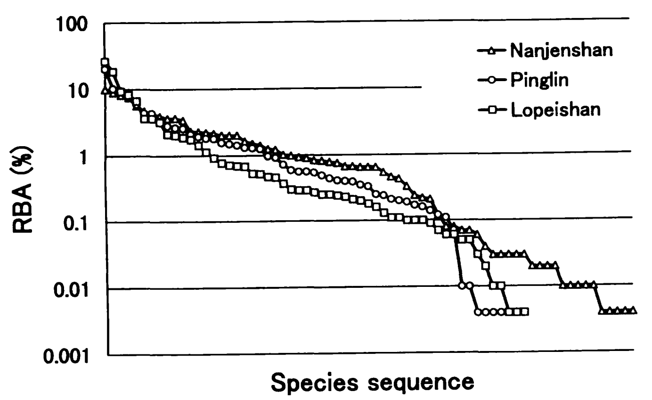

Fig. 11. Rank-abundance curves for the Nanjenshan, Pinglin and Lopeishan plots. The abundance is represented by the relative basal area of each species.

plots in the Ryukyus. As shown in Fig. 12, the floristic richness for tree and shrub species at the family, genus and species levels all overlapped between the plots in Taiwan and those in the Ryukyu Islands, with considerable variation within each area. Among the three Taiwan plots, the values at the family, genus and species levels were all higher in Nanjenshan than in the other two plots in North Taiwan. In the Ryukyu Islands, the plot on Iriomote similarly showed a higher value than the plots on the other three islands. The values of the two plots in North Taiwan (Pinglin Plot and Lopeishan Plot) were closer to values for the Ryukyu Island plots except Iriomote, and the values for the Nanjenshan Plot were closer to those for Iriomote.

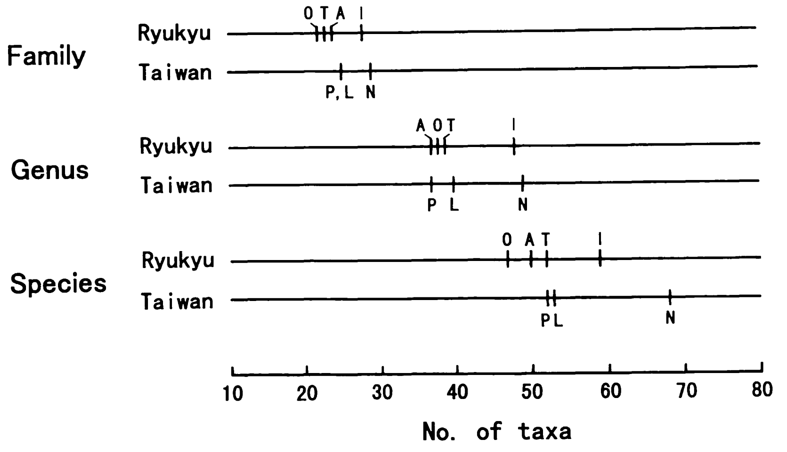

Fig. 12. Comparison of floristic richness for tree and shrub species between plots in Taiwan and the Ryukyu Islands. The richness at three levels of taxonomical hierarchy (family, genus and species) is shown. The location of each plot is shown with alphabetical abbreviations: A, Amami Ohshima; I, Iriomote; L, Lopeishan; N, Nanjenshan; O, Okinawa; P, Pinglin; T, Tokunoshima. For geographical location of each plot, see Fig. 1.

In terms of the topographical condition, every plot contained a similar range of habitat covering a whole slope from a ridge to a valley bottom, on a similar spatial scale. Thus, from this viewpoint, species with a similar range of habitat were included. However, the plot area differed among plots because of the difference in the length and inclination of the slopes. Three plots (Iriomote, 1161 m^2; Amami Ohshima, 1311 m^2; Tokunoshima, 1962 m^2) in the Ryukyu Islands were larger than those in Taiwan (678–975 m^2), but the Okinawa Plot (648 m^2) was smaller. Thus, in comparison with the Taiwan plots, the richness of the Okinawa Plot would have been somewhat underestimated, and the values for the remaining three plots would have been overestimated, although the difference appears to have been relatively small.

The higher floral richness in Nanjenshan and Iriomote might have been the factor most responsible for the higher richness of the two plots at stand level. Hengchun peninsula, where Nanjenshan plot is located, lies at the southern end of Taiwan and is famous for its diverse flora including many endemic and tropical elements (Hsieh *et al.*, 1994). Iriomote Island is also located near the southern end of the Ryukyus (at a latitude and altitude actually lower than Pinglin and Lopeishan), and thus the value of the warmth index (WI) is 203℃·month which is higher than that of Pinglin or Lopeishan, and closer to the value for Nanjenshan. Iriomote Island is also characterized by many of the southern elements which are absent in the northern and middle parts of the Ryukyus (Hatusima, 1975).

2. Species diversity of the canopy layer

Irrespective of the similar richness of taxa at the stand level in Taiwan and the Ryukyu Islands, the dominance-diversity relationships of the stands differ markedly between the two areas. In the Ryukyus, more than half of the total basal area of each plot is usually shared by only two or three dominant species (Hara *et al.*, 1996a, 1996b; and unpublished data), indicating the lower species diversity of the canopy layer. Furthermore, the dominant species are common to the islands and are relatively few; usually *Castanopsis sieboldii* (Makino) Hatusima ex Yamazaki et Mashiba ssp. *lutchuensis* (Koidz.) H. Ohba and *Quercus miyagii* Koidz., and sometimes *Distylium racemosum* Sieb. et Zucc. and *Schima wallichii* (DC.) Korthals are additionally included. On the other hand, in Taiwan, no species shared such a large portion of RBA as *Castanopsis sieboldii* ssp. *lutchuensis* or *Quercus miyagii* did in the Ryukyus. In addition to many Fagaceae spp., many other species, particularly Lauraceae such as *Machilus kusanoi, Cryptocarya chinensis, Beilshmiedia* spp. etc., became the dominant species in Taiwan. Variations in the composition of dominant species among the plots were also much larger there.

The floristic paucity of canopy elements in the Ryukyu Islands as compared with Taiwan should be one of the most important, direct causes of the difference in the diversity of the canopy layer between the two areas. For example, the richness of Fagaceae species is appreciably higher in Taiwan: 37 spp. according to Liao (1996), as compared with 6 spp. in the Ryukyus (Hatusima, 1975). Lauraceae species, which can reach as high as Fagaceae spp., such as *Machilus kusanoi* or *Cryptocarya chinensis* in Taiwan, are also absent in the Ryukyu Islands. The different biogeographical histories of the Ryukyus and Taiwan appear to explain this difference in their tree flora. It is considered that Taiwan was connected to mainland China more frequently during Pleistocene, and that the vast majority of species now characteristic of the Taiwanese lowland flora must have arrived at the beginning of the Holocene (10,000 yr BP) onward (Shen, 1994). On the other hand, Kira (1989, 1991) has stated that the dominant oak (*Castanopsis* and *Quercus*) species in the Ryukyu Islands may be relics of an age when a cooler climate prevailed and the islands were connected either with the continent or with the main islands of Japan, and have survived in coexistence with the tropical flora that arrived later from across the sea.

Furthermore, the strong wind in Taiwan might affect the species diversity of the forest canopy layer. One of the characteristic features of evergreen broad-leaved forests in Taiwan is that they are strongly affected by monsoon winds in winter, in addition to strong Typhoon winds in summer (Suzuki, 1952; Hsieh *et al.*, 1994). Frequent canopy gap formation by strong wind might increase the species diversity of the canopy by reducing the competitive exclusion among canopy species, as predicted by the intermediate disturbance hypothesis (Connell, 1978; Huston, 1979). In addition, strong and continuous winds such as the winter monsoon in Taiwan usually reduce the extension growth of branches, and make trees shorter in stature (Telewski, 1995). As a result, not only tree species but also small-tree and shrub species can comprise the canopy altogether, and the species diversity of the canopy might increase as a result. Sun *et al.* (1996) reported that the Nanjenshan forest on the slopes windward to the winter monsoon was characterized by lower tree heights, higher trunk densities and smaller, thicker leaves than those on the leeward slopes. Although our plot in Nanjenshan included a leeward slope and a valley site, trees were only 16 m or less in height, the density of canopy trees was relatively low, and most of the canopy trees were partly broken, suggesting frequent disturbance of the forest canopy. Also in Lopeishan, the canopy was not so high and broken crowns of canopy trees were common, particularly near the ridge. Thus, both chronic stress due to monsoon wind, and rare but strong disturbance by typhoon wind might increase the species diversity of the forest canopy layer in Taiwan by reducing the competitive exclusion of canopy species through changing the canopy lower to a more open form. The strong effects of typhoon and winter monsoon wind on the vegetation of the Ryukyus and neighboring islands have been pointed out in some reports (Suzuki, 1979; Bellingham *et al.*, 1996), although the knowledge on this topic is still quite limited, and further studies are necessary in order to compare the effects of wind between Taiwan and the Ryukyus.

3. Some ecological differences between Group A and Group B

Recent studies on the relationship between vegetation pattern and micro-landform, have shown that differences in the disturbance regime of the land surface affect the vegetation pattern in addition to differences in water and nutrient conditions (Kikuchi and Miura, 1993; Sakai and Ohsawa, 1993, 1994; Hara *et al.*, 1996a, b; Yoshida and Ohsawa, 1996). As compared with an upper slope, the land surface of a lower slope is more unstable (Tamura, 1987; Kikuchi and Miura, 1993). The unstable land surface of a lower slope often limits the distribution and growth of tree species (Hara *et al.*, 1996b), resulting in relatively lower trunk density and total basal area on the lower slope, as observed in this study.

In addition, the present study revealed that among component species of each stand, species whose distribution was biased to the upper slope were more common than those with a distribution bias to the lower slope; the number of Group A species was far larger (11, 12 and 13 in each plot) than the number of Group B species (2 in all plots) in every plot. Many of the Group A species were also relatively abundant in terms of number, showing the highest representation for the smallest size class. Individuals were usually scattered throughout the upper slope. Thus, these Group A species have many successor trees in the understorey and appear to have the potential to regenerate successfully there.

On the other hand, the population density of some species which were clustered on the lower slope was relatively low, and one reason for the far lower number of Group B species than Group A species might be to the lower population density of these species. For example, in Pinglin Plot, large trees of *Cryptocarya chinensis* and *Machilus kusanoi* were found on the lower slope and thus became the dominant species there. However, successor trees of smaller size were absent for these species, and the number of individuals were very small, only two and four for each species, respectively. As a result, these species could not be classified into Group B but into Group C because of the small number of individuals. Not only for the above species but also for *Astronia formosana,* which was classified into Group B in Nanajenshan, individuals of the smallest DBH class were relatively few, indicating that these species did not have sapling banks in the understorey.

In contrast, some species of Group B (*Blastus cochinchinensis, Turpinia formosana, Itea parviflora* and *Hydrangea angustipetala*) showed a relatively higher trunk density. These species were shrub or small-tree species which cannot reach the canopy. Sprouting from leaning old trunks was frequently observed for these species. Such a sprouting habit is an effective regeneration strategy in unstable sites (Sakai *et al.,* 1995). Thus, some Group B species can maintain their higher trunk density by frequent sprouting of trunks.

It is also interesting that the family composition of Group A also differed from that of Group B. Group A comprised many species belonging to various families such as Fagaceae, Lauraceae, Theaceae, Aquifoliaceae, Myrsinaceae, Rubiaceae, Elaeocarpaceae and Illiciaceae, whereas Group B species belonged to families different from those in Group A, such as Melastomataceae, Saxifragaceae, Staphyleaceae and Araliaceae. Thus, it is suggested that a certain extent of habitat differentiation between upper and lower slopes may exist at the family level.

4. Dominant species of the upper vs. lower slopes

There was a considerable overlap of floristic composition between the two slopes, as indicated by the relatively high values of CC (59.2%–83.6%). However, the quantities (basal area and trunk density) of many of the component species differed considerably between the slopes, and there were larger differences in vegetation when the quantities of each species were considered, as indicated by the lower values of PS(N) and PS(BA).

The most important, dominant taxon on the upper slopes in Taiwan was Fagaceae such as *Castanopsis* and *Quercus.* On the other hand, Lauraceae such as *Machilus* and *Cryptocarya,* and Melatomataceae such as *Astronia* were the most dominant taxa on the lower slopes. In particular, the prevalence of *Machilus kusanoi* on the lower part of slope was reported elsewhere (Suzuki, 1952; Liu and Su, 1976; Su and Lin, 1979). *Quercus* species are also seen on the lower slopes but only in lesser amounts.

Also in the Ryukyu Islands and Kyushu Island, the most important, dominant taxon on the upper slopes is Fagaceae. In the Ryukyu Islands, the most dominant species of the upper slope was *Castanopsis sieboldii* ssp. *lutchuensis* (Hara *et al.,* 1996a, b). Forest in which the upper slope is dominated by *Quercus* spp. is absent in the Ryukyus, except for *Q. glauca* Thunb. var. *amamiana* (Hats.) Hats. forest on raised coral reef, because of the low altitudes of these islands. However, this type of forest is found on mainland Japan. For example, *Quercus sessilifolia,* which was one of the dominant species at Lopeishan, is also one of the common species in the evergreen oak forest on mainland Japan (Fujiwara, 1981).

On the other hand, the most important, dominant taxon on lower slopes in the Ryukyus and Kyushu is usually *Quercus,* and Lauraceae species appear to be less dominant there. The most common dominant species on the lower slopes in the Ryukyus is *Quercus miyagii* (Hara *et al.,* 1996a, b and unpublished data). In Kyushu, *Q. gilva* is also one of the most common dominant species on lower slopes (Suzuki, 1960; Itow and Kawasato, 1974; Hirata *et al.,* unpublished data). *Q. gilva* is also distributed in Taiwan but seems to be less dominant than in Kyushu. *Machilus japonica* Sieb. et Zucc., which is sometimes treated as the same taxon as *Machilus kusanoi* at the species level (Liao, 1988), is also found on lower slopes in the Ryukyus and Kyushu, but this species does not become as large a tree as *M. kusanoi,* and thus rarely becomes dominant on lower slopes. *Machilus thunbergii* is also distributed in Japan and often becomes a dominant species near the coast (Hattori, 1992), a dominant species of the successional sere to *Castanopsis* forest (Kamijo and Okutomi, 1993), or sometimes a dominant species on lower slopes (Suzuki and Wada, 1949). However in the Ryukyus (Hara *et al.,* 1996a, b and unpublished data) and Kyushu (Hirata *et al.,* unpublished data), except for coastal areas, the distribution of this species is mostly restricted to upper slopes, and it rarely become dominant species on lower slopes.

Conclusion

The evergreen broad-leaved forests of Taiwan show a floristic richness for tree and shrub species at the stand level similar to the forests of the same type in the Ryukyu Islands, although there is a large variation within each area. However, the species diversity of the forest canopy is considerably higher in Taiwan than that in the Ryukyus. The paucity of canopy elements in the Ryukyus, which can be attributed to the paleogeography of the islands, would be one of the main causes of this difference in diversity of the canopy layer. In addition, the combined effect of a strong, winter monsoon and frequent typhoons in Taiwan might increase the diversity of the canopy layer by reducing the competitive exclusion of canopy trees, changing the canopy to a lower and more open form. From the viewpoint of vegetation structure in relation to micro-landform, lower slopes are characterized by lower values of basal area and trunk density than upper slopes. Species with a distribution biased to the upper slopes (Group A) are more common than species biased to lower slopes (Group B). Fagaceae, such as *Castanopsis* and *Quercus,* are the most important dominant taxon on the upper slopes, whereas Lauraceae such as *Machilus* are more conspicuous on lower slopes.

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台湾の 3 地点における常緑広葉樹林の種組成と構造 —特に微地形と植生の関係について—

原　正利[1]・平田和弘[1]・藤原道郎[1]・大野啓一[1]・謝　長富[2]

[1] 千葉県立中央博物館
〒260 千葉市中央区青葉町 955–2
[2] 国立台湾大学植物学系
台北市 106，台湾

台湾の 3 地点（南仁山，Nanjenshan；坪林，Pinglin；羅培山，Lopeishan）において，尾根から谷にかけて，ひとつの斜面を全て含むように調査区を設置し，常緑広葉樹林の種組成と構造を特に微地形との関連で調べた．各調査区では地表面の形態に基づいて微地形単位を区分し，それらを上部斜面と下部斜面にまとめて，両斜面間で樹木の分布や植生構造を比較した．各調査区内に出現した科，属および種の数は，いずれも Nanjenshan 区で最も多く，他の 2 調査区では，あまり違いがなかった．各調査区における林分全体での胸高断面積合計および高さ 2m 以上の幹の密度はそれぞれ，41.0–46.7 m^2ha^{-1} および 61.6–84.1/100 m^2 の範囲にあった．いずれの調査区においても，胸高断面積合計と幹密度の値は，下部斜面に比べ上部斜面で高く，また，上部斜面に分布の偏る種の方が，下部斜面に分布の偏る種に比べ，種数の点ではるかに多かった．上部斜面と下部斜面の植生は種組成の点ではかなり重複していたが，各構成種の胸高断面積合計や幹密度は両斜面間で大きく異なっていた．両斜面の優占種は，調査区により異なったが，上部斜面ではブナ科（シイ属やコナラ属）が，下部斜面ではクスノキ科（タブノキ属など）が共通して重要な要素であった．各調査区の結果を，これまでに同様の調査データが得られている琉球列島の調査区の結果と比較すると，種や属，科の豊富さの点では，あまり違わなかったが，林冠層の種多様性が琉球列島に比べかなり高かった．冬期の季節風と台風による強風が，台湾の常緑広葉樹林の構造に与える影響について議論した．