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Forest Structure and Biomass of a Tropical Seasonal Rain Forest in Xishuangbanna, Southwest China[1]

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ABSTRACT

Xishuangbanna is a region located at the northern edge of tropical Asia. Biomass estimates of its tropical rain forest have not been published in English literature. We estimated forest biomass and its allocation patterns in five 0.185–1.0 ha plots in tropical seasonal rain forests of Xishuangbanna. Forest biomass ranged from 362.1 to 692.6 Mg/ha. Biomass of trees with diameter at 1.3 m breast height (DBH) $\geq$ 5 cm accounted for 98.2 percent of the rain forest biomass, followed by shrubs (0.9%), woody lianas (0.8%), and herbs (0.2%). Biomass allocation to different tree components was 68.4–70.0 percent to stems, 19.8–21.8 percent to roots, 7.4–10.6 percent to branches, and 0.7–1.3 percent to leaves. Biomass allocation to the tree sublayers was 55.3–62.2 percent to the A layer (upper layer), 30.6–37.1 percent to the B layer (middle), and 2.7–7.6 percent to the C layer (lower). Biomass of *Pometia tomentosa*, a dominant species, accounted for 19.7–21.1 percent of the total tree biomass. The average density of large trees (DBH $\geq$100 cm) was 9.4 stems/ha on two small plots and 3.5 stems/ha on two large plots, illustrating the potential to overestimate biomass on a landscape scale if only small plots are sampled. Biomass estimations are similar to typical tropical rain forests in Southeast Asia and the Neotropics.

Key words: forest biomass; forest community; forest structure; tropical Asia; tropical forest.

VEGETATION PLAYS A MAJOR ROLE in nutrient cycling and energy flux of terrestrial ecosystems, and biomass is an important parameter for characterizing a forest ecosystem. The storage of carbon in a forest reflects environmental conditions such as climate, soil structure, nutrient availability, and disturbance (Brunig 1983, Chave *et al.* 2001). Atmospheric carbon uptake by vegetation will play an important role for mediating global climate changes over the next century (Fan *et al.* 1998, Phillips *et al.* 1998). An estimated 37 percent (428 Pg = 428 $\times$ 10^{15} g) of the world's living terrestrial carbon pool (1146 Pg) is stored in tropical forests (Dixon *et al.* 1994). Therefore, biomass and its dynamics in tropical forests can have a major influence on both the global carbon cycle and the global climate change. An accurate estimation of biomass in tropical forests is fundamental for realistic global and regional carbon budgets and resource assessments.

Biomass estimates of pantropical rain forests vary widely (170.3–689.7 Mg/ha), and their reliability is rather poor (Brunig 1983, Brown & Lugo 1984, Clark *et al.* 2001). The wide differences in biomass estimates may result from variations in the tree and stand structures within mature forest types on different soils or landform units, at different altitudes, or in different regions (Brunig 1983). Also, little is known about the intersite and temporal variability of forest biomass in tropical zones (Brown 1997). Reliable, sufficient, and representative data on total biomass of stands or forest types are limited for tropical humid evergreen forests (Brunig 1983).

Xishuangbanna is located on the northern edge of tropical Asia, at the ecotone between the Asian tropics and subtropics, and is dominated by tropical seasonal rain forests. Compared to typical lower latitude Southeast Asian tropical rain forests, the forests in Xishuangbanna have lower annual mean temperatures and rainfall (Cao *et al.* 2006). Seasonal changes in the forests are manifested by the shedding of leaves by plants constituting the upper canopy during the hot-dry season (March–April; Liu 1987).

Limited studies have been done on the biomass of the tropical seasonal rain forest in Xishuangbanna. A few studies have developed allometric regression equations for trees and woody lianas, and used quadrant harvests for estimating biomass of shrubs and herbs (Dang *et al.* 1997, Feng *et al.* 1998, Zheng *et al.* 2000). These biomass estimates varied widely, due to differences in plot size, landform, and the intensity of disturbance. In addition, inadequate sample size and area have limited the estimation of standing biomass in this rain forest.

The aims of this study are to assess forest structure and species composition, and estimate forest biomass and allocation patterns in the tropical seasonal rain forest in Xishuangbanna. Furthermore, we analyzed the influence of plot area, the presence of large trees, and vegetation disturbance on biomass estimates and compared our biomass estimates with other reports from the Asian tropics and Neotropics.

METHODS

STUDY AREA AND SITE DESCRIPTION.—Xishuangbanna has a typical monsoon climate with three distinct seasons: a humid hot rainy season (May–October), a foggy cool-dry season (November–February), and a hot-dry season (March–April). The foggy cool-dry season and hot-dry season together represent the annual dry season (Cao *et al.* 2006).

Tropical seasonal rain forest is one of the main primary forest vegetation types in Xishuangbanna (Zhang & Cao 1995, Zhu *et al.* 2006). There are three tropical seasonal rain forest formations in this region: (1) *Terminalia myriocarpa* and *Pometia tomentosa* formation;

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(2) *Antiaris toxicaria*, *Pouteria grandifolia*, and *Canarium album* formation; and (3) *Shorea wangtianshuea* formation. Among the three formations, *T. myriocarpa* and *P. tomentosa* formation occupies the largest area. It usually occurs in valleys or on foothills, with altitudes ranging from 500 to 900 m (Liu 1987). In Xishuangbanna, areas on hills and mountains have been used for shifting agriculture for centuries, and most of the seasonal rain forest remains on northern slopes and in steep valleys. The seasonal rain forest is confined to below 900 m on northern slopes due to deficiencies of light and temperature. However, on the southern slopes of large mountains, this forest can extend to an elevation of about 1100 m along valleys (Zhu *et al.* 2000). The habitat is wet, so it is locally termed as "tropical ravine rain forest" (Liu 1987). In Mengla County, this type of rain forest extends in long, narrow strips along valleys. Features of this rain forest habitat include narrow terrain with less solar radiation and abundant soil moisture, and the forest has vegetative characteristics typical of other Southeast Asian rain forests (Liu 1987).

Five plots in the tropical seasonal rain forest were chosen for the study. Four plots (Manzhanggou, Baka, Tietahe B, and Tietahe A) were located within the Menglun Nature Reserve (21°55′–21°59′N, 101°08′–101°13′E, 650–730 m elev.), and another plot (22°33′N, 101°06′E, 1130 m elev.) was located in Caiyanghe Nature Reserve. The tropical seasonal rain forest is only distributed in the valleys on the southern slopes of the main cordillera below 1200 m in the Caiyanghe Nature Reserve (22°30′N–22°38′N, 101°7′E–101°15′E, 980–1698 m elev.). At present, it is the northernmost reported tropical seasonal rain forest at the highest elevation (Zhu *et al.* 2000; Table 1). The criteria for choosing the research plots were: mature rain forests stands with minimum disturbance, and homogeneous forest structure and topography. Soils of all plots are rhodic ferralsol, according to the world soil classification system (FAO/Unesco 1988).

FOREST STRUCTURE AND SPECIES COMPOSITION.—Detailed vegetation surveys were done in three of the five plots (Baka, Tietahe A, and Caiyanghe). The tree layer was divided into three sublayers based on canopy continuity: A layer (upper), B layer (middle), and C layer (lower). For the three plots, individual trees in each layer were identified and measured for height, diameter, and coverage. Height and coverage for herb and shrub layers were also estimated. The Tietahe A and Caiyanghe 1-ha plots were divided into 100 subplots of 10 × 10 m for the vegetation surveys and biomass estimations.

TREE AND WOODY LIANA BIOMASS.—Tree biomass was estimated as the sum of leaf, stem, branch, and root biomass. These organ biomass estimates were obtained using allometric regressions relating tree organ mass to diameter at 1.3 m breast height (*D* or DBH) or D^2H (*H* stands for tree height). In most assessments of tropical forests, biomass for trees with DBH ≤ 10 cm is usually neglected because it comprises a very small fraction of total forest biomass. However, in this study, the estimation of tree biomass included all trees with DBH ≥ 5 cm (Chave *et al.* 2003, Hoshizaki *et al.* 2004). For a few large trees of *P. tomentosa*, the DBH was determined at the trunk above buttresses. Woody liana biomass was estimated by measuring DBH and the length (*L*) of all woody lianas (DBH ≥ 2 cm), and calculating biomass using allometric regression relating liana mass to D^2L. Regression equations for the biomass of tree and woody lianas in the Xishuangbanna tropical seasonal rain forest are given in Table 2. At the Tietahe A plot, biomass was estimated using the regressions of Feng *et al.* (1998) using *H* and DBH. Tree heights below 20 m were determined using a pole with a meter tape. Tree heights above 20 m were determined by climbing to the tree canopy and then using a pole and meter tape lowered to the ground. Due to the dangers of climbing, biomass on the other four plots (Manzhanggou, Baka, Tietahe B, and Caiyanghe) was estimated using the regressions of Zheng *et al.* (2000; Table 2), which only rely on the *D* parameter. The regressions of Feng *et al.* (1998) and Zheng *et al.* (2000) were derived from the same sample trees. Measurement of the length of lianas was similar to tree height. Both sets of allometric regression equations calculated by Feng *et al.* (1998) and Zheng *et al.* (2000) were developed for estimating above- and belowground (root) biomass.

The surveys at the Baka, Tietahe B, Tietahe A, Manzhanggou, and Caiyanghe plots were carried out in January of 1988, 1991, 1994, 1999, and 2002, respectively.

BIOMASS OF THE SHRUB AND HERB LAYER.—Five quadrants of 5 × 5 m were established to measure shrub biomass at each site. In each quadrant, two 2 × 2 m subquadrants were established to measure herb biomass. The biomass of shrubs and herbs (including small trees and seedlings) was determined by the quadrant harvest method (Chapman 1986). The number of quadrants was limited to five

TABLE 1. *Characteristics of the tropical seasonal rain forest on the five study plots in Xishuangbanna, China.*

Plot	Area (ha)	Elevation (m)	Slope (deg.)	Aspect	Tree density DBH ≥ 5 cm (trees/ha)	No. of tree species DBH ≥ 5 cm	DBH of largest tree (cm)	Basal area (m^2/ha)
Manzhanggou	0.185	650	20	SE	567	39	157	47.49
Baka	0.25	650	33	N	796	60	154	55.96
Tietahe B	0.88	730	5–35	N	793	147	147	43.32
Tietahe A	1	740	5–35	N	730	145	145	31.28
Caiyanghe	1	1130	5–40	S	489	86	138	32.81

TABLE 2. *Tree and woody liana biomass allometric regression equations of the tropical seasonal rain forest in Xishuangbanna, China.*

	DBH classes	Organs	Regression equations	Correlation coefficients (*r*)	References
Tree	5–20 cm	Stems	$W_s = 0.0296(D^2H)^{0.9539}$	0.9861***	Feng *et al.* (1998)
		Branches	$W_b = 0.0158(D^2H)^{0.8285}$	0.8430***	
		Leaves	$W_l = 0.0488(D^2H)^{0.5027}$	0.6596**	
		Roots	$W_r = 0.0112(D^2H)^{0.9045}$	0.9535***	
		Total	$W_t = 0.0675(D^2H)^{0.9040}$	0.9790***	
	>20 cm	Stems	$W_s = 0.0606(D^2H)^{0.8976}$	0.9797***	
		Branches	$W_b = 0.5962(D^2H)^{0.5226}$	0.8661***	
		Leaves	$W_l = 0.1707(D^2H)^{0.4280}$	0.8336**	
		Roots	$W_r = 0.0069(D^2H)^{0.9781}$	0.9555***	
		Total	$W_t = 0.1341(D^2H)^{0.8599}$	0.9758***	
Woody liana	>2 cm	Total	$W_t = 0.0740(D^2L)^{0.8495}$	0.9756***	
Tree	5–20 cm	Stems	$W_s = 0.06006D^{2.59187}$	0.9724***	Zheng *et al.* (2000)
		Branches	$W_b = 0.01500D^{2.57887}$	0.9023***	
		Leaves	$W_l = 0.05943D^{1.45775}$	0.7186**	
		Roots	$W_r = 0.01989D^{2.46110}$	0.9063***	
	> 20 cm	Stems	$W_s = 0.17259D^{2.32016}$	0.9637***	
		Branches	$W_b = 0.86250D^{1.40861}$	0.8768***	
		Leaves	$W_l = 0.25134D^{1.10819}$	0.8143**	
		Roots	$W_r = 0.02203D^{2.52334}$	0.9373***	

***$P < 0.001$, **$P < 0.01$.

per plot due to the destructive sampling of the harvesting method (Murphy & Lugo 1986). The quadrats were arranged quincuncially in the plots.

LEAF AREA INDEX.—Tree leaves of 12 dominant species were sampled from Tietahe A and their areas were measured using a CI-203 laser leaf area meter. These leaves were then oven-dried to determine dry mass in order to obtain specific leaf area (SLA, leaf area/leaf dry mass). Leaf area index (LAI) of trees on the Tietahe A plot was estimated by multiplying the plot leaf biomass by the average SLA of the dominant species. LAI for the Baka and Caiyanghe plots was estimated by multiplying the tree leaf biomass of each plot by the average SLA.

RESULTS

FOREST STRUCTURE AND SPECIES COMPOSITION.—Biomass allocation and stem density of dominant species in each plot are listed in Appendix 1. On the Baka plot, the rain forest canopy reached 50 m. Trees of the A layer had an average height of more than 40 m with emergent and disjunct canopy covering approximately 30 percent of the plot area. The main species were *P. tomentosa*, *Amoora tetrapetala*, and *Mitrephora wangii*. Trees of the B layer were 20–40 m in height with approximately 80 percent canopy cover. The main species were *Barringtonia macrostachya*, *Knema erratica*, and *Knema cinerea*. Trees of the C layer were 3–20 m in height with approximately 10 percent canopy cover. The main species were *Myristica yunnanensis, Lasiococca comberi, Saprosma ternatum*, *Baccaurea ramiflora*, and some young trees of the species in the A and B layers. The height of the shrub layer was less than 3 m and the cover was about 10 percent. This layer mostly consisted of juveniles of dominant tree species. The shrub species were mainly *Psychotria henryi* and *Mycetia gracilis*. The herb layer (height < 2 m and cover < 10%) mainly consisted of *Phrynium capitatum*, *Commelina paludosa*, and *Bolbitis angustipinne*. The woody lianas were mainly in the B and C tree layers, with a maximum height of 38 m and a maximum DBH of 13.8 cm. The dominant species were *Tetrastigma planicaulum*, *Combretum yunnanensis*, and *Byttneria grandifolia*. Herbaceous lianas included *Strychnos wallichiana*.

On the Tietahe A plot, the height of the forest was about 48 m. The tree layer mainly consisted of *P. tomentosa*, *Garuga floribunda*, *B. macrostachya*, *Gironniera subaequalis*, *T. myriocarpa*, and *Ardisia tenera*. In addition, there were some secondary tree species in this layer resulting from regeneration in a forest gap. Trees of the A layer were >30 m tall with approximately 30 percent canopy cover. Trees of the B layer had a height of 15–30 m, and formed an even canopy with approximately 70 percent cover. The height of the trees in the C layer was less than 15 m with canopy cover of approximately 10 percent. This plot was disturbed as some trees had been felled in order to cultivate *Amomum villosum*, a Chinese medicinal plant. Although part of the natural understory had been cleared, the shrub and herb layers that remained were similar to the Baka plot. The community structure and species composition on the Tietahe B and Manzhanggou plots were similar to those on the Baka and Tietahe A plots.

The rain forest canopy in Caiyanghe was more than 40 m tall. The dominant species were typical of the tropical seasonal rain forest in the region such as *P. tomentosa, T. myriocarpa, Acrocarpus fraxinifolius, M. wangii*, *G. floribunda*, *Garcinia cowa*, *Cleidion spiciflorum*, *B. ramiflora*, and *Ostodes paniculata.* The trees of the A layer exceeded 30 m in height with approximately 15 percent canopy cover. The trees of the B and C layers were 15–30 and 2–15 m tall, respectively, both with 50 percent canopy cover. The height of the shrub layer was <3 m with 30 percent cover. The shrub layer mainly consisted of *Mycetia sinensis*, *M. gracilis*, and *Leea compactiflora*. The height of herb layer was <2 m, with about 25 percent cover. Common species were *P. capitatum* and *Mananthus patentiflora*. The Caiyanghe plot was also disturbed to some extent by a large natural treefall gap, and by the harvesting of some trees in 2000.

BIOMASS ESTIMATION.—The total biomass estimates varied widely among the five plots, from 362.1 to 692.6 Mg/ha with a mean of 511.4 Mg/ha (Table 3). Biomass estimates were much higher in small plots (mean 648.1 Mg/ha) than large plots (mean 420.2 Mg/ha). Most of the total biomass was concentrated in the tree layers, which accounted for 98.2 percent of the total biomass on average. Shrub, woody liana, and herb biomass accounted for 0.9, 0.8, and 0.2 percent of total biomass, respectively (Table 3). Higher herb biomass on the Tietahe A plot was associated with disturbance from the cultivation of *A. villosum*. Total biomass correlated negatively with plot size (Fig. 1), and tree layer biomass followed the same pattern. Biomass of woody lianas, shrubs, and herbs were not significantly correlated with plot sizes.

TREE BIOMASS ALLOCATION TO DIFFERENT ORGANS.—The allocation of biomass to different tree organs followed the order: stems > roots > branches > leaves for each plot (Table 4). There were a few large trees (DBH > 100 cm) in these plots, which had long and straight trunks with umbrella-shaped small crowns. These large trees contributed greatly to the total biomass. The LAI of the tree layers in the three plots ranged from 3.8 to 6.9 (Table 4).

BIOMASS ALLOCATION IN DIFFERENT DBH SIZE-CLASSES.—In the Manzhanggou plot, the biomass was mainly allocated to trees of the large DBH classes (Fig. 2). The trees in the 150–160 cm size-class contributed 30.9 percent of the total tree biomass and trees in the 130–140 cm size-class accounted for 23.2 percent. In the Baka plot, the biomass was mainly allocated in three DBH classes: 60–70 cm (19.2%), 130–140 cm (14.2%), and 150–160 cm (20.0%). In the Tietahe A plot, biomass was mostly allocated to trees of the medium DBH classes (20–80 cm), which accounted for 72.5 percent (255.5 Mg/ha) of the total tree biomass compared to 7.4 percent (26.2 Mg/ha) and 20.1 percent (70.9 Mg/ha) for the smaller DBH classes (5–20 cm) and large DBH classes (>80 cm), respectively. On the Caiyanghe plot, the biomass allocation in DBH classes had two peaks. The 80–100-cm class accounted for 33.2 percent of total biomass and the 120–140-cm class accounted for 24.1 percent. Tree biomass for DBH class of 5–10 cm only accounted for a small fraction of total tree biomass, which was 2.8 Mg/ha (0.5%) for Manzhanggou plot, 3.1 Mg/ha (0.8%) for Caiyanghe, 5.9 Mg/ha (1.2%) for Tietahe B, 7.9 Mg/ha (1.2%) for Baka, and 4.9 Mg/ha (1.4%) for Tietahe A.

ALLOCATION OF BIOMASS IN THE TREE SUBLAYERS.—Biomass allocation greatly increased from the C layer to the A layer (Table 5). The biomass of the C, B, and A layers were 2.7–7.6, 30.6–37.1, and 55.3–62.2 percent of the total biomass, respectively.

Differences of biomass in stems and roots of different sublayers were similar to that of the total biomass, which increased from the C layer to A layer. The maximum leaf biomass occurred in the B layer instead of the A layer, which contrasts with the patterns of biomass allocation in stems and roots. The highest branch biomass occurred in the B layer in the Tietahe A and Baka plots, while a marginal increase in branch biomass occurred in the tree A layer on the Caiyanghe plot, due to severe canopy disturbance. Stem density in the sublayers also contrasts the patterns of biomass, where 69.4–78.0 percent of trees were in the C layer, 16.0–24.6 percent in the B layer, and 6.0–6.7 percent in the A layer (Table 5).

TABLE 3. *Biomass (Mg/ha) of the tropical seasonal rain forest in Xishuangbanna, China, on five plots.*

Plot size	Plot	Trees	Shrubs	Woody lianas	Herbs	Total
Small area (0.185–0.25 ha)	Manzhanggou	594.523	4.603	4.218	0.336	603.680
	Baka	683.291	5.243	3.444	0.612	692.590
	Mean	638.907	4.923	3.831	0.474	648.135
Large area (0.88–1.0 ha)	Tietahe B	488.581	4.135	3.911	0.501	497.128
	Tietahe A	352.563	4.737	3.108	1.677	362.085
	Caiyanghe	390.617	5.126	4.822	0.756	401.321
	Mean	410.587	4.666	3.947	0.978	420.178
All	Mean	501.915	4.769	3.901	0.776	511.361

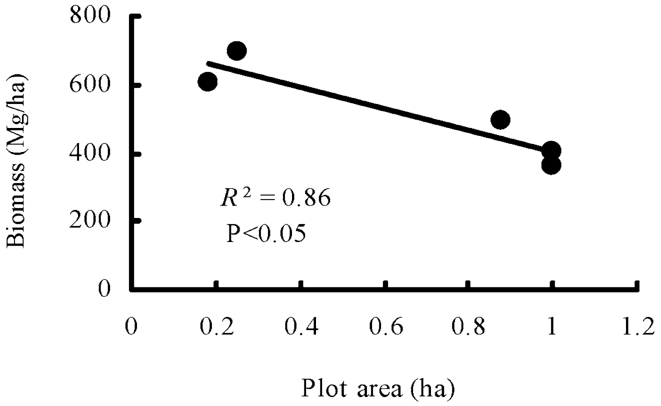

FIGURE 1. Relationships between total biomass estimates and plot area in the tropical seasonal rain forest in Xishuangbanna, China.

TREE BIOMASS ALLOCATION BY DIFFERENT SPECIES.—Tree species whose biomass was >1.0 percent of the total tree biomass included 17 species in the Baka plot, 18 in the Tietahe A plot, and 12 in the Caiyanghe plot. Biomass and density of each species are provided in Appendix 1. The biomass of *P. tomentosa*, the major dominant species in the tropical seasonal rain forests, accounted for 20.1, 19.7, and 21.1 percent of the total biomass in the Baka, Tietahe A, and Caiyanghe plots, respectively. Biomass of *P. tomentosa* was the highest in the Baka and Tietahe A plots, and the second highest in the Caiyanghe plot. *T. myriocarpa*, one of the dominant species in this rain forest, contributed 5.3 and 6.2 percent of the total biomass in the Tietahe A and Caiyanghe plots, respectively.

In the Baka plot, there were five species (*P. tomentosa*, *A. tetrapetala*, *M. wangii*, *K. erratica*, and *Michelia hedyosperma*) which contributed to >5 percent of the tree biomass. These species accounted for 57.7 percent of the total biomass. Of the B layer species, the biomass of *K. erratica* was the highest (6.3%), followed by *B. macrostachya* (5.0%).

Of the 18 species in the Tietahe A plot, 17 were found in the A layer. The exception was *B. macrostachya*, a B layer species. Some A layer species had only one plant on the plot, but made a large contribution to overall biomass. For example, single trees of five species, *T. myriocarpa*, *Chukrasia tabularis*, *Sapium baccatum*, *Pterospermum menglunense*, and *Trema orientalis*, accounted for 13.7 percent of the tree layer biomass. On the Tietahe A plot, *B. macrostachya,* the B layer species, had more biomass (5.4%) than all A layer species except *P. tomentosa*. The total biomass of the 18 species was 215.8 Mg/ha and accounted for 61.2 percent of the tree biomass. In the Caiyanghe plot, the tree species that contributed to >5 percent of the tree biomass were *Duabanga grandiflora*, *P. tomentosa*, *A. fraxinifolius*, and *T. myriocarpa*. These four species accounted for 67.5 percent of the total biomass. *M. wangii* had the maximum biomass among the B layer species, and accounted for 3.1 percent of tree biomass.

These results indicate that a few dominant species make the greatest contribution to the biomass of this tropical seasonal rain forest, and most of these species occur in the A layer. Large individuals

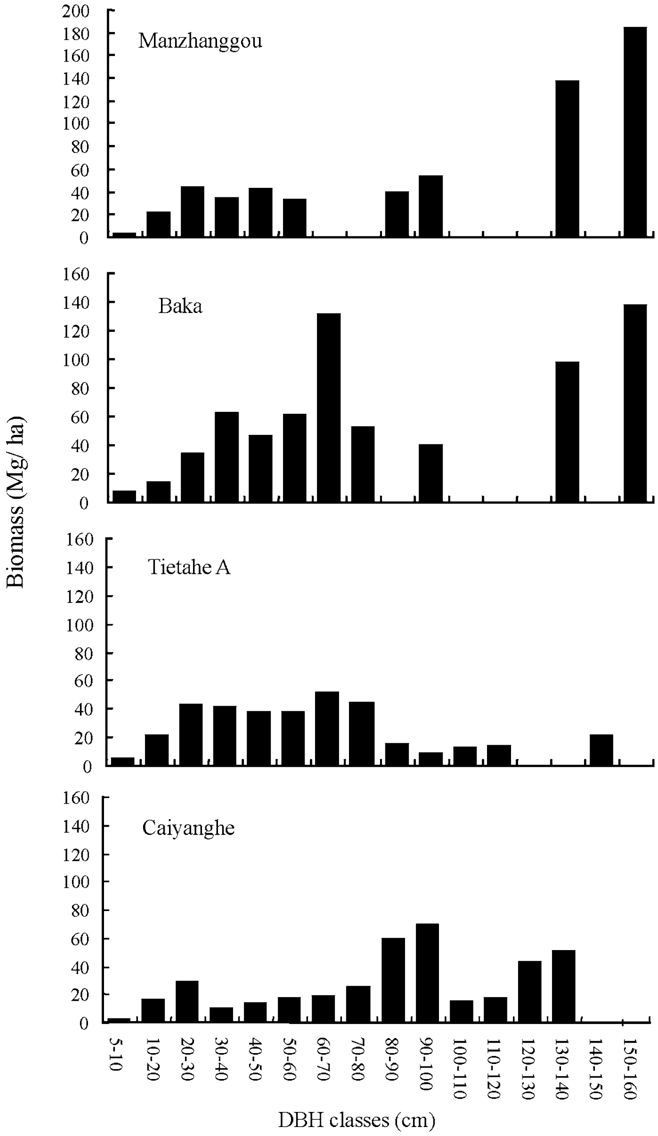

FIGURE 2. Allocation of tree biomass to different DBH classes on four plots of the tropical seasonal rain forest in Xishuangbanna, China.

TABLE 4. *Allocation of biomass to organs for the tree layers and leaf area index (LAI) on three plots of the tropical seasonal rain forest in Xishuangbanna, China.*

Plots		Stems	Branches	Leaves	Roots	LAI
Baka	Mg/ha	477.375	53.172	5.291	147.453	6.91
	Percent	69.80	7.77	0.77	21.56	
Tietahe A	Mg/ha	241.270	37.287	4.392	69.614	5.72
	Percent	68.43	10.57	1.25	19.75	
Caiyanghe	Mg/ha	273.601	28.983	2.905	85.128	3.79
	Percent	70.04	7.42	0.74	21.79	

TABLE 5. *Allocation of tree biomass and plants in tree sublayers on three plots in the tropical seasonal rain forest in Xishuangbanna, China.*

			Biomass (% of tree layer)				
Plot	Sublayer	Plants (% of tree layer)	Stems	Branches	Leaves	Roots	Total
Baka	A (>40m)	6.03	42.85	3.38	0.26	14.06	60.55
	B (20–40 m)	24.62	25.27	3.97	0.39	7.09	36.72
	C (2–20 m)	69.35	1.74	0.43	0.13	0.42	2.73
Tietahe A	A (>30m)	6.72	43.82	4.57	0.42	13.41	62.22
	B (15–30 m)	21.03	20.13	4.70	0.52	5.21	30.56
	C (2–15 m)	72.25	4.48	1.30	0.31	1.13	7.22
Caiyanghe	A (>30m)	6.00	39.21	3.12	0.24	12.70	55.27
	B (15–30 m)	16.00	25.90	3.02	0.28	7.92	37.12
	C (2–15 m)	78.00	4.93	1.28	0.23	1.17	7.61

of these dominant species are infrequent, although they contribute a large proportion of the stand biomass due to their huge size.

DISCUSSION

PLOT AREA, COMMUNITY HETEROGENEITY, AND BIOMASS ESTIMATES.—Generally, 0.25 ha is the minimum area for studying a tropical rain forest community, and it is a standard area for biomass estimation and studying forest productivity in tropical forests (Clark *et al.* 2001). The plot areas in the present study ranged between 0.185 and 1.0 ha. Total biomass estimates on the smaller plots (0.185–0.25 ha) were much higher than those of the larger plots (1.0 ha), similar to results from a rain forest in Malaysia (Hoshizaki *et al.* 2004). The differences among the plot size resulted from the study design, which was limited by the high community heterogeneity. In this study, the aim was to estimate biomass of the primary tropical seasonal rain forest. The rain forest occurs on lower slopes in valleys. Curving ravines and complicated landforms characterize the site. The 0.185- and 0.25-ha plots met our criteria for a research plot, and biomass estimates were considerably high. The Tietahe A and Caiyanghe plots (1.0 ha) were composed of mature and gap phase stands. Streams and human activities caused large gaps in the plots, with trees being badly damaged in some parts. The disturbance in Caiyanghe plot was evident. Of the 100 subplots with areas of 100 m^2 each, 7 had no trees (DBH $\geq$ 5 cm), and 14 had only one tree. Consequently, these plots were considerably lower in biomass. The Tietahe B plot (0.88 ha) was mainly composed of mature forest with little disturbance, thus it had higher biomass estimates than Tietahe A. The biomass estimate for this plot seems to be the most representative estimate for this type of undisturbed tropical seasonal rain forest in Xishuangbanna.

In 32 of 39 studies throughout the world, the total plot area assessed was $\leq$1 ha with a median of 0.25 ha. Few (9 of 39) of these studies were done on harvested plots, and in six of these cases the plot size was extremely small (0.04–0.16 ha; Clark *et al.* 2001). In a tropical rain forest at La Selva Biological Station of Costa Rica, estimated aboveground biomass (AGBM) were similar among three plot sizes of 0.1, 0.5, and 4 ha, and had a relatively small error bound for the three means (Clark & Clark 2000). Those results suggest that estimation of biomass with levels of environmental variation similar to La Selva is insensitive to plot size (Clark & Clark 2000). However, in a lowland tropical rain forest in Malaysia, AGBM varies spatially. AGBM estimated by 0.2 and 1.0 ha plots ranged from 212 to 655 and 365 to 440 Mg/ha, respectively, indicating that sampling smaller plots can result in higher variation for biomass estimates among plots, which could produce over- or underestimation of forest biomass if small plots are used (Hoshizaki *et al.* 2004). Clark and Clark (2000) suggested that a plot of 0.35–0.5 ha would be the most efficient way to sample basal area and AGBM in a tropical rain forest at La Selva. Because we lacked intermediate plot sizes (including 0.5 ha) for the seasonal rain forest in Xishuangbanna, the most efficient plot area could not be determined.

LARGE TREES AND BIOMASS ESTIMATES.—The presence of large trees is a sign of mature rain forest, and was one of the criteria for our plot selection. However, in smaller plots, the presence of large trees could result in an overestimate of total tree biomass (Brown & Lugo 1992, Brown *et al.* 1995, Clark *et al.* 2001). There are few large trees (DBH > 100 cm) in the Xishuangbanna rain forest, and their spatial distribution is uneven. There were three and four large trees on the 1.0-ha plots of Tietahe A and Caiyanghe, respectively, and the mean density was 3.5 trees/ha. There were two large trees on the 0.25-ha Baka plot and the 0.185-ha Manzhanggou plots, and mean density was 9.4 trees/ha, much higher than the 1.0-ha Tietahe A and Caiyanghe plots. The difference in density for large trees is the main reason for higher biomass in the Manzhanggou and Baka plots than Tietahe A and Caiyanghe plots.

INFLUENCE OF DISTURBANCE ON THE SPECIES ALLOCATION OF BIOMASS.—*P. tomentosa*, the dominant species in the tropical seasonal rain forest, had the highest biomass in most of the plots because of its large population and trunk size. However, the biomass of fast growing *D. grandiflora* was higher than that of *P. tomentosa* on the Caiyanghe plot and accounted for 27.6 percent of the total

TABLE 6. *Comparison of tree estimated aboveground biomass (AGBM) between tropical seasonal rain forest in Xishuangbanna and other rain forests having similar or higher rainfall in the tropics.*

Site	Forest	Altitude (m)	Mean annual temp. (°C)	Rainfall (mm)	Plot area (ha)	No. of plots	AGBM (Mg/ha)	Dry period (mo)	Source
Menglun, Xishuangbanna, China	Tropical seasonal rain forest	650–740	21.8	1492.9	0.18–1.0	4	283–536 (279–529 for DBH ≥10 cm)	6	Present study[a]
Caiyanghe, Xishuangbanna, China	Tropical seasonal rain forest	1130	19.7	1862.5	1.0	1	305 (302 for DBH ≥10 cm)	6	Present study[a]
Ping Kong, Thailand	Tropical monsoon forest	500		1500	0.16	1	268	5	Ogawa *et al.* (1965)[b]
Kampong Thom, Cambodia	Tropical deciduous forest	9–100	28.0	1700	0.12	46	189	6	Top *et al.* (2004)[c]
Kampong Thom, Cambodia	Tropical mixed/Semideciduous forest		28.0	1700	0.12	302	244	6	Top *et al.* (2004)[c]
Kampong Thom, Cambodia	Tropical evergreen forest		28.0	1700	0.12	192	256	6	Top *et al.* (2004)[c]
Pasoh, Malaysia	Lowland tropical rain forest		25	1842	0.2	30	212–655	0	Hoshizaki *et al.* (2004)[a]
Mount Kinabalu, Borneo	Hill dipterocarp rain forest	700	25	2300	1.0	1	437	0	Kitayama and Aiba (2002)[c]
Khao Chong, Thailand	Tropical rain forest		27.2	2696	0.16	1	334	2–3	Kira *et al.* (1967)[b]
Sarawak, Malaysia	Lowland tropical rain forest	50–300		5090	1.0	4	250–650	0	Proctor *et al.* (1983)[c]
Karnataka, India	Tropical rain forest	200–800		5310–7670	0.44–1.0	4	420–649	5–6	Rai and Proctor (1986)[a]
Central Amazon, Brazil	Tropical rain forest (terra firme)			1900–2500	1.0	65	231–492	5	Laurance *et al.* (1999)[c]
Nouragues, French Guiana	Lowland wet tropical forest			2757	1.0	22	230–416	2	Chave *et al.* (2001)[c]

[a]DBH ≥5.0 cm; [b]DBH ≥4.5 cm; [c]DBH ≥10.0 cm.

tree biomass. Previous studies on plant biomass and community composition in Xishuangbanna indicated the dominance of species such as *P. tomentosa*, *T. myriocarpa*, *M. wangii*, *B. macrostachya*, and an absence of *D. grandiflora* in the mature rain forests (Liu 1987, Zhang & Cao 1995, Cao *et al.* 1996, Zheng *et al.* 2000). Because seedlings of *D. grandiflora* are shade intolerant, this species occurs mostly on the roadsides, in forest gaps or on forest edges. The large gap in the Caiyanghe plot caused by a small stream and intense human activities could have favored the growth and higher biomass of *D. grandiflora* in this plot.

COMPARISONS WITH OTHER TROPICAL FORESTS.—The tree AGBM of some tropical forests with rainfall close to or higher than that in Menglun, Xishuangbanna are listed in Table 6. Studies with AGBM estimates determined from stems ≥4.5 cm (Ogawa *et al.* 1965), 5.0 cm (Rai & Proctor 1986, Hoshizaki *et al.* 2004, present study), and 10.0 cm (others) are included (Table 6). In the five plots studied in Xishuangbanna, the AGBM with DBH 5–10 cm only contributed a small fraction of total AGBM, for they were all mature rain forest. The fraction ranged from 0.5 to 1.4 percent of total AGBM. In the Asian tropics, the AGBM of the tropical monsoon forest in Ping Kong, with rainfall similar to Menglun, was 268 Mg/ha, and the AGBM of three types of forests in Kampong Thom, with rainfall between Menglun and Caiyanghe, ranged from 189 to 256 Mg/ha. These estimates are less than ours for the tropical seasonal rain forests in Menglun and Caiyanghe. The AGBM of a forest in Pasoh varied widely (212–665 Mg/ha), and rainfall is close to that in Caiyanghe. The rainfall in Mount Kinabalu (2300 mm), Khao Chong (2696 mm), Sarawak (5090 mm), and Karnataka (5310–7670 mm) is higher than that of Xishuangbanna, and the AGBM of these forests are similar (250–650 Mg/ha) to our results from Xishuangbanna (283–536 Mg/ha). The AGBM of some plots in Pasoh, Sarawak, and Karnataka reached nearly 650 Mg/ha (Table 6), exceeding our highest AGBM estimate of 536 Mg/ha in Xishuangbanna. The tree AGBM of seasonal rain forest in Xishuangbanna averaged 393.8 Mg/ha (of which 389.9 Mg/ha for trees DBH $\geq$ 10 cm), which accounted for 78.6% of tree biomass for the five plots; this value is higher than in Khao Chong and similar to that in Mount Kinabalu. AGBM estimates from 65 plots of 1 ha in Neotropical rain forests (terra firme) in the Central Amazon of Brazil (rainfall from 1900 to 2500 mm) ranged from 231 to 492 Mg/ha (mean of 356 Mg/ha), which are similar to our estimates for Xishuangbanna (Laurance *et al.* 1999). In another lowland wet tropical forest in Nouragues French Guiana, the AGBM of 22 plots of 1 ha ranged from 230 to 416 Mg/ha, with a mean of 309 Mg/ha, slightly under our estimates for Xishuangbanna (Chave *et al.* 2001).

The biomass estimates of tropical seasonal rain forest in Xishuangbanna, located on the northern edge of tropical Asia, are similar to those of typical rain forests in the Asian tropics and the Neotropics. In Xishuangbanna the rain forest flourishes and has a tall stature. The relatively high biomass in this forest is probably due to the obstruction of cold air movement southward by the Qinghai–Tibet Plateau, adequate soil moisture in the rain forest distributed in valleys with continuously flowing streams, and the humid air during four foggy months over the 6-mo dry season. However, future studies on the biomass of other rain forests in Xishuangbanna, such as those dominated by *S. wangtianshuea* (with a height reaching 70 m), are likely to produce different results than the tropical seasonal rain forests dominated by *T. myriocarpa* and *P. tomentosa* studied here. Studies are currently in progress to obtain biomass estimates for other rain forests in Xishuangbanna.

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LITERATURE CITED

BROWN, S. 1997. Estimating biomass and biomass change of tropical forests: A primer. FAO forestry paper. FAO, Rome, Italy.

———, AND A. E. LUGO. 1984. Biomass of tropical forests: A new estimate based on forest volumes. Science 223: 1290–1293.

———, AND A. E. LUGO. 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17: 8–18.

BROWN, I. F., L. A. MARTINELLI, W. W. THOMAS, M. Z. MOREIRA, C. A. C. FERREIRA, AND R. A. VICTORIA. 1995. Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil. For. Ecol. Manage. 75: 175–189.

BRUNIG, E. F. 1983. Vegetation structure and growth. *In* F. B. Golley (Ed.). Tropical rain forest ecosystems, pp. 49–75. Elsevier Scientific Publishing Company, Amsterdam.

CAO, M., J. ZHANG, Z. FENG, J. DENG, AND X. DENG. 1996. Tree species composition of a seasonal rain forest in Xishuangbanna, southwest China. Trop. Ecol. 37: 183–192.

CAO, M., X. ZOU, M. WARREN, AND H. ZHU. 2006. Tropical forests of Xishuangbanna, China. Biotropica 38: 306–309.

CHAPMAN, S. B. 1986. Production ecology and nutrient budgets. *In* P. D. Moore and S. B. Chapman (Eds.). Methods in plant ecology, 2nd edition, pp. 1–59. Blackwell Scientific Publications, London.

CHAVE, J., B. RIÉRA, AND M. A. DUBOIS. 2001. Estimation of biomass in a Neotropical forest of French Guiana: Spatial and temporal variability. J. Trop. Ecol. 17: 79–96.

———, R. CONDIT, S. LAO, J. P. CASPERSEN, R. B. FOSTER, AND S. P. HUBBELL. 2003. Spatial and temporal variation of biomass in a tropical forest: Results from a large census plot in Panama. J. Ecol. 91: 240–252.

CLARK, D. B., AND D. A. CLARK. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Manage. 137: 185–198.

CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, J. Ni, AND E. A. HOLLAND. 2001. Net primary production in tropical forests: An evaluation and synthesis of existing field data. Ecol. Appl. 11: 371–384.

DANG, C., Z. WU, AND Q. ZHANG. 1997. A study on biomass of the ravine tropical rain forest in Xishuangbanna. Acta Bot. Yun. Suppl. IX: 123–128 (in Chinese with English abstract).

DIXON, R. K., S. BROWN, R. A. HOUGHTON, A. M. SOLOMON, M. C. TREXLER, AND J. WISNIEWSKI. 1994. Carbon pools and flux of global forest ecosystems. Science 263: 185–190.

FAN, S., M. GLOOR, J. MAHLMAN, S. PACALA, J. SARMIENTO, T. TAKAHASHI, AND P. TANS. 1998. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science 282: 443–446.

FAO/UNESCO. 1988. Soil map of the world, revised legend. FAO, Rome, Italy.

FENG, Z., Z. ZHENG, J. ZHANG, M. CAO, L. SHA, AND J. DENG. 1998. Biomass and its allocation of a tropical seasonal rain forest in Xishuangbanna. Acta Phytoecol. Sin. 22: 481–488 (in Chinese with English abstract).

HOSHIZAKI, K., K. NIIYAMA, K. KIMURA, T. YAMASHITA, Y. BEKKU, T. OKUDA, E. S. QUAH, AND N. M. D. SUPARDI. 2004. Temporal and spatial variation of forest biomass in relation to stand dynamics in a mature, lowland tropical rainforest, Malaysia. Ecol. Res. 19: 357–363.

KIRA, T., H. OGAWA, K. YODA, AND K. OGINO. 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production, with special reference to the Khao Chong rain forest. Nat. Life Southeast Asia 5: 149–174.

KITAYAMA, K., AND S. AIBA. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. J. Ecol. 90: 37–51.

LAURANCE, W. F., P. M. FEARNSIDE, S. G. LAURANCE, P. DELAMONICA, T. E. LOVEJOY, J. M. RANKIN-DE MERONA, J. Q. CHAMBERS, AND C. GASCON. 1999. Relationship between soils and Amazon forest biomass: A landscape-scale study. For. Ecol. Manage. 118: 127–138.

LIU, L. 1987. Rain forest. *In* Z. WU, Y. ZHU, AND H. JIANG (Eds.). Vegetation of Yunnan, pp. 97–163. Science Press, Beijing (in Chinese).

MURPHY, P. G., AND A. E. LUGO. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18: 89–96.

OGAWA, H., K. YODA, K. OGINO, AND T. KIRA. 1965. Comparative ecological studies on there main types of forest vegetation in Thailand. II. Plant Biomass. Nat. Life Southeast Asia 4: 49–81.

PHILLIPS, O. L., Y. MALHI, N. HIGUCHI, W. F. LAURANCE, P. V. NÚÑEZ, R. M. VÁSQUEZ, S. G. LAURENCE, L. V. FERREIRA, M. STERN, S. BROWN, AND J. GRACE. 1998. Changes in the carbon balance of tropical forests: Evidence from long-term plots. Science 282: 439–442.

PROCTOR, J., J. M. ANDERSON, P. CHAI, AND H. W. VALLACK. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. J. Ecol. 71: 237–260.
RAI, S. N., AND J. PROCTOR. 1986. Ecological studies on four rainforests in Karnataka, India I. Environment, structure, floristics and biomass. J. Ecol. 74: 439–454.
TOP, N., N. MIZOUE, AND S. KAI. 2004. Estimating forest biomass increment based on permanent sample plots in relation to woodfuel consumption: A case study in Kampong Thom Province, Cambodia. J. For. Res. 9: 117–123.
ZHANG, J., AND M. CAO. 1995. Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. Biol. Conserv. 73: 229–238.
ZHENG, Z., Z. FENG, M. CAO, H. LIU, AND L. LIU. 2000. Biomass and net primary production of primary tropical seasonal rainforest in Xishuangbanna. Acta Phytoecol. Sin. 24: 197–203 (in Chinese with English abstract).
ZHU, H., B. LI, S. DENG, Y. CAO, AND X. ZHANG. 2000. Tropical rain forest of Caiyanghe Nature Reserve, Simao and its biogeographical significance. J. Northeast For. Univ. 28: 87–93 (in Chinese with English abstract).
———, M. CAO, AND H. HU. 2006. Geological history, flora and vegetation of Xishuangbanna, Southern Yunnan, China. Biotropica 38: 310–317.

APPENDIX 1. *Biomass allocation to some common species of the tree layer in three plots in the tropical seasonal rain forest of Xishuangbanna, China.*

		Biomass		Density	
Plot	Species	Mg/ha	Percent of tree layer	Stems/ha	Percent of tree layer
Baka	*Pometia tomentosa* (Bl.) Teysm. et Binn.	137.152	20.07	12	1.51
	Amoora tetrapetala (Pierre) C. Y. Wu var. *macrophylla* (H. L. Li) C. Y. Wu	97.171	14.22	4	0.50
	Mitrephora wangii Hu.	82.508	12.08	36	4.52
	Knema erratica (Hook. f. et Thoms.) J. Sincl.	42.811	6.27	12	1.51
	Michelia hedyosperma Low	34.818	5.10	8	1.01
	Barringtonia macrostachya (Jack) Kurz	33.982	4.97	48	6.03
	Litsea dilleniifolia P. Y. Bai et P. H. Huang	29.022	4.25	12	1.51
	Dysoxylum lenticellatum C. Y. Wu	26.442	3.87	12	1.51
	Knema cinerea (Poir.) Warb. var. *glauca* (Bl.) Y. H. Li	24.569	3.60	20	2.51
	Chukrasia tabularis A. Juss. var. *velutina* (Wall.) King	22.942	3.36	8	1.01
	Semecarpus reticulata Lecte.	19.374	2.84	4	0.50
	Homalium laoticum Gagnep. var. *glabretum* C. Y. Wu	18.544	2.71	8	1.01
	Sumbaviopsis albicans (Bl.) J. J. Sm.	14.812	2.17	36	4.52
	Vitex quinata (Lour.) Will. var. *puberula* (Lam.) Moldenke	12.889	1.89	4	0.50
	Gironniera subaequalis Planch.	11.819	1.73	12	1.51
	Myristica yunnanensis Y. H. Li	8.936	1.31	12	1.51
	Lasiococca comberi Haines var. *pseudoverticellata* (Merr.) H. S. Kiu	7.171	1.05	32	4.02
	Total	624.962	91.49	280	35.19
Tietahe A	*P. tomentosa*	69.349	19.67	37	5.07
	B. macrostachya	19.179	5.44	55	7.53
	Terminalia myriocarpa Heurck et Muell.-Arg.	18.580	5.27	1	0.14
	C. tabularis	11.881	3.37	1	0.14
	Sloanea tomentosa (Benth.) Rehd. et Wils.	9.872	2.80	10	1.37
	G. subaequalis	9.837	2.79	43	5.89
	Garuga floribunda Decne. var. *gamblei* (King ex Smith) Kalkm.	9.413	2.67	8	1.10
	Elaeocarpus varunua Buch.-Ham. ex Mast.	8.497	2.41	5	0.68
	Drypetes perreticulata Gagnep.	8.426	2.39	7	0.96
	Sapium baccatum Roxb.	7.510	2.13	1	0.14
	Pouteria grandifolia (Wall.) Pierre	6.593	1.87	9	1.23
	Pterospermum menglunense Hsue	6.452	1.83	1	0.14
	Terminalia bellirica (Gaertn.) Roxb.	5.782	1.64	3	0.41

APPENDIX 1. *Continued.*

Plot	Species	Biomass		Density	
		Mg/ha	Percent of tree layer	Stems/ha	Percent of tree layer
	Lithocarpus leucostachyus A. Camus	5.641	1.60	10	1.37
	Firmiana colorata (Roxb.) R. Br.	5.465	1.55	2	0.27
	S. reticulata	5.288	1.50	6	0.82
	Phoebe puwenensis Cheng	4.195	1.19	7	0.96
	Trema orientalis (Linn.) Bl.	3.808	1.08	1	0.14
	Total	215.768	61.20	207	28.36
Caiyanghe	*Duabanga grandiflora* (Roxb. et DC.) Walp.	107.717	27.58	10	1.95
	P. tomentosa	82.581	21.14	25	5.12
	Acrocarpus fraxinifolius Arn. et Wight	48.955	12.53	11	2.19
	T. myriocarpa	24.327	6.23	1	0.24
	M. wangii	12.188	3.12	126	25.85
	Machilus sp. 1	12.079	3.09	1	0.24
	Sp. 2	10.873	2.78	1	0.24
	G. floribunda	8.926	2.28	4	0.73
	S. baccatum	8.388	2.15	1	0.24
	Winchia calophylla A. DC.	5.742	1.47	1	0.24
	Horsfieldia pandurifolia Hu	5.043	1.29	2	0.49
	Bischofia javanica Bl.	4.693	1.20	6	1.22
	Total	331.512	84.86	189	38.75