

Species Composition and Structure of a Montane Rainforest of Mt. Lopei in Northern Taiwan

Huan-Yu Lin⁽¹⁾, Kuoh-Cheng Yang⁽²⁾, Tsung-Hsin Hsieh⁽³⁾ and Chang-Fu Hsieh^(1,4)

(Manuscript received 22 March, 2005; accepted 15 June, 2005)

ABSTRACT: The forest structure and woody species composition were investigated in a montane rainforest of Mt. Lopei in northern Taiwan. All stems ≥ 1 cm dbh were measured and identified for a permanent plot of 1-ha (1,136 to 1,164 m asl.). Approximately 12,934 stems of 70 taxa in 31 families were found. The most abundant families were Fagaceae, Illiciaceae, and Theaceae, representing 51.5% of the individuals. The dominant species, based on basal areas were *Cyclobalanopsis longinux*, *Machilus thunbergii*, *Cyclobalanopsis sessilifolia*, *Illicium arborescens*, *Diospyros morrisiana*, and *Meliosma seqimulata*. Comparison of TWINSpan groupings with the DCA ordination showed a definitive separation of forest types along a topographic gradient. The categorized forest types were the *Cyclobalanopsis longinux*-*Myrsine seguinii* type on the ridgetop and northeastern slope facing strong northeastern monsoon, and the *Illicium arborescens*-*Itea parviflora* type on the relatively protected southwestern slope. Evident differences of the composition and structure were observed between these two forest types. Size-class structures of most species showed an inverse J-shaped or an inverse L-shaped distribution, both indicators of a continuous recruitment in this permanent plot.

KEY WORDS: Permanent plot, forest type, classification, ordination, size-class distribution, diversity.

INTRODUCTION

The broad-leaved evergreen forests occur from sea level to about 2,500 m above sea level (asl) in Taiwan. These forests are usually categorized as Lauro-Fagaceous forests (Kudo and Sasaki, 1931). Many of the dominant tree species are evergreen members of Fagaceae, Lauraceae, Theaceae, Symplocaceae and other broad-leaved evergreen species. Regardless of being one of the most rich and diverse subtropical rain forests in east Asia, only a few studies (e.g., Liu, 1968; Su, 1984; Chen, 1993; Hsieh *et al.*, 1997, 1998) have been conducted to explore the composition and distribution of plant communities. Furthermore, comprehensive researches are still scanty.

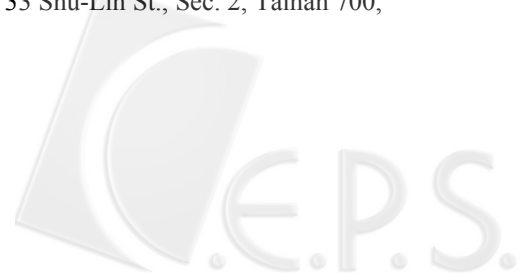
This study was conducted in a montane rainforest in northern Taiwan, where a large continuous pristine forest can still be found. In this study, we present preliminary results of the first investigation conducted in a permanent plot established between 1989 and 1994. The goal is to examine changes in forest structure and composition across a topographic gradient. The information provided here will also serve as the basis for further comparisons with other biodiversity monitoring plots in Taiwan.

1. Institute of Ecology and Evolutionary Biology, National Taiwan University, 1 Roosevelt Road, Sec. 4, Taipei 106, Taiwan.

2. Department of Ecology, Providence University, 200 Chung-Chi Rd., Shalu, Taichung 433, Taiwan.

3. Department of Natural Sciences Education, National University of Tainan, 33 Shu-Lin St., Sec. 2, Tainan 700, Taiwan.

4. Corresponding author. Tel: 886-2-33662474; Email: tnl@ntu.edu.tw



Study area

The study area is located on the northwestern slope of Mt. Lopei (120°27'15"N, 24°48'42"E, 1,553 m in altitude), ca. 20 km south of Taipei City in northern Taiwan (Fig. 1). The Lopei main ridge extends in a northeast to southwest direction with the highest peak rising to 1,907 m in the south. The 1-ha plot was established on a branch ridge running southeast-northwest. Elevation ranges from 1,136 to 1,164 m. This area is humid with a mean annual precipitation of 3,100 mm and a mean annual temperature of 16.2°C (estimated from three nearby weather stations). Dense clouds or mists cover the ridge most of the year. High-intensity rainfalls are often caused by typhoons and thunderstorms from June to September. However, the average precipitation fluctuates within a certain range throughout the year. Occasional snow occurs in January above 1,000 m in elevation. Strong northeast monsoon winds occur frequently during the winter, from November to April (Fig. 2).

Soil depth is estimated from 20 to 30 cm, and soil profiles are classified as Inceptisols with clay content mostly greater than 40% and silt content of 30-50% (Hsieh & Chen, 1989).

Evergreen broad-leaved forests cover most of the area, while patches of Japanese cedar (*Cryptomeria japonica*) plantation exist on the lower and middle slopes. In addition, nearly pure stands of Taiwan beech (*Fagus hayatae*) occur above 1,400 m on the top of ridges.

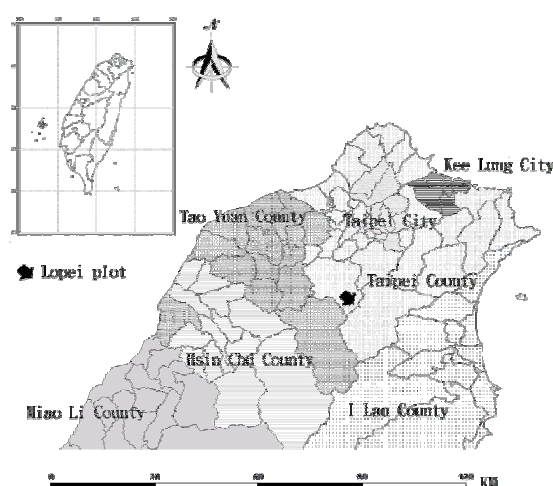


Fig. 1. Location of the 1-ha Lopei Plot in northern Taiwan.

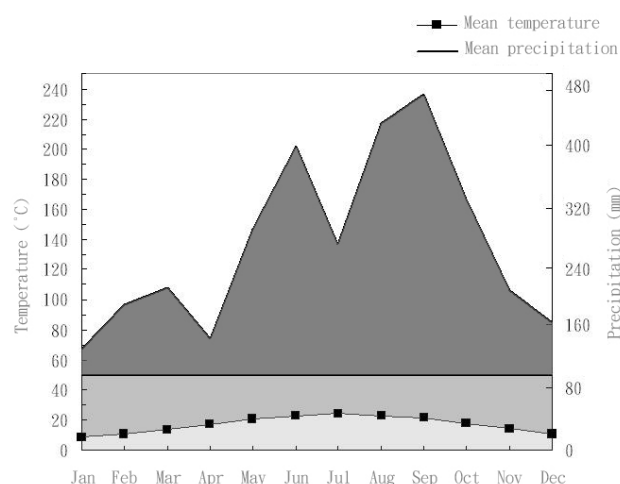


Fig. 2. Climate diagram of the Lopei montane area.

METHODS

A 1-ha plot (100 × 100 m) was established in 1989 and was partitioned into one hundred 10 × 10 m quadrats for vegetation investigations. The first census of woody plants was conducted in 1993-1994. All free-standing woody plants ≥ 1 cm dbh (diameter at breast height, 1.3 m above ground) were tagged, measured, mapped, and identified.

Individuals with multiple stems were considered as one unit for density calculation, and basal areas of separate stems were summed up for a total value. Important value (IV) was calculated as the mean of the relative abundance and basal area of a particular species in each quadrat. A primary matrix of species IV by quadrats (70 species × 100 quadrats) was subjected to TWINSpan classification (Hill, 1979a). Major gradients in vegetation composition were identified using Detrended Correspondence Analysis (DCA; Hill, 1979b).

TWINSPAN and DCA were carried out using PC-ORD (McCune and Mefford, 1999).

For size-class analysis, only species with >15 individuals in the plot were included. The dbh class width (R) for each species was determined as:

$$R = (\text{Max. dbh} - \text{Min. dbh}) / M$$

$$M = \text{INT} (6 \times \log_{10} N)$$

Where N is the individual number of species, and M is the number of dbh classes

Species diversity (Hill, 1973) was measured based on the values of relative basal areas using species richness (number of species per plot), the Shannon-Wiener index, and Hill's diversity numbers N1 and N2, where N1 measured the number of abundant species in the sample, and N2 was the number of very abundant species. Evenness was calculated as the modified Hill's ratio E5, which approached zero as a single species became more and more dominant. Species richness was evaluated at the site scale using rarefaction method (Hurlbert, 1971). This method estimates the number of species expected in a random sample of individuals taken from a collection.

Diversity indices for the 3-ha Lanjenchi plot (Sun *et al.*, 1998) of the southernmost Taiwan were also calculated for comparison.

RESULTS

Floristic composition

The woody flora of the Lopei plot was composed of 70 species in 49 genera of 31 families. The most speciose family was Theaceae, followed by Symplocaceae, Rosaceae, Aquifoliaceae, Lauraceae, Fagaceae, and Oleaceae (Fig. 3). Canopy height varied markedly within the plot, ranging from 13 m on the southwestern slope and creek bottom to about 5 m on the ridgetop and northeastern slope.

A total of 12,934 stems with dbh ≥ 1 cm was recorded in this census. There were 2,460 stems ≥ 8 cm dbh, accounted for 19.02% of all stems in the plot. Woody individuals in 10×10 m quadrats varied between 29 and 320 with an average of 125. Stem density was obviously higher on the northeast side slope and ridge than on the southwest slope (Fig. 4). The basal area of all individuals was 47.27 m²/ha, varying from 20.47 to 81.64 m²/ha in the 10×10 m quadrats. In contrast to the density, the basal areas were higher for the quadrats on the southwestern slope (Fig. 5). The most abundant families were Fagaceae, Illiciaceae, and Theaceae, together constituting 51.5% of the individuals. Other abundant families included Lauraceae and Myrsinaceae. The most abundant species were *Illicium arborescens*, *Cyclobalanopsis longinux*, *Cyclobalanopsis sessilifolia*, *Myrsine seguinii*, *Meliosma seqimulata*, *Machilus thunbergii*, *Syzygium buxifolium*, *Diospyros morrisiana*,

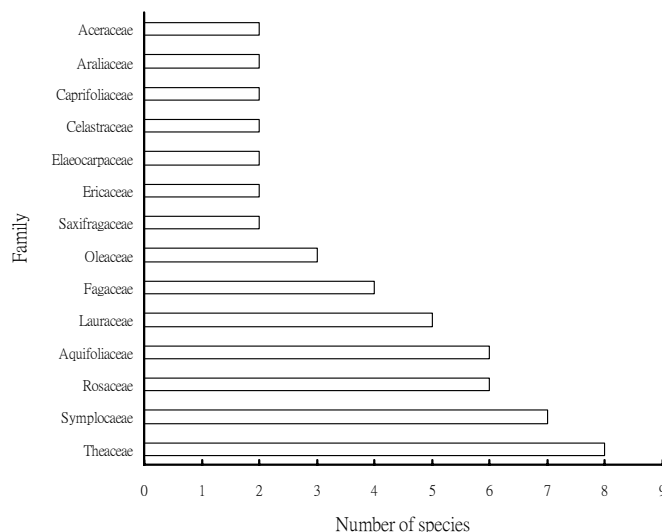


Fig. 3. Dominant families which possess the most species in the Lopei Plot.

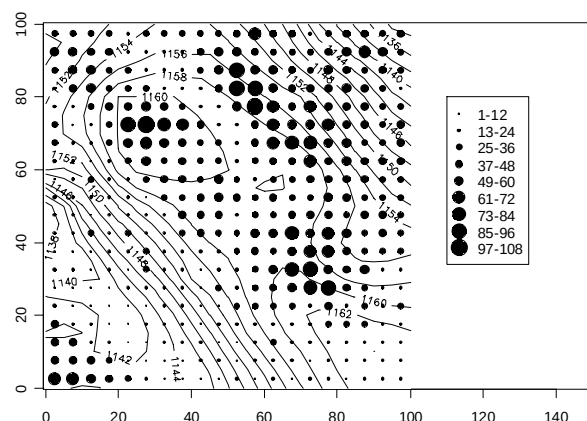


Fig. 4. The distribution of number of stems per 5×5 m quadrat in the Lopei Plot.

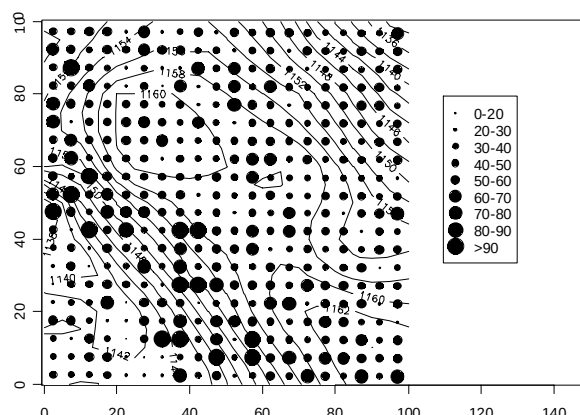


Fig. 5. Total basal area (m^2/ha) obtained for each 5×5 m quadrat in the Lopei Plot.

Cleyera japonica, and *Symplocos sumuntia*. The five most abundant species collectively comprised 53.38% and the first 32 species 95.41% of all stems in the plot (Fig. 6).

The families with the highest basal area were Fagaceae, Lauraceae, Illiciaceae, Ebenaceae, Sabiaceae, Theaceae, Myrsinaceae, Symplocaceae, and Myrtaceae, and the first three families accounted for 63% of the total basal area. The dominant species, based on basal area, were *Cyclobalanopsis longinix*, *Machilus thunbergii*, *Cyclobalanopsis sessilifolia*, *Illicium arborescens*, *Diospyros morrisiana*, and *Meliosma sequimulata*. The cumulative basal area of the three most dominant species was $24.09 \text{ m}^2/\text{ha}$, and that represented 50.68% of the total basal area of all recorded species. *Illicium arborescens* (usually a subcanopy tree) had the greatest stem density in the plot, but it did not contribute much to the total basal area since most stems were less than 20 cm dbh.

The most important family, as indicated by IV, was Fagaceae, followed by Illiciaceae, Lauraceae, Theaceae, Sabiaceae, and Ebenaceae. Cumulative important values of the first five families reached 55.88%. The most important species were *Cyclobalanopsis longinix*, *Illicium arborescens*, *Cyclobalanopsis sessilifolia*, *Machilus thunbergii*, *Meliosma sequimulata*, *Diospyros morrisiana*, *Myrsine sequinii*, *Syzygium buxifolium*, *Symplocos sumuntia*, and *Itea parviflora*.

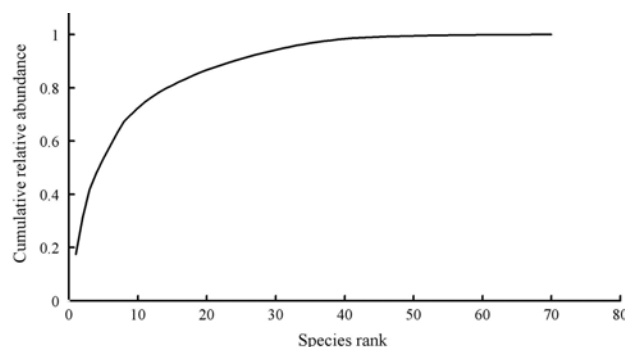


Fig. 6. Relationship between cumulative relative abundance of species and their rank (left to right: from the most common to the rarest) in the Lopei Plot.

Size-class structure

Population structures of the 44 sufficiently abundant species (total stems ≥ 15) indicated relatively continuous regeneration within the plot. Most species were represented by numerous saplings and 3-7 cm dbh stems and by gradually diminishing numbers of stems in successively larger size classes. However, three patterns of population structure could be recognized (Figs. 7-9): the inverse J-shaped, L-shaped, and fluctuating distributions.

The inverse J-shaped pattern (Fig. 7) was shown by 19 species (e.g., *Illicium arborescens*, *Cyclobalanopsis longinix*, *Cyclobalanopsis sessilifolia*, *Meliosma squimulata*, and *Machilus thunbergii*, while the L-shaped pattern (Fig. 8) was determined for 18 species (e.g., *Syzygium*

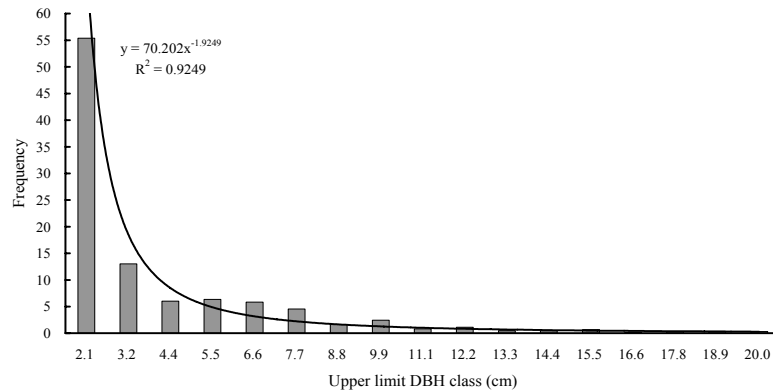


Fig. 7. Inverse J-shaped size-class distribution. Typical species is *Cyclobalanopsis sessilifolia*.

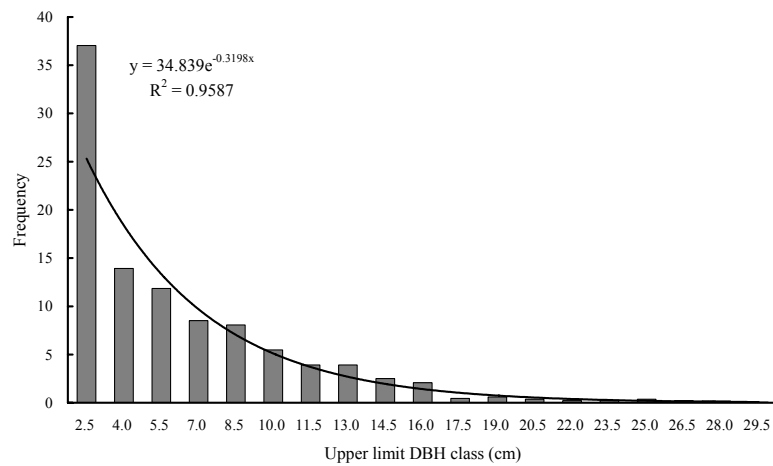


Fig. 8. L-shaped size-class distribution. Representative species is *Syzygium buxifolium*.

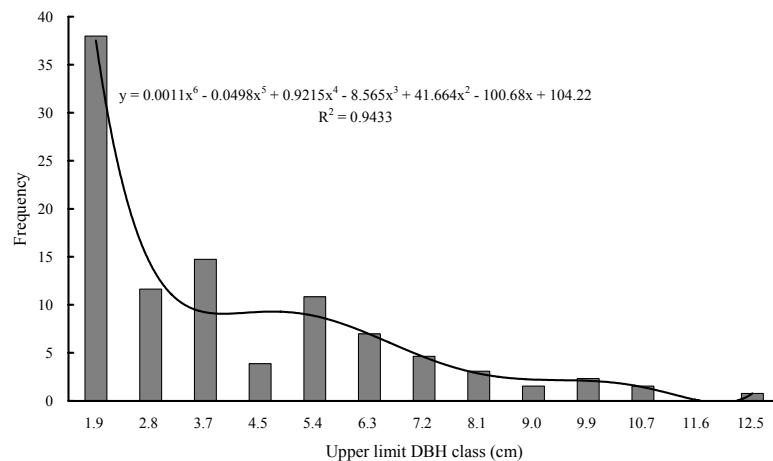


Fig. 9. Fluctuating size-class distribution. Species with this pattern is *Ligustrum japonicum*.

buxifolium, *Litsea acuminata*, *Tricalysia dubia*, *Prunus phaeosticta*, and *Ilex ficoidea*). Both patterns show a decrease of abundance with increasing dbh classes. However, the inverse J-shaped contains more individuals than the L-shaped in the small size classes. A third pattern was shown by seven species (e.g., *Myrsine seguinii*, *Itea parviflora*, and *Ligustrum japonicum*) that had multi-modal distribution, but with more individuals in the smaller size classes (Fig. 9). This type of structure implies periodic regeneration.

Community classification

Results of TWINSpan classification of 100 quadrats based on species important value (IV) suggested two distinctive habitat types at the first dichotomy. When quadrats containing the identified habitat types were superimposed on the topographic map, these clusters were easily identified as occurring on the ridgetop & northeastern slope, and southwestern slope & creek bottoms (Fig. 10). The forest of the first type contained 56 quadrats and was densely stocked with trees only 5-6 m tall. The other type consisted of 44 quadrats, and the height of trees ranged from 13 to 15 m.

The results of DCA ordination (Fig. 11) shows a configuration that agreed in general with the results of the TWINSpan classification. The eigenvalues for the first two DCA axes were 0.173 and 0.068 respectively and together they explained 21% of the overall amount of variance in species data. The ordering across axis 1 of the DCA ordination is also very similar in its species placement (Fig. 12) to that of the TWINSpan classification. *Ilex pedunculosa*, *Viburnum foetidum* var. *rectangulatum*, *Acer kawakamii*, *Callicarpa remotiflora*, *Vaccinium bracteatum*, *Symplocos heishanensis*, *Myrsine seguinii*, *Osmanthus heterophyllus*, *Photinia parvifolia*, *Rhododendron ellipticum*, and, at low values on axis 1, are predominantly found on the ridgetop and northeastern slope. Conversely, at high values on axis 1, the species are those found solely or mainly on

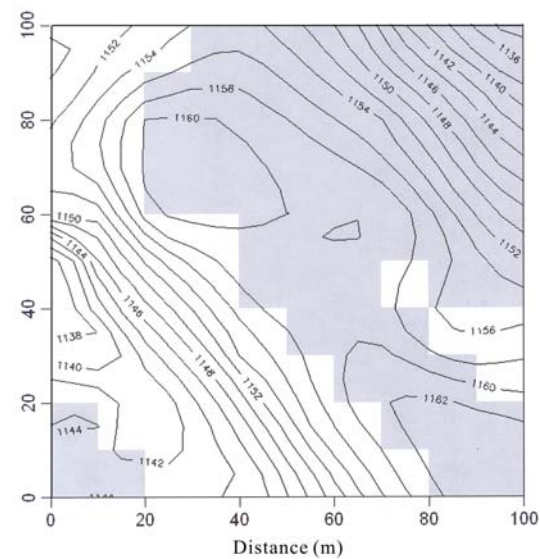


Fig. 10. Topographic map of the Lopei Plot with the TWINSpan clusters superimposed. One hundred quadrats were classified into two habitat types (shaded areas are ridgetops and northeastern slopes, the remaining areas denote southwestern slopes).

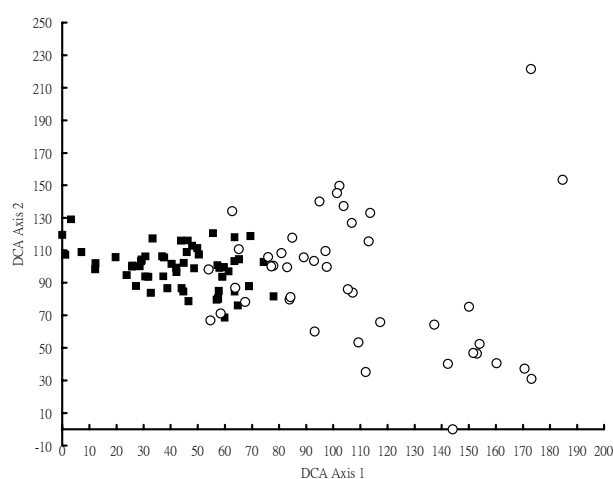


Fig. 11. First two axes of the DCA ordination with the two habitat types delimited by TWINSpan superimposed. Closed square symbols denote quadrats on the ridgetop and northeastern slope, and circular symbols denote quadrats from the southwestern slope.

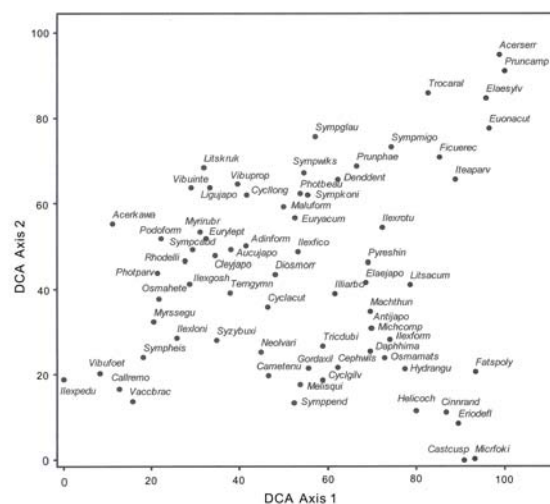


Fig. 12. DCA ordination diagram of the species. Species names are abbreviated by the first four letters of the genus followed by the first four letters of the species. See appendix for full species names.

southwestern slopes, such as *Prunus campanulata*, *Acer serrulatum*, *Euonymus acuto-rhombifolia*, *Elaeocarpus sylvestris*, *Fatsia polycarpa*, *Microtropis fokienensis*, *Castanopsis cuspidata* var. *carlesii*, *Eriobotrya deflexa*, *Itea parviflora*, *Cinnamomum randaiense*, and *Ficus erecta* var. *beeheyana*, etc.

Forests of these two habitats differed both in species composition and structure (Tables 1 and 2). The two forest types, thus identified, are designated below by their respective dominant species and characteristic species.

1. *Cyclobalanopsis longinux*-*Myrsine sequinii* type

A total of 64 species and 9,741 individuals were recorded on the ridgetop and northeastern slope. Stem density was high (17,394 stems/ha). Most trees were quite small and the mean dbh was 5.76 cm. The most important species here, as indicated by importance value, were *Cyclobalanopsis longinux*, and followed by *Cyclobalanopsis sessilifolia*, *Illicium arborescens*, *Machilus thunbergii*, *Myrsine sequinii*, *Diospyros morrisiana*, and *Meliosma squimulata*.

2. *Illicium arborescens*-*Itea parviflora* type

Stem density is lower on the southwestern slope (7,257 stems/ha), but with a relatively larger average dbh of 9.35 cm. A total of 59 species and 3,193 individuals were recorded there. The tree stratum was dominated by *Illicium arborescens*, with an importance value of 17.55%. Other species present, in descending order of importance, were *Cyclobalanopsis longinux*, *Machilus thunbergii*, *Cyclobalanopsis sessilifolia*, *Meliosma squimulata*, *Diospyros morrisiana*, and *Itea parviflora*.

Species diversity

Woody species richness within the 10 × 10 m quadrats varied from 12 to 40 with an average of 25. The total number of species and the number of species per quadrat were consistently greater on the ridgetop and northeastern slope (Table 2). However, the expected species richness for a sample of 1000 individuals was slightly higher on the southwestern slope. Results for other diversity measures (Shannon-Wiener index, Hill's N1 and N2 numbers, and evenness index) revealed comparable values. Species-area curves (Fig. 13) show that the levels of accumulation are in the range of 45-50 species at the 0.01 ha scale. Each of the curves also shows that the number of species is approaching an asymptote, but is still increasing slowly.

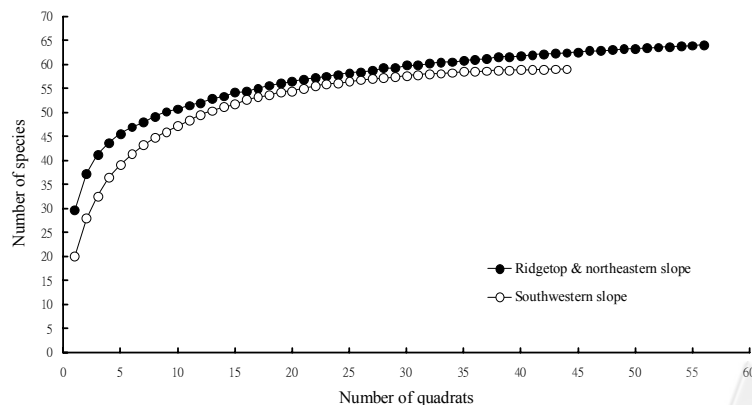


Fig. 13. Species-area curves for the two habitat types of the Lopei Plot.

Table 1. Composition and structure for the two forest types in the Lopei Plot. Species of the first type are ordered by important value (IV).

Species	<u><i>Cyclobalanopsis longinix</i>- <i>Myrsine sequinii</i> type</u>				<u><i>Illicium arborescens</i>- <i>Itea parviflora</i> type</u>			
	Density (stems/ha)	BA (m ² /ha)	% BA	IV	Density (stems/ha)	BA (m ² /ha)	% BA	IV
<i>Cyclobalanopsis longinix</i>	2516	11.79	26.04	20.27	864	7.91	15.90	13.95
<i>Cyclobalanopsis sessilifolia</i>	1870	6.51	14.36	12.57	680	5.66	11.37	10.41
<i>Illicium arborescens</i>	2663	4.18	9.23	12.29	1725	5.54	11.12	17.55
<i>Machilus thunbergii</i>	788	5.26	11.62	8.08	400	11.03	22.15	13.86
<i>Myrsine sequinii</i>	1380	2.45	5.42	6.69	91	0.22	0.43	0.85
<i>Diospyros morrisiana</i>	850	2.77	6.11	5.51	277	3.24	6.51	5.18
<i>Meliosma squimulata</i>	814	2.38	5.27	4.98	507	3.22	6.48	6.76
<i>Syzygium buxifolium</i>	914	1.44	3.19	4.23	230	0.90	1.81	2.50
<i>Symplocos caudata</i>	513	1.17	2.59	2.77	55	0.22	0.44	0.60
<i>Cleyera japonica</i>	484	0.42	0.92	1.85	89	0.19	0.38	0.81
<i>Adinandra formosana</i>	427	0.42	0.92	1.69	127	0.27	0.55	1.16
<i>Osmanthus heterophyllus</i>	150	0.89	1.96	1.41	11	0.15	0.30	0.23
<i>Michelia compressa</i>	288	0.48	1.05	1.36	150	1.04	2.08	2.08
<i>Pyrenaria shinkoensis</i>	263	0.53	1.18	1.35	200	1.00	2.02	2.40
<i>Elaeocarpus japonicus</i>	213	0.56	1.23	1.23	45	0.52	1.05	0.84
<i>Ligustrum japonicum</i>	207	0.31	0.68	0.94	30	0.09	0.19	0.30
<i>Myrica rubra</i>	75	0.51	1.13	0.78	11	0.05	0.10	0.13
<i>Rhododendron leptosanctum</i>	114	0.39	0.86	0.76	16	0.03	0.05	0.14
<i>Symplocos migoii</i>	145	0.28	0.61	0.72	84	0.57	1.14	1.16
<i>Ilex ficoidea</i>	184	0.17	0.37	0.72	102	0.26	0.52	0.97
<i>Daphniphyllum himalaense</i>	141	0.27	0.60	0.71	73	0.79	1.58	1.30
<i>Pourthiaea villosa</i> var. <i>parvifolia</i>	189	0.11	0.25	0.67	11	0.01	0.01	0.09
<i>Prunus phaeosticta</i>	188	0.10	0.22	0.65	120	0.36	0.72	1.20
<i>Tricalysia dubia</i>	166	0.13	0.30	0.63	161	0.20	0.39	1.32
<i>Ternstroemia gymnanthera</i>	154	0.13	0.29	0.59	25	0.03	0.06	0.20
<i>Camellia tenuifolia</i>	159	0.11	0.24	0.58	45	0.06	0.12	0.37
<i>Litsea acuminata</i>	161	0.08	0.18	0.55	170	0.64	1.29	1.83
<i>Dendropanax dentiger</i>	75	0.28	0.62	0.52	39	0.13	0.27	0.40
<i>Ilex lonicerifolia</i>	145	0.08	0.17	0.50	9	0.01	0.02	0.08
<i>Ilex goshiensis</i>	127	0.10	0.23	0.48	18	0.04	0.09	0.17
<i>Neolitsea aciculata</i> var. <i>variabilissima</i>	129	0.06	0.14	0.44	27	0.20	0.40	0.39
<i>Ilex rotunda</i>	84	0.12	0.27	0.38	55	0.22	0.45	0.60
<i>Eurya loquaiana</i>	111	0.04	0.08	0.36	70	0.03	0.06	0.52
<i>Pourthiaea beauverdiana</i> var. <i>notabilis</i>	59	0.15	0.33	0.33	20	0.29	0.58	0.43
<i>Itea parviflora</i>	80	0.08	0.18	0.32	309	2.07	4.15	4.22
<i>Acer kawakamii</i>	71	0.09	0.21	0.31	0	0.00	0.00	0.00
<i>Symplocos wikstroemifolia</i>	50	0.14	0.30	0.30	7	0.07	0.13	0.11
<i>Eurya leptophylla</i>	95	0.01	0.03	0.29	39	0.00	0.01	0.27
<i>Osmanthus matsumuranus</i>	52	0.05	0.10	0.20	48	0.31	0.62	0.64
<i>Castanopsis cuspidata</i> var. <i>carlesii</i>	32	0.05	0.10	0.14	20	0.98	1.97	1.13
<i>Ilex formosana</i>	36	0.02	0.03	0.12	68	0.17	0.35	0.65
<i>Helicia cochichinensis</i>	25	0.04	0.08	0.11	16	0.31	0.62	0.42
<i>Viburnum foetidum</i> var. <i>rectangulatum</i>	29	0.01	0.01	0.09	0	0.00	0.00	0.00
<i>Symplocos heishanensis</i>	21	0.02	0.04	0.08	0	0.00	0.00	0.00
Subtotal	17232	45.16	99.71	99.53	7045	49.03	98.49	98.22
Total	17394	45.29	100.00	100.00	7257	49.78	100.00	100.00

Table 2. Structural characteristics and diversity measures for the two forest types in the Lopei Plot and the 3-ha Lanjenchi Plot at Nanjenshan of the southernmost Taiwan.

Plot	Lopei		Lanjenchi	
Habitat	Ridgetop & northeastern slope (windward site)	Southwestern slope (leeward site)	Windward site	Leeward site
Forest type	<i>Cyclobalanopsis longinux-Myrsine seguinii</i>	<i>Illicium arborescens-Itea parviflora</i>		
Quadrat number	56	44	195	105
Tree density (stems/ha)	17,394	7,257	15,157	6,809
Basal area (m ² /ha)	45.29	49.78	42.70	38.12
Mean dbh (cm)	5.76	9.35	4.13	5.25
Total number of species	64	59	111	104
Mean number of species (0.01 ha)	30	20	37	29
Shannon-Wiener index	2.61	2.66	3.44	3.58
Hill' diversity number N1	14	14	31	36
Hill' diversity number N2	9	10	19	21
Hill' E5 evenness index	0.62	0.65	0.59	0.59
Richness E (S1000)	48	51	74	84

DISCUSSION

The species composition of the Lopei Plot is considered to be characteristic of the Lower *Quercus* forest zone (Su, 1984) of Taiwan montane forests with *Cyclobalanopsis longinux*, *Illicium arborescens*, *Cyclobalanopsis sessilifolia*, and *Machilus thunbergii* as the most dominant species. Locally the *Cyclobalanopsis longinux-Myrsine seguinii* forest type is comparable to the *Myrsine seguinii-Cyclobalanopsis sessilifolia* type (Wang, 1987) in Wulai of northern Taiwan. The *Myrsine seguinii-Cyclobalanopsis sessilifolia* community occurs mainly on mountain ridges and hilltop between 800 to 1,200 m asl., and is composed of *Cyclobalanopsis sessilifolia*, *Machilus thunbergii*, and *Cyclobalanopsis longinux* in the canopy layer, and *Myrsine seguinii*, *Syzygium buxifolium*, *Cinnamomum subavenium*, *Prunus phaeosticta*, and *Ilex goshiensis* in the subcanopy stratum. The species composition of the *Illicium arborescens-Itea parviflora* forest type is similar to that of the *Ilex formosana-Machilus thunbergii* type occurring mainly on the middle slope between 700 to 1,200 m asl. in Wulai area. Major canopy tree species of this type are *Machilus thunbergii*, *Diospyros morrisiana*, *Castanopsis cuspidata* var. *carlesii*, and *Limlia uraiana*, and the subcanopy is dominated by *Cleyera japonica*, *Meliosma squimulata*, *Tricalysia dubia*, *Illicium arborescens*, *Litsea acuminata*, *Michelia compressa*, and *Elaeocarpus japonicus*. The forest type corresponds to the *Cyclobalanopsis paucidentata* Association (under the *Symplocos macrostroma* Alliance) mentioned by Suzuki (1935) which was usually found in northern Taiwan between 900-1,220 m on the ridges straddling the boundary between Taipei and Ilan counties. It is also closely comparable to the *Cyclobalanopsis sessilifolia-C. longinux* forest type recognized by Liu & Su (1976) and Chen (1993) in Wulai area, and the

Cyclobalanopsis longinux-Machilus thunbergii-Cyclobalanopsis sessilifolia dominance-type by Hsieh *et al.* (1998) on the nearby ridge.

Vegetation patterns of the broad-leaved forests of Taiwan have been shown to be determined mainly by the steep gradients in temperature that followed the altitudinal and latitudinal gradients (Su, 1984; Hsieh *et al.*, 1997). However, local variations in topography strongly influence the vegetation pattern at smaller scales (Hsieh *et al.*, 1990; Chen, 1993; Sun *et al.*, 1998). The influence of topographic features, particularly slope aspect, on vegetation is commonly related to prevailing winds. Changes in forest structure and composition along a strong wind-stress gradient have been documented in Taiwan (Sun *et al.*, 1998) and elsewhere in subtropical and tropical regions (Howard 1968; Lawton and Dryer, 1980; Sugden, 1986).

In the Lopei Plot, the ridgetop and northeastern slope generally experiences strong northeasterly monsoon winds in the winter season. The average maximum wind speed was 8-10 m/s (measured by a 3-cup anemometer during Jan. and Feb. 1997), producing marked differences in plant community composition and structure. It has been mentioned that the monsoon winds did not usually cause massive damage to the forests, but had profound effects on the structural and floristic features (Sun *et al.*, 1998; Chen *et al.*, 1997). Typhoons are also common during the period from July to September, and usually cause uprooting and treefall. Most of the typhoon damages were concentrated on the ridgetop and northeastern-facing slope, and this was well reflected by the occurrence of many small gaps created by single treefall or limbfall. The density of standing dead trees was greater on the ridgetop (538 stems) than that on the southwestern slope (201 stems), although the total basal areas were comparable (2.69 vs. 2.84 m²/ha). The canopy openings caused by dead canopy trees and limbfall resulted from natural disturbances greatly change stand structure and improve the light environment in the understory, and provide favorable conditions for certain species (e.g., Kubota, 1995). In the study plot, the density of widespread gap colonist, *Diospyros morrisiana*, was much higher in the windward forest (474 stems) than the leeward forest (125 stems). Its persistence in the forest is assured by the numerous treefalls and dead trees associated with wind disturbance. Studies in the subtropical rain forest in Nanjenshan Forest Dynamics Plot in the southernmost of Taiwan also showed that forest structure and species composition changed dramatically with exposure over short distance (Sun *et al.*, 1998; Hsieh *et al.*, 2000). Chen (1993) surmised that monsoon winds might be one of disturbance agents shaping forest structure in the old-growth forests of northern Taiwan.

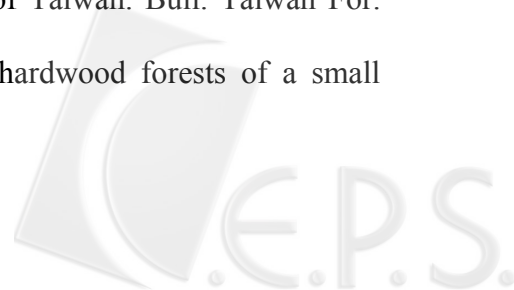
A comparison of the species composition of the Lopei Plot with the Lanjenchi Plot (Sun *et al.*, 1998) at 300-340 m asl. in the southernmost part of Taiwan reveals that only 18 species occur at two study sites. Although the number of shared taxa between two plots is low, the most abundance species, *Illicium arborescens*, is the same. Besides, *Cyclobalanopsis longinux* is dominant in both plots.

In this study stem density of the windward and leeward forests are 17,394 and 7,257 stems/ha, respectively, and these values are slightly higher than those reported for the Lanjenchi Plot (Table 2). The comparison of total basal areas also shows a distinctive difference between the two plots. An increase in monsoon wind exposure not only affected plant composition and structure in these forests, but also plant diversity (Hsieh *et al.*, 2000). It seemed that under a heavy wind stress, diversity measures tended to be lower at the windward sites. However, the present data show comparable values between the windward and leeward forests with the latter only slightly richer (Table 2).



LITERATURE CITED

- 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**: 127-146. (In Chinese)
- Chen, Z.-S., C.-F. Hsieh, F.-Y. Jiang, T.-H. Hsieh and I.-F. Sun. 1997. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. *Plant Ecol.* **132**: 229-241.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* **54**: 427-249.
- Hill, M. O. 1979a. 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., USA.
- Hill, M. O. 1979b. DECORANA—A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. *Ecology and Systematics*, Cornell University, Ithaca, NY., USA.
- 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. and Z.-S. Chen. 1989. Developing an Ecological Data System for Nature Preserves, pp. 58-59. Technical Report, No. 22. Council of Agriculture, Taiwan. (In Chinese)
- Hsieh, C.-F., T.-C. Huang, T.-H. Hsieh, K.-C. Yang and S.-F. Huang. 1990. Structure and composition of the windward and leeward forests in the Wushipi Nature Preserve, northern Taiwan. *J. Taiwan Mus.* **43**: 157-166.
- Hsieh, C.-F., W.-C. Chao, C.-C. Liao, K.-C. Yang and T.-H. Hsieh. 1997. Floristic composition of the evergreen broad-leaved forests of Taiwan. *Nat. Hist. Res. Special Issue* **4**: 1-16.
- Hsieh, C.-F., Z.-S. Chen, Y.-M. Hsueh, K.-C. Yang and T.-H. Hsieh. 1998. Altitudinal zonation of evergreen broad-leaved forest on Mount Lopei, Taiwan. *J. Veg. Sci.* **9**: 201-212.
- Hsieh, C.-F., I.-F. Sun and C.-C. Yang. 2000. Species composition and vegetation pattern of a lowland rain forest at the Nanjenshan LTER site, southern Taiwan. *Taiwania* **45**: 107-119.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577-586.
- Kubota, Y. 1995. Effects of disturbance and size structure on the regeneration process in a sub-boreal coniferous forest, northern Japan. *Ecol. Res.* **10**: 135-142.
- Kudo, Y. and S. Sasaki. 1931. An ecological survey of the vegetation of the border of Lake Jitsugetsutan. *Ann. Rep. Taihoku Bot. Gard.* **1**: 1-50.
- Lawton, R. O. and V. Dryer. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* **18**: 101-116.
- 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*. 25 pp. (In Chinese)
- Liu, T.-S. and H.-J. Su. 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)
- McCune, B. and M. J. Mefford. 1999. *PC-ORD: Multivariate Analysis of Ecological Data* (version 4). MjM Software Design, Gleneden Beach, Oregon, USA.
- Su, H.-J. 1984. Studies on the climate and vegetation types of the natural forest in Taiwan. (II). Altitudinal vegetation zones in relation to temperature gradient. *Quar. J. Chin. For.* **17**: 57-73.
- Sugden, A. M. 1986. The montane vegetation and flora of Margarita Island, Venezuela. *J. Arnold Arbor.* **67**: 187-232.
- Sun, I.-F., C.-F. Hsieh and S. P. Hubbell. 1998. The structure and species composition of a subtropical monsoon forest in southern Taiwan on a steep wind-stress gradient. In: Francisco Dallmeier and James A. Comiskey (eds.). *Forest Diversity Research, Monitoring and Modeling: Conceptual background and Old World Case Studies*, pp. 565-635. Parthenon Publishing Co. Paris, France.
- Suzuki, T. 1935. A preliminary report on the associations in the Laurisilvae in Togokeyi-district, North Taiwan. *Ecol. Rev.* **4**: 298-314.
- Wang, L.-C. 1987. *Multivariate Analysis on the Natural Vegetation in Wulai Area, northern Taiwan*. M.S. thesis, Department of Forestry, National Taiwan University. 82 pp. (In Chinese)



Appendix: List of woody plant species in the Lopei Plot**I. Gymnosperms**

1. Cephalotaxaceae
 1. *Cephalotaxus wilsoniana* Hayata
2. Podocarpaceae
 2. *Nageia nagi* (Thunb.) O. Ktze.

II. Dicotyledons

3. Aceraceae
 3. *Acer kawakamii* Koidz.
 4. *Acer serrulatum* Hayata
4. Aquifoliaceae
 5. *Ilex ficoidea* Hemsl.
 6. *Ilex formosana* Maxim.
 7. *Ilex goshiensis* Hayata
 8. *Ilex lonicerifolia* Hayata
 9. *Ilex pedunculosa* Miq.
 10. *Ilex rotunda* Thunb.
5. Araliaceae
 11. *Dendropanax dentiger* (Harms ex Diels) Merr.
 12. *Fatsia polycarpa* Hayata
6. Caprifoliaceae
 13. *Viburnum foetidum* Wall. var. *rectangulatum* (Graebn.) Rehder
 14. *Viburnum propinquum* Hemsl.
7. Celastraceae
 15. *Euonymus tashiroi* Maxim.
 16. *Microtropis fukienensis* Dunn
8. Cornaceae
 17. *Aucuba japonica* Thunb.
9. Daphniphyllaceae
 18. *Daphniphyllum himalaense* (Benth.) Müll. Arg. subsp. *macropodum* (Miq.) T. C. Huang
10. Ebenaceae
 19. *Diospyros morrisiana* Hance
11. Elaeocarpaceae
 20. *Elaeocarpus japonicus* Sieb. & Zucc.
 21. *Elaeocarpus sylvestris* (Lour.) Poir.
12. Ericaceae
 22. *Rhododendron leptosantherum* Hayata
 23. *Vaccinium bracteatum* Thunb.
13. Euphorbiaceae
 24. *Antidesma japonicum* Sieb. & Zucc. var. *densiflorum* Hurus.
14. Fagaceae
 25. *Castanopsis cuspidata* (Thunb.) Schottky var. *carlesii* (Hemsl.) Yamaz.
 26. *Cyclobalanopsis gilva* (Blume) Oerst.



- 27. *Cyclobalanopsis longinux* (Hayata) Schott.
- 28. *Cyclobalanopsis sessilifolia* (Blume) Schottky
- 15. Illiciaceae
 - 29. *Illicium arborescens* Hayata
- 16. Lauraceae
 - 30. *Cinnamomum subavenium* Miq.
 - 31. *Litsea acuminata* (Blume) Kurata
 - 32. *Litsea hypophaea* Hayata
 - 33. *Machilus thunbergii* Sieb. & Zucc.
 - 34. *Neolitsea aciculata* (Blume) Koidz. var. *variabilissima* (Hayata) J. C. Liao
- 17. Magnoliaceae
 - 35. *Michelia compressa* (Maxim.) Sargent
- 18. Moraceae
 - 36. *Ficus erecta* Thunb. var. *beeheyana* (Hook. & Arn.) King
- 19. Myricaceae
 - 37. *Myrica rubra* (Lour.) Sieb. & Zucc.
- 20. Myrsinaceae
 - 38. *Myrsine seguinii* Lev.
- 21. Myrtaceae
 - 39. *Syzygium buxifolium* Hook. & Arn.
- 22. Oleaceae
 - 40. *Ligustrum japonicum* Thunb.
 - 41. *Osmanthus heterophyllus* (G. Don) P. S. Green
 - 42. *Osmanthus matsumuranus* Hayata
- 23. Proteaceae
 - 43. *Helicia cochichinensis* Lour.
- 24. Rosaceae
 - 44. *Eriobotrya deflexa* (Hemsl.) Nakai
 - 45. *Malus docmeri* (Bois) Chev.
 - 46. *Pourthiaea beauverdiana* (C. K. Schneid.) Hatus. var. *notabilis* (Rehder & Wilson) Hatus.
 - 47. *Pourthiaea villosa* (Thunb. ex Murray) Decne. var. *parvifolia* (Pritz.) Iketani & H. Ohashi
 - 48. *Prunus campanulata* Maxim.
 - 49. *Prunus phaeosticta* (Hance) Maxim.
- 25. Rubiaceae
 - 50. *Tricalysia dubia* (Lindl.) Ohwi
- 26. Sabiaceae
 - 51. *Meliosma squimulata* Hance
- 27. Saxifragaceae
 - 52. *Hydrangea angustipetala* Hayata
 - 53. *Itea parviflora* Hemsl.
- 28. Symplocaceae
 - 54. *Symplocos konishii* Hayata
 - 55. *Symplocos glauca* (Thunb.) Koidz.
 - 56. *Symplocos heishanensis* Hayata
 - 57. *Symplocos migoi* Nagam.



- 58. *Symplocos pendula* Wight var. *hirtystylis* (Clarke) Noot.
- 59. *Symplocos caudata* Wall. ex G. Don
- 60. *Symplocos wikstroemifolia* Hayata
- 29. Theaceae
 - 61. *Adinandra formosana* Hayata
 - 62. *Camellia tenuifolia* (Hayata) Cohen-Stuart
 - 63. *Cleyera japonica* Thunb.
 - 64. *Eurya loquaiana* Dunn
 - 65. *Eurya leptophylla* Hayata
 - 66. *Gordonia axillaris* (Roxb.) Dietr.
 - 67. *Pyrenaria shinkoensis* (Hayata) H. Keng
 - 68. *Ternstroemia gymnanthera* (Wight & Arn.) Sprague
- 30. Trochodendraceae
 - 69. *Trochodendron aralioides* Sieb. & Zucc.
- 31. Verbenaceae
 - 70. *Callicarpa remotiflora* W. F. Lin & J. L. Wang



台灣北部羅培山山地雨林的物種組成及森林結構

林奐宇⁽¹⁾、楊國禎⁽²⁾、謝宗欣⁽³⁾、謝長富^(1,4)

(收稿日期：2005 年 3 月 22 日；接受日期：2005 年 6 月 15 日)

摘 要

本文旨在探討台灣北部羅培山山地雨林之森林結構及物種組成，於 1989 年起在海拔 1,136-1,164 m 處設立一公頃之永久樣區，樣區內所有胸高直徑 (dbh) ≥ 1 cm 之木本植物均加以標定、鑑別、度量及記錄。總共記錄 12,934 株植物，分屬於 70 分類群及 31 科。植株數量最多之科為殼斗科、八角茴香科及茶科，總計為所有植株之 51.5%。依據植株之總底面積之大小，優勢種分別為錐果櫟、紅楠、槲櫟、紅花八角、山紅柿及綠樟。雙向指標種分析法 (TWINSPAN) 及降趨對應分析法 (DCA) 同時可將本樣區畫分成二種林型，其分佈與坡向及暴露程度有密切相關。所區分出之林型以優勢種及特徵種命名之，各為錐果櫟—大明橘型及紅花八角—小花鼠刺型。前者生長於稜脊及東北向坡地，面對強烈東北季風吹襲；後者則分部於隱蔽之西南向坡地及溪谷。兩種林型不論在結構及物種組成上均有明顯區別。樣區中大部分的物種在徑級結構上多呈現反 J-型或 L-型分佈，表示在樣區中均能維持良好之更新狀態。

關鍵詞：永久樣區、林型、植群分類、植群排序、徑級結構、多樣性。

1. 國立台灣大學生態學與演化生物學研究所，台北市 106 羅斯福路 4 段 1 號，台灣。

2. 靜宜大學生態學系，台中縣 433 沙鹿鎮中棲路 200 號，台灣。

3. 國立台南大學自然科學教育學系，台南市 700 樹林街 2 段 33 號，台灣。

4. 通信作者。Tel. 886-2-33662474; Email: tnl@ntu.edu.tw

