

STRUCTURE AND DIVERSITY OF SEASONAL MIXED EVERGREEN-DECIDUOUS TROPICAL FOREST, WESTERN THAILAND

Edward L. Webb^{1,5}, *Robert Steinmetz*², *Naret Seuaturian*²,
*Wanlop Chutipong*³ and *Martin van de Bult*⁴

ABSTRACT

This paper describes the composition and structure of the tree community in mixed evergreen-deciduous forest with bamboo, at 700 m elevation in Thung Yai Naresuan Wildlife Sanctuary, western Thailand. This forest type covers large portions of western and northern Thailand but is little-studied. All trees with a diameter ≥ 5 cm diameter and bamboo clumps were identified, mapped and measured for diameter and height in a 1 ha (100 m \times 100 m) plot. We recorded 330 individuals, 64 tree species in 36 families. The most common species were *Colona floribunda* Craib, *Wendlandia scabra* Kurz var. *scabra*, *Castanopsis tribuloides* (Sm.) A. DC, *Schima wallichii* (DC.) Korth. and *Eurya acuminata* DC. var. *acuminata*. Basal area was dominated by *S. wallichii*, *C. floribunda* and *C. tribuloides*. Canopy cover was 43% for trees only, but 75% when bamboo cover was included. Tree density was 19% lower within a 5 m buffer around bamboo clumps, with small tree distributions being more affected than large trees, strongly suggesting that bamboo suppresses tree recruitment. In comparison with other forests of similar origin, this plot exhibited lower tree stem density, abundant stems from deciduous, disturbance-specialist species, and abundant bamboo. These three factors likely reflect the influence of fire and possibly previous agriculture on the structure and composition of the plot. Monitoring of this plot and the surrounding area will provide important information about the trajectory of forest change. Because much of the forest at middle elevations in SE Asia is influenced by people, we encourage replication of quantitative forest monitoring at other sites.

Keywords: bamboo, disturbance, forest composition, survey, Thung Yai, vegetation

INTRODUCTION

There is a long history of vegetation study in Thailand (MAXWELL, 2004), and recent work on forest classification demonstrates the importance of elevation, precipitation, seasonality and human disturbance on forest conditions and phenology (MAXWELL & ELLIOTT, 2001). Forest composition below 700–800 m elevation in continental Thailand consists of evergreen and deciduous tree species mixed with bamboo to varying degrees, depending on precipitation

¹ Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543

² WWF Thailand, 2549/45 Paholyothin Road, Bangkok, 10900, Thailand

³ King Monkut's Institute of Technology Thonburi, 83 Mu 8, Thakham, Bangkhuntien, Bangkok, 10150, Thailand

⁴ Doi Tung Development Project, 920 M. 7, T. Mae Fah Luang, A. Mae Fah Luang, Chiang Rai 57240, Thailand

⁵ E-mail: ted.webb@nus.edu.sg

Received 28 October 2010 ; accepted 7 February, 2011.

patterns, human disturbances, and soil conditions (SANTISUK, 1988). As elevation increases, forest composition becomes increasingly dominated by evergreen tree species (MAXWELL & ELLIOTT, 2001). Recent research by VAN DE BULT & GREIJMANS (2006) in Mae Wong National Park (western Thailand) demonstrated that a shift from deciduous to evergreen tree species' dominance occurred from 700–1000 m elevation. This 'middle elevation' zone in northern Thailand consists largely of mixed evergreen-deciduous (MXF) forest (MAXWELL & ELLIOTT, 2001; MAXWELL, 2004; FORRU, 2006), which is considered a distinct forest type.

Research in the middle elevation zone is important because although MXF forest has the fewest restricted tree species of the main forest types in Thailand (i.e. species found only in that forest type) (FORRU, 2006), the middle elevation may be significantly affected by climate change. Changing climate may favor a shift in species assemblages (PETEETE, 2000; PARMESAN & YOHE, 2003). For example, increases in disturbances such as fire may favor disturbance specialist species such as bamboo, which in turn may affect tree species regeneration through competitive exclusion (KEELEY & BOND, 1999; MAROD *ET AL.*, 1999). Additionally, the middle elevation forests of Thailand are extensively utilized by humans and therefore tend to be affected by anthropogenic disturbances such as fire. Thus, baseline information on the composition and structure of middle elevation plant communities is important for long-term monitoring of environmental change.

In order to develop a more comprehensive understanding of MXF vegetation in the middle elevation zone, we quantitatively surveyed the tree community at 700 m elevation in Thung Yai Naresuan Wildlife Sanctuary, western Thailand. This paper describes the composition and structure of this forest, and additionally tests for an impact of bamboo on the spatial distributions (and by extension, the dynamics) of trees in this community.

STUDY SITE

Thung Yai Naresuan Wildlife Sanctuary (hereafter, Thung Yai) is a large protected area covering 3200 km² adjacent to the Thai-Burma border (15° 00'–15° 23' N, 98° 30'–99° 05' E). It is part of the Western Forest Complex of Thailand, one of the largest contiguous blocks of protected forest in continental SE Asia. For this paper we follow the forest type terminology of MAXWELL (2004). Major habitats in Thung Yai are bamboo-deciduous forest (BB/DF), mixed evergreen-deciduous forest (MXF), and evergreen forest (EGF). The Sanctuary is characterized by rugged mountainous terrain, with elevations mostly above 400 m and a maximum elevation of 1811 m asl. Thung Yai receives 2000–2400 mm of rain annually, most falling between May and October. During the dry season (November to April) monthly rainfall is typically below 100 mm.

We inventoried natural forest in the western region of Thung Yai (Fig. 1). This site, called Ti Thay Khi, was at 700 m elevation along a footpath between forest-dwelling villages (Fig. 2 and 3). The closest village was *ca.* 10 km from the site. The site was on a gradual slope of less than 5 degrees. BB/DF was found within several hundred meters downslope. On steep slopes several hundred meters above the plot, EGF occurred which was not affected by fire.

Swidden agriculture is a traditional land use practice of the Karen villagers that have inhabited Thung Yai for several centuries (WONG *ET AL.*, 2007). Through conversations with local village elders about the history of the plot site, we learned that the site had not been

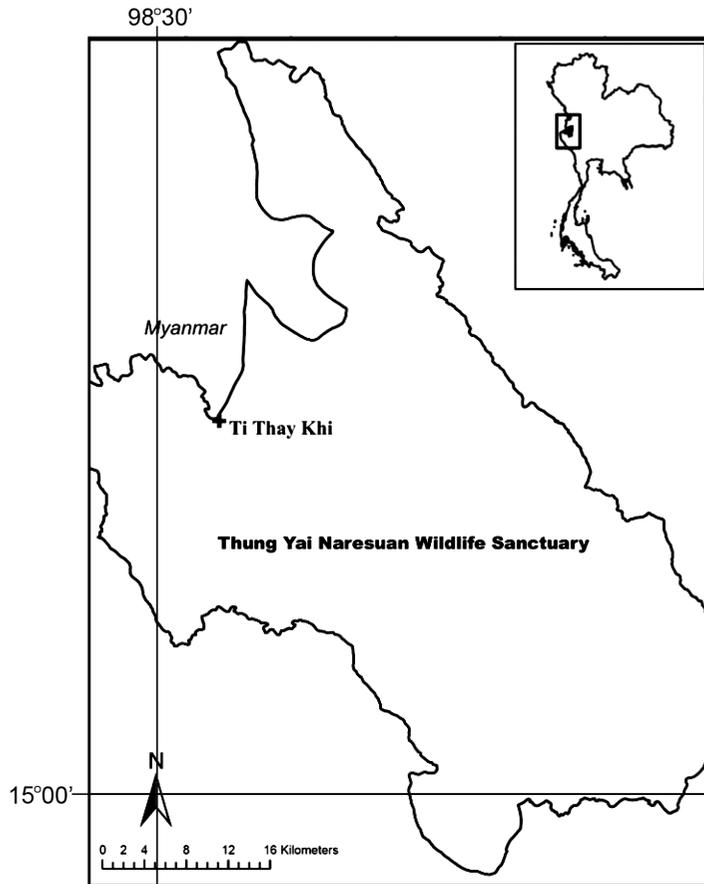


Figure 1. Map of Thailand showing the location of Thung Yai Naresuan Wildlife Sanctuary and the one hectare research plot.

used for swidden agriculture for a minimum of 80–100 years, if at all. Domestic cattle occasionally enter the site during the dry season and lightly browse the understory. Low-intensity ground fires, common in seasonal forests of SE Asia (BAKER *ET AL.*, 2009), occur at the site with semi-annual frequency.

METHODS

We established a 1 ha (100 m × 100 m) plot using a compass and measuring tape, with stakes placed every 20 m. We measured the DBH (diameter at 1.4 m height) of all trees ≥5 cm DBH, identified them to species, calculated their heights using a Suunto® clinometer, and mapped their Cartesian coordinates to the nearest 50 cm. We also mapped all bamboo clumps. Herbarium samples were collected and deposited at the BKF herbarium of the National Park, Wildlife and Plant Conservation Department (Royal Forest Department, Bangkok) and the CMU herbarium of Chiang Mai University.



Figure 2. Disturbed MXF habitat at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary, western Thailand.



Figure 3. Disturbed MXF forest with large *Schima wallichii* tree (on the right).

There were 13 multiple-stemmed trees in the plot, that is, trees whose stems branched below 1.4 m above the base. For these trees we measured each stem and recorded them as belonging to the same individual. When calculating tree densities we used only individuals, but for basal area calculations we used all stems.

A map of tree crowns was drawn by measuring the extent of the crown in four cardinal directions from the trunk and interpolating crown shape in between. The canopy maps were digitized into a Geographic Information System (GIS), which we used to calculate canopy cover after merging all overlapping crowns. A profile diagram was drawn for a 10 m × 50 m strip of representative forest in the plot (e.g. RICHARDS, 1996; SANTISUK, 1998).

We classified tree species according to leafing phenology (deciduous, evergreen or tropophilous), which was then used to assess the proportion of trees in each class contributing to overall species composition. This proportion changes across elevation, according to VAN DE BULT & GREIJMANS (2006).

We conducted a spatial analysis to test whether bamboo was partitioning space with trees and therefore likely affecting tree recruitment. Lower tree density or basal area closer to bamboo clumps could indicate an influence of bamboo on various life history stages of trees, such as seed germination, seedling survival, or growth. In the GIS we constructed a 5-m buffer around all bamboo clumps and compared stem density and basal area of trees inside and outside the bamboo buffer zone. The 5-m buffer size was based on field observations and the profile diagram indicating a 1 m clump radius plus 4 m canopy extent for a 'typical' mature clump. While this is a rather crude approximation of bamboo cover and ignores variation across clumps, we expect that it was a legitimate approximation to make exploratory calculations. We calculated density and basal area statistics for all stems, and thereafter for three diameter classes, 5–9.9 cm DBH, 10–19.9 cm DBH, and ≥20 cm DBH.

RESULTS

A total of 330 individuals were in the plot, of which 301 were identified to species level; these were from 60 species in 33 families (Table 1). Of the remainder, 14 were identified to genus (many of which were too small to provide fertile herbarium specimens), three were identified to family, four remained unidentified and eight died before we could identify them. At least four additional species were added to the complete list (bamboo [not *Gigantochloa*], *Canarium*, *Nephelium*, *Oreocnide*), bringing the minimum tree richness of the plot to 64 species in 36 families.

Lauraceae was the most species-rich family (7 species), followed by Euphorbiaceae (6 species). *Colona floribunda* Craib was the most abundant species (49 trees ha⁻¹ ≥5 cm DBH), followed by *Wendlandia scabra* Kurz var. *scabra* (31 ha⁻¹), *Castanopsis tribuloides* (Sm.) A. DC. (26 ha⁻¹), *Schima wallichii* (DC.) Korth. (25 ha⁻¹) and *Eurya acuminata* DC. var. *acuminata* (23 ha⁻¹) (Table 1). In terms of basal area, *S. wallichii* ranked first (3.5 m² ha⁻¹) and co-dominated with *C. floribunda* (2.3 m² ha⁻¹) and *C. tribuloides* (2.1 m² ha⁻¹) (Table 1).

Basal area of the plot was 18.5 m² (Table 1). Diameter size class distributions of species with at least 10 stems reveal that populations of most common species were recruiting in the plot, with two possible exceptions being *C. floribunda* and *Dillenia aurea* Sm. var. *aurea* (Fig. 4).

Table 1. Species list and structural summary for a one hectare (100 m × 100 m) plot in mixed evergreen plus deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary, Thailand. For deciduousness, D refers to deciduous, E refers to evergreen, T refers to tropophyllous. The “Habitat” column describes the forest type (MAXWELL, 2004) in which the species is most typically found (VAN DE BULT & GREIJMANS, 2006). Basal area (BA) was calculated using all stems and is presented as cm², except the last row where it is given in m².

Family	Species	Leaf phenology ¹	Habitat ²	≥5 cm DBH		≥10 cm DBH	
				N	BA	N	BA
Alangiaceae	<i>Alangium kurzii</i> Craib	D	MXF, EGF	2	643.3	2	643.3
Apocynaceae	<i>Alstonia rostrata</i> Fischer	E		7	13914.8	7	13914.8
Bignoniaceae	<i>Markhamia stipulata</i> (Wall.) Seem. <i>ex K.</i> Sch. var. <i>stipulata</i>	D	BB/DF, MXF	2	464.6	1	422.7
	<i>Stereospermum colais</i> (B.-H. <i>ex Dillw.</i>) Mabb.	D		3	3213.6	3	3213.6
Burseraceae	<i>Canarium subulatum</i> Guill.			1	598.3	1	598.3
	<i>Garuga floribunda</i> Decne.	D		2	140.7	1	116.9
Celastraceae	Unidentified			1	28.3	.	.
Dilleniaceae	<i>Dillenia aurea</i> Sm. var. <i>aurea</i>	D		10	9770.2	10	9770.2
Ebenaceae	<i>Diospyros glandulosa</i> Lace	E		1	54.1		
Elaeocarpaceae	<i>Elaeocarpus floribundus</i> Bl.	D		6	495.5	3	336.1
	<i>Elaeocarpus</i> sp.			4	771.7	1	611.4
	<i>Elaeocarpus stipularis</i> Bl.	E		4	143.5		
Euphorbiaceae	<i>Antidesma velutinsum</i> Bl.	E		1	33.2		
	<i>Antidesma</i> sp.			3	382.7	1	274.
	<i>Aporosa octandra</i> (B. -H. <i>ex D. Don</i>) Vick. var. <i>octandra</i>	D	BB/DF	6	236.5		
	<i>Baccaurea ramiflora</i> Lour.	E	MXF, EGF	1	103.9	1	103.9
	<i>Balakata baccata</i> (Roxb.) Esser	E		2	1819.0	2	1819.0
	<i>Glochidion sphaerogynum</i> (M.-A.) Kurz	D		2	74.8		

Table 1 (continued)

Family	Species	Leaf phenology ¹	Habitat ²	≥5 cm DBH		≥10 cm DBH	
				N	BA	N	BA
Fagaceae	<i>Ostodes paniculata</i> Bl.	E	MXF, EGF	5	426.0	3	343.7
	<i>Castanopsis tribuloides</i> (Sm.) A. DC.	E	EGF	26	21496.7	21	21278.4
	<i>Lithocarpus elegans</i> (Bl.) Hatus. ex Soep.	E	MXF, EGF	2	1819.4	2	1819.4
	<i>Lithocarpus truncatus</i> (King) Rehd. & Wils. var. <i>truncatus</i>	E		1	8494.9	1	8494.9
Flacourtiaceae	<i>Homalium ceylanicum</i> (Gard.) Bth.	D	BB/DF	2	2886.5	2	2886.5
Gramineae, Bambusoideae	<i>Gigantochloa nigrociliata</i> (Buse) Kurz	D		84	0.0		
	Unidentified			17	0.0		
Guttiferae	<i>Cratoxylum cochinchinense</i> (Lour.) Bl.	D		1	188.7	1	188.7
Juglandaceae	<i>Garcinia speciosa</i> Wall.	E	MXF	1	193.6	1	193.6
	<i>Garcinia</i> sp.			1	20.4		
	<i>Engelhardia serrata</i> Bl. var. <i>serrata</i>	D		1	26.4		
	<i>Engelhardia spicata</i> Lechen. ex Bl. var. <i>spicata</i>	D		4	12646.6	4	12646.6
Lauraceae	<i>Alseodaphne</i> sp.			1	36.3		
	<i>Cinnamomum bejolghota</i> (B.-H.) Sweet	E	EGF	2	408.4	2	408.4
	<i>Litsea albicans</i> Kurz	E		1	45.4		
	<i>Litsea salicifolia</i> (Roxb. ex Nees) Hk.f.	E	MXF, EGF	2	169.8	1	113.1
	<i>Machillus bombycina</i> King ex Hk.f.	E		1	44.2		
	<i>Machillus</i> sp. (prob. <i>bombycina</i> King ex Hk.f.)			1	149.6	1	149.6
	<i>Phoebe lanceolata</i> (Wall. ex Nees) Nees	E	EGF	2	491.1	1	460.0
	<i>Phoebe paniculata</i> Nees	E		1	2034.8	1	2034.8

Table 1 (continued)

Family	Species	Leaf phenology ¹	Habitat ²	≥5 cm DBH		≥10 cm DBH	
				N	BA	N	BA
Lecythidaceae	<i>Barringtonia acutangula</i> (L.) Gaertn.	D	BB/DF	5	476.6	3	426.5
Leeaceae	<i>Leea indica</i> (Burm. f.) Merr.	E	DDF	1	50.3		
Leguminosae, Mimosoideae	<i>Archidendron clypearia</i> (Jack) Niels. ssp. <i>clypearia</i> var. <i>clypearia</i>	D		2	171.2	1	113.1
	<i>Archidendron jiringa</i> (Jack) Niels.	D		11	4606.5	8	4523.7
Leguminosae, Papilionoideae	<i>Callerya atropurpurea</i> (Wall.) Schot	D	BB/DF, MXF, SG	5	3195.2	4	3174.0
	<i>Dalbergia lanceolaria</i> L.f. var. <i>errans</i> (Craib) Niyo.	D		9	2655.2	9	2655.2
	<i>Dalbergia</i> sp.			2	1153.4	1	1122.2
	<i>Erythrina stricta</i> Roxb.	D		1	759.6	1	759.6
Magnoliaceae	<i>Magnolia baillonii</i> Pierre	D	MXF	1	502.7	1	502.7
Meliaceae	<i>Toona ciliata</i> M. Roem.	D		1	430.1	1	430.1
Moraceae	<i>Artocarpus rigidus</i> Bl.	E		3	8635.9	3	8635.9
	<i>Ficus annulata</i> Bl.	E		1	0.0		
	<i>Ficus hirta</i> Vahl	E		1	21.2		
	<i>Ficus</i> sp.			1	0.0		
Myristicaceae	<i>Horsfieldia amygdalina</i> (Wall.) Warb. var. <i>amygdalina</i>	E		9	1183.4	4	983.3
Myrtaceae	<i>Eugenia siamensis</i> Craib	E		1	33.2		
Olacaceae	<i>Schoepfia fragrans</i> Wall.	E		1	35.3		
Proteaceae	<i>Helicia attenuata</i> (Jack) Bl.	E		1	29.2		
	<i>Helicia formosana</i> Hemsl.	E	MXF, EGF	2	1001.7	1	962.1
Rhizophoraceae	<i>Carallia brachiata</i> (Lour.) Merr.	E	BB/DF, EGF, MXF	1	263.0	1	263.0
Rosaceae	<i>Prunus arborea</i> (Bl.) Kalk. var. <i>montana</i> (Hk. f.) Kalk.	E		3	1008.4	2	944.8

Table 1 (continued)

Family	Species	Leaf phenology ¹	Habitat ²	≥5 cm DBH		≥10 cm DBH	
				N	BA	N	BA
Rubiaceae	<i>Diplospora singularis</i> (Korth.) K. Sch.	E		1	86.6	1	86.6
	<i>Tarennoidea wallichii</i> (Hk.f.) Tirv. & Sastre	E		1	1086.9	1	1086.9
	<i>Wendlandia scabra</i> Kurz var. <i>scabra</i>	D		31	2761.7	10	1679.2
	Unidentified			2	139.6	1	80.1
Rutaceae	<i>Tetradium glabrifolium</i> (Champ. ex Benth.) T. Hart.	E		1	490.9	1	490.9
Sapindaceae	<i>Nephelium</i> sp.			1	130.7	1	130.7
Sterculiaceae	<i>Sterculia urens</i> Roxb.	D	BB/DF, MXF, SG	3	195.2	1	143.1
Symplocaceae	<i>Symplocos cochinchinensis</i> (Lour.) S. Moore ssp. <i>laurina</i> (Retz.) Noot.	E	EGF	1	1885.7	1	1885.7
Theaceae	<i>Adinandra integerrima</i> T. And. ex Dyer	E		1	196.1	1	196.1
	<i>Eurya acuminata</i> DC. var. <i>acuminata</i>	E	EGF	23	2693.8	13	2179.8
	<i>Schima wallichii</i> (DC.) Korth.	T	MXF, EGF	25	34760.0	17	34416.3
Tiliaceae	<i>Colona floribunda</i> Craib	D		49	23138.5	44	22811.5
	<i>Microcos paniculata</i> L.	D	BB/DF	17	5867.1	12	5676.0
Urticaceae	<i>Oreocnide</i> sp. (probably <i>rubescens</i> (Bl.) Miq.)			1	41.9		
Unknown	Unidentified			3	88.8		
Unknown	Dead before ID possible			8	473.1	2	252.2
Totals				343	18.5	220	17.9

¹ D = deciduous, E = evergreen, T = tropophilous² BB/DF = bamboo—deciduous forest, DDF = deciduous dipterocarp forest, EGF = evergreen forest, MXF = mixed evergreen—deciduous forest, SG = secondary degraded forest

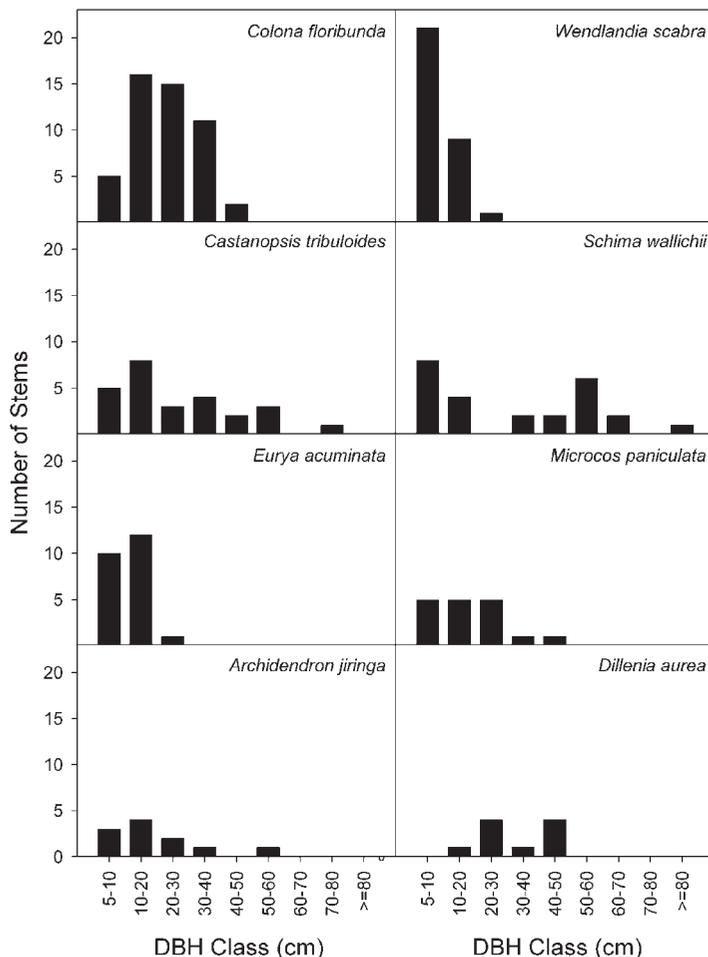


Figure 4. Diameter size class distributions of the most abundant tree species ≥ 5 cm DBH in mixed evergreen-deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary.

Table 2. Summary of leafing phenology and preferred forest type of identified species in one hectare of mixed evergreen plus deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary.

Leafing phenology	Species total	N individuals	BA (m ²)
Deciduous	25	255	7.6
Evergreen	34	106	7.0
Tropophyllous	1	24	3.5
Total	60	385	18.1

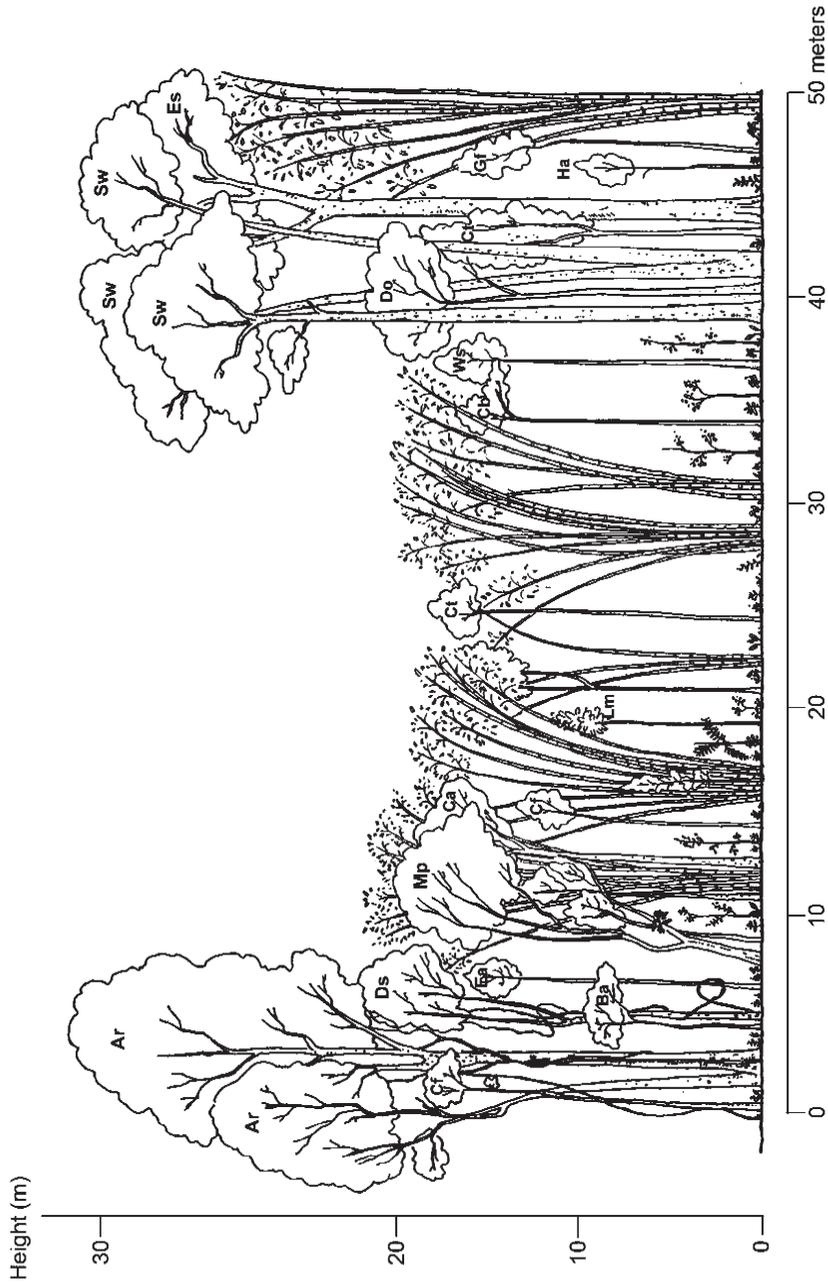


Figure 5. Profile diagram of a 50 m \times 10 m strip of mixed evergreen-deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary. Species abbreviations are: Ar (*Alstonia rostrata*), Ba (*Barringtonia actiangula*), Ca (*Callerya atropurpurea*), Cb (*Carallia brachiata*), Cf (*Colona floribunda*), Ct (*Castanopsis tribuloides*), Do (*Dillenia ovata*), Ds (*Dalbergia* sp.), Ea (*Eurya acuminata*), Es (*Engelhardtia spicata*), Gf (*Garuga floribunda*), Ha (*Horsfieldia amygdalina*), Lm (*Litsea monopetala*), Mp (*Microcos paniculata*), Sw (*Schima wallitchii*), Ws (*Wendlandia scabra*).

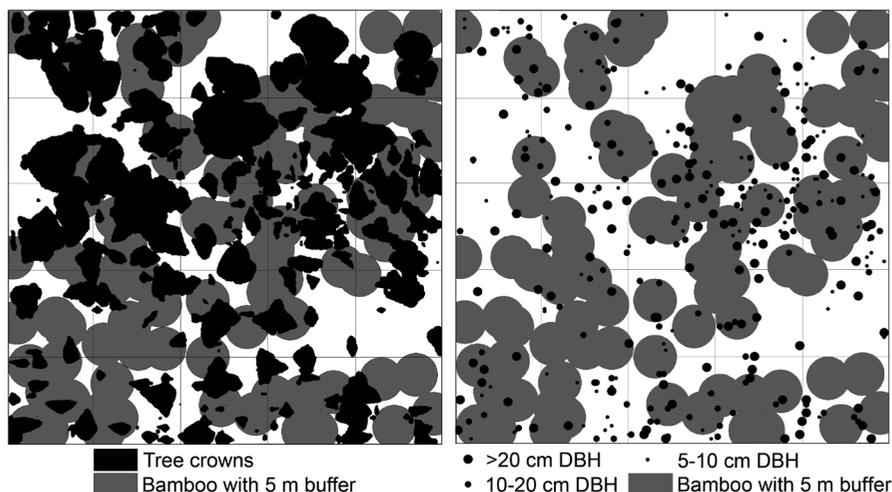


Figure 6. Canopy map of one hectare (100 m \times 100 m) of mixed evergreen-deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary. Left panel: map of tree crowns (black) and bamboo with 5 m buffer (grey). Right panel: location of all tree stems (points) and bamboo with 5 m buffer (grey).

Table 3. Density and basal area of trees inside and outside a 5 m buffer from bamboo clump centroids in one hectare of mixed evergreen plus deciduous forest at 700 m elevation, Thung Yai Naresuan Wildlife Sanctuary. Values are transformed to a per hectare basis.

Structural parameter	Inside 5 m buffer	Outside 5 m buffer	% Difference
No. individuals ≥ 5 cm DBH ha ⁻¹	300.3	359.6	+19.7
BA of stems ≥ 5 cm DBH ha ⁻¹	14.4	23.1	+59.7
No. individuals 5–9.9 cm DBH ha ⁻¹	93.8	132.7	+41.4
No. individuals 10–20 cm DBH ha ⁻¹	90.1	115.6	+28.3
No. individuals ≥ 20 cm DBH ha ⁻¹	116.4	111.3	-4.4

Of 60 identified species (including the bamboo *Gigantochloa nigroculiata* (Buse) Kurz), 34 (57%) were evergreen, 25 (42%) deciduous and one (*S. wallichii*) tropophyllous (Table 2). Deciduous species had far more individuals in the plot (255) than evergreen species (106).

The canopy was broken, fairly open and attained a height of 30–35 m with several emergent trees 35–40 m height (Fig. 5 and 6). Species with trees above 35 m tall were *Alstonia rostrata* Fischer, *Artocarpus rigidus* Bl., *Castanopsis tribuloides*, *Colona floribunda*, *Engelhardia spicata* Lechen. ex Bl. var. *spicata*, *Homalium ceylanicum* (Gard.) Bth., and *Schima wallichii*. Canopy cover of trees ≥ 5 cm DBH, as estimated by GIS analysis, was 43%. When a 5 m buffer was added to bamboo clump centroids and merged with the tree crown map, total canopy cover was 75% (Fig. 6).

Spatial analysis of stem distributions in relation to bamboo (buffers) revealed that for all stems ≥ 5 cm DBH there was a 19% reduction in tree (individual) density inside the 5 m buffer compared to outside (Fig. 6, Table 3). Basal area statistics for all stems were $23.1 \text{ m}^2 \text{ ha}^{-1}$ outside versus $14.4 \text{ m}^2 \text{ ha}^{-1}$ inside the buffer. Small tree densities were the most affected by bamboo (Table 3).

DISCUSSION

The Ti Thay Khi plot exhibits the tree phenological composition of MXF forest described elsewhere. The phenological composition of the Ti Thay Khi plot, 57% evergreen and 42% deciduous, is similar to the proportional representation of species of MXF forest found by others in Thailand (MAXWELL, 2004; VAN DE BULT & GREIJMANS, 2006). According to FORRU (2006), MXF in northern Thailand consists of about 43% deciduous tree species. MXF at Ti Thay Khi also exhibited a nearly identical community diameter class structure as MXF in Mae Wong National Park (Fig. 7).

There were several differences between Ti Thay Khi and other mixed evergreen/deciduous forests. Tree density and basal area in Ti Thay Khi were substantially lower than in MXF at 600–1100 m elevation of Mae Wong (33% and 53%, respectively, of Mae Wong values). VAN DE BULT & GREIJMANS (2006) established their plots in the least disturbed locations they could find, so the higher figures for Mae Wong would be expected. MXF at Ti Thay Khi exhibited very little species overlap with nearby deciduous, and evergreen, forest types. Only 23 of the identified 60 species overlapped with the Mae Wong species list (VAN DE BULT & GREIJMANS,

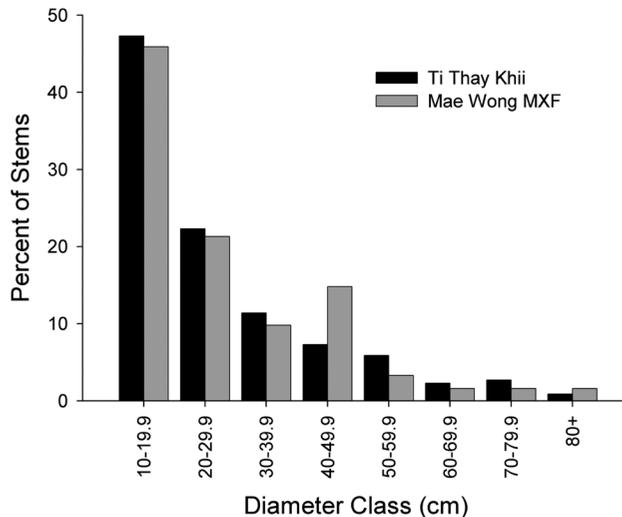


Figure 7. Comparison of diameter class distributions between mixed evergreen-deciduous forest at 700 m elevation in Thung Yai Naresuan and mixed evergreen-deciduous forest at 600–1100 m elevation in Mae Wong National Park (VAN DE BULT & GREIJMANS, 2006).

2006). Further, Ti Thay Khi shared almost no species with a 4 ha plot in ‘mixed deciduous forest’, western Thailand (MAROD *ET AL.*, 1999, plot elevation not published). Furthermore, the ten dominant tree families, genera, and species at Ti Thay Khi (in terms of relative abundance) were almost completely absent from the 50 ha vegetation plot in ‘seasonal dry evergreen forest’ at 550–640 m elevation in Huai Kha Khaeng (BUNYAVEJCHEWIN *ET AL.*, 2001; BUNYAVEJCHEWIN *ET AL.*, 2004).

The distinctiveness of Ti Thay Khi from other MXF or mixed evergreen and deciduous forests could be explained two ways. First, natural variation in MXF will account for some of the difference. However, another major contributor to the differences between Ti Thay Khi and other sites is human impacts. The structure and diversity of Ti Thay Khi was probably altered as a result of fire (even infrequent), and also possibly by agriculture in the past.

Two aspects of our results suggest such disturbances have shaped the tree community at Ti Thay Khi: the preponderance of deciduous tree species, and the abundance of bamboo. First, the particular deciduous tree species dominating the site are generally considered indicators of past disturbance. Local people informed us that the site had not been used for agriculture in recent memory (at least 80 years), but it could have been used in the more distant past. Together, *C. floribunda*, *S. wallichii* and *C. tribuloides* accounted for 22.5% of the trees and 42.9% of the basal area of the plot. Although *Schima* occurs across a wide range of forest types, it establishes after disturbances and is long-lived, so it persists for many decades (BOOJH & RAMAKRISHNAN, 1983; OHSAWA *ET AL.*, 1985, 1986; BARIK *ET AL.*, 1996; SANTISUK, 1998). The mixture of *Schima* with *Colona*, *Eurya*, and *Castanopsis* also occurred in both “old-growth” forest and in regenerating swidden fallows in northern Thailand, which were usually >12 years since cultivation (SCHMIDT-VOGT, 1999). CHOKKALINGAM & DE JONG (2001) used the *Schima-Colona-Eurya-Castanopsis* mixture as an example of secondary fallow in their typology of secondary forest types.

Second, MXF at our site exhibited a very high abundance of bamboo, which may increase in abundance where primary forest has been affected by agriculture and fire. Bamboo (*Bambusa tulda*) was common in our plot and in MXF of Mae Wong (VAN DE BULT & GREIJMANS, 2006), and notably both sites experience periodic fire. Bamboo appeared to suppress tree regeneration at this site, with the spatial distribution of smaller trees most heavily affected (Fig. 6, Table 3). These results correspond to other studies that have demonstrated the suppression of tree regeneration by bamboo (MAROD *ET AL.*, 1999; TABARELLI & MANTOVANI, 2000; LARPKERN *ET AL.*, 2011). However, bamboo death, occurring on a cyclical basis in many species (JANZEN, 1976), creates gaps that may assist in tree regeneration if seedlings can establish and outcompete bamboo seedlings for space and light, and as long as fire does not kill the young seedlings (KEELEY & BOND, 1999; MAROD *ET AL.*, 1999; FRANKLIN & BOWMAN, 2003; MAROD *ET AL.*, 2005). *Gigantochloa* at our site gregariously flowered and died about 26 years prior to the study, according to local people familiar with the area. This sudden disappearance of bamboo from the understorey may have resulted in large scale recruitment by *Colona floribunda*, whose hump-shaped size class distribution (Fig. 4) suggests a single-age cohort that established after the disturbance (BUNYAVEJCHEWIN, 1999) and a population into which young trees were no longer being recruited. *Colona floribunda* is a fast growing species that establishes well after disturbance; it can attain a DBH of 50 cm in roughly 30–40 years (D. Marod, pers. comm.).

Although only 42% of the species in Ti Thay Khi were deciduous, 66% of the stems were deciduous. To our knowledge the present study is the first in Thailand to report the relative

abundances of deciduous and evergreen stems. In contrast, recent forest descriptions have reported only the proportion of deciduous and evergreen species in the florula (e.g. FORRU, 2006; VAN DE BULT & GREIJMANS, 2006). We encourage the publication of both statistics. The species-proportion statistic may be useful for describing natural, undisturbed or “original” (*sensu* FORRU, 2006) forest types, but it is not weighted by species’ relative abundances, so therefore is not a good estimator of the relative deciduousness of the forest. Changes in species relative abundances due to disturbance may have an effect on the relative deciduousness of the forest. By calculating the relative abundances of deciduous and evergreen stems, the relative intensity of deciduousness could be compared across sites.

The Ti Thay Khi plot is a good representation of MXF that has been subject to a long history of relatively low human impact. This is an important forest type that requires further research attention. Monitoring the plot will provide information on the process of regeneration. We advocate replication of this research across other locations in northern and western Thailand.

ACKNOWLEDGEMENTS

Permission to work in Thung Yai was given by the Department of National Parks, Wildlife and Plant Conservation and the National Research Council of Thailand. Field assistance was provided by Karen villagers Mon Bey, Gong Khieow and Mon Dabwe, and by U Tin Than, Kietiphun Kaewplang, Thiha, Ngo Tri Dung and Rachel Webb. J. F. Maxwell processed and identified herbarium specimens, and provided numerous comments on an earlier version of the manuscript. This research was supported by the National Geographic Society’s Research and Exploration Grant number 6798-00 to ELW, and by WWF Thailand.

REFERENCES

- BAKER, P. J., S. BUNYAVEJCHEWIN, AND A. P. ROBINSON. The impacts of large-scale, low-intensity fires on the forests of continental South-east Asia. *Journal of Wildland Fire* 17: 782–792.
- BAKIK, S. L., R. S. TRIPATHI, H. N. PANDEY, AND P. RAO. 1996. Tree regeneration in a subtropical humid forest: effect of cultural disturbance on seed production, dispersal and germination. *J. Appl. Ecol.* 33: 1551–1560.
- BOOJH, R., AND P. S. RAMAKRISHNAN. 1983. The growth pattern of two species of *Schima*. *Biotropica* 15(2): 142–147.
- BUNYAVEJCHEWIN, S. 1999. Structure and dynamics in seasonal dry evergreen forest in northeastern Thailand. *J. Veg. Sci.* 10: 787–792.
- BUNYAVEJCHEWIN, S., P. BAKER, J. V. LAFRANKIE, AND P. ASHTON. 2001. Stand structure of a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. *Nat. Hist. Bull. Siam Soc.* 49: 89–106.
- BUNYAVEJCHEWIN, S., P. BAKER, J. V. LAFRANKIE, AND P. ASHTON. 2004. Huai Kha Khaeng Forest Dynamics Plot, Thailand. Pages 482–491 in E. Losos and E. G. Leigh, eds. *Forest Diversity and Dynamism: Findings from a Large-scale Plot Network*. University of Chicago Press, Chicago.
- CHOKKALINGAM, U., AND W. DE JONG. 2001. Secondary forest: a working definition and typology. *Int. For. Rev.* 3(1): 19–26.
- FORRU (THE FOREST RESTORATION UNIT CMU). 2006. *How to Plant a Forest: the Principles and Practice of Restoring Tropical Forests*. Biology Department, Science Faculty, Chiang Mai University, Thailand.
- FRANKLIN, D. C., AND D. J. M. S. BOWMAN. 2003. Bamboo, fire and flood: regeneration of *Bambusa arnhemica* (Bambuseae: Poaceae) after mass-flowering and die-off at contrasting sites in monsoonal northern Australia. *Aust. J. Bot.* 51: 529–542.

- KEELEY, J. E., AND W. J. BOND. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *Am. Nat.* 154(3): 383–391.
- LARPKERN, P., S. R. MOE, AND O. TOTLAND. 2011. Bamboo dominance reduced tree regeneration in a disturbed tropical forest. *Oecologia* 165: 161–168.
- JANZEN, D. H. 1976. Why bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* 7: 347–391.
- MAROD, D., U. KUTINTARA, C. YARWUDHI, H. TANAKA, AND T. NAKASHISUKA. 1999. Structural dynamics of a natural mixed deciduous forest in western Thailand. *J. Veg. Sci.* 10: 777–786.
- MAROD, D., V. NEUMRAT, S. PANUTHAI, T. HIROSHI, AND P. SAHUNALU. 2005. The forest regeneration after gregarious flowering of bamboo (*Cephalostachyum pergracile*) at Mae Klong Watershed Research Station, Kanchanaburi. *Kasetsart J. (Nat. Sci.)* 39: 588–593.
- MAXWELL, J. F. 2004. A synopsis of the vegetation of Thailand. *Nat. Hist. J. Chulalongkorn Univ.* 4(2): 19–29.
- MAXWELL, J. F., AND S. ELLIOTT. 2001. Vegetation and vascular flora of Doi Sutep-Pui National Park, Chiang Mai Province, Thailand. *Thai Studies in Biodiversity* 5. Biodiversity Research and Training Programme, Bangkok.
- OHSAWA, M., P. H. J. NAINGGOLAN, N. TANAKA, AND C. ANWAR. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of East Asia. *J. Trop. Ecol.* 1: 193–216.
- OHSAWA, M., P. R. SHAKYA, AND M. NUMATA. 1986. Distribution and succession of West Himalayan forest types in the eastern part of the Nepal Himalaya. *Mtn. Res. Dev.* 6(2): 143–157.
- PARMESAN, C., AND G. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- PETEETE, D. 2000. Sensitivity and rapidity of vegetational response to abrupt climate change. *Proc. Nat. Acad. Sci., U.S.A.* 97(4): 1359–1361.
- RICHARDS, P. W. 1996. *The Tropical Rain Forest*. Cambridge, Cambridge University Press.
- SANTISUK, T. 1998. *An Account of the Vegetation of Northern Thailand*. Steiner-Verlag, Stuttgart.
- SCHMIDT-VOGT, D. 1999. Swidden farming and fallow vegetation in northern Thailand. Steiner-Verlag, Stuttgart.
- TABARELLI, M., AND W. MANTOVANI. 2000. Gap-phase regeneration in a tropical montane forest: the effects of gap structure and bamboo species. *Plant Ecol.* 148: 149–155.
- VAN DE BULT, M., AND M. GREJMANS. 2006. Vegetation types and the deciduous-evergreen forest continuum along an elevation gradient in Mae Wong National Park, western Thailand. *Nat. Hist. Bull. Siam. Soc.* 54(1): 27–74.
- WONG, T., C. O. DELANG, AND D. SCHMIDT-VOGT. 2007. What is a forest? Competing meanings and the politics of forest classification in Thung Yai Naresuan Wildlife Sanctuary, Thailand. *Geoforum* 38: 643–654.