

## Research paper

## Species Composition, Size-Class Structure, and Diversity of the Lienhuachih Forest Dynamics Plot in a Subtropical Evergreen Broad-Leaved Forest in Central Taiwan

Li-Wan Chang,<sup>1,2)</sup> Jeen-Lian Hwong,<sup>3)</sup> Shau-Ting Chiu,<sup>2,4,7)</sup>  
 Hsiang-Hua Wang,<sup>5)</sup> Kuoh-Cheng Yang,<sup>6)</sup> Hsiu-Ying Chang,<sup>6)</sup>  
 Chang-Fu Hsieh<sup>4)</sup>

### [ Summary ]

The Lienhuachih Forest Dynamics Plot (FDP), measured 500 m by 500 m square, is located in central Taiwan. The collected data, followed a unified method adopted for the worldwide FDP network, were analyzed for floristic composition, size-class structure, and species diversity. In total, the censused trees and shrubs belonged to 144 species in 88 genera and 46 families. The most dominant families were the Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and Melastomataceae. In total, 153268 (6131 ha<sup>-1</sup>) individuals were recorded, and the total basal area was 34.77 m<sup>2</sup> ha<sup>-1</sup>. Of the 144 species, the most abundant were *Randia cochinchinensis* and *Blastus cochinchinensis*. *Pasania nantoensis* had the highest basal area (8.38%), followed by *Engelhardtia roxburghiana* (8.12%) and *Schefflera octophylla* (7.23%). Calculation of the importance value (IV, incorporating relative values of abundance and basal area) showed that *R. cochinchinensis*, *B. cochinchinensis*, *S. octophylla*, *Cryptocarya chinensis*, and *E. roxburghiana* were the most dominant species with the highest IV values in the plot. The sum of the 30 top species' IV reached 83.06% of the whole. Although the 1st 2 species were understory and very dominant due to the large number of individuals, certain numbers of rare species however increased the floristic diversity in the plot. Based on the species composition, the forest is characteristic of the *Machilus-Castanopsis* forest

<sup>1)</sup> Technical Service Division, Taiwan Forestry Research Institute, 53 Nanhai Rd., Taipei 10066, Taiwan. 林業試驗所技術服務組，10066台北市南海路53號。

<sup>2)</sup> Institute of Ecology and Evolutionary Biology, National Taiwan University, 1 Roosevelt Rd., Sec. 4, Taipei 10617, Taiwan. 國立台灣大學生態學與演化生物學研究所，10617台北市羅斯福路四段1號。

<sup>3)</sup> Lienhuachih Research Center, Taiwan Forestry Research Institute, 43 Hwalung Ln., Wucheng Vil., Yuchi Township, Nantou 55541, Taiwan. 林業試驗所蓮華池研究中心，55541南投縣魚池鄉五城村華龍巷43號。

<sup>4)</sup> Department of Botany, National Museum of Natural Science, 1 Guanqian Rd., Taichung 40453, Taiwan. 國立自然科學博物館植物學組，40453台中市館前路1號。

<sup>5)</sup> Fushan Research Center, Taiwan Forestry Research Institute, 1 Shuangpi Rd., Huxi Vil., Yuanshan Township, Yilan 26445, Taiwan. 林業試驗所福山研究中心，26445宜蘭縣員山鄉湖西村雙埤路1號。

<sup>6)</sup> Department of Ecology, Providence University, 200 Zhongqi Rd., Shalu Township, Taichung 43301, Taiwan. 靜宜大學生態學系，43301台中縣沙鹿鎮中棲路200號。

<sup>7)</sup> Corresponding author, e-mail: stchiu@mail.nmns.edu.tw 通訊作者。

zone of Taiwan, with certain dominant understory species and possessing 2 pioneer species in the major canopy composition.

For the size-class structure, 102 (each with total stems  $\geq 25$ ) species showed 4 patterns of size-class distribution: L-shaped, inverse J-shaped, fluctuating, and bell-shaped. The former 3 patterns in a total of 98 species, including a great number of small-sized individuals, imply that most current species in this study site can display good recruitment with rich resources of saplings. The woody plant richness of the Lienhuachih FDP is the highest among low-elevation FDPs in Taiwan. Compared to other Center of Tropical Forest Science forest dynamics plots on islands, Fisher's alpha diversity ( $ha^{-1}$ ) index of the subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of other FDPs in the tropics.

**Key words:** species composition, size class structure, diversity, subtropical evergreen broad-leaved forest, Lienhuachih Forest Dynamics Plot.

**Chang LW, Hwong JL, Chiu ST, Wang HH, Yang KC, Chang HY, Hsieh CF. 2010.** Species composition, size-class structure and diversity of the Lienhuachih Forest Dynamics Plot in a subtropical evergreen broad-leaved forest in central Taiwan. *Taiwan J For Sci* 25(1):81-95.

研究報告

## 蓮華池常綠闊葉林動態樣區之物種組成、徑級結構 與多樣性研究

張勵婉<sup>1,2)</sup> 黃正良<sup>3)</sup> 邱少婷<sup>2,4,7)</sup> 王相華<sup>5)</sup> 楊國楨<sup>6)</sup> 張秀瑩<sup>6)</sup> 謝長富<sup>4)</sup>

### 摘要

依據CTFS長期進行永久樣區研究所發展而成之作業模式，進行木本植物普查，於蓮華池天然林內設置一處25公頃(500 m × 500 m)之森林動態學研究永久樣區。調查項目包含每一棵樹的物種名稱、胸高直徑(DBH)與每一棵樹木的位置，調查結果區域內共計有144種木本植物，分屬於46科，88屬；其中DBH在1 cm以上的木本植物株數共計153,268株(6131株/公頃)。

以全樣區各科重要值指數而言，以樟科、殼斗科、茜草科最為優勢。統計數量最多的種類者為茜草樹，次多者為柏拉木。全樣區平均每公頃底面積為34.77 m<sup>2</sup>。南投石櫟底面積最大，佔全部底面積的8.38%，黃杞及鵝掌柴分別位居第二8.12%及第三7.23%。以重要值IV(相對密度及相對底面積加總)而言，樣區內最優勢的種類分別為茜草樹8.34%及柏拉木5.50%，其次為鵝掌柴5.41%，前30名物種累計可達83.06%。總體而言，優勢組成的集中於少數物種，而株數稀少之種類增加樣區物種的多樣性。

各種類徑級分佈呈現4型，分別為L型、倒J型、波動型及鐘型。前3型共98種，表此森林大部份的物種有足夠的幼苗，更新良好。以生物多樣性而言，與台灣其他低海拔動態樣區比較，蓮華池動態樣區為最為豐富；另與世界上島嶼動態樣區比較，其多樣性值低於其它熱帶的樣區，卻和波多黎各動態樣區相當。

**關鍵詞：**物種組成、徑級結構、多樣性、亞熱帶常綠闊葉林、蓮華池動態樣區。

張勵婉、黃正良、邱少婷、王相華、楊國楨、張秀瑩、謝長富。2010。蓮華池常綠闊葉林動態樣區之物種組成、徑級結構與多樣性研究。台灣林業科學25(1):81-95。

## INTRODUCTION

In order to study spatial and temporal patterns of tree and shrub populations, recent studies of forest plots frequently adopted a large plot area. These large datasets that might encompass environmental variations can be used to examine the mechanisms that maintain species diversity, study the consequences of rarity of local species survival, and monitor long-term changes to detect effects of climate change (Hubbell and Foster 1983, Masaki et al. 1992, Tanouchi and Yamamoto 1995, Yamakura et al. 1995, Yamamoto et al. 1995, Condit et al. 1996, Condit 1998, Sato et al. 1999, Manabe et al. 2000). Forest Dynamics Plots (FDPs) were established and used a standardized sampling methodology which allowed researchers to compare directly data collected at different sites (Losos and Leigh 2004).

Taiwan is a mountainous island with the rich ecological resources. To understand forest dynamic changes, several FDPs have been successively established since 1990 (Yang et al. 2008), but large intact FDPs of > 5 ha in area in the low-elevation zone included only the Fushan FDP in northern and the Kenting FDP in southern Taiwan. Both are surrounded by intact conserved forests: the Hapen Natural Conservation area (Su et al. 2007) and Kenting National Park (Wang et al. 2004), respectively. Due to the early and sustained development in central Taiwan, it is difficult to find an intact large forest with no artificial disturbances. However, to monitor forest ecological changes and succession for all of Taiwan, the Lienhuachih forest is the largest one remaining at low elevations in central Taiwan.

The Lienhuachih forest was an aboriginal hunting ground so it was conserved intact with few disturbances. More than half of the species of the Lauraceae and Fagaceae were

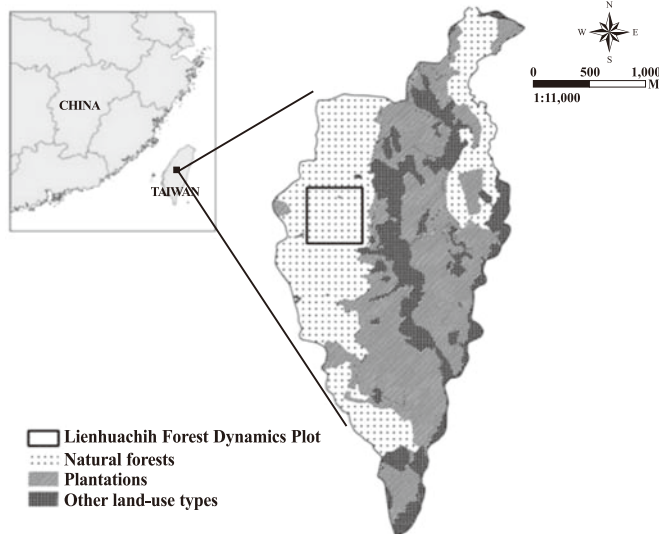
concentrated in this area, and many rare endemic species existed in this unique habitat (Lu et al. 2001). Lienhuachih was a conserved natural broad-leaved forest representative of central Taiwan. Therefore, establishing an FDP at Lienhuachih can conserve the natural vegetation of central Taiwan, and also allow the monitoring and study of broad-leaved forest dynamics to accumulate knowledge of northern, central, and southern forests throughout all lowlands of Taiwan.

This study includes the species composition, size-class structure, and diversity of the forest of the Lienhuachih FDP. It can serve as a foundation for cross-site comparisons with other FDPs and ecosystems in Taiwan.

## MATERIALS AND METHODS

### Study site

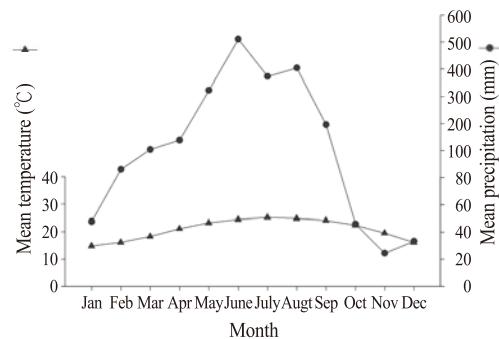
In July 2008, a 25-ha (500 m × 500 m) FDP (23°54'49"N, 120°52'43"E) was established within the evergreen, broad-leaved forest in the Lienhuachih Experimental Forest (LEF), Nantou County, central Taiwan (Fig. 1), as part of the Taiwan Forest Dynamics Monitoring Network. The study was conducted in a 25-ha (500 m × 500 m) FDP (23°54'49"N, 120°52'43"E) in a natural forest of the LEF, Nantou County, central Taiwan (Fig. 1). The substrate consisted of alternating argillaceous sandstone and shale. The dominant soils could be classified into 2 types, Typical Dystrochrept and Typical Hapleudults red soils (King 1986). The mean annual temperature was 20.8°C. The hottest month of the year was July with a mean temperature of 25.2°C, and the coldest was January with a mean temperature of 14.8°C. The annual precipitation was 2285.0 mm with seasonal variation throughout the year. More than half of the annual rainfall occurred between May



**Fig. 1.** Location of the 25-ha Lienhuachih Forest Dynamics Plot in the Lienhuachih Experimental Forest, Nantou County, central Taiwan.

and September, while the dry season usually began in October and lasted through February with 5 consecutive months averaging <100 mm precipitation a month. The mean relative humidity was 87.1% (Fig. 2) (Lu et al. 2008). Typhoons, a common occurrence in the LEF, swept through the area with violent winds and extremely heavy rainfall, and often caused severe damage (Lee et al. 2008). Landslides also took place, mainly caused by heavy rainfall events and the reshaping of stream channels (Lee et al. 2008).

The LEF covered a total area of 461 ha with elevations ranging 576~925 m. About half of the LEF was composed of natural forests, while the other half was made up of various artificial plantations. In total, 879 vascular plant species, belonging to 177 families and 561 genera, had been recorded within the entire LEF (Hwong et al. 2002). The dominant vegetation type in the LEF was considered to be a Lauro-Fagaceous forest (Su 1984). Most of the trees were *Castanopsis* spp., *Cyclobalanopsis* spp., *Machilus* spp., and *Schima superba* (Hwong et al. 2002). Other human



**Fig. 2.** Climate diagram for the Lienhuachih Experimental Forest.

activities in small, widely spaced villages, with agricultural fields and small plantations, occurred within and around the LEF. Natural vegetation in the area was fragmented, degraded, and isolated (Lee et al. 2008).

### Field inventory

Electronic total-station theodolites were used for precise topographic measurements. The field teams measured all horizontal points at 20-m intervals within the 25-ha plot. The plot was divided into 625 quadrats of 20 m

× 20 m, each with other subsidiary points at 10-m intervals. Each 20 m × 20 m quadrat was further divided into 16 subquadrats of 5 m × 5 m.

All freestanding trees ≥ 1 cm in diameter at breast height (DBH) were mapped, measured, identified, and tagged. The botanical nomenclature, life-form, and endemism of all species, following the Flora of Taiwan (Huang 1993-2000), were determined. Species rareness of fewer than 25 total individuals (< 1 individual ha<sup>-1</sup>) was considered a rare species in the plot (Hubbell and Foster 1986).

### Statistical analysis

Three parameters, stem density, basal area, and the importance value [IV, which is (relative density + relative basal area)/2], were used to describe the population structure of tree species. The relative dominance of each family and species was determined based on its IV. The main stems of plants with multiple branches at breast height were counted as 1 individual for the density calculation. However, the sum of the basal areas of all stems was used for the basal area.

For the size-class analysis, species with >25 individuals in the plot were analyzed, and each species was carried out by constructing a bar chart with DBH size classes against the numbers of individuals (Hough 1932, Tubbs 1977, McCarthy et al. 1987, Fan et al. 2005). Due to the varied growth rates, limitations of DBH sizes for different species, and non-unified size structures among species, the determination of wide-ranging size class scales followed the modified Sturges's equation instead of using a log-normal equation.

Modified Sturges' equation:  $M = 6 \times \log n_i$ ; where  $n_i$  is the number of individuals of species  $i$ . The class interval of each species = (DBHmax - DBHmin) /  $M$ .

For floristic diversity, the species rich-

ness, evenness, the Shannon-Wiener diversity index, and Fisher's alpha were used (Hurlbert 1971). Fisher's alpha is a mathematical calculation for determining the diversity within a population, which is usually expressed as the species richness of an area (Fisher et al. 1943, Rosenzweig 1995). It is independent of the sample size and is used to extrapolate species richness to large areas (Losos and Leigh 2004).

Richness is the number of species.

Evenness is  $H' / \ln(\text{Richness})$ .

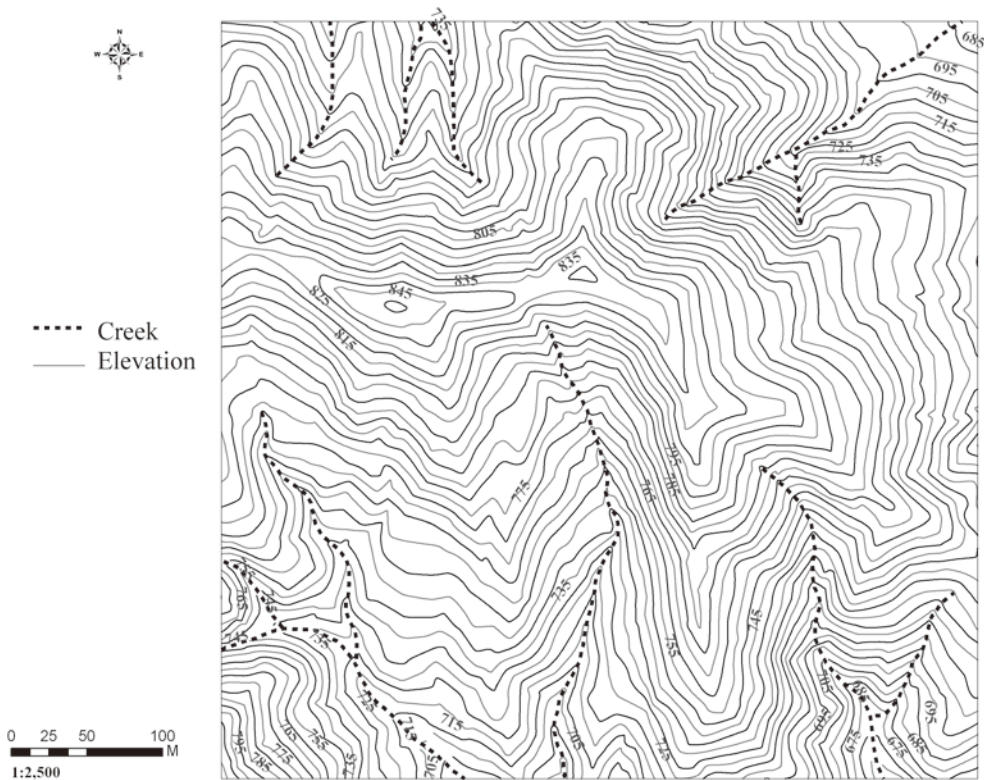
The Shannon-Wiener diversity index ( $H'$ ) is  $-\sum [P_i \times \ln(P_i)]$ ; where  $P_i$  is the  $n_i/N$ ;  $n_i$  is the number of individuals in species  $i$ ; the abundance of species  $i$ ; and  $N$  is the total number of all individuals.

Fisher's alpha:  $S = \alpha \ln(1 + n / \alpha)$ ; where  $S$  is the number of species; and  $n$  is the number of individuals.

## RESULTS

### Topographic features

The elevation of the plot ranged from 667 m to 845 m above the sea level. The average slope of the plots was about 35.3°, so the land was very steep. The topography of the plot was characterized by hills with valleys, steep slopes, and ridges. The ridge lies between 2 slopes, a steep slope facing north and gentler slope facing south. Seepage ways, spurs, small hillocks, and several seasonal streamlets cut through these slopes (Fig. 3). Small streams seasonally appeared to carry water in wet seasons. When typhoons with heavy rains passed nearby, instant large amounts of rainfall particularly caused landslides and the collapse of steep slopes and stream banks. In the dry season, small streams usually showed an anhydrous state. The topographic features displayed high spatial heterogeneity within the Lienhuachih FDP (Fig. 3).



**Fig. 3.** Contour map of the Lienhuachih Forest Dynamics Plot with 5-m contour intervals. The dotted lines indicate creeks.

### Floristic Composition

The 153,268 (6131 stems  $\text{ha}^{-1}$ ) trees surveyed within the 25-ha plot included 144 species in 88 genera and 46 families. The basal area was  $869.31 \text{ m}^2 (25 \text{ ha})^{-1}$  ( $34.77 \text{ m}^2 \text{ ha}^{-1}$ ). With the exception of 2 gymnosperms (*Podocarpus nakaii*, and *Pinus morrisonicola*) and 1 monocotyledon (*Arecae catechu*), all woody species were dicotyledons. These included of 27 canopy species, 72 sub-canopy species, and 45 shrubs species. Among these, 23 species are endemic in Taiwan.

The 5 most abundant species in descending order were *Randia cochinchinensis* (Rubiaceae), *Blastus cochinchinensis* (Melastomataceae), *Euonymus laxiflorus* (Celastraceae), *Cryptocarya chinensis* (Lauraceae), and *Tricalysia dubia* (Rubiaceae). The first

2 species are small trees or shrubs which are distributed throughout most of the plot. Both accounted for 24.32% of the total abundance, but only 3.53% of the total basal area. Based on the basal area, the dominant species were large-statured, less-abundant trees, including *Pasania nantoensis* (Fagaceae), *Engelhardtia roxburghiana* (Juglandaceae), *Schefflera octophylla* (Euphorbiaceae), *Cryptocarya chinensis* (Lauraceae), and *Schima superba* (Theaceae). Most of them, except *C. chinensis*, are canopy species. The most important species as indicated by the IVs were *R. cochinchinensis*, *B. cochinchinensis*, *S. octophylla*, *C. chinensis*, and *E. roxburghiana*. The top 30 dominant species contributed over 80% to the total IV (Table 1). Among the 20 most dominant species, *Mallotus paniculatus* at

10th and *Sapium discolor* at 20th are pioneer species, and both reached the top 10 major canopy species with the highest IV.

Families with the most number of species in the plot were the Lauraceae, followed

by the Rubiaceae, Fagaceae, Theaceae, and Euphorbiaceae. Families with the greatest basal areas were the Fagaceae (26.47% of the total basal area), followed by the Lauraceae, Juglandaceae, Euphorbiaceae, and Araliaceae.

**Table 1. Top 30 species with the highest importance values in the Lienhuachih Forest Dynamics Plot**

Species	Basal area [m <sup>2</sup> (25 ha) <sup>-1</sup> ]	Relative basal area (%)	Abundance [stems (25 ha) <sup>-1</sup> ]	Relative density (%)	Importance Value (%)	Mean DBH (cm)
<i>Randia cochinchinensis</i> +	26.95	3.10	21075	13.75	8.43	2.88
<i>Blastus cochinchinensis</i> *	3.77	0.43	16199	10.57	5.50	1.44
<i>Schefflera octophylla</i>	62.88	7.23	5490	3.58	5.41	7.34
<i>Cryptocarya chinensis</i> +	53.06	6.10	6936	4.53	5.31	5.16
<i>Engelhardtia roxburghiana</i>	70.55	8.12	1769	1.15	4.63	12.45
<i>Pasania nantoensis</i>	72.89	8.38	821	0.54	4.46	11.28
<i>Cyclobalanopsis pachyloma</i>	36.17	4.16	3875	2.53	3.34	6.80
<i>Diospyros morrisiana</i>	26.82	3.09	5001	3.26	3.17	5.16
<i>Cinnamomum subavenium</i> +	30.64	3.52	3800	2.48	3.00	5.27
<i>Mallotus paniculatus</i>	30.35	3.49	3794	2.48	2.98	6.40
Top 10	414.08	47.63	68,760	44.86	46.25	
<i>Tricalysia dubia</i> +	15.62	1.80	6251	4.08	2.94	4.12
<i>Schima superba</i>	44.86	5.16	744	0.49	2.82	16.88
<i>Helicia formosana</i> +	17.47	2.01	5241	3.42	2.71	3.81
<i>Euonymus laxiflorus</i> *	2.94	0.34	7767	5.07	2.70	1.83
<i>Syzygium buxifolium</i> +	11.82	1.36	5962	3.89	2.63	3.59
<i>Castanopsis fargesii</i>	31.97	3.68	1277	0.83	2.26	7.71
<i>Ormosia formosana</i>	11.08	1.27	4779	3.12	2.20	2.93
<i>Psychotria rubra</i> *	5.09	0.59	5720	3.73	2.16	2.12
<i>Ardisia quinquegona</i> *	3.35	0.38	5693	3.71	2.05	2.08
<i>Sapium discolor</i>	24.32	2.80	1176	0.77	1.78	10.05
Top 20	582.59	67.02	113,370	73.97	70.49	
<i>Helicia rengetiensis</i> +	8.23	0.95	3196	2.09	1.52	3.46
<i>Litsea acuminata</i> +	1300	1.49	2183	1.42	1.46	5.06
<i>Castanopsis kawakamii</i>	22.07	2.54	331	0.22	1.38	8.28
<i>Neolitsea aciculata</i> +	3.10	0.36	3514	2.29	1.32	2.39
<i>Podocarpus nakaii</i>	8.26	0.95	2494	1.63	1.29	4.69
<i>Glochidion acuminatum</i>	12.47	1.43	1396	0.91	1.17	7.56
<i>Castanopsis cuspidata</i>	16.58	1.91	647	0.42	1.16	8.04
<i>Pasania konishii</i>	11.86	1.36	1320	0.86	1.11	4.26
<i>Pasania harlandii</i>	13.42	1.54	986	0.64	1.09	7.52
<i>Machilus zuihoensis</i>	15.35	1.77	544	0.35	1.06	10.46
Top 30	706.92	81.32	129,981	84.81	83.06	

+ sub-canopy species; \* shrub species. No marks indicating canopy species. DBH, diameter at breast height.

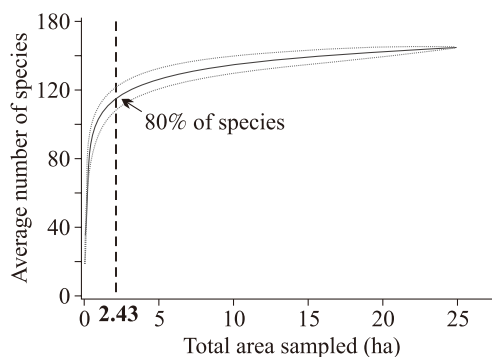
The Rubiaceae had the greatest density, consisting of 20.86% of the total. The top 15 families in terms of IVs are shown in Table 2. The most dominant families were ranked in the order of the Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and then the Melastomataceae.

The species-area curve shows that the number of species increased rapidly, and the curve inclined to nearly a plateau after an area of 10 ha (Fig. 4). The curve appears to approach an asymptote, and very few species were added to the plot beyond the point.

The species-area curve showed that the number of species increased rapidly until the incline plot area reached 2.43 ha, when about 80% of species had accumulated (Fig. 4). The curve inclined to nearly a plateau after an accumulated total area of 10 ha. Then, the curve appeared to approach an asymptote and very few species were added as the plot size was

enlarged.

The species-abundance pattern (Fig. 5) showed that a few species contributed a great proportion to the stem abundance. The sum of ranks 1 and rank 2 was 37,274 individuals as 24.32% of the total. From ranks 3 to 22, the curve exhibited a shallow gradient, and the total of the top 22 species reached 80%

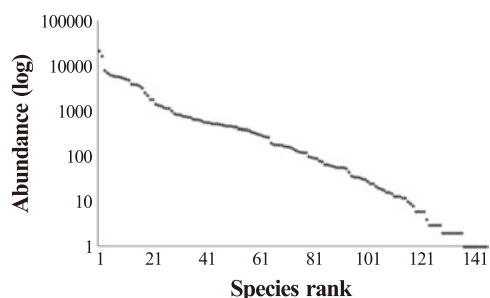


**Fig. 4. Species-area curve for the 25-ha Lienhuachih Forest Dynamics Plot.**

**Table 2. Top 15 families with the highest importance values in the Lienhuachih Forest Dynamics Plot**

Family	Basal area (m <sup>2</sup> /25 ha)	Relative basal area (%)	Density (stems/25 ha)	Relative Density (%)	Important Value (%)	Number of Species
Fagaceae	230.15	26.47	21597	10.62	18.55	11
Lauraceae	152.41	17.53	25771	12.68	15.10	17
Rubiaceae	51.97	5.98	42417	20.86	13.42	13
Euphorbiaceae	67.60	7.78	7166	3.52	5.65	8
Melastomataceae	3.83	0.44	21274	10.46	5.45	2
Araliaceae	62.88	7.23	6359	3.13	5.18	1
Proteaceae	26.22	3.02	14101	6.94	4.98	3
Juglandaceae	70.55	8.12	2401	1.18	4.65	1
Theaceae	58.63	6.74	3013	1.48	4.11	9
Ebenaceae	27.66	3.18	5875	2.89	3.04	2
Myrsinaceae	8.16	0.94	8789	4.32	2.63	5
Celastraceae	2.95	0.34	9907	4.87	2.61	3
Myrtaceae	13.88	1.60	7226	3.55	2.58	2
Leguminosae (Fabaceae)	11.08	1.27	5180	2.55	1.91	2
Aquifoliaceae	6.93	0.80	5048	2.48	1.64	7
Others	74.41	8.56	17191	8.46	8.51	59
Total	869.31	100.00	203315	100.00	100.00	144





**Fig. 5. Species-abundance curve for the Lienhuachih Forest Dynamic Plot.**

relative abundance. Among 144 species, 43 species (29.86%) had < 25 individuals (< 1 individual  $\text{ha}^{-1}$ , and were considered to be rare species), and 9 of them were represented by a single stem.

#### Size-class structure

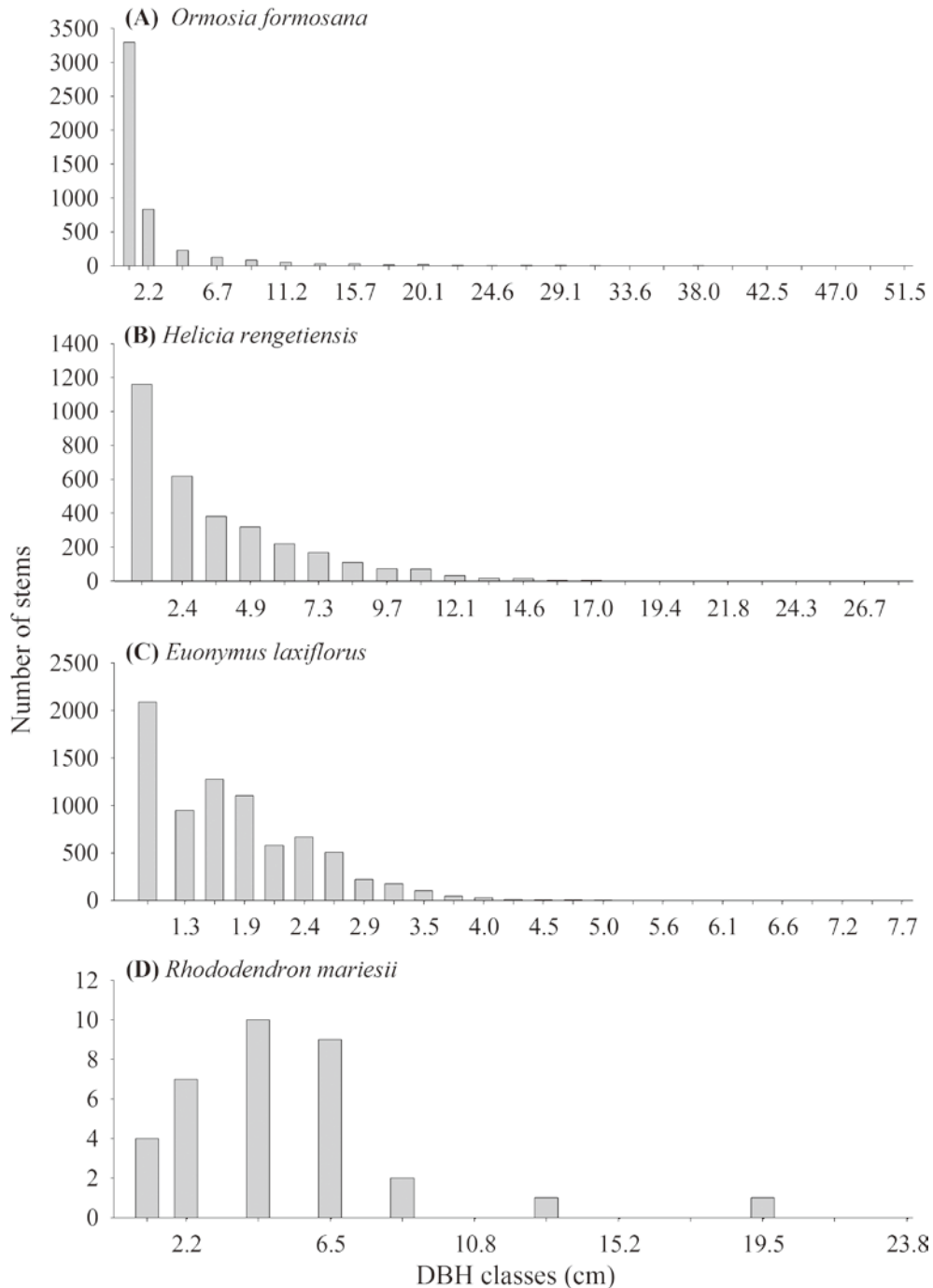
One hundred and two (each with total stems  $\geq 25$ ) out of 144 species were examined by size class. The charts exhibited 4 patterns: L-shaped, inverse J-shaped, fluctuating, and bell-shaped (Fig. 6). The L-shaped pattern was found in 9 species, such as *Ormosia formosana* and *Psychotria rubra*, and it showed a dramatic drop in the number of individuals in the small size-class. The inverse J-shaped pattern had a smooth, downward curve, which was shown by 60 species; for example, *E. roxburghiana* and *Helicia rengetiensis*. Twenty-nine species showed the fluctuating pattern, having the greatest number of individuals in the smallest size and a varied number of individuals in the other size classes, such as *Mallotus paniculatus* and *E. laxiflorus*. Only 4 species, such as *Antidesma japonicum* and *Rhododendron mariesii*, showed a bell-shaped pattern, and appeared to have quite a few saplings.

#### Floristic diversity

The composition and diversity of the size-classes of all woody individuals in the

Lienhuachih FDP showed that trees of the size class  $\geq 10$ -cm dbh included 16,513 stems (10.77%) and made up 710.08  $\text{m}^2$  (81.68%) of the total basal area and those in the size class  $\geq 30$ -cm dbh only included 2,267 stems (1.48%) with 370.11  $\text{m}^2$  (42.57%) in basal area. The Evenness index for those with dbh  $\geq 10$  cm of the 25-ha plot was 0.79, which was very high, and 0.86  $\text{ha}^{-1}$ . The Shannon-Wiener diversity index ( $H'$ ) for those dbh  $\geq 10$  cm was 3.64 in the 25-ha plot and 3.40  $\text{ha}^{-1}$ , which was the highest among those  $\geq 1$ -, 10-, 30-, 60-cm dbh ranks. The Evenness index inclined with increases along the diameter of the size class, but Fisher's alpha diversity showed the opposite trend.

A comparison of CTFS FDPs on islands used Fisher's alpha diversity index to evaluate their phytodiversity. Fisher's alpha diversity index for all woody plants with DBH  $\geq 1$  cm was the highest at the Lienhuachih FDP among those of 4 large lowland FDPs in Taiwan (Table 3). Its highest number of species and the second highest abundance resulted in the richest diversity on the island of Taiwan (Table 3). Compared to other CTFS FDPs on islands, Fisher's alpha diversity ( $\text{ha}^{-1}$ ) index of the subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of the Palana FDP in the Philippines, Sinhaja FDP in Sri Lanka, or Barro Colorado Island (BCI) FDP in Panama in the tropics. Meanwhile, Lienhuachih FDP was in a status between the Luquillo FDP and other tropical FDPs in terms of diversities of those large trees communities with DBH  $\geq 10$  cm and  $\geq 30$  cm. However, for those with a DBH  $\geq 60$  cm, the canopy diversity of the Lienhuachih FDP was much higher than those of the Fushan FDP in Taiwan, Luquillo FDP in the Philippines, and Sinhaja FDP in Sri Lanka, but was lower than that of the BCI FDP in Panama.



**Fig. 6.** Size-class structure of 4 representative species. **A**, L-shaped size-class pattern, representative species: *Ormosia formosana*; **B**, inverse J-shaped size-class pattern, representative species: *Helicia rengetiensis*; **C**, fluctuating size-class pattern, representative species: *Euonymus laxiflorus*; **D**, bell-shaped size-class pattern, representative species: *Rhododendron mariesii*.

**Table 3. Lowland forest dynamics plots of Taiwan**

Location	Elevation (m)	Location	Area (ha)	Number of species	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Abundance (individual ha <sup>-1</sup> )	Fisher's alpha
Fushan*	600~733	North	25	110	41.40	4580	12.0
Lienhuachih	667~845	Central	25	144	34.77	6631	15.8
Nanjenshan <sup>+</sup>	300~340	South	3	118	36.30	12209	15.2
Kenting	280~300	South	10	110	45.12	4785	13.5

\* Data of Fushan adopted from Su et al. 2007.

<sup>+</sup> Data of others than Lienhuachih and Fushan adopted from Losos and Leigh 2004.

## DISCUSSION

### Floristic composition and size-class structure

The vegetation of the Lienhuachih FDP is dominated by the families Fagaceae, Lauraceae, Rubiaceae, Euphorbiaceae, and Melastomataceae. These dominant families of forests are found widely in humid areas of low elevations in the Northern Hemisphere (Kira 1991, Tagawa 1995). Although our studied dominant canopy species were characterized by *P. nantoensis*, *E. roxburghiana*, *S. octophylla*, and *Cryptocarya chinensis*, the top 30 dominant canopy species also including *Castanopsis fargesii*, *Cast. kawakamii*, *Cast. cuspidate*, and *Machilus zuihoensis* were similar to species in the *Machilus-Castanopsis* forest zone (Su 1984). Even the sub-canopy and shrub species such as *Cryptocarya chinensis* and *B. cochinchinensis* are also common species found in this zone. These 2 species are very dominant due to the large number of individuals. Characteristics of the vegetation might be defined by the dominant families, genera or species but nearly never by non-canopy species. Prior to further analysis, the Lienhuachih FDP can be roughly recognized as a *Pasania-Engelhardtia-Schefflera* forest with dominant under-canopy of *R. cochinchinensis*, *Cryptocarya chinensis* and *B. cochinchinensis*, which refer to the vegetation zone of Lauro-Fagaceous forests as well as

*Machilus-Castanopsis* forests.

Most mature forests do not consist of pioneer species, except in areas of frequent disturbances or large gaps. Among the 20 most dominant species, 2 pioneer and canopy species, *Mallotus paniculatus* and *Sapium discolor*, with a sum IV of 4.76 contributed 6~11% importance to the composition of the top 20 dominant species and the top 10 canopy species, respectively. It is possible that new niches are created by disturbances such as typhoons and artificial plantations. Large disturbed areas might result from landslides due to heavy rains or artificial plantations. Small disturbances might be twig self-shaving, tree falls, hunting trails, medical plant collection, etc. Due to nearly no barriers between the Lienhuachih FDP and the surrounding human developments, the pioneer species can easily invade and colonize the forest gaps and disturbed areas, and then develop greater numbers. The alternate natural and artificial disturbances may also encourage the development of a great amount of sub-canopy and shrub species which are composed of rapidly growing saplings for recruitment. This is might be why the shrubby *B. cochinchinensis* and the sub-canopy *R. cochinchinensis* have great numbers of individuals resulting in major contributions to IV and dominance.

Both L-shaped and inverse J-shaped patterns of size-class structure analysis included 69 species comprising 67.6% of the total

102 analyzed species. The great numbers of small-sized individuals in these 2 patterns imply that most current species in this study site display good recruitment with rich sapling resources. The forest stand structure had a reverse J-shaped curve for tree and for seedling/sapling size-class distributions, which indicated that the forest as a whole is probably adequately regenerating (McLaren et al. 2005). When new niches occur, those with many saplings would generally have great chances for regeneration of forests through species competition. On the contrary, species with the bell-shaped pattern with only a few saplings usually face understory inhibition of sapling development and the fate of exclusion after elimination of young trees. The fluctuating pattern, also similar to a multi-modal size-class distribution pattern, may result from the numbers of individuals in different size classes being controlled by external physical stresses or internal physiological rhythms, such as periodicity of reproduction (Fan et al. 2005).

#### Comparisons with other lowland FDPs in Taiwan and other FDPs of the world on islands

Among the 4 low-elevation FDPs in Taiwan, the Lienhuachih FDP has the lowest basal area per hectare, whereas the Fushan FDP has the highest (Table 4). This might be

because of the great proportion of small trees and shrubs at the Lienhuachih FDP. However, the number of individuals is very high in the Nanjenshan FDP instead of the Lienhuachih FDP because the strong windward effect of monsoon results in numbers of small-diameter trees in high densities (Sun et al. 1996). The woody plant density of the Lienhuachih FDP was still higher than that of the Fushan FDP in the north and the Kenting FDP in the south. This is possibly due to forest management, aboriginal development of the Thao, and local agricultural reclamation at the Lienhuachih FDP (Lu et al. 2001). Both the Fushan FDP and Kenting FDP are located in conservation areas (Su et al. 2007, Wang et al. 2004), and intact forests usually contain large-sized trees but are distributed at low densities.

For the diversity of those trees with DBH  $\geq 1$  cm and  $\geq 10$  cm, Fisher's alpha diversity of the Lienhuachih FDP was the highest in Taiwan, higher than that of the Nanjenshan FDP and much higher than that of the Fushan FDP. However, it was obviously lower than the BCI, Palanan, and Sinharaja FDPs. In general, the greatest diversity occurs in humid tropical rainforests with no dry seasons. As a result, the Lienhuachih FDP with obvious dry and wet seasons should show not as high diversity. It is surprising that the diversity of those trees with DBH  $\geq 30$  cm and  $\geq 60$  cm for most canopy trees at the Lienhuachih FDP

**Table 4. Fisher's alpha diversity (per 1 ha) index of different ranks of diameter at breast height for CTFs forest dynamics plots on islands**

Size class (cm)	Lienhuachih (Taiwan)	Fushan* (Taiwan)	Najenshan <sup>+</sup> (Taiwan)	Luquillo <sup>+</sup> (Puerto Rico)	Palanan <sup>+</sup> (Philippines)	Sinharaja <sup>+</sup> (Sri Lanka)	BCI <sup>+</sup> (Panama)
$\geq 1$	15.7	12.1	15.6	13.5	43.4	24.4	34.6
$\geq 10$	14.0	9.9	14.0	9.3	36.5	20.4	35.6
$\geq 30$	10.6	5.9	5.5	8.8	16.0	14.1	23.9
$\geq 60$	8.9	2.8		5.8	4.0	4.3	17.8

\* Data of Fushan adopted from Su et al. 2007.

<sup>+</sup> Data of others than Lienhuachih and Fushan adopted from Losos and Leigh 2004.

was much higher than those at the Fushan and Nanjenshan FDPs. Prior to this comparison, biodiversity and species richness of Nanjenshan and the Hengchun Peninsula were considered superior than those in other areas of Taiwan. It is also surprising that the canopy diversity of the Lienhuachih FDP was only lower than that of the BCI FDP in Panama. This indicates that the high canopy diversity at Lienhuachih results from the maintenance of natural species richness, influences of aboriginal activities and forest management, and natural disturbances by typhoons, and landslides from the steep topography generating new niches for recruitment. All disturbances including the introduction of cultivation such as *Prunus* and being too close to artificial forest management near the eastern boundary encourage pioneer species to colonize the newly generated niches. That is why 2 pioneer species were in the top 30 dominant species. The Lienhuachih FDP is a forest that combines the characteristics of natural diversity and disturbed niches in succession, so its floristic diversity is high and rich.

## CONCLUSIONS

The floristic composition of the Lienhuachih FDP is dominated by the Fagaceae and Lauraceae. This is considered to be characteristic of the *Machilus-Castanopsis* forest zone. The under-canopy species, *R. cochinchinensis* and *B. cochinchinensis*, are very dominant due to the large numbers of individuals. Two pioneer and canopy species, *M. paniculatus* and *S. discolor*, as a part of the composition of the top 20 dominant species and the top 10 canopy species indicate that the Lienhuachih FDP with mingled niches may involve natural and artificial disturbances. Certain numbers of rare species, unexpected pioneer species and waste cultivated

species result in the high floristic diversity in the Lienhuachih FDP. Patterns of the size-class structure including a majority of small-sized individuals for 98 of the analyzed 102 species indicate that most current species in this study site display good recruitment with rich sapling resources. Among low-elevation FDPs in Taiwan, the Lienhuachih FDP has a higher density of individuals than the Fushan FDP and Kenting FDP, but much less than the Nanjenshan FDP. For diversity (Fisher's alpha diversity), the Lienhuachih FDP is the highest among these 4 plots. Compared to other CTFS forest dynamics plots on islands, Fisher's alpha diversity (per 1 ha) index of the subtropical Lienhuachih FDP was similar to that of the Luquillo FDP in Puerto Rico but much lower than that of other FDPs in the tropics. However, it is surprising that the canopy diversity of the Lienhuachih FDP was only lower than that of the BCI FDP in Panama. Due to the maintenance of natural species richness, influences of the aboriginal activities, forest management, and the natural disturbances by typhoons, and landslides from steep topography which generate new niches for recruitment, a high and rich floristic diversity of the Lienhuachih FDP in a forest combining the characteristics of natural diversity and disturbed niches in succession can be maintained.

## ACKNOWLEDGEMENTS

We appreciate numerous volunteers, co-workers, and research assistants of the Lienhuachih Research Center for field assistance. Dr. Hen-Biau King, Dr. I-Fan Sun, Dr. Ying-ching Lin, and Dr. Yu-Yun Chen helped with the fieldwork and discussed in the statistical analysis. We also greatly appreciate Dr. Sheng-You Lu and Dr. Tsung-Hsin Hsieh for identifying the specimens. This

study was supported by a Taiwan Forestry Research Institute grant under the project 97 AS-7.1.1.F1-G1. Some financial support was provided by the Forestry Bureau (No. tfbm-960226).

## LITERATURE CITED

- Condit R. 1998.** Tropical forest census plot. New York: Springer-Verlag.
- Condit R, et al. 1996.** Species area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *J Ecol* 84: 549-62.
- Fan SW, Chao WC, Hsieh CF. 2005.** Woody floristic composition, size class distribution and spatial pattern of a subtropical lowland rainforest at Nanjen Lake, southernmost Taiwan. *Taiwania* 50:307-26.
- Fisher RA, Corbet AS, Williams CB. 1943.** The relation between the number of species and the number of individuals in a random sample of an animal population. *J Anim Ecol* 12:42-58.
- Hough AF. 1932.** Some diameter distributions in forest stands of northwestern Pennsylvania. *J For* 30:933-43.
- Huang TC (Chief Editor). 1993~2000.** Flora of Taiwan, 2<sup>nd</sup> ed., Vols. 1-5. Taipei, Taiwan: Department of Botany, National Taiwan Univ.
- Hubbell SP, Foster RB. 1983.** Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton SL, Whitmore TC, Chadwick AC, editors. *Tropical rain forest: ecology and management*. Oxford, UK: Blackwell Scientific Publications. p 25-41.
- Hubbell SP, Foster RB. 1986.** Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soule M. editor *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Press, Sunderland, UK, p 205-31.
- Hurlbert SH. 1971.** The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577-86.
- Hwong JL, Liaw SC, Chen MC, King HB, Lu SY. 2002.** Review and analysis of forest hydrological researches in the Lienhuachi Experimental Forest. *J Exp Nat Taiwan Univ* 16(2): 95-114. [in Chinese with English summary].
- King HB. 1986.** The classification of two forest soils in Lien-Hua-Chih experimental watershed: an attempt to use USDA comprehensive system of soil classification. *Bull Taiwan For Res Inst New Ser* 1(2):155-76. [in Chinese with English summary].
- Kira T. 1991.** Forest ecosystems of east and Southeast Asia in global perspective. *Ecol Res* 6:185-200.
- Lee MF, Lin TC, Vadeboncoeur M, Hwong JL. 2008.** Changes in the vegetation cover in relation to the 1996 strong Typhoon Herb at the Lienhuachi Experimental Forest in central Taiwan. *For Ecol Manage* 255(8-9):3297-306.
- Losos EC, Leigh Jr. EG. 2004.** Tropical forest diversity and dynamism: findings from a large-scale plot network. Chicago, IL: Univ of Chicago Press. 645 p.
- Lu SY, Hwang LS, Huang HH. 2008.** Complication of meteorological records for the Lienhuachih station 1997-2007. Taipei, Taiwan: Taiwan Forestry Research Institute. 166 p. [in Chinese with English summary].
- Lu SY, Sun CC, Tseng YH. 2001.** The legend of Lienhuachuh. *Nat Conserv Q* 35:28-42. [in Chinese].
- Manabe T, Nishimura N, Miura M, Yamamoto S. 2000.** Population structure and spatial patterns for trees in a temperate old-growth evergreen broad-leaved forest in Japan. *Plant Ecol* 151:181-97.
- Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashizuka T. 1992.** Community structure of a species-rich temperate forest, Ogawa forest reserve, central Japan. *Vegetatio* 98:97-111.

- McCarthy BC, Hammer CA, Kauffman GL, Cantino PD. 1987.** Vegetation patterns and structure of an old-growth forest in south-eastern Ohio. *Bull Torr Bot Club* 114:33-45.
- McLaren KP, McDonald MA, Hall JB, Healey JR. 2005.** Predicting species response to disturbance from size class distributions of adults and saplings in a Jamaican tropical dry forest. *Plant Ecol* 181:69-84.
- Rosenzweig ML. 1995.** Species diversity in space and time. New York: Cambridge Univ Press.
- Sato T, et al. 1999.** An introduction to the Aya research site, a long-term ecological research site, in a warm temperate evergreen broad-leaved forest ecosystem in southwestern Japan: research topics and design. *Bull Kitakyushu Mus Nat Hist* 18:157-80.
- Su HJ. 1984.** Studies on the climate and vegetation types of the natural forest in Taiwan II. Altitudinal vegetation zones in relation to temperature gradient. *Q J Chin For* 17:57-73.
- Sun IF, Hsieh CF, Hubbell SP. 1996.** The structure and species composition of a subtropical monsoon forest in southern Taiwan on a steep wind-stress gradient. In: Tuner IM, Di-ong CH, Lim SSL, Ng PKL, editors. Biodiversity and the dynamics of ecosystems. DIWPA Series Vol. 1. Kyoto, Japan: Center of Ecological Research, Kyoto Univ. p 147-69.
- Su SH, et al. 2007.** Fushan subtropical forest dynamics plot: tree species characteristics and distribution patterns. Taipei, Taiwan: Taiwan Forestry Research Institute. 271 p.
- Tagawa H. 1995.** Distribution of lucidophyll oak-laurel forest formation in Asia and other areas. *Tropics* 5:1-40.
- Tanouchi H, Yamamoto S. 1995.** Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. *Vegetatio* 117:51-60.
- Tubbs CH. 1977.** Age and structure of a northern hardwood selection forest, 1929-1976. *J. For.* 75:22-24.
- Wang HH, et al. 2004.** Tree species composition and habitat types of a karst forest in kenting, southern Taiwan. *Taiwan J For Sci* 19(4): 323-35.
- Yamakura T, et al. 1995.** Topography of a large-scale research plot established within a tropical rain forest at Lambir, Sarawak. *Tropics* 5:41-56.
- Yamamoto S, Nishimura N, Matsui K. 1995.** Natural disturbance and tree species coexistence in an old-growth beech-dwarf bamboo forest, southwestern Japan. *J Veg Sci* 6:875-86.
- Yang KC, et al. 2008.** Vegetation pattern and woody species composition of a broad-leaved forest at the upstream basin of Nantzuhsienhsi in mid-southern Taiwan. *Taiwania* 53(4):325-37.

