Woody Floristic Composition, Size Class Distribution and Spatial Pattern of a Subtropical Lowland Rainforest at Nanjen Lake, Southernmost Taiwan

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ABSTRACT: A permanent 2.21 ha plot of lowland subtropical rainforest was established at Nanjen Lake of the Nanjenshan Nature Reserve in southern Taiwan. All free-standing woody plants in the plot with DBH ≥ 1 cm were identified, measured, tagged, and mapped. A total of 120 tree species (21,592 stems), belonging to 44 families and 83 genera, was recorded. The community structure was characterized by a relative dominance of Castanopsis carlesii in the canopy, Illicium arborescens in the subcanopy, and Psychotria rubra in the understory. The dominant families were Fagaceae, Illiciaceae, Aquifoliaceae, Lauraceae and Theaceae. However, typical species of lowland area in Taiwan, such as members of Euphorbiaceae and Moraceae, were relatively rare. Thus, floristic composition of this area was comparable with that found in some of the subtropical rain forests or even warm-temperate rain forests of the Central Range in Taiwan. The analysis of size-class distributions of individual species showed good recruitment patterns with a rich sapling bank for each species. TWINSPAN analysis revealed four distinct groups of samples, with the ridge top and northwest streamside plant communities representing two opposite extremes of the gradient. The dominant families of the ridge group were Fagaceae, Illiciaceae, Theaceae, Aquifoliaceae and Lauraceae, whereas those dominating the streamside group were Rubiaceae, Araliaceae, Lauraceae, Fagaceae, and Staphyleaceae. Most species had a patchy distribution and many were distributed randomly. Among those with a patchy distribution, Cyclobalanopsis championii and Rhododendron simsii only occurred on the ridge top, while Drypetes karapinensis and Ficus fistulosa occurred along the streamside. Illicium arborescens and Ilex cochinchinensis were commonly distributed on the intermediate slope. Species that appeared to be randomly or near-randomly distributed over the plot included Schefflera octophylla and Daphniphyllum glaucescens ssp. oldhamii. The distribution patterns of species also suggested that there was strong niche differentiation among species. It is found that the community of Nanjenshan forest is organized by different topographic plant associations. Maintenance of tree species diversity in the forests is largely due to differentiated environmental factors related to plot topography.

KEY WORDS: Subtropical rainforest, species diversity, floristic composition, size distribution, distribution pattern, Nanjenshan.

INTRODUCTION

Many ecologists have studied the maintenance of species richness in forest communities. Niche differentiation was proposed to illustrate how one species can avoid direct competition with other species in a stable community (Whittaker, 1975). Connell (1978) proposed that the degree to which species diversity is maintained in a community depended upon the scale of disturbance upon it. Pickett (1980) also proposed patchy dynamics that frequent disturbances enable species with different competitive abilities to coexist. The importance of differentiated microhabitat and disturbance to create species diversity in the subtropical rainforest of Nanjenshan Nature Reserve has also been discussed (Liu and Liu, 1978; Chen and Huang,

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The Nanjenshan Nature Reserve, on the southern tip of Taiwan, harbors some of the best examples of lowland rain forest in Taiwan. The Nanjenshan forests are particularly noteworthy biogeographically because of their mixture of holarctic and tropical floral elements (Li and Keng, 1950; Huang et al., 1980), and ecologically because of the importance of chronic monsoon wind-stress in organizing their communities. In addition, the phenomenon of vegetation compression where forest is tropical, subtropical and temperate species within a range of 200-400 m in elevation, is interesting for local botanists (Su, 1984; Liao, 1995).

A previous census has showed the existence of different environmental factors, such as soil characters (Chen et al., 1997; Tsui et al., 2004), topographic differences and monsoon effects (Sun et al., 1998; Hsieh et al., 2000), to be highly related to plant associations. Plants have also been reported to have morphological and physiological responses to the environmental factors, such as leaf structure (Su, 1993), photosynthetic rate (Yang, 1997; Lee, 1999) and tree architecture (Yeh, 2002). Previous studies have examined patterns of tree species composition, diversity and structure in plots, including those greater than 0.1 ha in area (Hsieh et al., 2000). However, these studies, have not discussed combined influence of chronic monsoon and habitat fragmentation by natural bodies of water. The objective of this paper is to describe the results of the census of a long term plot across a swamp. The information provided here will serve as evidence of how forest composition is affected by a combination of monsoon winds and land fragmentation.

STUDY AREA

The Nanjenshan Reserve, centered approximately at 22°3’N and 120°51’E, is part of Kenting National Park. It is located at the east side of a Central mountain range near the coast of the Pacific Ocean in the Hengchun Peninsula of southern Taiwan (Fig. 1). The climate is hot, humid and coastal with prevailing northeasterly monsoon winds during October and May. Typhoons sweeping through the reserve between July and September usually bring heavy rains. The climate data collected in the plot from 1998 to 2004 indicates that the average annual rainfall is 2,809 mm. However, the monthly averages for precipitation varies from 84 to 592 mm with 56% of the total falling between July and October. The mean annual temperature is 23.0°C and monthly means range from 18.4°C in January to 26.7°C in July (Fig. 2). The mean daily average wind velocity was 5.9 ms⁻¹ and the maximum was 7.22 ms⁻¹ in monsoon season. The wind velocity in the open area by Nanjen Lake is more variable and usually higher than at the study plot (Fig. 3).

METHODS

Census and Record

In 1995, a permanent 2.21 ha plot of lowland (324 to 360 meters above sea level) subtropical rain forest was established near Nanjen Lake in the Nanjenshan Nature Reserve in southern Taiwan. The topography of this plot is rugged, with steep slopes, ridges and valleys. A low-lying swamp and stream pass through the plot and divide the forest into relatively high west part and a lower and relatively open east part (Fig. 4). Each part has its own ridge, leeward slope and windward slope. The plot was divided into 221 10 m × 10 m quadrats, and all free-standing woody plants in the plot with DBH (Diameter of Breast Height) ≥ 1cm were measured, tagged, mapped and identified in 1998.
Fig. 1. Location of the Nanjenshan Reserve in the southernmost Taiwan. Major vegetation types and three permanent plots are also shown.

Fig. 2. Monthly average temperature and precipitation at the Nanjen Lake Plot (data collected in 1998-2004).

Fig. 3. Monthly average maximum wind speeds at Najen Lake-side (data collected in 1997-2001) and the study plot (1998-2004).

**Analyses**

**Forest composition**

The collected data were entered into Excel (Microsoft) and dBASE (Ashton-Tate) programs. The relative dominance of each species was determined based on its density (stems per hectare), basal area (m²ha⁻¹), and Importance Value (IV = (relative density + relative basal area)/2). Botanical nomenclature followed the Flora of Taiwan (Huang, 1993-1998) throughout.
Fig. 4. Topographic chart of study plot. Numbers indicate meters above sea level. ER indicates the east ridge, LS indicates leeward slope, SS indicates the streamside and WR indicates the west ridge of the study plot. The weather stations are labeled by 🌠.

Classification
A plant with multiple stems was considered to be a single individual when calculating the density of species. When calculating basal area for such a plant, the sum of basal area of all stems was used. A primary matrix of species basal area by quadrat (120 species × 186 quadrats, excluding quadrats with only grass and shrubs) was subjected to TWINSPAN classification (Hill, 1979), an option through the PC-ORD program (MjM software design). For detailed explanation of PC-ORD program, please refer to McCune and Grace (2002).

Size-class distribution
Analysis of the size-class distribution for each species was carried out by constructing a bar chart with DBH size-classes against numbers of individuals (Hough, 1932; Tubbs, 1977; McCarthy et al., 1987). Only the species with more than 15 stems in the plot were analyzed. The number of size-classes (M) for each species was determined by the equation below:

\[ M = 6 \times \log_{10} N_i \]  
(modified form Sturges’ equation)

Ni: number of individuals of species i

The interval of each class = \( \frac{DBH_{\text{max}} - DBH_{\text{min}}}{M} \)

Spatial pattern
The numbers of individuals for each species in every 5 m × 5 m subquadrat of the 2.21 ha plot were counted and labeled on the topographic map in order to demonstrate the species’ spatial distribution (Yang, 1994; Tanouchi and Yamamoto, 1995).
RESULTS

Woody floristic composition

The woody flora of the study plot was composed of 120 species in 83 genera and 44 families, of these species 99 were trees and 21 were shrubs. The numbers of the free-standing woody species in 10 m × 10 m quadrats ranged from 1 to 64, with an average of 32 species. Families with the greatest species in descending order, were Lauraceae, Euphorbiaceae, Fagaceae, Rubiaceae, Theaceae, Aquifoliaceae, Moraceae and Myrsinaceae. These eight families were represented by 63 species and 52.5% of the total number of species in the plot.

A total of 21,592 individuals (10,905 stems/ha) were recorded in the census (Table 1). The number of individuals per 0.01 ha quadrat ranged from 2 to 303, with an average of 109 individuals. The quadrats near the ridge had more individuals than those on the streamside. The canopy reached a height of 10-15 m on the leeward slopes and streamside, but only 3-5 m high on the ridge tops. On the plot as a whole, the numbers of individuals of subcanopy and understory species were greater than those in the canopy. The subcanopy tree species, *Illicium arboresens*, *Ilex cochinchnensis* and *Litsea acutivena*, and the understory shrub species, *Psychotria rubra*, *Aucuba chinensis*, *Antidesma hiiranense* and *Melastoma cadidum*, had more than 200 individuals per hectare. But only two canopy species, *Daphniphyllum glaucesens* ssp. *oldhamii* and *Schefflera octophylla*, had species abundances exceeding 200 individuals per hectare.

The mean basal area was 42.49 m² per hectare, with the families having the largest basal areas are with descending order: Fagaceae, Theaceae, Aquifoliaceae, Illiciaceae, Araliaceae, Lauraceae, Myrsinaceae, Melastomataceae and Myrtaceae. The most important and dominant species, as indicated by having a greater importance value than four percent, were *Castanopsis carlesii*, *Illicium arborescens*, *Ilex cochinchnensis*, *Psychotria rubra* and *Schefflera octophylla* (Table 1). The other species with more than two percent IV were *Castanopsis fabri*, *Cyclobalanopsis longinux*, *Daphniphyllum glaucescens* ssp. *oldhamii*, *Ilex uraiensis*, *Lithocarpus amygdalifolius*, *Litsea acutivena*, *Melastoma candidum*, and *Schima superba* var. *kankoensis*. These 13 species accounted for 51.51% of the total IV. Two of the most important species, *Ilex cochinchnensis* (IV = 5.17%) and *Illicium arborescens* (IV = 10.37%) occurred at high densities, which accounted for their high importance values, while *Castanopsis carlesii* (IV = 7.32%) and *Schefflera octophylla* (IV = 4.68%) had high important value due to their large diameters. The dominant families with the largest importance values (in descending order of IV) were Fagaceae, Illiciaceae, Aquifoliaceae, Lauraceae, Theaceae, Rubiaceae and Melastomataceae.

Size-class distribution

Eighty-nine out of 120 woody species were represented by more than 15 individuals in the plot and the numbers of individuals for each these species were counted by each size class. The bar charts showing size-class against individual numbers among 89 species displayed three patterns: Inverse-J shape, L-shape and Multi-modal distribution. The L-shape distribution pattern showed a dramatic drop in number of individuals in the small size-class such as *Aucuba chinensis* (Fig. 5a), *Illicium arborescens*, *Melastoma candidum*, *Microtropis japonica* and *Psychotria rubra* (42 spp. in total), while the Inverse-J shape size-class distribution pattern had smooth-downward curve seen in *Engelhardia roxburghiana* (Fig. 5b), *Castanopsis carlesii*, *Daphniphyllum glaucesens* ssp. *oldhamii*, *Ilex cochinchnensis*, *I.
Table 1. Woody species composition of the Nanjen Lake Plot. Only the species with IV > 0.5% are included. Species order is based on Importance Value. DBH = Diameter of Breast Height, BA = Basal Area, IV = (relative density + relative basal area)/2.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of individuals (Stem)</th>
<th>DBH &lt; 2cm</th>
<th>2cm ≤ DBH &lt; 5cm</th>
<th>DBH &gt; 5cm</th>
<th>Total</th>
<th>BA (m²ha⁻¹)</th>
<th>IV</th>
</tr>
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<td>875</td>
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<td>254</td>
<td>414</td>
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<td>678</td>
<td>3010</td>
<td>5.02</td>
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<tr>
<td>Total</td>
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<td>7655</td>
<td>5144</td>
<td>21592</td>
<td>42.49</td>
<td>100</td>
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A subtropical lowland rainforest of the southernmost Taiwan

**Classification of plant community**

Four types of plant communities classified by using TWINSPLAN in correspondence of topographic positions (Fig. 6). For each forest type, the character species were defined here as those that have more than half of their total number of individuals from the plot appearing in that forest type and for which this distribution had been shown to be non-random. Some examples of ridge forest character species were *Anneslea fragrans* var. *lanceolata*, *Cleyera japonica*, *Eurya nitida* var. *nanjenshanensis*, *Machilus obovatafolia*, *Myrsine sequinii*, *Rhapiolepis indica* var. *hiiranensis*, *Rhododendron simsii*, *Syzygium buxifolium* and *Wikstroemia taiwanensis* (Table 2). The character species of streamside forest type were *Drypetes karapinensis*, *Dysoxylum hongkongense*, *Machilus japonica* var. *kusanoi*, *Ficus fistulosa* and *Glycosmis citrifolia*. The mid-slope forest had only three character species: *Diospyros eriantha*, *Ilex cochinchinensis* and *Litsea acutivena*. The TWINSPLAN analysis indicated that ridge and streamside forests were the extremes of four plant community types, with relatively more character species, while mid-slope and valley forests were transitional between the ridge and streamside forests and had relatively fewer character species of their own.

The association names of four forest types, designated by dominant species following character species, were *Cyclobalanopsis championii—Illicium arborescens* type in the ridge,
Fig. 6. The swamp, shrub-land and four types of woody plant community in study plot.

Table 2. The character species of each woody plant community. N = number of individuals of species in a forest type.

<table>
<thead>
<tr>
<th>Ridge type</th>
<th>Mid-slope type</th>
<th>Valley type</th>
<th>Streamside type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyclobalanopsis championii – Illicium arborescens type</td>
<td>Litsea acutivena – Illicium arborescens type</td>
<td>Mallotus paniculatus – Schefflera octophylla type</td>
<td>Machilus japonica var. kusanoi – Schefflera octophylla type</td>
</tr>
<tr>
<td>Ilex lonicerifolia var. matsudai N = 278</td>
<td>Ilex cochinensis N = 1004</td>
<td>Mallotus paniculatus N = 53</td>
<td>Ficus fistulosa N = 38</td>
</tr>
<tr>
<td>Microtropis japonica N = 265</td>
<td>Litsea acutivena N = 537</td>
<td>Callicarpa remotiserrulata</td>
<td>Drypetes karapinensis N = 34</td>
</tr>
<tr>
<td>Eurya nitida var. nanjenshanensis N = 258</td>
<td>Diospyros eriantha N = 143</td>
<td>N = 18</td>
<td>Machilus japonica var. kusanoi N = 18</td>
</tr>
<tr>
<td>Myrsine sequinii N = 152</td>
<td></td>
<td></td>
<td>Dysoxylum hongkongense N = 12</td>
</tr>
<tr>
<td>Neolitsea buisanensis N = 106</td>
<td></td>
<td></td>
<td>Glycosmis citrifolia N = 9</td>
</tr>
<tr>
<td>Rhododendron simsi* N = 144</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gordonia axillaries N = 98</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Symphocarpos congesta N = 85</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Symphocarpos shihanensis N = 76</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclobalanopsis championii N = 74</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meliosma squamulata N = 64</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nageia nagi N = 52</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhaphiolepis indica var. hiiranensis N = 66</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclobalanopsis pachyloma N = 55</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anneslea fragrans var. lanceolata N = 53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Syzygium buxifolium N = 50</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cleyera japonica N = 39</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tersteroemia gymnanthera N = 37</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wikstroemia taiwanensis* N = 28</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ilex maximovicziana N = 9</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Shrubs are indicated with an “*”

Litsea acutivena — Illicium arborescens association in the mid-slope, Mallotus paniculatus — Schefflera octophylla type in the valley and Machilus japonica var. kusanoi — Schefflera octophylla type in the streamside. Each forest type had its own dominant species and distinct tree densities. The Machilus japonica var. kusanoi — Schefflera octophylla type in streamside, of which there were 23 quadrats, had lowest total density (5791 stems ha⁻¹) and basal area
(32.2 m² ha⁻¹), while those 41 quadrats of Cyclobalanopsis championii—Illicium arborescens type in the west and east ridge had the greatest total density (14,729 stems ha⁻¹), and larger basal area (43.58 m² ha⁻¹). Species composition of the two extreme forest types, the ridge and the streamside, also varied. The Cyclobalanopsis championii—Illicium arborescens type at ridge was dominated by Castanopsis carlesii, Cyclobalanopsis championii, Cyclobalanopsis longinux and Gordonia axillaris in (in descending order of IV) in the canopy layer and Illicium arborescens, Ilex lonicerifolia var. matsudai and Melastoma candidum in the understory layer (Table 3). In the Machilus japonica var. kusanoi—Schefflera octophylla type at streamside, the principal canopy species were Schefflera octophylla, Turpinia ternate, Machilus japonica var. kusanoi, Castanopsis fabri, Astronia ferruginea, Sloanea formosana, Wendlandia formosana, Ardisia sieboldii, Ficus fistulosa, Daphniphyllum glaucescens ssp. oldhamii and Adinandra formosana and the main shrub species were Psychotria rubra and Helicia formosana. The Litsea acutivena—Illicium arborescens association located between the ridge and streamside forest types, had the highest species richness out of all four types. The dominant species of the Litsea acutivena—Illicium arborescens forest canopy were Castanopsis carlesii, Schefflera octophylla, Cyclobalanopsis longinux, Lithocarpus amygdalifolius, Schima superba var. kankoensis and Daphniphyllum glaucescens ssp. oldhamii, while those of the subcanopy were Illicium arborescens, Ilex cochinchinensis, Litsea acutivena and Ilex uraiensis, and the dominant shrubs were Melastoma candidum and Psychotria rubra. The Mallotus paniculatus—Schefflera octophylla forest located on the westernmost of the study plot was dominated by Schefflera octophylla, Turpinia ternate and Machilus japonica var. kusanoi in canopy, Psychotria rubra and Helicia formosana in understory. Fig. 7. shows that the character species for each type has a great quantity only in that type of forest (cf. Cyclobalanopsis championii, Litsea acutivena, Mallotus paniculatus and Machilus japonica var. kusanoi). The abundances of most species in the study plot appeared unevenly among the four forest types, even the dominant species such as Illicium arborescens and Schefflera octophylla.

**Woody plant spatial pattern**

Based on distribution maps of the species, most species were patchily distributed and many were random. Among those with patchy distribution, species could be located distinctly on the ridge, slope or streamside (Fig. 8). Rhododendron simsii (Fig. 8a) and Cyclobalanopsis championii (Fig. 8b) only occurred on ridge tops in the east and west, while Drypetes karapinensis (Fig. 8c) and Ficus fistulosa occurred along the streamside. One of the most abundant subcanopy species, Litsea acutivena, was mostly found on the mid-slope (Fig. 8d). Two of most densely distributed species in the plot, Illicium arborescens (Fig. 8e) and Ilex cochinchenensis, were commonly located from the intermediate slope to the hilltop. Many species appeared to be randomly or near-randomly distributed over the plot including Schefflera octophylla and Daphniphyllum glaucescens ssp. oldhamii (Fig. 8f).

**DISCUSSION**

The community structure was characterized by a relative dominance of Castanopsis carlesii in the canopy, Illicium arborescens in the subcanopy, and Psychotria rubra in the understory. The dominant families, Fagaceae, Illiciaceae, Aquifoliaceae, Lauraceae and
Table 3. Woody species composition of four association types. For each association type, the 19 species with highest IVs are listed in descending order according to IV.

**Type 1: Ridge**

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cyclobalanopsis championii</strong></td>
<td>313</td>
<td>14.16</td>
<td>12</td>
<td><strong>Ilex arborescens</strong></td>
<td>781</td>
<td>7.81</td>
<td>39.4</td>
</tr>
<tr>
<td><strong>Pericopsis sieboldii</strong></td>
<td>371</td>
<td>18.22</td>
<td>10</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td>Melastoma candidum</td>
<td>270</td>
<td>9.12</td>
<td>9</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Castanopsis carlesii</strong></td>
<td>249</td>
<td>9.12</td>
<td>9</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
</tbody>
</table>

**Type 2: Mid-slope**

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cyclobalanopsis longinux</strong></td>
<td>134</td>
<td>1.49</td>
<td>2.1</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
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<td>63.6</td>
</tr>
<tr>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
</tbody>
</table>

**Type 3: Valley**

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Daphniphyllum glaucescens</strong></td>
<td>317</td>
<td>1.76</td>
<td>1.96</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Myrsine sequinii</strong></td>
<td>429</td>
<td>0.24</td>
<td>1.74</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Psychotria rubra</strong></td>
<td>249</td>
<td>0.60</td>
<td>1.60</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Blechnum truncatum</strong></td>
<td>371</td>
<td>0.43</td>
<td>1.81</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
</tbody>
</table>

**Type 4: Streamside**

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
<th>Species</th>
<th>Density (stem ha⁻¹)</th>
<th>BA (m² ha⁻¹)</th>
<th>IV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Daphniphyllum glaucescens</strong></td>
<td>317</td>
<td>1.76</td>
<td>1.96</td>
<td><strong>Ilex chinensis</strong></td>
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</tr>
<tr>
<td><strong>Psychotria rubra</strong></td>
<td>249</td>
<td>0.60</td>
<td>1.60</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
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</tr>
<tr>
<td><strong>Blechnum truncatum</strong></td>
<td>371</td>
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<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
<tr>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
<td><strong>Ilex chinensis</strong></td>
<td>473</td>
<td>7.23</td>
<td>63.6</td>
</tr>
</tbody>
</table>

Shrubs are indicated with an “*”
Theaceae in this study, are similar to those in the Lanjenchi plot (Fig. 1) in the Nanjenshan area (Sun et al., 1998). However, the members belonging to Euphorbiaceae, Moraceae and Rubiaceae that are considered as the dominant species in most tropics and lowland Taiwan, were relatively rare. Many species that are typically considered members of the warm-temperate montane forests in central Taiwan above 500 m in elevation, such as *Illicium arborescens* and *Ilex* spp., display a down-shift of their altitudinal distribution at the study area. The floristic composition of the study plot was comparable not only with that found in some of the other subtropical rain forests in Taiwan, but also in some warm-temperate montane forests of the island. The species down-shift at both northern and southern tips of Taiwan has been noticed by many botanists (Su, 1984; Liao, 1995).
Fig. 8. Distribution map of species in the Nanjen Lake Plot. (a) and (b): Species occurring only on the ridge-top. (c): Species appearing only near the streamside. (d): Species distributing mainly on the mid-slope. (e): Species growing from the mid-slope to ridge-top. (f): Species appeared to be distributed near-randomly.

The species richness and diversity of this study site compared favorably with the plots in the Nanjenshan Reserve (Yang, 1994; Liao, 1995; Hsieh et al., 2000) and in the 1 ha plot in Dinghushan of southern China, where only 99 woody species were found (Kong et al., 1998). The total basal area of woody plants in this forest is approximately 42 m² ha⁻¹, which is similar to the values obtained from a variety of evergreen broad-leaved forests in Taiwan (Song, 1996) and Forest Dynamic Plots in tropics (Losos et al., 2004). The canopy of the study forest is relatively low in height and not continuous comparing to the Bischofia dominant forest in the creek plot nearby (Yang, 1994). However, the tree density of the study plot is much higher than that of the creek plot and even those of Forest Dynamic Plots in tropics. Studies examining the relationship between northeastern monsoon winds and vegetation in the same area indicate that a high density of small and short stems may result from the chronic wind stress on the windward slopes (Sun et al., 1998).

Despite little variation in elevation and distance between ridge and streamside forest types, distinct floristic and structural factors were detected by TWINSPAN analysis. For example, some species never occurred in the leeward slope and streamside forest, such as *Anneslea fragrans* var. *lanceolata*, *Rhaphiolepis indica* var. *hiiranensis*, *Rhododendron simsii* and
Wikstroemia taiwanensis, while others were not observed in the windward ridge forest, like Dyssoxylum hongkongense and Glycosmis citrifolia. The asymmetry in the floristic composition and physiognomic characteristics of vegetation at windward and leeward sites of the plot are thought to be the results of interaction of wind stress and resource availability. Similar results are reported, particularly due to varied light and soil properties, in Lanjenchi and Nanjenshan Plots (Fig. 1) (Chen et al., 1997; Sun et al., 1998; Tsui et al., 2004). The forest of the east ridge (338 m above sea level) in the plot had a similar composition to the one on the west (ca. 360 m above sea level), the main hilltop of this study plot. This might indicate that under chronic wind-blowing, the east ridge, isolated by a swamp, also has a suitable habitat for the ridge species. Distinct floristic composition for each forest type in the study plot may imply that the tree species comprising this forest may be classified into different functional groups to adapt to varied environments. Most species in the study plot have patchy distributions responds to varied topographic positions. With the different patterns of spatial distribution among species, the performance of niche differentiation in the study forest may also be supported.

The size-class distribution of all species had an Inverse-J shape pattern or a modified Inversed-J shape pattern (L-shape and Multi-modal distribution). This means that species presently in this study site have good recruitment patterns with a rich saplings bank. In general, the regeneration of canopy species in a primary forest is considered to include an understory inhibition period in which canopy species endure a low light condition and wait for gap formations and space releasing. During this period there may be a massive death of saplings, resulting in an L-shape size-class distribution for most canopy species. In this study, most tree species showed an L-shape distribution and most shrubs have Inverse-J shape size-class distribution patterns. Multi-modal size-class distribution patterns may result from the number of individuals in different size classes being controlled by external physical stress or internal physiological rhythms, such as periodicity of reproduction.

In this research, the strong relationship between forest types and varied topographic features is shown in the Nanjenshan area of southern Taiwan. Although the forest at the Nanjen Lake area has chronic wind-stress in winter and disturbance of typhoons in summer, the trees there still show complete population structure in whole size-classes, possibly indicating that this forest has good recruitment mechanisms. The maintenance of tree species diversity in the forest might be due to the existence of different environmental factors that are related to topography in this area and the varied responses of different species to these environmental factors.

ACKNOWLEDGEMENTS

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台灣南部南仁湖地區亞熱帶低地雨林的木本植物組成、徑級結構與空間分佈

范素瑋(1,2)、趙偉村(1)、謝長富(1)

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摘要

為了解台灣南部低海拔雨林之物種多樣性及森林結構，並作為未來森林動態監測之用，於南仁湖附近設立一橫跨草澤及森林之2.21公頃樣區。進行胸高直徑大於等於1公分之木本植物調查，共發現44科83屬120種木本植物(共21,592棵)。總底面積為每公頃42.49平方公尺。各樹種優勢的組成上，冠層以長尾栲、江某、錐果櫟及港口木荷為優勢，次冠層優勢植物為紅花八角及革葉冬青。在林下灌木植物重要值高的有：九節木、野牡丹、桃葉珊瑚及南仁五月茶。森林主要由殼斗科、八角茴香科、冬青科、樟科及茶科所組成。各種類之徑級結構，可分為三種類型，即反J型(42種)、L型(38種)及波動型(9種)，各樹種均呈現豐富小樹庫，表示現存的種類有良好的更新狀態。將調查資料經雙向指標種分析法(TWINSPAN)進行植群分類後，再將植物社會與地形圖搭配，發現各植物社會與地形有密切相關。因此可將當地森林分為四型：位於稜脊的嶺南椆－紅花八角型、坡面的銳脈木薑子－紅花八角型、谷地的白匏子－江某型及溪畔的大葉楠－江某型。優勢科的組成由稜脊之殼斗科、八角茴香科、茶科、冬青科、樟科，轉變為溪谷的茜草科、五加科、樟科、殼斗科及省沽油科，密度也由稜脊向溪谷降低。檢視各樹種在樣區內的分布狀況，可歸納為下列之空間分布類型：1. 稜脊型：如長尾栲、嶺南椆、唐杜鵑等；2. 山坡型：如小葉樹杞、銳脈木薑子等；3.溪谷型：如水同木、交力坪鐵色等；4.廣佈型：如江某、奧氏虎皮楠、港口木荷等。南仁山森林在徑級結構上，顯示良好的更新狀態，該森林在組成上短期內應能維持穩定不變，但森林林冠破碎及陽性樹種存在，顯示該環境具經常性干擾，其異質度的維持亦有部分來自於干擾。在空間分布上，樹種的分布與地形及環境異質性有關，顯示環境提供不同條件，以適合不同植物生長更新。環境異質性使得物種區隔而免於競爭，呈現出生境分化情況，如此多種森林樹種能共存於一地區。

關鍵詞：亞熱帶雨林、種異度、物種組成、徑級結構、分佈模式、南仁山。
Appendix: Woody species of the study plot at Nanjen lake

A. Gymnosperms
1. Podocarpaceae 罗汉松科
   1. Nageia nagi (Thunb.) O. Ktze. 竹柏 (T, V, M)*

B. Angiosperms
2. Actinidiaceae 猕猴桃科
   2. Saurauja tristyla DC. var. oldhamii (Hems.) Finet & Gagnep. 水冬瓜 (T, V, C)
3. Anacardiaceae 漆树科
   3. Rhus succedanea L. 山漆 (T, V, C)
4. Aquifoliaceae 冬青科
   4. Ilex cochinchinensis (Lour.) Loes. 萃叶冬青 (T, V, R)
   5. Ilex lonicerifolia Hayata var. matsumai Yamamoto 松田氏冬青 (T, E, M)
   6. Ilex maximowicziana Loes. 倒卵叶冬青 (T, V, M)
   7. Ilex rotunda Thunb. 鐵冬青 (T, V, C)
   8. Ilex uraiensis Mori & Yamamoto 烏來冬青 (T, V, M)
5. Araliaceae 五加科
   9. Schefflera octophylla (Lour.) Harms 鵝掌柴 (T, V, C)
6. Bignoniaceae 紫葳科
   10. Radermachia sinica (Hance) Hemsl. 山菜豆 (T, V, C)
7. Boraginaceae 紫草科
   11. Ehretia longiflora Champ. ex Benth. 長葉厚殼樹 (T, V, M)
8. Caprifoliaceae 忍冬科
   12. Viburnum luzonicum Rolfe 呂宋莢迷 (T, V, C)
   13. Viburnum odoratissimum Ker 珊瑚樹 (T, V, R)
9. Celastraceae 衛矛科
   14. Euonymus pallidifolia Hayata 淡緑葉衛矛 (S, E, E)
   15. Microtropis japonica (Fr. & Sav.) Hall. 日本賽衛矛 (T, V, M)
10. Clusiaceae 金絲桃科
    16. Garcinia multiflora Champ. 恆春福木 (T, V, R)
11. Cornaceae 山茱萸科
    17. Aucuba chinensis Benth. 桃葉珊瑚 (S, V, M)
12. Daphniphyllaceae 虎皮楠科
    18. Daphniphyllum glaucescens Bl. ssp. oldhamii (Hems.) Huang 奧氏虎皮楠 (T, V, C)
13. Ebenaceae 檀香科
    19. Diospyros eriantha Champ. ex Benth. 軟毛柿 (T, V, C)
    20. Diospyros maritima Blume 黃心柿 (T, V, M)
    21. Diospyros morrisiana Hance 山紅柿 (T, V, C)
14. Elaeocarpaceae 杜英科
    22. Elaeocarpus syalvestris (Lour.) Poir. 杜英 (T, V, C)
   23. Sloanea formosana Li 猴歡喜 (T, E, C)
15. Ericaceae 杜鹃花科
    24. Rhododendron simii Planch. 唐杜鵑 (S, E, R)
16. Euphorbiaceae 大戟科
    25. Antidesma hitranense Hayata 南仁五月茶 (S, E, M)
    26. Bischofia javanica Blume 茶葉 (T, V, C)
    27. Bridelia balansae Tutcher 斜柱密 (T, V, C)
    28. Drypetes karapinensis (Hayata) Pax 交力坪鐵色 (T, E, M)
    29. Glochidion rubrum Blume 細葉槭果 (T, V, C)
    30. Glochidion zeylanicum (Gaertn.) A. Juss. 搖葉槭果 (T, V, C)
31. Mallotus japonicus (Thunb.) Muell. -Arg. 野桐 (T, V, C)
32. Mallotus paniculatus (Lam.) Muell. -Arg. 野匏子 (T, V, C)
33. Melanolepis multiglandulosa (Reinw.) Reich. f. & Zoll. 蟲屎 (T, V, C)
34. Sapium discolor Muell.-Arg. 白臼 (T, V, C)

17. Fabaceae 豆科
35. Archidendron lucidum Benth. 單垂豆 (T, V, C)
36. Ormosia hengchuniana Huang, Yang & Huang 恆春紅豆樹 (T, E, R)

18. Fagaceae 殼斗科
37. Castanopsis carlesii (Hemsl.) Hayata 長尾栲 (T, V, C)
38. Castanopsis fabri Hance 星刺栲 (T, V, M)
39. Castanopsis formosana (Skan) Hayata 臺灣栲 (T, V, C)
40. Castanopsis indica (Roxb.) A. DC. 印度栲 (T, V, C)
41. Cyclobalanopsis championii (Benth.) Oerst. ex Schott. 嶺南椆 (T, V, R)
42. Cyclobalanopsis longinux (Hayata) Schott. 錐果櫟 (T, V, C)
43. Cyclobalanopsis pachyloma (O. Seem.) Schott. 金斗椆 (T, V, M)
44. Lithocarpus amygdalifolius (Skan ex Forbes & Hemsl.) Hayata 杏葉石櫟 (T, V, C)
45. Pasania harlandii (Hance) Oersted 短尾柯 (T, V, C)

19. Illiciaceae 八角茴香科
46. Illicium arborescens Hayata 紅花八角 (T, E, C)

20. Juglandaceae 胡桃科
47. Engelhardtia roxburghiana Wall. 黃杞 (T, V, C)

21. Lauraceae 樟科
48. Beilschmiedia erythrophloia Hayata 瓊楠 (T, V, C)
49. Cryptocarya chinensis (Hance) Hemsl. 厚殼桂 (T, V, M)
50. Litsea acutivena Hayata 銳脈木薑子 (T, V, M)

22. Magnoliaceae 木蘭科
51. Magnolia kachirachirai (Kanehira & Yamamoto) Dandy 烏心石舅 (T, E, R)
52. Michelia compressa (Maxim.) Sargent 烏心石 (T, V, C)

23. Melastomataceae 野牡丹科
53. Astronia formosana Kanehira 銹葉野牡丹 (T, E, M)
54. Myrica adenophora Hance 青楊梅 (T, V, M)

24. Meliaceae 檀科
55. Moraceae 桑科
60. Michelia compressa (Maxim.) Sargent 烏心石 (T, V, C)
27. Myrsinaceae 紫金牛科
   70. Ardisia cornudentata Mez 鐵雨傘 (S, E, C)
   71. Ardisia quinquegona Blume 小葉樹杞 (T, V, C)
   72. Ardisia sieboldii Miq. 樹杞 (T, V, C)
   73. Maesa perlarius (Lour.) Merr. var. formosana (Mez) Yuen P. Yang 臺灣山桂花 (S, V, C)
   74. Myrsine sequinii Lev. 大明橘 (T, V, C)

28. Myrtaceae 桃金孃科
   75. Decaspermum gracilentum (Hance) Merr. & Perry 十子木 (T, V, R)
   76. Syzygium buxifolium Hook. & Arn. 小葉赤楠 (T, V, C)
   77. Syzygium euphlebium (Hayata) Mori 細脈赤楠 (T, E, R)
   78. Syzygium kusukusense (Hayata) Mori 高士佛赤楠 (T, E, R)

29. Oleaceae 木犀科
   79. Osmanthus marginatus (Champ. ex Benth.) Hemsl. 小葉木犀 (T, V, M)

30. Opiliaceae 山柚科
   80. Champerea manillana (Blume) Merr. 山柚 (T, V, C)

31. Proteaceae 山龍眼科
   81. Helicia formosana Hemsl. 山龍眼 (T, V, C)
   82. Helicia rengetiensis Masamune 蓮花池山龍眼 (T, E, M)

32. Rosaceae 蔷薇科
   83. Prunus phaeosticta (Hance) Maxim. 黑星櫻 (T, V, C)
   84. Rhaphiolepis indica (L.) Lindl. var. hiiranensis (Kanehira) Li 恆春石斑木 (S, E, R)

33. Rubiaceae 茜草科
   85. Gardenia jasminoides Ellis 山黃梔 (T, V, C)
   86. Lasianthus cyanocarpus Jack 毛雞屎樹 (S, V, C)
   87. Lasianthus fordii Hance 琉球雞屎樹 (S, V, C)
   88. Lasianthus obliquinervis Merr. 雞屎樹 (S, V, C)
   89. Lasianthus wallichii Wight 圓葉雞屎樹 (S, V, C)
   90. Psychotria rubra (Lour.) Poir. 九節木 (S, V, C)
   91. Tarenna gracilipes (Hayata) Ohwi 薄葉玉心花 (S, E, C)
   92. Tricalysia dubia (Lindl.) Ohwi 狗骨仔 (T, V, C)
   93. Wendlandia formosana Cowan 水金京 (T, V, C)

34. Rutaceae 芸香科
   94. Glycosmis citrifolia (Willd.) Lindl. 石苓舅 (S, V, C)
   95. Melicope semecarpifolia (Merr.) T. Hartley 山刈葉 (T, V, C)
   96. Tetradium meliaefolia (Hance) Benth. 賊仔樹 (T, V, C)

35. Sabiaceae 清風藤科
   97. Meliosma rigda Sieb. & Zucc. 筆羅子 (T, V, C)
   98. Meliosma squamulata Hance 綠樟 (T, V, C)

36. Saxifragaceae 虎耳草科
   99. Hydrangea chinensis Maxim. 華八仙 (S, V, C)
   100. Itea parviflora Hemsl. 小花鼠刺 (T, E, C)

37. Staphyleaceae 省沽油科
   101. Turpinia ternata Nakai 三葉山香圓 (T, V, C)

38. Sterculiaceae 槭樹科
   102. Reevesia formosana Sprague 臺灣梭羅木 (T, E, R)

39. Symplocaceae 灰木科
   103. Symplocos congesta Benth. 楊桐葉灰木 (T, V, C)
   104. Symplocos modesta Brand 小葉白筆 (T, E, C)
   105. Symplocos shilanensis Liu & Lu 南仁灰木 (T, E, R)
106. *Symplocos theophrastaeifolia* Sieb. & Zucc. 山豬肝 (T, V, C)

40. **Theaceae** 茶科

107. *Adinandra formosana* Hayata 臺灣楊桐 (T, E, C)
108. *Anneslea lanceolata* (Hayata) Kanehira 細葉茶梨 (T, E, R)
109. *Camellia hengchunensis* Chang 恆春山茶 (T, E, R)
110. *Cleyera japonica* Thunb. var. *mori* (Yamamoto) Masamune 森氏紅淡比 (T, V, C)
111. *Eurya chinensis* R. Br. 米碎柃木 (T, V, C)
112. *Eurya nitida* Korthals var. *nanjenshanensis* Hsieh, Ling & Yang 南仁山柃木 (T, E, R)
113. *Gordonia axillaris* (Roxb.) Dietr. 大頭茶 (T, V, C)
114. *Schima superba* Gardn. & Champ. var. *kankoensis* (Hayata) Keng 港口木荷 (T, E, M)
115. *Ternstroemia gymnanthera* (Wight & Arn.) Sprague 厚皮香 (T, V, C)

41. **Thymelaeaceae** 瑞香科

116. *Wikstroemia taiwanensis* C. E. Chang 臺灣蕘花 (S, E, M)

42. **Urticaceae** 蕁麻科

117. *Dendrocnide meyeniana* (Walp.) Chew 咬人狗 (T, V, C)

43. **Verbenaceae** 馬鞭草科

118. *Callicarpa remotiflora* Lin & Wang 疏花紫珠 (S, E, M)
119. *Callicarpa remotiserrulata* Hayata 恆春紫珠 (S, E, R)
120. *Clerodendrum cyrtophyllum* Turcz. 大青 (S, V, C)

* Codes in parentheses show the characteristics for each species. Growth form in the first: T is representative of Tree species and S is Shrubs. Source of species in the second: E is representative of endemic species and V is Native. Degree of abundance in the third: C is representative of common species, M means Moderate abundance, and R is Rare.

Statistical information of the woody species in the study plot.

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