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Long-term ecological research in the Yuanyang Lake forest ecosystem I. Vegetation composition and analysis[4]

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Abstract. The Yuanyang Lake Nature Preserve is located in the northeastern part of Hsinchu County, Taiwan. It is the uppermost head water of the Tahan River watershed at 1,650-2,432 m altitude. The total area of the natural preserve is about 374 ha, of which the lake occupies about 3.6 ha and the marshy area encircling the lake about 2.2 ha. The surrounding hillsides are dominated by cypress forests. Floristic analyses by means of Two-Way Indicator Species Analysis (TWINSPAN) and Detrend Correspondence Analysis (DCA) were conducted at the site. The findings of the former analysis concluded that the forest could be divided into two communities, namely a coniferous-hardwood community, and a swamp or early succession community. The former comprises (a) *Chamaecyparis formosensis*, *C. obtusa* var. *formosana*, *Tsuga chinesis* and (b) *Rhododendron mariseii-Rhamus cranata*. The swamp or early succession community comprises (a) *Potamogeton octandrus*, *Sparganium fallax* and *Schaenoplectus mucronatus*, (b) *Miscanthus transmorrisonesis* and *Schoenoplectus morrisonensis*. In total, there are 185 species of vascular plants, in 115 genera and 71 families. The cypress community has reached its stable stage, and *Chamaecyparis* species are capable of self regeneration. A successional trend of vegetation in the nature preserve area was proposed; however, the mechanism of the successional trend on the aquatic communities needs further investigation.

Keywords: *Chamaecyparis*; Community formation; Florisitc analysis; *Miscanthus transmorrisonesis*; *Potamogeton octandrus*; *Rhododendron mariseii*; *Sparganium fallex*; Successional trend; Yuanyang Lake.

Introduction

The Long-Term Ecological Research (LTER) program is one of the core projects of the Global Change and Terrestrial Ecosystem program (GCTE), which is under the umbrella of the International Geosphere-Biosphere Programme (IGBP). The Taiwan LTER project was initiated by the senior author in 1992 under the auspices of the Academia Sinica and the National Science Council of Taiwan. The main objectives of the Taiwan LTER are: (1) to understand long-term ecological changes in Taiwan, (2) to elucidate the mechanisms involved in ecological processes, (3) to provide suitable ecological information for social and economic development, and (4) to merit membership in an international LTER network in order to provide ecological information of regional and global interest. Taiwan LTER studies put emphasis upon the structure and function of the forest ecosystem as well as the hydrological and nutrient flux of the ecosystem in Taiwan. The database will also be made available in the global change research program. Such information is valuable for ecological and environmental education, as it will call upon people's awareness of the importance of natural conservancy and the impact of environmental change on the terrestrial ecosystem. Studying the structure and function of forest ecosystems is particularly important for Taiwan because forests cover 52% of the island and forest management and conservation are extremely important for the survivors of all living organisms in Taiwan. Forests are also the fundamental basis for water, timber and clean air for all organisms, and the forest composition and vegetation pattern are particularly important for biogeochemical and hydrological cycles in the forest ecosystems.

The Yuanyang Lake (YYL) Nature Preserve is one of the five Taiwan LTER sites. Located in the northeastern part of Hsinchu County, it consists of coniferous forest, hardwood forest, pteridophytes, epiphytes, such as mosses and liverworts, grassland species and several aquatic plants. The vegetation of the YYL was previously studied by Liu (1966) and Kuo and Tsian (1993), who reported that the predominant *Chamaecyparis formosensis* and *C. obtusa* var. *formosana* are distributed mainly in a fog zone. Lin and Chiu (1994) also reported that six plant communities and 252 species were found. Subsequent studies conducted much emphasized the cypress forest (Chang, 1963; Liu and Ying, 1973; Liu and Hsu, 1973; Chen, 1996; Lin and Chiu, 1994) and pollen analysis of associated species, e.g., Q*uercus* and *Alnus* (Chen and Yang, 1996). Nevertheless, a detailed analysis of the vegetation pattern and composition at the YYL is not available. The present study thus aims to describe not only floristic com-

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position but also the vegetation pattern of the YYL forest ecosystem.

Study Site

The Yuanyang Lake Forest Ecosystem Research (called YYLFER) is conducted at the Yuanyang Lake Nature Preserve, which is located at N24°35', E121°24' in the northeastern part of Hsinchu County, Taiwan, at the uppermost head water of the Tahan River watershed with an elevation of 1,650-2,432 m. The total area of the natural preserve is about 374 ha, of which the lake is about 3.6 ha and the marsh area encircling the lake is about 2.2 ha. (Figure 1A). The surrounding hillsides are dominated by cypress forest. Supported by Taiwan's Central Weather Bureau, a weather station was established near the site in 1992. Weather data, including monthly rainfall and air temperature, have been collected since 1992 and 1993, respectively. Daily solar radiation data at the YYL, collected from October 1992 to September 1995, ranged from 0 to 25 MJ/m^2/day (Hwang et al., 1966). The maximum air temperature was in the summer, ranging from 16 to 27°C; the minimum air temperatures ranged from -5 to 13.5°C, and the mean air temperatures ranged from 5 to 17.5°C. Thus, YYL has a temperate, heavy moist climate.

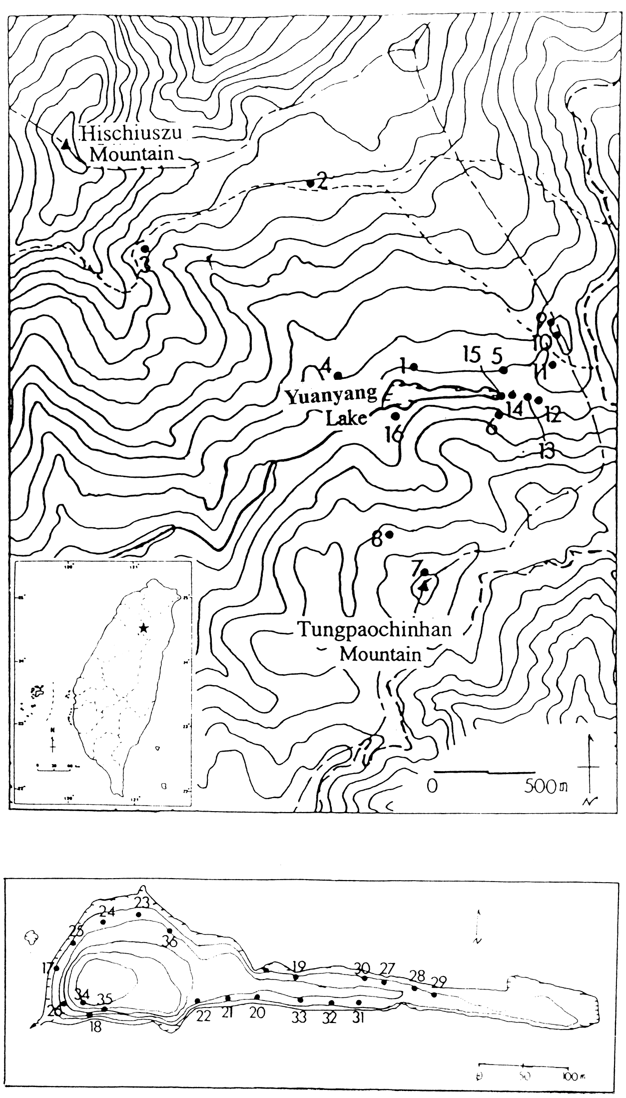

Figure 1. The geographic location of the Yuanyang Lake (YYL) forest site. Numbers indicate the sampling plots. A, sampling plots in the YYL forest site; B, sampling plots around the YYL area.

Materials and Methods

Sampling and Measuring Techniques

Regarding the sampling, sixteen plots were selected in the YYL forest area for the vegetation composition study. Of them, 10 quadrats, 10×10 m^2 or 5×5 m^2 each were employed for detailed forest analysis (Figure 1A). For aquatic community study, on the other hand, 36 plots were selected around the lake area. Of them, 10 quadrates, 5×5 m^2 or 3×3 m^2 each, were selected for detailed analysis (Figure 1B). In the forest community DBH (diameter at breast height) was measured for all plants above 1 meter tall. The number of plants of each species per plot and coverage of basal area at breast height of each plant was measured. Dominance value (DV) of each species is the sum of relative density and relative coverage of each species in the community (Curtis and McIntosh, 1951). By using an Octave scale (Gauch, 1982), the data were divided into 10 scale indexes from 0 to 9 and were analyzed by a Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979) and by a Detrend Correspondence Analysis (DCA) (Hill and Gauch, 1980).

For environmental factor analysis, information of altitude, slope, orientation, geographical position, and elevation above lake surface was analyzed to obtain a correlation between the environmental parameters and sampling plots. These environmental parameters are as follows:

Altitude. The data of altitude is important for environmental analysis and is ranked high in the hierarchy of environmental factors (Billings, 1952).

Slope. The slope recorded by using a slope meter is thought to be associated with soil development, water drainage, and water content.

Orientation. Different orientation may affect temperature, radiation, humidity, and soil moisture. The orientation was based on the major facing side. The degree of slope is associated with water gradient and is designated as 1(=southwest), 2(=south), 3(=west), 4 (=southeast), 5(=northwest), 6(=east), 7(=north), and 8 (=northeast).

Geographic position. The geographic position is defined as the correlation between habitat position and topographic position. The geographic positions are designated as follows: 1(=summit ridge), 2(=middle hill or branch), 3(=downhill), 4(=valley, creek side, riverside) and 5(=lake surface). The numbers used to evaluate the degree of soil moisture are in an increasing order, i.e., 1 is the driest land, and 5 is the most moist area.

Table 1. Vegetation composition of the Yuanyang Lake forest.

Species name	Relative coverage, %	Relative density, %	Dominance, %
Chamaecyparis obtusa formosana	38.87	3.36	21.11
Tsuga chinensis formosana	40.92	0.39	20.65
Illicium philippinense	0.78	7.29	4.03
Rhododendrum formosanum	0.09	6.11	3.10
Schefflera taiwaniana	2.01	4.32	3.17
Dendropanax pellucidopunctata	0.13	4.57	2.35
Barthea formosana	1.31	3.44	2.37
Adinandra lasiostyla	0.23	3.33	1.78
Illex pedunculosa	0.14	2.72	1.43
Neolitsea acuminatissima	0.52	2.44	1.48
Skimmia arisanensis	0.68	2.32	1.50
Eurya leptophylla	0.09	2.48	1.29
Eurya glaberrima	0.18	2.03	1.10
Vaccinium randaiense	0.42	1.61	1.01
Elaeocarpus japonicus	0.67	1.20	0.93
Neolitsea variabillima	0.53	1.04	0.79
Daphniphyllum himalaense	1.12	0.64	0.88
Creptomeria japonica	0.19	0.98	0.59
Ternstroemia gymnanthera	1.99	0.21	1.10
Ilex sugeroki brevipedunculata	0.63	0.64	0.64
Viburnum furcatum	1.27	0.37	0.82
Ardisia crenata	0.55	0.57	0.56
Trochodendron aralioides	0.37	0.59	0.48
Symplocos anomala	0.50	0.42	0.46
Symplocos lancifolia	0.07	0.57	0.32
Stranvaesia niitakayamensis	0.18	1.00	0.59
Ilex hayataiana	0.54	0.38	0.46
Eurya strigillosa	0.15	0.51	0.33
Prunus takasagomontana	0.02	0.41	0.21
Osmanthus heterophyllus	0.51	0.20	0.35
Viburnum foetidum	0.67	0.11	0.39
Photinia beauverdiana	0.05	0.33	0.19
Acer morisonensis	0.66	0.09	0.37
Lasianthus japonicus	0.04	0.29	0.16
Rhododendron ellipticum	0.01	0.26	0.13
Viburnum taiwanianum	0.61	0.01	0.31
Litsea mushaensis	0.03	0.21	0.12
Symplocos lucida	0.14	0.15	0.14
Damnacanthus angustifolius	0.15	0.12	0.13
Litsea cubeba	0.43	0.01	0.22
Rhododendron morii	0.26	0.07	0.16
Rhododendron mariesii	0.37	0.01	0.19
Ligustrum japonicum	0.01	0.13	0.07
Machilus japonica	0.25	0.03	0.14
Lindera thunbergii	0.01	0.12	0.06
Daphne arisanensis	0.04	0.10	0.07
Lonicera apodonta	0.01	0.11	0.06
Pieris taiwanensis	0.07	0.08	0.08
Rhaphiolepis indica tashiroi	0.21	0.01	0.11
Rhamnus crenata	0.08	0.05	0.07
Symplocos heishanensis	0.05	0.04	0.04
Ilex yunnanensis parvifolia	0.02	0.04	0.03
Microtropis fokienensis	0.01	0.03	0.02
Machilus thunbergii	0.05	0.01	0.03
Pittosporum illicioides	0.02	0.03	0.02
Symplocos stellaris	0.01	0.03	0.02
Ilex lonicerifolia hakkuensis	0.04	0.01	0.02
Ilex tsugitakayamensis	0.04	0.01	0.02
Acer palmatum pubscence	0.01	0.01	0.01
Ilex suzukii	0.02	0.01	0.02
Ilex goshiensis	0.01	0.01	0.01
Itea oldhamii	0.01	0.01	0.01
Total	100.00	100.00	100.00

Elevation above lake surface. A negative value indicates a submerged plant, while a positive value indicates a terrestrial plant. These data were used to classify vegetation patterns of the plant community in the YYL forest ecosystem.

Results

Floristic Composition of the YYL Forest

Based on the data of relative coverage, relative density, and dominance value (DV), the order of dominance among plants in the YYL area is given in Table 1. It shows that *Chamaecyparis obtusa* var. *formosana* and *Tsuga chinese* are predominant species with dominance over 20%. Floristically there are 185 species in 115 genera and 71 families. Pteridophytes comprise 33 species in 23 genera and 14 families. Gymnosperms comprise 4 species in 3 genera and 3 families. Regarding dicots, there are, 108 species in 70 genera and 46 families; while for monocots there are 22 species in 19 genera and 8 families. The most common plants found in the area include 7 species of Polypodiaceae (pteridophytes), 9 species of Rosaceae, 8 species of Aquifoliaceae, and 10 species of Ericaceae. These plants are representative of warm temperate flora; however, the most abundant warm temperate plants in Taiwan, such as Lauraceae and Fagaceae, were scarcely present in the area. A comparison of plants of YYL with those of neighboring areas, such as Fushan, was made. The number of species in Lauraceae and Fagaceae was much lower in the YYL area than in the Fushan area, suggesting that the dominant species, such as *Chamaecyparis* and *Rhododendron*, took over Lauraceae and Fagaceae.

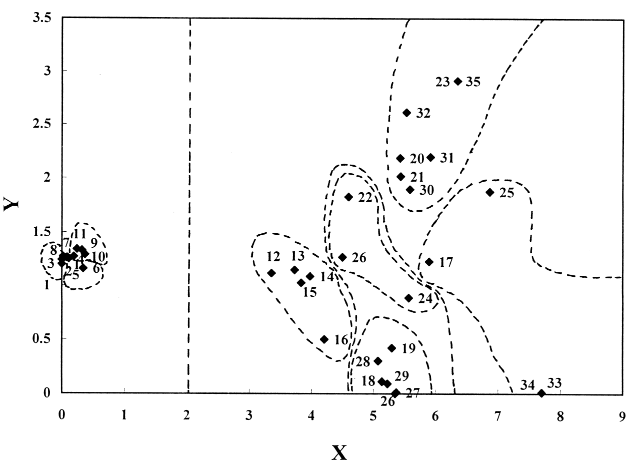

Figure 2. The cluster formation of sampling plots at the YYL site between the X and Y axes based on DCA analysis. The designations of plots are: I, Stands of *Chamaecyparis obtusa* var. *formosana* and its association; II, Stands of *Cryptomeria japonica* plantation; III, Stands of dominant community of *Miscanthus transmorrisonensis*; IV, Stands of submerged plants community; V, Stands of emergent hydrophyte dominated by *Sparganium fallax* and scattered by *Schoenoplectus mucronatus*; VI, Stands of dominant community of *Schenoplectus mucronatus*.

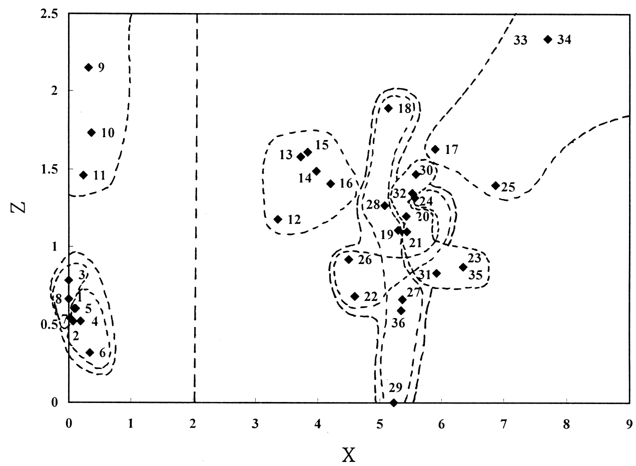

Figure 3. The cluster formation of sampling stands at the Yuanyang Lake site between the X and Z axes based on DCA analysis. The designations I, II, III, IV, V, and VI are the same as Figure 2.

Vegetation Analysis

Statistical analysis of TWINSPAN reveals that the plant community in the YYL area can be divided into two major sub-communities in the first run of computing, namely, a forest community and a swamp or early succession plant community (Table 2). In the second computing run, the forest community then can be divided into two groups, *Chamaecyparis* spp. (natural vegetation) and *Cryptomeria joponica* (plantation). The forest community can be grouped into two subtypes: *Chamaecyparis—Rhododendron* type and *Chamaecyparis—Tsuga* type (Table 2). On the other hand, the swamp vegetation can be divided into two groups, submerged hydrophytes (e.g., *Potamogeton octandrus*) and emergent hydrophytes (e.g., *Schoenoplectus mucronatus* and *Sparganium fallax*). *Miscanthus transmorrisonesis* was out of the *S. mucronatus* group.

By using DCA analysis, the data can be formed into three axes, representing three dimensions based on environmental factors mentioned previously. This is shown in Tables 3 and 4. The correlation between the X axis and environmental factors was significant, but a negative correlation was revealed with slope, altitude, content of sand, and distance from lake surface. However, the other two axes, Y and Z, were not statistically correlated to the environmental factors given. Therefore, if the correlation is based on the X and Y axis, two distinct communities are shown (Figure 2). Plots 1-11 belong to A group, comprising types I and II, while plots 12-36 belong to B group comprising types III, IV, V, and VI. Furthermore, correlation between the X and Z axes also reveals two community sub-groups (Figure 3), in which vegetation patterns are similar to that of Figure 2. These findings conclude that six vegetation types are represented in the YYL plant community.

Table 2. The vegetation types of species distribution in the Yuanyang Lake forest community. The data were analyzed by TWINSPAN method.

Species name	Vegetation type								
	I		II	III	IV		V	VI	
	Sampling plot								
	000 378	00000 24561	011 901	11111 23456	112223 899796	222 246	3322233 0201315	1233 7534	
Elaeocarpus japonicus	111	12212	---	-----	------	---	-------	----	000011
Myrsin stolonifera	-1-	111-1	---	-----	------	---	-------	----	000011
Tsuga chinensis formosana	556	5----	---	-----	------	---	-------	----	000100
Monachosorum henryi	131	----1	---	-----	------	---	-------	----	000100
Yushania niitakayamensis	-58	-----	---	-----	------	---	-------	----	000100
Neolitsea acuminatissima	545	31133	2-2	-----	------	---	-------	----	000101
Oxalis acetosella japonica	23-	---31	--1	-----	------	---	-------	----	000101
Pleione formosana	4--	2----	--1	-----	------	---	-------	----	000101
Polypodium amoenum	2-1	12-1-	-1-	-----	------	---	-------	----	000110
Ilex hayataiana	111	1--21	-1-	-----	------	---	-------	----	000111
Viburnum furcatum	132	22332	111	-----	------	---	-------	----	000111
Lyonia ovalifolia lanceolata	13-	31211	-11	-----	------	---	-------	----	000111
Ternstroemia gymnanthera	212	32213	-11	-----	------	---	-------	----	000111
Xiphopteris okuboi	111	11113	---	-----	------	---	-------	----	000111
Vittaria flexuosa	11-	111-4	--1	-----	------	---	-------	----	000111
Shortia exappendiculata	212	43141	--2	-----	------	---	-------	----	000111
Nertera nigricarpa	111	11111	---	-----	------	---	-------	----	000111
Skimmia arisanensis	321	44322	111	-----	------	---	-------	----	000111
Schefflera taiwaniana	425	43524	455	-----	------	---	-------	----	001000
Vaccinium randaiense	-11	----2	-11	-----	------	---	-------	----	001000
Symplocos anomala	211	2--11	11-	-----	------	---	-------	----	001000
Araiostegia perdurans	221	111--	-21	-----	------	---	-------	----	001000
Rhus orientalis	121	11111	112	-----	------	---	-------	----	001000
Asarum macranthum	22-	1-111	211	-----	------	---	-------	----	001000
Rhododendron kawakamii	-11	-11-1	-11	-----	------	---	-------	----	001000
Vaccinium japonicum lasiostemon	131	11111	-11	-----	------	---	-------	----	001000
Rubus pectinellus	43-	----1	1-2	-----	------	---	-------	----	001000
Daphne arisanensis	111	1--11	1-1	-----	------	---	-------	----	001000
Chamaecyparis obtusa formosana	777	67777	-56	-----	------	---	-------	----	001001
Illicium philippinensis	626	54565	466	-----	------	---	-------	----	001001
Barthea formosana	354	25545	223	-----	------	---	-------	----	001001
Adinandra lasiostyla	423	33534	323	-----	------	---	-------	----	001001
Mecodium polyanthos	553	35364	355	-----	------	---	-------	----	001001
Elaphoglassum conforme	11-	11211	11-	-----	------	---	-------	----	001001
Plagiogyria euphlebia	553	46654	656	-----	------	---	-------	----	001001
Arthromeris lehmanni	111	11321	111	-----	------	---	-------	----	001001
Ainsliaea reflexa	11-	111--	-11	-----	------	---	-------	----	001001
Vaccinium merrillianum	2-2	31111	-13	-----	------	---	-------	----	001001
Tripterospermum lanceolatum	1-1	11111	-11	-----	------	---	-------	----	001001
Sarcopyramis delicata	432	13641	253	-----	------	---	-------	----	001001
Ardisia japonica	511	36552	235	-----	------	---	-------	----	001001
Damnacanthus angustifolius	1-1	1111-	111	-----	------	---	-------	----	001001
Pellionia trilobulata	56-	32551	214	-----	------	---	-------	----	001001
Smilacina formosana	11-	111--	-11	-----	------	---	-------	----	001001
Neolitsea variabillima	-42	-41--	321	-----	------	---	-------	----	00101
Lycopodium serratum longipetiolatum	---	-1311	11-	-----	------	---	-------	----	00101
Rhododendron formosanum	162	65565	--4	-----	------	6-6	-------	----	0011
Viburnum taiwanianum	2-1	111-1	121	-----	------	---	-------	----	01000
Symplocos lancifolia	--1	-1111	21-	-----	------	---	-------	----	010010
Ophiopogon japonica	22-	14331	444	-----	------	---	-------	----	010010
Ilex pedunculosa	111	11111	-34	-----	------	---	-------	----	010011
Ilex sugeroki brevipedunculata	112	11221	223	-----	------	---	-------	----	010011
Dendropanax pellucidopunctata	344	35223	256	3----	------	---	-------	----	010011

Table 2. (Continued)

	Vegetation type								
	I		II	III	IV		V	VI	
Species name	Sampling plot								
	000	00000	011	11111	112223	222	3322233	1233	
	378	24561	901	23456	899796	246	0201315	7534	
Viburnum foetidum rectangulatum	111	1111-	331	-----	------	---	-------	----	010011
Osmanthus heterophyllus bibracteatus	3-1	-1---	211	-----	------	---	-------	----	010011
Eurya glaberrima	113	11-31	643	-----	------	---	-------	----	010011
Berberis kawakamii	2--	111-1	121	-----	------	---	-------	----	010011
Rubus liuii	11-	1-2-1	231	-----	------	---	-------	----	010011
Nertera depressa	111	211-1	223	-----	------	---	-------	----	010011
Pellionia arisanensis	-4-	-----	5--	-----	------	---	-------	----	010011
Smilax sp.	111	11111	411	-----	------	---	-------	----	010011
Cryptomeria japonica	---	-----	766	-----	------	---	-------	----	010100
Daphniphyllum himalaense macropodum	1-1	11-1-	542	-----	------	---	-------	----	010100
Vaccinium dulanianum caudatifolium	---	----1	122	-----	------	---	-------	----	010100
Stranvaesia niitakayamensis	1-1	1---1	343	-----	------	---	-------	----	010100
Symplocos lucida	1--	-----	423	-----	------	---	-------	----	010100
Trochodendron aralioides	---	---11	451	-----	------	---	-------	----	010100
Peranema cyatheoides	---	----1	342	-----	------	---	-------	----	010100
Diplopterygium glaucum	--2	-2--1	454	-----	------	---	-------	----	010100
Plagiogyria stenoptera	---	----1	113	-----	------	---	-------	----	010100
Hydrangia integrifolia	11-	--1--	4-1	-----	------	---	-------	----	010100
Ligustrum japonicum	---	2----	321	-----	------	---	-------	----	01011
Akebia chingshuiensis	---	-11--	321	-----	------	---	-------	----	01011
Eurya leptophylla	214	12212	554	-4-5-	------	---	-------	----	011
Lonicera acuminata	111	111-1	111	----3	------	---	-------	----	011
Coptis quinquefolia	421	34331	113	-55--	------	---	-------	----	011
Prunus tagasagomontana	111	1-1--	211	-----	------	---	-------	----	10
Rhododendron mariesii	---	-1-5-	---	5----	------	---	-------	----	110
Rubus shinkoensis	121	-1111	211	5--54	------	---	-------	----	110
Arisaema consanguineum	1--	1-11-	---	----4	------	---	-------	----	110
Potemogeton octandrus	---	-----	---	-----	3-----	---	-------	9599	11100
Viburnum matsudai	---	-----	---	33---	------	---	-------	----	111010
Hydrangea paniculata	---	-----	---	63353	------	---	-------	4---	111010
Baeothryon subcapitatum	---	-----	---	88777	------	---	-------	----	111010
Carex sp.	1--	-----	21-	-56-3	------	---	-------	----	111010
Parathelypteris japonica	---	-11--	-2-	-4-5-	--3---	---	-------	----	111011
Schoenoplectus mucronatus robustus	---	-----	---	-5764	888888	588	--58-5-	5---	11110
Miscanthus transmorrisonensis	---	-----	454	88788	566334	766	6665---	5---	11110
Alnus formosana	---	----1	---	-----	4-----	---	-------	----	111110
Rhododendron ellipticum	---	-1-1-	---	-----	----7-	---	-------	----	111110
Vaccinium bracteatum	---	-1---	---	-----	------	4--	-------	----	111110
Machilus japonica	---	----1	---	-----	------	-76	-------	----	111110
Polygonum dichotomum	---	-----	---	----3	6777-7	-53	5------	----	111110
Polygonum thunbergii biconvex	---	-----	---	----6	565565	-6-	-------	----	111110
Rosa taiwanensis	---	-----	-1-	----4	5-----	-46	-------	----	111110
Galium trifidum	---	-----	---	-----	64-776	44-	-------	----	111110
Hydrocotyle nepalensis	---	---2-	---	-----	---667	--3	-------	----	111110
Carex onoei	---	-----	---	-----	--5-33	---	-------	----	111110
Juncus effusus decipiens	---	-----	-2-	-----	6-4---	---	-------	----	111110
Sparganium fallax	---	-----	---	-----	----3-	663	9999999	69--	111111
	000	00000	000	11111	111111	111	1111111	1111	
	000	00000	111	00000	000000	000	0000000	1111	
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Vegetation Types

Based on the analysis of DCA of the aforementioned 36 sampling plots, two plant communities with six vegetation types are described as follows:

Community A. Forest community. The forest community comprises two vegetation types.

Type I: *Chamaecyparis obtusa* var. *formosana* and its associates.

Chamaecyparis obtusa appeared in plots 1-8. They were tall and distributed from the lake side up to mountain summit. The tree height was above 20 m and classified as T1 layer, where *Chamaecyparis obtusa* var. *formosana* was the dominant species and *Tsuga chinensis*

Table 3. Information of eight environmental parameters for each stand at the YYL sites.

Stand No.	Environmental parameter[a]							
	FSL	DSS	Aspect	Slope	Topography	Elevation	Stoniness	DLS
1	57	72	4	40	4	1700	30	28
2	75	88	7	13	6	1900	10	228
3	63	72	7	6	5	2000	5	328
4	51	64	7	25	3	1800	28	128
5	33	29	7	40	3	1685	35	13
6	60	71	8	22	4	1725	0	153
7	52	51	8	38	6	1930	15	258
8	66	74	1	6	5	1900	3	228
9	55	81	1	35	4	1870	19	198
10	60	76	1	26	4	1820	15	148
11	52	62	3	25	4	1850	15	178
12	57	75	1	0	2	1675	0	2
13	53	60	1	4	2	1675	0	2
14	53	69	1	3	2	1675	0	3
15	59	75	1	0	2	1675	0	2
16	59	70	1	0	2	1675	0	2
17	65	79	1	0	1	1672	0	-2.2
18	63	78	1	0	1	1672	0	-0.6
19	59	76	1	0	1	1672	0	-0.8
20	51	58	1	0	1	1672	0	-1
21	60	80	1	0	1	1672	0	-0.9
22	51	61	1	0	1	1672	0	-0.9
23	58	74	1	0	1	1672	0	-1.1
24	59	76	1	0	1	1672	0	-0.8
25	58	73	1	0	1	1672	0	-1
26	57	73	1	0	1	1672	0	-0.7
27	57	77	1	0	1	1672	0	-0.3
28	60	77	1	0	1	1672	0	-0.3
29	56	73	1	0	1	1672	0	-0.8
30	59	74	1	0	1	1672	0	-1
31	55	68	1	0	1	1672	0	-1.1
32	55	72	1	0	1	1672	0	-1.4
33	59	70	1	0	1	1672	0	-2.1
34	56	70	1	0	1	1672	0	-2.4
35	61	77	1	0	1	1672	0	-1.3
36	61	79	1	0	1	1672	0	-0.5

[a]The abbreviation of parameters are: FSL=Full sky light space; DSS=Direct sky light space; DLS=Distance from lake surface.

Table 4. Correlation between environmental axis and environmental parameter.

Environmental axis[a]	Environment parameter[b]					
	FSL	DSL	Slope	Elevation	Stoniness	DLS
X	0.097	0.255	-0.811	-0.773	-0.723	-0.802
Y	-0.113	-0.109	0.042	0.035	0.042	0.033
Z	0.059	0.172	-0.191	-0.173	-0.200	-0.217

[a]X, Y, Z: indicates the dimension of environmental factor.

[b]Abbreviations of environmental parameters are: FSL=Full sky light space; DSL=Direct sky light space; DLS=Distance from lake surface.

var. *formosana* was the second dominant. However, *Tsuga chinensis* var. *formosana* was distributed only in higher elevation above 2,500 m. On the other hand, tree height between 10 and 20 meters was classified as T2 layer. Trees of *Lauraceae* and *Fagaceae* were grouped into T2 layer. These plants, however, were scarce in the YYL site.

Trees below 10 m height were classified as T3 layer and distributed in the area around the lakeside, where *Illicium philippinense* and *Rhododendron formosanum* were predominant. Other common trees are *Neolitsea cuminatissima*, *Schefflera taiwaniana, Barthea formosana, Ternstroemia gymnanthera, Adinandra formosanum, Damnacanthus angustifslius, Dendropanax pellcidopunctata* and *Skimumia arisamensis* (Figure 4). Grassland species are *Miscanthus transmorrisonensis, Plagiogyria glauca* var. *philippinensis, Coptis quinquefolia, Ardisia japonica, Asarum* spp., *Pellionia trilobulata*. Epiphytes are *Mecodium polyanthos* and *Sarcopyramis delicata*. Vine tree is dominated by *Smilax* spp.

Type II: *Cryptomeria japonica* plantation.

Regarding type II of *Cryptomeria* and plantation trees, plots 9, 10 and 11 are distributed in the eastern range area of the YYL natural preserve. Forest plantation, such as *Cryptomeria joponica* was dominant but substantial old deforested *Chamaecyparis* trees were still there. Several native species have gradually reappeared in the area. These native species include *Chamaecyparis formosensis*, *C. obtusa* var. *formosana*, *Viburnum furcatum*, *Skimmia arisanensis*, *Illicium philippinense*, *Symplocos anomala*, *Barthea formosana*, *Ilex sugeroki* var. *brevipedunculata*, *Dendropanax pellcidopunctata*, *Berberis Kawakamii*, *Daphniphyllum himalaense* subsp. *macropodum*, *Symplocos lucida*, *Eurya glaberrima*, *Trochodendron aralioides*, *Vaccinium dunaliannum* var. *caudatifolium*, *Ligustrum japonicum* and *Shefflera taiwaniana.*

Community B. Aquatic and grassland community.

The aquatic and grassland community appeared in the lake and swamp area around the lake. Based on DCA analysis, four types of vegetation are recognized:

Type III: *Miscanthus transmorrisonensis*.

Type III vegetation is represented by *M. transmorrisonensis* based on sampling plots 12, 13, 14, 15, and 16. The vegetation was the dominant species in marsh area, and the mean coverage was above 5% of the area. The other common species were *Carex onoei, Baeothryon subcapitatum,* and *Juncus effusus* var. *decipiens,* which were typical marsh plants. Other Gramminae occupied only a small area with relatively low coverage. There were a few shrubs, such as *Hydrangia paniculata* (most common)*, Rhamnus crenata* and *Alnus formosana.*

Type IV*: Potamogeton octandrus*.

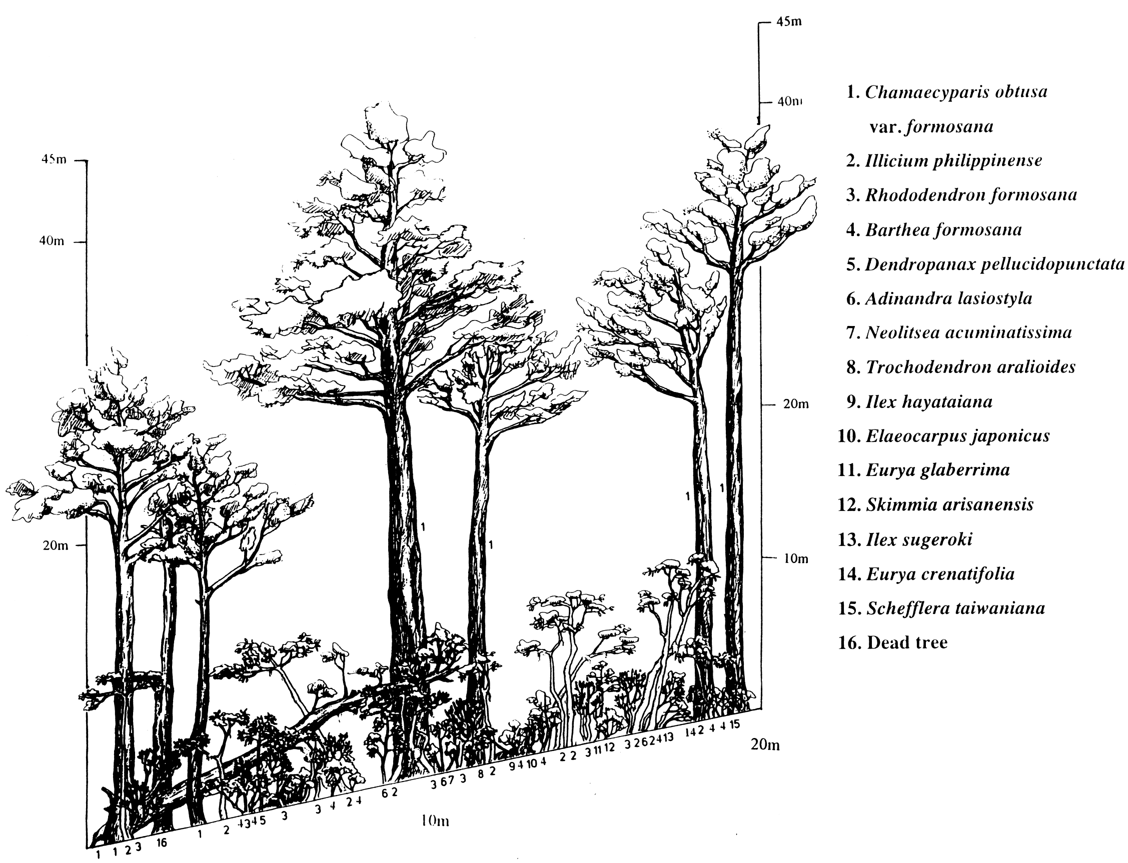

Figure 4. A general diagram of the forest community in the area of the Yuanyang Lake .

Potamogeton octandrus appeared in plots 17, 25, 33, and 34 and was a submerged plant. Its leaves floated on the lake water.

Type V: *Sparganium fallax*.

Sparganium fallax appeared in plots 20, 21, 23, 30, 32, 31, and 35 and was an emergent hydrophyte. It grew mostly along the lakeside. *Sparganium fallax* was dominant at the site, and *Schoenoplectus mucronata* was scattered throughout the stand of *S. fallax*.

Type VI: *Schoenoplectus mucronatus*.

Schoenoplectus mucronatus appeared in plots 18, 19, 22, 24, 26, 27, 28, 29, 36. It was an emergent hydrophyte, frequently forming a pure stand. It was also found in the surrounding swamp. The associated species are *Polygonum dichotomum, Polygonum thunbergii* f. *biconvexum, Hydrocotyle nepalensis,* and *Galium trifidum.* This vegetation type often forms two subtypes, namely the *Schoenoplectus-Polygonum* subtype and the *Schoenoplectus-Sparganium* subtype based on the population size of *Polygonum thunbergii.*

The growth habitat of vegetation types IV, V and VI can be contrasted as follows: *Potamogeton octandrus* grows in deep water; *Schoenoplectus* grows in the shallow water; and *Sparganium fallax* grows in between.

Regeneration of Chamecyparis obstusa var. formosana Trees in YYL Forest

We measured the diameter at breast height (DBH) of all *Chamaecyparis* trees in 0.8 ha of the forest at the YYL. Results based on 5 cm set of diameter are given in Figure 5. It shows that the number of individuals with a 5 cm diameter is the highest (118), while the number of individual trees with 50, 10, and 45 cm diameters is less than 20. Only four trees have diameter over 70 cm, and only about one or two trees with diameter over 90 cm were found (Figure 5). This fact indicates that the forest is relatively mature and that the cypress trees are regenerating and sustainable as a dominant community there. The young (less than 10-year old) cypress trees were abundant although some old trees were also present. That lack of old trees could be due to some physical factors, such as shallow soil and frequent typhoons. An old cypress tree was destroyed and broken in half by a thunderstorm in 1994.

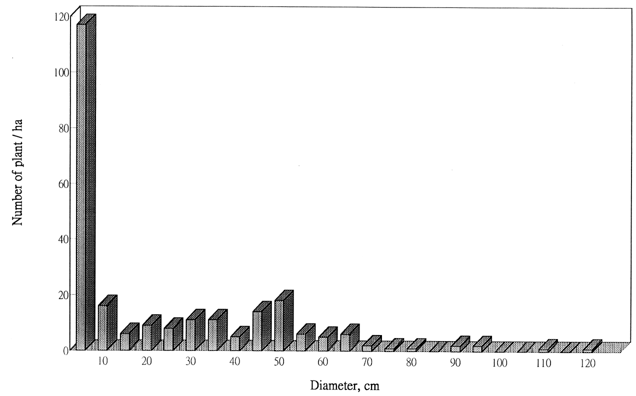

Figure 5. Number of plants of *Chamaecyparis obtusa* var. *formosana* per hectare based on the stem diameter at breast height at the Yuanyang Lake site.

Successional Trend in the YYL Forest

Most alpine lakes contain organic debris or other matter coming from the upper stream to a narrow creek mouth. The continuous accumulation of deposition causes the lakeside to become shallow and aquatic plants gradually invaded the land. A hydrosere will occur at all alpine lakes if organic debris is allowed to continuously deposit. The present vegetation of aquatic plants occurring in the center and surrounding lake is obvious. The succession has begun from the east and southwest side of the lake where the creek passes through. *Potamogeton octandrus* (submerged plant), *Schoeneplectus mucronatus* and *Sparganium fallax* (both are emergent hydrophyte) are pioneer species growing in the area. In the second stage of plant succession, *Miscanthus transmorrisonensis* and *Alnus formosana* become dominant, and in the final successional stage the *Chamaecyparis* species becomes dominant. The cypress trees and seedlings are found everywhere, indicating a regeneration by natural reseeding has occurred. A proposed pathway of the succes-

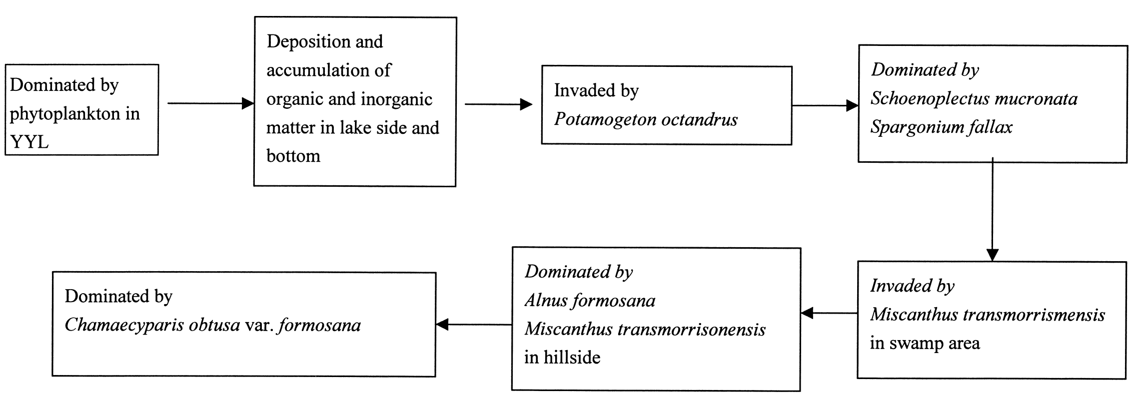

Figure 6. A proposed succession trend of the Yuanyang Lake forest community.

sional trend of vegetation at the Yuenyang Lake forest is given in Figure 6. Our findings are very much in agreement with that of Moir (1992), who stated that an old growth forest should possess big fallen trees or dead trees with a large diameter, and large vine trees as well.

Discussion

In the YYL forest community, many dead and fallen trees of *Chamaecyparis obtusa* var. *formosana* were found. Many seedlings of this plant grew luxuriantly on the decaying wood and in open areas. It has been reported that the cypress forest has been there for many thousands of years and has become a climax vegetation (Chang, 1963; Liu and Hsu, 1973; Liu, 1975). Chen and Yang (1996) further indicated that pollen of *Chamaecyparis* have been dominant for 3,000 years. They also found pollen of the Fagaceae species at around 3,000, 2,500, 1,800, 1,380 and 300 years ago, indicating that the climate change led temperatures to rise temporarily. The rise of temperature is presumably favorable for the growth of hardwood forests, such as Fagaceae and Lauraceae; however, these plants were not dominant due to the short duration of temperature rise. Consequently, the *Chamaecyparis* seedlings established themselves in the open gap area where the hardwood forest died. In the present study, we did not find plants of Fagaceae and Lauraceae, which are dominant at similar altitudes, at other places in Taiwan. This fact reflects that the climatic and edaphic development might have been stable for many thousands of years and the trees of *Chamaecyparis* species have been able to resist the invasion of other species. Many recent workers have reported that the productivity of *Chamaecyaris* plants has reached its maximum and is stablized at the YYL area. The aforementioned evidence may lead one to conclude that the YYL site is favorable to the growth of *Chamaecyparis* plants, which might reach a climax stage as defined by Clements (1936) and Daubenmire (1968).

One of the nature preserve's naturalized and rare species is *Sparganium fallax*, which is native to northeast China. The plants may have been introduced by birds to YYL and some other alpine lakes or swamp land, such as Nantau (1,150 m in elevation), Fushan pond (700 m), Shenmi lake (1,000-1,150 m) or Taolin (1,300 m) in Taiwan. These areas are favorable for the growth of Fagaceae trees. However, *Sparganium* growing in the lake or swamp area can be regarded as an important indicator plant. The adaptive mechanisms of *Sparganium* were studied by Hwang and his associates (1996). Other physiological ecology studies conducted by Lee et al. (1996a and b) concluded that abscisic acid and putresine played an important role in the plant growth of *Schoenoplectus mucronata* (*Scirpus mucronatus*). Furthermore, these plants could grow in water of rather high acidity (pH 3.5-4.5), indicating that a good adaptive strategy of plant growth could be developed. We have conducted an alleopathic study on the dominant species of *Sparganium,* which revealed allelopathic potential (Chou, unpublished data). Chou (1993) indicated that allelopathy is an important species survival strategy when the plant grows under a stressful environment. Further clarification of this, however, is needed.

The aforementioned findings conclude that the cypress forests of *Chamaecyparis* and its related species are stable and can self-regenerate due to the favorable weather conditions of high humidity and low temperature. *Chamaecyparis obtusa* var. *formosanus*, *Tsuga chinese, Illicium philippinense*, *Schefflera taiwaniana*, and *Rhododendron formosanum* are the top five dominant forest species (Table 1), while *Potamogeton octandrus, Sparganium fallax, Schoenoplectus mucronntus*, and *Miscanthus transmorrisonensis* are the most dominant species in the YYL and its surrounding swamp area. These plants form a plant community of six major vegetation types, which is unique among alpine lakes and very different from other areas of subtropical forest at the same altitude in Asia. The unique, unspoiled YYL ecosystem is significant for performing long-term research. Permanent plots need to be established in order to elucidate the structure and function of the alpine lake forest ecosystem and to provide valuable information about ecological processes that help forest management.

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鴛鴦湖森林生態系長期生態研究
I. 植被組成及分析

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鴛鴦湖自然保留區位於台灣東北部新竹縣及桃園縣境交界，其集水區係源自大漢溪之上游，高度自 1,650 公尺至 2,432 公尺。自然保留區面積共 374 公頃，全湖包括沼澤區面積共約 3.6 公頃，但湖面僅 2.2 公頃。此自然保留區蘊育著豐富的珍稀植物，其植物相共 185 種維管束植物，分屬 71 科 115 屬；蕨類植物 14 科，23 屬，33 種；裸子植物 3 科，3 屬，4 種；雙子葉植物 46 科，70 屬，108 種；單子葉植物 8 科，19 屬，22 種。出現種類較多之科有蕨類的水龍科 7 種，薔薇科 9 種，冬青科 8 種，杜鵑花科 10 種，均屬溫帶樹種。然而，在溫帶較優勢的殼斗科與樟科植物在本區內極為罕見，只出現 7 種。以優勢度（包括相對密度及覆蓋度），雙向列表分析法及降趨對應分析本區之植被，再配合環境因子而歸納出六型植物即：(一)森林植物社會，包括：第一型：台灣扁柏型 （*Chamaecyparis obtusa* var. *formosensis* type)，第二型：柳杉人工型（*Cryptomeria japonica* plantation type)；(二)水、溼生草本植物社會，包括：第三型：高山芒型（*Miscanthus transmorrisonesis* type)，第四型：眼子菜型（*Potamogeton octandrus* type)，第五型：東亞黑三稜型（*Sparganium fallax* type）及第六型：水毛花型（*Schoenoplectus mucronatus* type)。此六型植物以扁柏林為主要優勢種，並有自然更新的機能，吾等認為其植物消長已近末期而呈現一個穩定的植物社會。

關鍵詞：扁柏；群系；植被分析；高山芒；眼子菜；守城滿山紅；東亞黑三稜；演替；鴛鴦湖。