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Geological History, Flora, and Vegetation of Xishuangbanna, Southern Yunnan, China[1]

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ABSTRACT

Xishuangbanna of southern Yunnan is biogeographically located at a transitional zone from tropical Southeast (SE) Asia to subtropical East Asia, and is at the junction of the Indian and Burmese plates of Gondwana and the Eurasian plate of Laurasia. The flora of the region consists of a recorded 3336 native seed plant species, belonging to 1140 genera in 197 families, among which 83.5 percent are tropical genera and 32.8 percent are endemic to tropical Asia, suggesting a strong affinity to tropical Asian flora. The vegetation of Xishuangbanna is organized into four forest types: tropical rain forest, tropical seasonal moist forest, tropical montane evergreen broad-leaved forest, and tropical monsoon forest. The tropical rain forest in Xishuangbanna has the same floristic composition of families and genera as some lowland equatorial rain forests in SE Asia, and is dominated (with a few exceptions) by the same families both in species richness and stem dominance. The exceptions include some deciduous trees in the canopy layer, fewer megaphanerophytes and epiphytes, and a higher abundance of lianas and microphyllic plants. We consider the tropical rain forest of Xishuangbanna as a type of tropical Asian rain forest, based on their conspicuous similarities in ecological and floristic characteristics.

Key words: floristic composition; southern Yunnan; tropical rain forest; vegetation types; Xishuangbanna.

THE TROPICAL AREA OF SOUTHERN CHINA is climatically and biogeographically located at the northern edge of tropical Asia. The largest tropical area still covered by native forests is in southern Yunnan. C.W. Wang briefly mentioned the tropical flora and vegetation of southern China, especially those of southwestern China, for the first time in 1939 (Wang 1939). Tropical rain forests of southwestern China were little known to the scientific community until the late 1950s because of poor access to the region. For a long time there has been discussion as to whether there is true tropical rain forest in southern Yunnan owing to its location at the northern edge of tropical Southeast (SE) Asia and monsoon climate. It was commonly assumed that if there were tropical rain forests in the region, they would probably be intermediate between tropical rain forests and monsoon forests, as defined by Schimper (1903), or be types of subtropical rain forests which differ in various aspects from tropical rain forests described by Richards (1952). Some papers on the tropical rain forest vegetation (Fedorov 1958, Qu 1960, Wang 1961) and tropical flora (Fedorov 1957, Wu 1965) of this region were published after a China–Russia expedition that penetrated deep into the areas of southwestern China (including southern Yunnan) in the late 1950s. It was then accepted that true tropical rain forests exist in the southern Yunnan region of southwestern China. These forests were considered distinct from the Indo-Malaysian forests, however, because they lacked representatives of Dipterocarpaceae, which dominate the typical rain forests of tropical SE Asia.

Botanical interest in the area was rekindled in the 1970s by the discovery of a dipterocarp forest in southern Yunnan. From that finding, the Indo-Malaysian affinity of the tropical flora of China was taken into consideration. Further biogeographical and ecological studies on the vegetation and flora of tropical southern Yunnan revealed that it indeed comprises a part of Indo-Malaysian flora (Zhu 1992; 1993a, b; 1994; 1997; 2002; Zhu *et al.* 1998a, b; 2001; 2002; 2003; 2004). Furthermore, on a short visit to southern Yunnan, T. C. Whitmore felt that the birds in the tropical rain forest sing the same songs as those heard in the tropical rain forests of Malaysia (Whitmore 1982). He also confirmed that there is true evergreen rain forest present in the southern fringe of China (Whitmore 1984, 1990).

Xishuangbanna is an administrative region in southern Yunnan. It has a typical monsoon climate. Despite its relatively high latitude and elevation, Xishuangbanna has a tropical moist climate in the southern area due to the Hengduan Mountains which form a barrier, keeping out northern cold air during winter. Additionally, the montane topography produces dense radiation fog during the dry season, which can supplement the reduction in precipitation. Biogeographically, the region is located at a transitional zone with tropical SE Asia to the south, subtropical East Asia to the north, the Sino-Japanese floristic region to the east, and the Sino-Himalayan floristic region to the west. Southern Yunnan is therefore a key area in biogeography and a hotspot for biodiversity (Myers 1998).

GEOLOGICAL HISTORY

Southern Yunnan is at the junction of the Indian and Burmese plates of Gondwana and the Eurasian plate of Laurasia (Audley-Charles 1987, Hall 1998). Before the Mesozoic era, the area was a part of the Tethys margin, and later some fragments from Gondwanaland were combined. Since the Tertiary period, the region had gone through several stages of rising and descending with the intermittent uplift of the Himalayas, and gradually formed the modern topography in the mid-Tertiary period (Shi *et al.* 1998, 1999).

During the late Cretaceous period, the region was under a dry and hot climatic condition, based on fossil records from Mengla, where a relatively high proportion of *Ulmipollenites* and *Ephedripites*

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were found (Sun 1979). From the Paleocene to the Eocene periods, the region went through a rising stage with the uplift of the Himalayas, and was influenced by a dry climate with a high deposition of salt minerals. From the Miocene to the Neocene periods, the region descended to some extent, and formed a series of basins with a wet and warm climate. Since the Quaternary period, the region has gone through rapid rising again, associated with alternative climatic changes of wet and dry periods (Liu *et al.* 1986).

Paleobotanical work is insufficient in the region, especially for the Tertiary period. From pollen deposition in Mengla during the late Cretaceous to the early Tertiary periods (except *Ulmipollenites*, and *Ephedripites*), Sun (1979) found the presence of gymnosperms such as *Tsugaepollenites*, *Araucariacites*, *Taxodiaceaepollenites*, *Abietineaepollenites*, and *Pinuspollenites*, and angiosperms such as *Engelhardtioidites*, *Faguspollenites*, *Ilexpollenites*, *Symplocospollenites*, *Rhamnacidites*, *Cupuliferuipollenites*, *Caprifoliidites*, *Quercoidites*, *Fraxinoipollenites*, and *Liquidambarpollenites*. This evidence indicates that the representative vegetation in the period was a subtropical montane evergreen broad-leaved forest, which was similar to the present vegetation in subtropical Yunnan.

Song *et al.* (1976, 1983) defined the region and neighboring northern SE Asia as a paleo-phytogeographical region of *Quercus-Betula* vegetation of the Miocene–Neocene plateau, suggesting that the vegetation in Xishuangbanna could have been a subtropical montane evergreen broad-leaved forest during that period. From other available references (Wulff 1944, Editorial Group for Cenozoic Plants from China 1978, Song 1984, Zhou and Ren 1984, Wang 1996), the vegetation of regions neighboring southern Yunnan was considered to be subtropical evergreen broad-leaved forests during the Tertiary period. A 40,000-yr palynological record from northeast Thailand indicated that the region supported a Fagaceae-coniferous forest, similar to contemporary vegetation from subtropical southwest China, and climatic conditions were cooler and probably drier in the Pleistocene than present northern Thailand (Penny 2001). Xishuangbanna is geographically near northern Thailand. Therefore, it is possible that Xishuangbanna had vegetation and climatic conditions similar to northern Thailand during the Pleistocene period.

The present tropical rain forest in Xishuangbanna is at the altitudinal and latitudinal limits of tropical rain forests in the northern hemisphere. It was believed that the tropical moist climate in southern Yunnan did not form until the Himalayas lifted up to a certain elevation after the late Tertiary period. Thus, the tropical rain forests in the region were developed after the later Tertiary period. The fundamental topography and climate of the region have been strongly affected by the uplift of the Himalayas and the formation of the eastern monsoon climate (Shi *et al.* 1998, 1999).

THE FLORA

FLORISTIC COMPOSITION.—Based on more than 40 yr of intermittent field collections, 3336 native species of 1218 genera and 207 families of seed plants have been recognized from this region in southern Yunnan (Li 1996). The families with highest species richness include Orchidaceae (96 genera(334 species), Fabaceae (68(232), Rubiaceae (43(147), Poaceae (65(141), Euphorbiaceae (38(119), Asteraceae (59(107), Lamiaceae (36(105), Moraceae (6(77), Urticaceae (12(72), Lauraceae (12(68), Zingiberaceae (15(67), Asclepiadaceae (25(62), Apocynaceae (27(61), Annonaceae (15(52), Acanthaceae (32(50), and Cucurbitaceae (17(50). The family Orchidaceae has higher species richness in Xishuangbanna than in Laos and Cambodia (Chen & Tsi 1996).

Some families have only a small number of species in Xishuangbanna, but are the dominant families in phytosociological importance (dominant in stems) in the tropical forests of the region. Such families include: Sapindaceae, Anacardiaceae, Burseraceae, Elaeocarpaceae, Ebenaceae, Combretaceae, Ulmaceae, and Myrtaceae. The families Dipterocarpaceae, Barringtoniaceae, Tetrameleaceae, Myristicaceae, Clusiaceae, Icacinaceae, Ixonanthaceae, and Sapotaceae also have even few species, but high phytosociological importance.

At the generic level, *Ficus* has the highest species richness with 51 species. Other genera with high species richness include *Dendrobium* (43 species), *Bulbophyllum* (40), *Piper* (24), *Dioscorea* (23), *Syzygium* (23), *Eria* (22), *Litsea* (21), *Lasianthus* (17), *Lithocarpus* (17), *Millettia* (17), *Pilea* (17), *Castanopsis* (16), *Tetrstigma* (16), *Calamus* (16), *Elaeocarpus* (14), *Elatostema* (14), *Amomum* (14), *Clerodendrum* (14), *Ardisia* (12), *Dysoxylum* (10), and *Fissistigma* (10). *Pometia, Terminalia*, *Antiaris*, *Girroniera*, *Pouteria*, *Pterosperma*, and *Tetrameles* have fewer species but high phytosociological importance in the dominant tree layer, and *Lasiococca*, *Garcinia*, *Mitrephora*, *Alphonsea*, *Cleidion*, *Sumbaviopsis*, *Trigonostemon*, and *Pittosporopsis* in the lower tree layer of the tropical rain forest in the region. In the tropical montane rain forest of the region, *Castanopsis, Lithocarpus, Machilus, Litsea, Phoebe, Anneslea,* and *Schima* are the most dominant genera.

GEOGRAPHICAL ELEMENTS.—In the flora of Xishuangbanna, families of strictly tropical distribution contribute 18.2 percent of the total sum of the flora. These families include those of pantropical distribution, such as Dipterocarpaceae, Myristicaceae, Taccaceae, and Icacinaceae; Old World tropical distribution, such as Sonneratiaceae and Barringtoniaceae; tropical Asian, African, and American distribution, including Aristolochiaceae, Bombacaceae, and Ixonanthaceae; and the tropical Asian Carlemanniaceae, Mastixiaceae, Sladeniaceae, Crypteroniaceae, and Pentaphragmaceae. Families with tropical as well as nontropical species contribute 41 percent of the total flora. Such families include Rubiaceae, Acanthaceae, Euphorbiaceae, Moraceae, Apocynaceae, and Meliaceae. The families of mainly subtropical distribution contribute 17.7 percent of the total flora, including Fagaceae, Magnoliaceae, Theaceae, Symplocaceae, Hamamelidaceae, and Aquifoliaceae. Families of mainly temperate distribution contribute 22.2 percent of the total flora, such as Primulaceae, Ranuculaceae, Scrophulariaceae, and Lamiaceae.

At the generic level, patterns of seed plant distribution in China were summarized by the Chinese botanist Wu (1991). From Wu's documentation, the distribution patterns of genera from the flora of Xishuangbanna are quantified and given in Table 1.

The genera of tropical Asian distribution, such as *Alphonsea, Pterospermum, Mitrephora, Chukrasia, Crypteronia*, and *Knema*, show the highest percentage among all distribution types, contributing to 32.8 percent of the flora. Genera of pantropical distribution, such as *Gnetum, Cryptocarya, Piper, Lasianthus, Bauhinia,* and *Marsdenia*, contribute to 22.8 percent of the flora. Following are the genera with Old World tropical distribution, such as *Thunbergia*, *Dracaena*, *Pandanus*, *Carallia*, and *Canarium*. The flora of tropical distribution (see above) compose 83.5 percent of the total number of genera, while genera of temperate distribution such as *Betula*, *Salix*, *Cornus*, and *Sorbus* contribute 10.6 percent of the total genera. Other genera include those with distributions disjunct from East Asia to North America such as *Schizandra, Photinia, Nyssa,* and *Mahonia*, Old World temperate distributions such as *Ajuga, Elsholzia, Ligustrum, Paris*, etc., and East Asian distributions such as *Actinidia, Belamcandia,* and *Cephalotaxus*. The Chinese endemics are only in eight genera, which are *Craspedolobium, Cyphotheca, Dichotomanthes, Biondia, Styrophyton, Tapiscia, Thyrocarpus*, *and Tutcheria*. These data show that the flora of Xishuangbanna is tropical in nature and has strong tropical Asiatic affinity.

The tropical flora of Yunnan (from Southwest to Southeast Yunnan) is composed of 4815 species representing 1447 genera of seed plants (Li 1995). The flora of Xishuangbanna includes more than 3336 species and 1140 genera. Xishuangbanna is therefore the area with the highest species richness in Yunnan.

TABLE 1. *Distribution types of seed plants at the generic level from the flora of Xishuangbanna (1135 genera).*

Distribution types	Number of genera	Percent
1. Cosmopolitan	48	–
2. Pantropic	248	22.8
3. Tropical Asia and Tropical America disjunct	26	2.4
4. Old World Tropic	112	10.3
5. Tropical Asia to Tropical Australia	75	6.9
6. Tropical Asia to Tropical Africa	91	8.4
7. Tropical Asia	356	32.8
Type 2–7 (total tropical elements)	908	83.5
8. North temperate	57	5.2
9. East Asia and North America disjunct	34	3.1
10. Old World temperate	16	1.5
11. Temperate Asia	4	0.4
12. Mediterranean, W Asia to C Asia	4	0.4
13. Center Asia	1	0.1
14. East Asia	55	5.1
15. Endemic to China	8	0.7
Type 8–15	227	16.5

VEGETATION TYPES

Terminology and classification of tropical vegetation have not been standardized, and different researchers have used various methods of classification. For example, physiognomic and ecological characters, which were initiated by Drude (1913) and Warming (1909), were used as the main basis for vegetation classification by most American researchers, while floristic aspects (Braun-Blanquet 1932) were used by continental European researchers. Our vegetation classification is based on a combination of physiognomic and ecological characters, floristic composition, and habitats. Physiognomic and ecological characters were used mainly for classification at the vegetation type level, whereas floristic composition and habitats were combined mainly at the formation level. Thus, the vegetation of Xishuangbanna is classified into four main vegetation types: tropical rain forest, tropical seasonal moist forest, tropical montane evergreen broad-leaved forest, and tropical monsoon forest.

TROPICAL RAIN FOREST.—The tropical rain forest (vegetation type) in Xishuangbanna has been classified into two subtypes: tropical seasonal rain forest and tropical montane rain forest (Qu 1960; Wu 1980, 1987; Jin 1983; Zhang & Cao 1995; Cao *et al.* 1996, 1997; Zhu 1992, 1993a, 1997; Jin & Ou 1997; Zhu *et al.* 1998a). The tropical seasonal rain forest is found in the lowlands, usually below 900 m in elevation, while tropical montane rain forest occurs locally at higher elevation.

Like equatorial lowland rain forest, the tropical seasonal rain forest has 3–4 indistinct tree layers, of which the top layer is mainly emergent trees greater than 30 m tall (tallest up to 60 m), with about 30 percent crown coverage. The second layer is the main canopy layer, and is up to 30 m tall with an almost continuous canopy (70–80% coverage), and greatest stem density. The third layer is 5–18 m tall with crown cover of about 40 percent, consisting of small trees and juveniles of species from the upper layers. In some sites, the third tree layer can be further divided into two sublayers: the upper (10–18 m tall), and lower sub-layers (5–9 m tall). Buttresses and cauliflory are common, and both big woody lianas and vascular epiphytes are abundant. The forest is mainly evergreen despite the fact that there are some deciduous trees in the emergent layer.

Based mainly on habitats and floristic composition, the tropical seasonal rain forest of Xishuangbanna is further classified into two formation groups including lower hill seasonal rain forest and ravine seasonal rain forest (Wu 1980, 1987; Zhu 1992, 1997; Jin 1997; Jin & Ou 1997; Zhu *et al.* 1998a). Ravine seasonal rain forest occurs in wet ravine habitats, has relatively high species diversity, more epiphytes, and fewer deciduous trees than lower hill seasonal rain forest. Ravine seasonal rain forest is similar to classic Equatorial lowland tropical rain forest, whereas lower hill seasonal rain forest tends to be a transitional type to tropical montane rain forest.

The tropical montane rain forest in Xishuangbanna occurs in the wet montane habitats between 900 and 1600 m. Structurally, the forest is 20–30 m tall with 2–3 tree layers. A top tree layer with 70–80 percent crown cover forms a canopy without emergent trees. The dominant tree species are *Alstonia scholaris*, *Paramichelia baillonii*, *Michelia floribunda*, *Mastixia euonymoidos*, *Alcimandra cathcartii*, *Dysoxylun spicatum*, *Schima wallichii*, *Phoebe nanum*, *Calophyllum polyanthum*, *Phoebe megacalyx*, *Ostodes paniculata*, and *Gymnanthes remota* (Wang *et al.* 2001).

In floristic composition, the tropical montane rain forest is dominated by Magnoliaceae, Mastixiaceae, Lauraceae, Fagaceae, Theaceae, Meliaceae, Euphorbiaceae, and Elaeocarpaceae. In physiognomy, the montane rain forest is dominated by evergreen mesophanerophytes and microphanerophytes with simple, leathery, and entire mesophyllous leaves. The forest has frequent woody lianas and epiphytes, abundant herbaceous phanerophytes, few buttresses, and little cauliflory (Zhu *et al.* 2004).

TROPICAL SEASONAL MOIST FOREST.—Tropical seasonal moist forest occurs on the middle and upper limestone slopes with shallow soils ranging from 650 to 1300 m in elevation. This vegetation type is adjacent to the seasonal rain forest. The forest is evergreen, with two distinct tree layers. The top tree layer has a crown cover of 40–60 percent and is 15–25 m tall. The second tree layer has a crown cover of 70–80 percent and is 3–15 m tall. Woody lianas are very abundant, and vascular epiphytes with small thick leaves are frequent. *Lasiococca comberi* var. *pseudoverticillata,* and *Osmanthus polyneurus* are the dominant species in the top layer, and *Dracaena cochinchinensis* and *Cleistanthus sumatranus* are usually dominant in the second layer. The understory consists of saplings and creeping lianas. The most common lianas are *Loeseneriella yunnanensis* and *Hiptage benhalensis.* Herbaceous species of the family Urticaceae, such as *Procris crenata, Elatostemma* spp., and *Pilea* spp., are abundant. Epiphytes are also frequently found on rock substrates (Zhu *et al.* 1998b).

TROPICAL MONTANE EVERGREEN BROAD-LEAVED FOREST.—The primary montane vegetation type in Xishuangbanna is tropical montane evergreen broad-leaved forest. It is distributed on mountain slopes and summits above 1000 m elevation and valleys above 1300 m. The forest is mainly dominated by the families Fagaceae, Euphorbiaceae, Theaceae, and Lauraceae. Physiognomically, the forest is characterized by abundant (*ca* 70%) trees with mesophyllous and leathery leaves.

The tropical montane evergreen broad-leaved forest has two conspicuous tree layers, of which the top layer is 15–25 m tall with dense crown coverage and the lower layer is 3–15 m tall with coverage of *ca* 50 percent. The top layer is dominated by species in the Fagaceae and Lauraceae, such as *Castanopsis fleuryi, Lithocarpus leucostachyus*, *Lithocarpus grandifolius*, *Lithocarpus truncatus*, *Castanopsis mekongensis, Machilus tenuipila*, and *Machilus rufipes.* The frequent species in the lower layer are *Syzygium tetragonum*, *Tricalysia fruticosa*, *Cinnamomun bejolghota*, *Nephelium lappaceum* var. *pallens*, *Macropanax dispermus*, *Harpulia cupanioides*, *Aporusa yunnanensis*, and *Phobe lanceolata*. The frequent shrub species are *Ardisia* spp., *Psychotria symplocifolia*, *Lasianthus hookeri* var. *dunnuanus*, and *Evodia lepta*. Herbaceous plants are abundant. Common species are *Strobilanthus* spp., *Alpinia* spp., *Phrynium capitatum*, and ferns. The common liana species are *Tetrastigma* spp., *Celastrus paniculata*, *Parameria laevigata*, and *Millettia* spp. Common epiphytes are *Rhaphidophora hongkongensis*, *Pothos chinensis*, *Schefflera venulosa*, *Ficus* spp., *Dendrobium* spp., *Bulbophyllum* spp., and *Eria* spp.

MONSOON FOREST.—Monsoon forest is a tropical deciduous forest under the influence of strong monsoon climate as defined by Schimper (1903). In southern Yunnan and SE Asia, monsoon forest often has a mosaic distribution within seasonal rain forest. Monsoon forest seems to be a transitional forest type between seasonal rain forest and savanna. In Xishuangbanna, monsoon forest occurs on the banks of the Mekong River and at wide basins where there is evidently an annual dryness due to the strong monsoon climate. The monsoon forest is usually 20–25 m tall with 1–2 deciduous tree layers. Woody lianas and epiphytes are scarce. Frequent tree species are *Bombax ceiba, Ficus altissima*, *Chukrasia tabularis* var. *velutina*, *Erythrina stricta*, *Pterocarya tonkinensis*, *Albizia chinensis*, *Bischoffia javanica*, *Bauhinia variaegata*, *Anogeissus acumunata*, *Stereospermum tetragonum*, and *Mitragyna brunonis.* The monsoon forest is often a single dominant tree community or consociation (Wang & Zhu 1990, Li *et al.* 1993, Zhu 2005).

FLORISTIC AFFINITY TO TROPICAL ASIAN FLORA

The floristic similarity between Xishuangbanna and the Malay Peninsula was compared in order to demonstrate floristic affinity. The catalog of vascular plants of Malaya (Turner 1995) is the revised and relatively complete reference for the regional flora of West Malesia and was used in this study.

The top 20 families with high species richness from the flora of Xishuangbanna and the flora of the Malay Peninsula are relatively equivalent (Table 2). Except for the Urticaceae, Lamiaceae, Cucurbitaceae, Rosaceae, and Fagaceae, other families with species richness in the flora of Xishuangbanna are shared by Malesian floras as the top 20 families. Conversely, Arecaceae, Clusiaceae, Dipterocarpaceae, Gesneriaceae, Melastomaceae, and Myristicaceae are among the top 20 families in Malay Peninsula, but are not among the top 20 families in the flora of Xishuangbanna. The floristic similarity between the flora of Xishuangbanna and Malay Peninsula is more than 80 percent at the family level and more than 60 percent at the generic level (Zhu & Roos 2004). These results strongly support floristic affinity of southern Yunnan to Malesia.

The flora of Xishuangbanna occurs on the margin of tropical Asia. On the other hand, although tropical families and genera *sensu lato* contribute most to its total flora, the families and genera of strictly tropical distribution are still underrepresented as compared to the Malesian flora. For example, Dipterocarpaceae has only two species in the flora of Xishuangbanna, although it is the dominant tree (in individuals) in some forest types of the region. Many

TABLE 2. *Top 20 families with most species richness among the floras of Xishuangbanna and the Malay Peninsula. Names in bold indicate families unique to each location.*

Flora of Xishuangbanna, southern Yunnan (Li 1996)			Flora of Malay Peninsula (Turner 1995)		
Name of family	No. of genera	No. of species	Name of family	No. of genera	No. of species
Orchidaceae	96	334	Orchidaceae	147	853
Fabaceae	68	232	Rubiaceae	79	562
Rubiaceae	43	147	Euphorbiaceae	70	368
Poaceae	67	143	Fabaceae	81	298
Euphorbiaceae	38	119	Poaceae	92	238
Asteraceae	59	107	**Myrtaceae**	11	215
Lamiaceae	36	105	Lauraceae	16	214
Moraceae	6	77	Annonaceae	36	202
Urticaceae	12	72	**Arecaceae**	32	198
Lauraceae	12	68	**Gesneriaceae**	20	189
Zingiberaceae	15	67	**Melastomataceae**	22	172
Asclepiadaceae	25	62	Cyperaceae	29	162
Apocynaceae	27	61	Acanthaceae	29	158
Annonaceae	15	52	**Dipterocarpaceae**	9	156
Cucurbitaceae	17	50	Zingiberaceae	18	150
Acanthaceae	32	49	Araceae	23	141
Rosaceae	17	49	Moraceae	10	138
Fagaceae	6	45	**Clusiaceae**	7	120
Araceae	16	43	Apocynaceae	31	119
Cyperaceae	13	43	Asclepiadaceae	30	116

Malesian elements reach their northern limits in southern Yunnan. This implies that the flora of Xishuangbanna is on the northern limit of the Indo-Malaysian flora.

DISCUSSION

Holdridge (1947) established a scheme for the classification of plant formations based on the climatic factors of mean annual temperature, average total annual precipitation, and potential evapotranspiration to precipitation ratio combined. With a mean annual temperature of 21°C, annual precipitation of 1500 mm, and potential evapotranspiration to precipitation ratio of *ca* 0.9, the tropical forest in Xishuangbanna would be classified into the category of subtropical moist forest according to the Holdridge system. The forests of Xishuangbanna would also be classified into the climatic class between the tropical wet seasonal and the tropical wet–dry, or into the vegetation type between evergreen seasonal moist forest, and semievergreen seasonal moist forest according to Richard's climatic classification for tropical rain forest regions (Richards 1996).

Although the forests of Xishuangbanna could be classified as lower montane subtropical moist forests according to the Holdridge system, they share similar forest profiles, physiognomic characteristics, species richness per unit area, and numbers of individuals in each tree species and diameter size-classes as equatorial lowland rain forests (Zhu 1997). The distribution of tropical moist forests occurring in Xishuangbanna tends to be at higher elevation than would be expected under the Holdridge system, owing to the unique geography. Floristically and physiognomically, forests in Xishuangbanna are atypical of subtropical lower montane moist forests, and are more similar to lowland tropical rain forests elsewhere.

The tropical seasonal rain forest of Xishuangbanna, in terms of physiognomy and structure, is similar to the evergreen seasonal forest of tropical America following Beard (1944, 1955), which was reclassified by Richards (1952) as a subformation of tropical rain forest; or the moist evergreen type of African tropical rain forest following Hall and Swaine (1976, 1981). Xishuangbanna's tropical seasonal forest can also be compared to the Mesophyll Vine Forest of the Australian rain forest following Webb (1959), as well as semievergreen rain forest of Walter (1971). However, it is most equivalent to the semievergreen rain forests of SE Asia defined by Whitmore (1975, 1984). Because the rain forest in Xishuangbanna occurs at latitudinal and altitudinal limits, and shows pronounced seasonal changes in physiognomy, Chinese botanists prefer to describe this forest as "tropical seasonal rain forest" (Wu 1980, 1987; Jin 1983, 1997; Zhu 1992 1997; Zhang & Cao 1995; Cao *et al.* 1996; Zhu *et al.* 1998a). Nonetheless, the forest belongs to the tropical rain forest formation of SE Asia, and is a type of semievergreen rain forest on the northern edge of the tropical zone. The same forest type also occurs in northern Thailand (Smitinand 1966) and North Vietnam (Thin 1997), although different names have been used.

The tropical montane rain forest in Xishuangbanna is similar to the lower montane rain forest of tropical Asia (Whitmore 1984, 1990). Compared with the seasonal rain forest of the region, the montane rain forest has fewer megaphanerophytes and large woody lianas, and more micro- and nanophanerophytes, herbaceous phanerophytes, and plants with simple, leathery, and nonentire and microphyllous leaves. Although different from lowland rain forest in floristic and physiognomic characteristics, tropical montane rain forest is recognized as a type of tropical rain forest by most researchers (Beard 1944, 1955; Richards 1952, 1996; Grubb *et al.* 1964; Whitmore 1984, 1990).

Tropical seasonal moist forest has been called "monsoon forest" by some Chinese authors (Wu 1980, 1987). The term "seasonal moist forest" is preferred here, because the forest is not equivalent to Schimper's monsoon forest (Schimper 1903), despite the fact that it is affected by seasonal dryness and contains a variable percentage of deciduous trees (Zhu *et al.* 1998a, 2003). The seasonal dryness in the region is compensated to some extent by dense fog accompanied by low temperatures in the dry months from November to April (Whitmore 1984). Some deciduous trees shed leaves toward the end of the dry season, while others such as *Cratoxylon cochinchinensis* shed their old leaves as new ones develop. This suggests that deciduousness in the region is more frequently associated with locally dry habitats than the seasonal dryness of climate. Therefore, using the term monsoon forest for the evergreen or semievergreen forest on limestone soil is confusing, because Schimper's monsoon

forest is more or less completely leafless during the dry season (Zhu 2005).

The term "monsoon evergreen broad-leaved forest" was used for the tropical montane evergreen broad-leaved forest in Xishuangbanna by some Chinese authors (Jin 1979, Wu 1980, 1987). Again, "monsoon forest" is widely used for deciduous forest with a strong monsoonal climate in SE Asia (Schimper 1903). This evergreen forest in Xishuangbanna is evidently not a monsoon forest of the same type as in SE Asia. It is also different from the tropical montane rain forest of SE Asia due to a lack of epiphytes. The term "tropical montane evergreen broad-leaved forest" was suggested for this forest type in Xishuangbanna, considering its physiognomy, and habitats, and to avoid confusion with the "monsoon forest" and "tropical montane rain forest" of SE Asia and Xishuangbanna (Zhu *et al.* 2005).

The tropical forests of Xishuangbanna, though surprisingly far from the Equator, are not the northern-most types of tropical rain forest, because tropical rain forest has been recorded in northern Myanmar at about 27°30′N latitude (Kingdon-Ward 1945) and in northeastern India at 27°31′N latitude (Proctor *et al.* 1998). Both of these northern sites still have tropical wet climates due to their low elevations. However, the tropical rain forest in Xishuangbanna occurs at the altitudinal and latitudinal limits. This could be partially explained by the so-called *Massenerhebung* or mass elevation effect (see Whitmore 1990, Richards 1996).

The tropical rain forest in Xishuangbanna occurs quite locally in limited habitats, controlled mainly by topography, and forms a mosaic with tropical montane evergreen broad-leaved forests and monsoon forests in the region. The occurrence of tropical rain forest in the region is mainly controlled by topography and local habitats, not by the regional climate (Zhu 2004).

Flora in Xishuangbanna has a strong affinity to the Malesian flora, owing to the floristic similarity between the two regions at family and generic levels. A clear generic demarcation knot exists between Malesia and mainland SE Asia, as found by Van Steenis (1950) and further confirmed by Johns (1995). Certainly there is this kind of demarcation knot between southern Yunnan and Malesia, but the high percentage of shared taxa in both regions suggests that they should be considered as the same floristic region. We agree with Van Balgooy *et al.*'s (1996) conclusion that the number of taxa in common is the first step to survey floristic affinity.

Research on the geological history of SE Asia has revealed that the direct land connection between mainland SE Asia and west Malesia existed until the early Pliocene period (5 million yr ago; Hall 1998), and no geographical barrier to the natural distribution of plants between mainland SE Asia and west Malesia existed during most of the Tertiary period (Morley 1998). This geological history is a probable explanation for the close affinity between the flora of southern Yunnan and Malesia.

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