Stand Structure of A Seasonal Dry Evergreen Forest at Huai Kha Khaeng Wildlife Sanctuary, Western Thailand[1]

ลักษณะโครงสร้างของป่าดิบแล้ง ที่เขตรักษาพันธุ์สัตว์ป่าห้วยขาแข้ง

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บทคัดย่อ

ลักษณะโครงสร้างของป่าดิบแล้งในเขตรักษาพันธุ์สัตว์ป่าห้วยขาแข้ง ทำการศึกษาจากแปลงตัวอย่างถาวรขนาด 50 เฮกแตร์ (500x1000 เมตร) โดยวิเคราะห์จากข้อมูลการวัดครั้งแรก ป่าดิบแล้งในแปลง 50 เฮกแตร์ มีความหนาแน่นเฉลี่ย 1,613 ต้น/เฮกแตร์ (dbh $\geq$ 1 เซนติเมตร) 439 ต้น/เฮกแตร์ (dbh $\geq$ 10 เซนติเมตร) และ 3.74 ต้น/เฮกแตร์ (dbh $\geq$ 100 เซนติเมตร) พื้นที่หน้าตัดเฉลี่ย 30.45 ม^{2}/เฮกแตร์ (dbh $\geq$ 1 เซนติเมตร) 28.69 ม.^{2}/เฮกแตร์ (dbh $\geq$ 10 เซนติเมตร) และ 5.57 ม.^{2}/เฮกแตร์ (dbh $\geq$ 100 เซนติเมตร) โครงสร้างของหมู่ไม้ (ความหนาแน่น และพื้นที่หน้าตัด) ของป่าดิบแล้งที่เขตรักษาพันธุ์สัตว์ป่าห้วยขาแข้งใกล้เคียงกับป่าดิบแล้งอื่น ๆ ในประเทศไทย แต่จะมีความหนาแน่นน้อยกว่ามากเมื่อเทียบกับป่าดิบชื้นที่ศึกษาจากแปลงขนาดเดียวกันในมาเลเซีย (6,769 ต้น/เฮกแตร์, dbh $\geq$ 1 เซนติเมตร) และที่ปานามา (4,882 ต้น/เฮกแตร์, dbh $\geq$ 1 เซนติเมตร) แต่มีพื้นที่หน้าตัดจะใกล้เคียงกัน สิ่งที่แตกต่างกันอย่างมากคือปริมาณความหนาแน่นของลูกไม้ สำหรับต้นไม้ที่มี dbh $\geq$ 10 เซนติเมตร ป่าดิบแล้งที่เขตรักษาพันธุ์สัตว์ป่าห้วยขาแข้ง จะมีความหนาแน่นเท่า หรือหนาแน่นกว่าป่าดิบชื้นทั้งสองแปลง

ลักษณะโครงสร้างตามชั้นขนาดความโตของพันธุ์ไม้แต่ละชนิดประกอบด้วยหลายรูปแบบ จาก negative exponential ถึง unimodal ถึง irregular อย่างไรก็ตามสำหรับพันธุ์ไม้ที่มีความหนาแน่นสูงสุด 20 ชนิดแรก พบว่า มีรูปแบบการกระจายตามชั้นความโตแบบ Unimodal และ irregular จำนวนมากเป็นสองเท่าของรูปแบบ negative exponential ตะเคียนทองซึ่งเป็นพันธุ์ไม้ที่มีพื้นที่หน้าตัดรวมสูงสุดในแปลง มี

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[1] ลงพิมพ์เผยแพร่ใน Nat. Hist. Bull. Siam Soc. 49: 89-106, 2001

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การกระจายชั้นความโตแบบ normal ผลการศึกษานี้แสดงว่า พื้นที่ป่าในแปลง 50 เฮกแตร์ และพื้นที่โดยรอบเคย ถูกรบกวนอย่างรุนแรงเป็นพื้นที่ขนาดใหญ่ (large-scale catastrophic disturbance)

คำหลัก: แปลงตัวอย่างถาวร, การกระจายตามชั้นความโต, ตะเคียนทอง

ABSTRACT

We describe the structure of a stand of seasonal dry evergreen forest located in the Huai Kha Khaeng Wildlife Sanctuary (HKK), Uthai Thani Province based on a census of all trees ≥1 cm dbh in a 50 ha plot. Mean densities were 1613 trees ha^{-1} (≥1 cm dbh), 439 trees ha^{-1} (≥10 cm), and 3.74 trees ha^{-1} (≥100 cm). Mean basal area was 30.45 m^2 ha^{-1} (≥1 cm dbh), 28.69 m^2 ha^{-1} (≥10 cm dbh), 5.57 m^2 ha^{-1} (≥100 cm dbh). The stand structure (density and basal area) of the seasonal dry evergreen forest at HKK is comparable to published reports of stand structure for other seasonal evergreen forests in Thailand and would appear to be generally representative of the forest type. The HKK plot was much less dense (1613 trees ha^{-1} ≥1 cm dbh) than similar plots in Malaysia (6769 trees ha^{-1} ≥1 cm dbh) and Panama (4882 trees ha^{-1} ≥1 cm dbh), although had similar values for total basal area. The major difference between the forest types was in the density of the saplings. For trees ≥ 10 cm dbh the seasonal dry evergreen forest plot was as dense or denser than the lowland tropical forest plots. Individual tree species' diameter distributions exhibited a variety of forms, from negative exponential to unimodal to irregular; however, among the 20 most common species unimodal and irregular diameter distributions were twice as frequent as negative exponential distributions. The diameter distribution of *Hopea odorata* Roxb., the species with the greatest basal area on the plot, was unimodal and approximately normal. These results suggest that the area in and around the HKK plot may have been subject to a large-scale catastrophic disturbance.

Keywords: permanent plot, disturbances, diameter distributions, *Hopea odorata*

INTRODUCTION

Between 1992 and 1995 a large-scale permanent forest dynamics plot (FDP) was established in a seasonal dry evergreen forest at the Huai Kha Khaeng Wildlife Sanctuary (HKK) in western Thailand to monitor long-term changes in forest composition and structure. In this paper we summarize the results from the first census describing the stand structure at the HKK FDP to answer two questions: (1) Is the forest of the HKK FDP representative of seasonal evergreen forests of continental southeast Asia? (2) How does the structure of the seasonal dry evergreen forest differ from other lowland tropical forest types? and (3) Is there evidence that the stand has experienced severe disturbance in the past? The structure of this paper closely parallels Manokaran and LaFrankie (1990), which describes the results of the first census from a similar FDP in lowland evergreen forest of peninsular Malaysia. We have chosen to adopt a similar framework for describing the HKK forest to facilitate comparisons between these and other large-scale permanent plots (see Condit, 1995). A companion paper will describe the floristic structure of the FDP.

SITE DESCRIPTION AND METHODS

The study site is located in the Huai Kha Khaeng Wildlife Sanctuary at 15° 40' N latitude and 99° 10' E longitude in Uthai Thani province, west-central Thailand, approximately 300 km northwest of Bangkok (Figure 1). The sanctuary encompasses 2780 km^2 of the Huai Kha Khaeng River watershed. The topography consists of broad river valleys and moderately steep ridges running north-south. The sanctuary contains a mosaic of four forest types: seasonal dry evergreen forest, mixed deciduous forest, dry dipterocarp forest, and hill evergreen forest. The study site is located in an area of seasonal dry evergreen forest. Elevation within the study plot ranges from 550 to 640 meters above sea level. Mean annual rainfall is 1475 mm (1983-1993). The climate is monsoonal with a rainy season from May to October and a dry season from November to April (in which mean monthly rainfall is <100 mm) (Figure 2). The extent and severity of the dry season is variable. Some years have sporadic rainfall during the dry season; others have little or no rain for the entire dry season. Mean July temperature is 27° C; mean January temperature is 19° C. Minimum recorded temperatures are as low as 12° C and maximum temperatures as high as 38° C. Maximum daily relative humidity drops below 98% only during the height of the dry season in March and April. Minimum daily relative humidity varies between 40% and 60% except during the dry season, when it is frequently less than 20%.

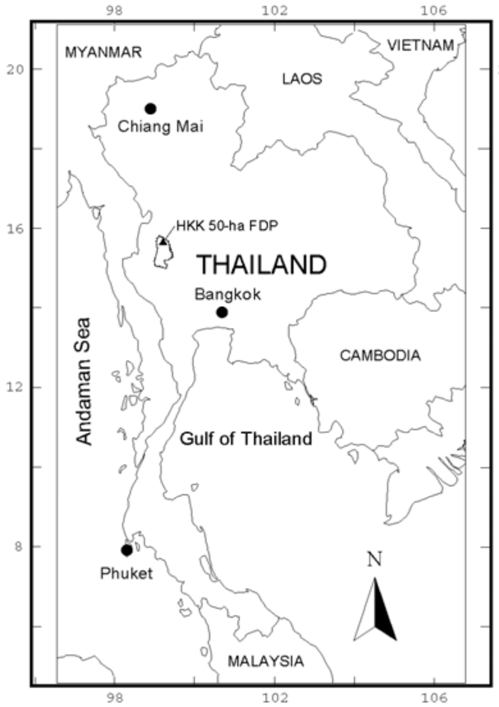


Figure 1. Location of the Huai Kha Khaeng Wildlife Sanctuary, western

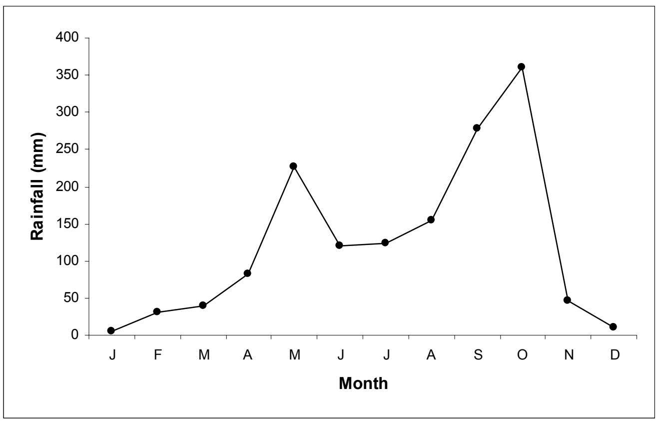


Figure 2. Mean monthly rainfall conditions at the Huai Kha Khaeng WS, Thailand (Khao Nang Ram Wildlife Research Station meteorological data; 1983-1993).

The FDP is a 50 ha rectangle 1 km long (north-south axis) and 0.5 km wide (east-west). The enumeration included all free-standing woody plants ≥ 1 cm dbh. Each tree was measured, mapped to plot coordinates, and identified following a standard protocol (Manokaran *et al.*, 1990; Condit, 1998; Bunyavejchewin *et al.*, 2000). All data are stored in a

Microsoft Access database to facilitate data retrieval and manipulation. Taxonomy and nomenclature follows Bunyavejchewin *et al.* (2000).

RESULTS

Stand-wide Distribution Among Diameter Classes

The forest within the 50 ha plot had a relatively low density with a total of 80640 trees or a mean density of 1613 trees ha^{-1} (SD = 311.0) The mean density for trees between 1 and 2 cm dbh was 434 ha^{-1} (SD = 190.56). Between 1 and 10 cm the mean density was 1171 ha^{-1} (SD = 299.0), decreasing in a log-linear fashion through 1 cm size class intervals (Figure 3). When compared to other 50 ha plots, the HKK forest has much lower densities among the small size classes (Table 1).

Figure 3. Density of trees 1 to 10 cm dbh (1 cm intervals) in the 50-ha plot, Huai Kha Khaeng WS, Thailand.

Table 1. Comparison of tree densities above specified diameters from other large-scale forest
dynamics plots (i.e., ≥50 ha).

Plot	Trees ha^{-1} (≥1 cm dbh)	Trees ha^{-1} (≥10 cm dbh)	Trees ha^{-1} (≥30 cm dbh)	Trees ha^{-1} (≥100 cm dbh)
Pasoh Forest, Peninsular Malaysia	6769	530	75	1.6
Lambir Hills NP, Sarawak	6687	622	117	
Barro Colorado Island, Panama	4844	414	83	3.4
Huai Kha Khaeng WS, Thailand	1609	438	83	5.6
Mudumalai WS, India	328	255	103	

Mean density of trees ≥10 cm dbh was 438 ha^{-1} (SD = 61.3). The mean density of trees ≥30 cm dbh was 83 ha^{-1} (SD = 18.1). The mean density of trees ≥100 cm dbh was 5.6 ha^{-}

^{1} (SD = 12.5). Mean density of trees classed in 10 cm intervals between 10 cm and 100 cm dbh decreased in a log-linear fashion (Figure 4).

The family Annonaceae had the greatest number of stems ≥1 cm dbh (16663 individuals), followed closely by the Euphorbiaceae (14595 individuals) and Sapindaceae (9823 individuals). No other families had more than 5000 stems (*i.e.*, mean density of 100 ha^{-1}). Because many of the genera at the HKK FDP have only one or two species, the patterns of abundance among the most populous genera and species are nearly identical. Thus, *Croton* (Euphorbiaceae), represented by *C. oblongifolius* Roxb. and *C. hutchinsonianus* Hosseus, was the most populous genus (9153 individuals), with *C. oblongifolius* being the most common species (9106 individuals). *Polyalthia* (Annonaceae) was the second most populous genus (6141 individuals) and *Polyalthia viridis* Craib was the second most common species with 5888 individuals. Table 2 summarizes the distribution of stems among the top 10 families, genera, and species.

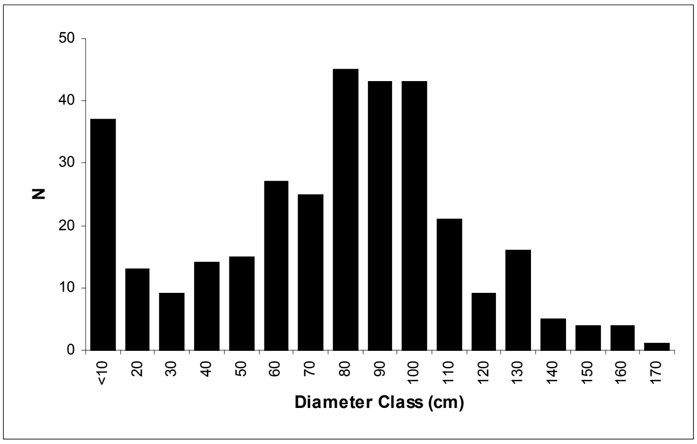


Figure 4. Density of trees in 10 cm size classes in the 50-ha plot, Huai Kha Khaeng WS, Thailand.

It is worth noting that the HKK plot contains some very large trees. Of the 26 trees over 150 cm dbh, 14 were *Ficus* species. Most of these were strangling (*i.e.*, hemi-epiphytic) figs for which dbh measurements represent the total diameter of fig and host tree. The remaining 12 trees larger than 150 cm dbh were divided among 4 species: *Afzelia xylocarpa* (Kurz.) Craib, *Anisoptera costata* Korth., *Hopea odorata* Roxb., and *Tetrameles nudiflora* R.Br. The largest tree (excluding strangling figs) was an *Anisoptera costata* with a dbh of 206 cm. In comparison, the Pasoh FDP had only 4 trees larger than 150 cm dbh (Manokaran & LaFrankie, 1990).

Species-specific Diameter Distributions

Stand-wide diameter distributions provide a general description of the stand's structure; however, diameter distributions of individual species can often provide additional information about past influences on stand development such as disturbances. The tree species at the HKK FDP exhibit a range of diameter distributions. The negative exponential distribution that is predicted for self-replacing populations is not as common among the HKK species as expected. In fact, the negative exponential distribution is found in only 6 of the 20 most common species (ranging in abundance from 1049 to 9101 individuals); of the remainder, 8 species have unimodal distributions that are approximately normal (although often positively skewed), 2 species have compound (or multimodal) distributions (*i.e.*, large numbers of individuals in the smallest size class and a unimodal distribution describing the remainder of the size classes), and 4 species have maximum dbh <10 cm and thus are not appropriate for comparison. The most notable species with a unimodal diameter distribution is *Hopea odorata*, the dominant canopy species. The diameter distribution of *Hopea odorata* is approximately normally distributed with a mean diameter of 71 cm (SD = 38, n=330) (Figure 5). Other important canopy species exhibiting unimodal diameter distributions include *Alphonsea ventricosa* Hk.f.& Th., *Duabanga grandiflora* Walp., *Dysoxylum grande* Hiern, and *Litsea cambodiana* H. Lec..

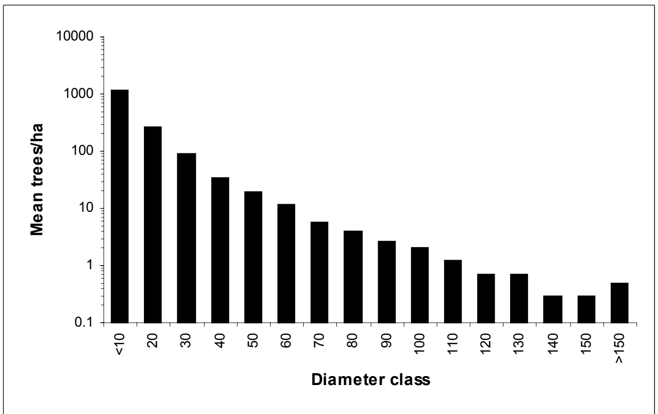
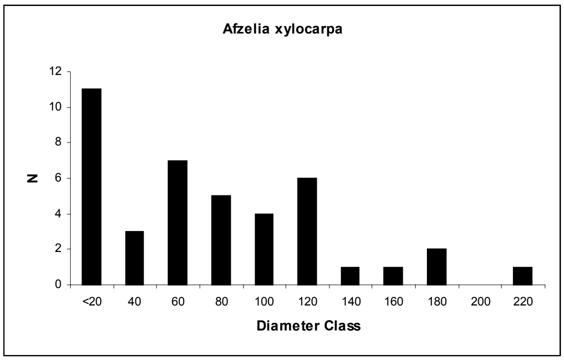


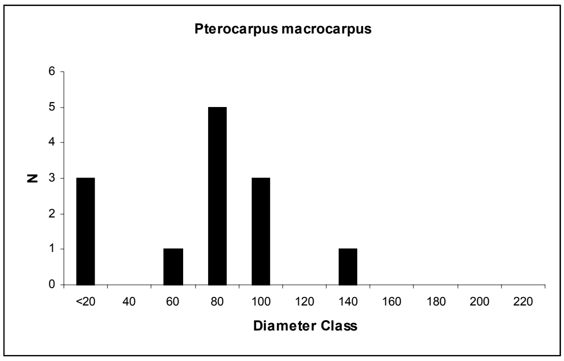
Figure 5. Diameter distribution of *Hopea odorata* (Dipterocarpaceae), the dominant tree species in the 50-ha plot, Huai Kha Khaeng WS, Thailand

Table 2. Densities of the 10 most populous families, genera, and species at the 50-ha plot, Huai Kha Khaeng WS, Thailand.

Rank	Family	Density	Genus	Density	Species	Density
1	Annonaceae	16663	*Croton* (Euphorbiaceae)	9153	*Croton oblongifolius* (Euphorbiaceae)	9106
2	Euphorbiaceae	14595	*Polyalthia* (Annonaceae)	6111	*Polyalthia viridis* (Annonaceae)	5888
3	Sapindaceae	9823	*Dimocarpus* (Sapindaceae)	5501	*Dimocarpus longan* (Sapindaceae)	5501
4	Rubiaceae	4899	*Orophea* (Annonaceae)	4379	*Orophea polycarpa* (Annonaceae)	4379
5	Lauraceae	4574	*Diospyros* (Ebenaceae)	4159	*Prismatomeris malayana* (Rubiaceae)	4137
6	Ebenaceae	4159	*Prismatomeris* (Rubiaceae)	4137	*Phoebe tovayana* (Lauraceae)	3018
7	Dipterocarpaceae	2874	*Phoebe* (Lauraceae)	3018	*Baccaurea ramiflora* (Euphorbiaceae)	2582
8	Rutaceae	2776	*Baccaurea* (Euphorbiaceae)	2582	*Arytera litoralis* (Sapindaceae)	2539
9	Leguminosae	2539	*Arytera* (Sapindaceae)	2539	*Mitrephora thorelii* (Annonaceae)	2248
10	Bignoniaceae	1897	*Mitrephora* (Annonaceae)	2248	*Vatica cinerea* (Dipterocarpaceae)	2080

Another group of species with diameter distributions that may be indicative of historical disturbance are those that are commonly associated with mixed deciduous or dry dipterocarp forests (Bunyavejchewin *et al.*, in press). Several traits suggest that many of these species are relict populations within the matrix of the seasonal dry evergreen forest at the HKK FDP: (1) small populations, (2) unimodal diameter distributions that are negatively skewed, and (3) large mean diameters. Examples include *Afzelia xylocarpa*, *Pterocarpus* *macrocarpus* Kurz., and *Terminalia bellirica* (Gaertn.) Roxb. (Figure 6). S*horea siamensis* Miq., one of the dominant species of the deciduous dipterocarp forests, is represented by a sole individual of 65 cm dbh that has the gnarled and tumescent bole typically associated with relict *S. siamensis* in dry dipterocarp stands elsewhere in the sanctuary (P.J. Baker, unpublished data).





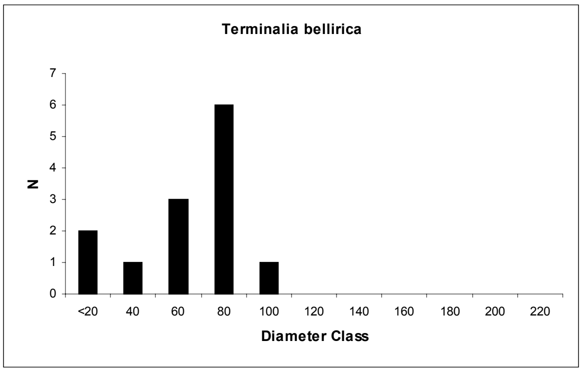
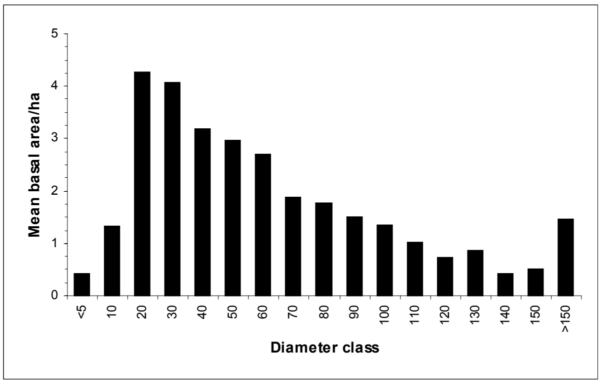


Figure 6. Diameter distributions of (a) *Afzelia xylocarpa* (Leguminosae), (b) *Pterocarpus macrocarpus* (Leguminosae), and (c) *Terminalia bellirica* (Combretaceae), three species with irregular size distributions dominated by large individuals, in the 50 ha
plot, Huai Kha Khaeng WS, Thailand.

Stand-Wide Distribution of Basal Area



Mean basal area of trees ≥1 cm dbh was 30.39 m^2 ha^{-1} (SD = 5.70). For trees ≥10 cm dbh the mean basal area was 28.64 m^2 ha^{-1} (SD = 5.70); for trees ≥30 cm dbh the mean basal area was 20.33 m^2 ha^{-1} (SD = 5.43); and, for trees ≥100 cm dbh the mean basal area was 5.57 m^2 ha^{-1} (SD = 4.46). Basal area peaked in the 10-20 cm size class and decreased in a linear fashion among the larger size classes (Figure 7).

Figure 7. Mean basal area of trees per hectare in the 50-ha plot, Huai Kha Khaeng WS, Thailand. (Note that the size classes are uneven.)

Members of the family Dipterocarpaceae dominated the FDP with respect to basal area. While they represented only 3.6% of the total number of stems in the FDP, the dipterocarps accounted for 21.9% of the basal area (332.24 m^2). (Table 3 summarizes the distribution of basal area among the top 10 families, genera, and species.) A single species, *Hopea odorata* (n = 330 individuals, or 0.41% of the total number of trees on the FDP), accounted for 169 m^2 of basal area (3.38 m^2 ha^{-1} and 0.51 m^2 $tree^{-1}$) —11.1% of the total basal area of the FDP. The Annonaceae had the second highest basal area among families (292.22 m^2 ha^{-1}), followed distantly by the Lauraceae (118.05 m^2 ha^{-1}) and Euphorbiaceae (83.94 m^2 ha^{-1}); all three of these families were ranked in the top five families for total number of individuals on the HKK FDP. The same pattern of similarity between genera and species that occurred for stem density is found in the distribution of basal area. The genus *Hopea* (Dipterocarpaceae), represented by the single species *H. odorata*, had the greatest basal area (see above). *Saccopetalum* (Annonaceae), also represented by a single species (*S. lineatum* Craib), had the second greatest basal area (128.74 m^2 ha^{-1}) among the genera at the HKK FDP.

Table 3. Basal area (m^2) of the top 10 families, genera, and species at the 50-ha plot, Huai Kha Khaeng WS, Thailand

Rank	Family	BA	Genus	BA	Species	BA
1	Dipterocarpaceae	332.24	*Hopea* (Dipterocarpaceae)	168.92	*Hopea odorata* (Dipterocarpaceae)	168.92
2	Annonaceae	292.22	*Saccopetalum* (Annonaceae)	128.73	*Saccopetalum lineatum* (Annonaceae)	128.73
3	Lauraceae	118.05	*Polyalthia* (Annonaceae)	84.72	*Polyalthia viridis* (Annonaceae)	84.28
4	Euphorbiaceae	83.94	*Ficus* (Moraceae)	77.25	*Vatica cinerea* (Dipterocarpaceae)	66.65
5	Sapindaceae	82.57	*Vatica* (Dipterocarpaceae)	66.65	*Tetrameles nudiflora* (Datiscaceae)	61.26
6	Moraceae	79.66	*Dipterocarpus* (Dipterocarpaceae)	62.42	*Dipterocarpus alatus* (Dipterocarpaceae)	59.27
7	Ebenaceae	61.76	*Diospyros* (Ebenaceae)	61.76	*Neolitsea obtusifolia* (Lauraceae)	48.15
8	Datiscaceae	61.26	*Tetrameles* (Datiscaceae)	61.26	*Lagerstroemia tomentosa* (Lythraceae)	44.45
9	Lythraceae	53.94	*Lagerstroemia* (Lythraceae)	53.94	*Alphonsea ventricosa* (Annonaceae)	43.60
10	Meliaceae	50.74	*Neolitsea* (Lauraceae)	48.15	*Arytera litoralis* (Sapindaceae)	35.77

Heterogeneity

The distribution of stems and basal area was not uniform across the plot. We divided the plot into 1250 20 m x 20 m quadrats and calculated the density for each quadrat. The density of stems (≥1 cm dbh) in the quadrats ranged from 11 to 249 trees; median density was 58 trees and 50 percent of the quadrats had total stem densities between 45 and 77 (Figure 8a). The distribution was not significantly different from a normal distribution (Shapiro-Wilk $W = 0.90$, $p < 0.001$; Zar 1984), although it was strongly positively skewed (skewness =

1.50). Variation in basal area among quadrats was similar (Figure 8b); the distribution was normally distributed (Shapiro-Wilk W = 0.85, p < 0.001), although strongly positively skewed (skewness = 2.25). The range of basal area was 0.11 to 7.02 m^2. The median basal area was 1.09 m^2 with 50% of the values falling between 0.73 and 1.53 m^2.

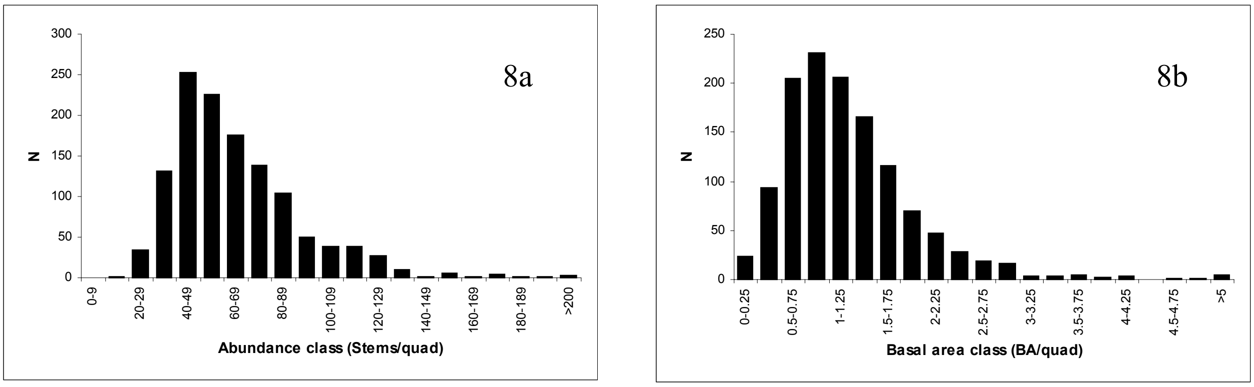


Figure 8. Density (a) and basal area (b) of 1250 20 m x 20 m quadrats within the 50-ha plot, Huai Kha Khaeng WS, Thailand.

Figure 9 shows the distribution of all trees ≥100 cm dbh. The northern half of the FDP has greater proportion of these large trees. The two areas along the eastern and southeastern edges of he plot that have no large trees correspond to the top of hills, both of which are covered with short dense thickets of bamboo and scrub forest.

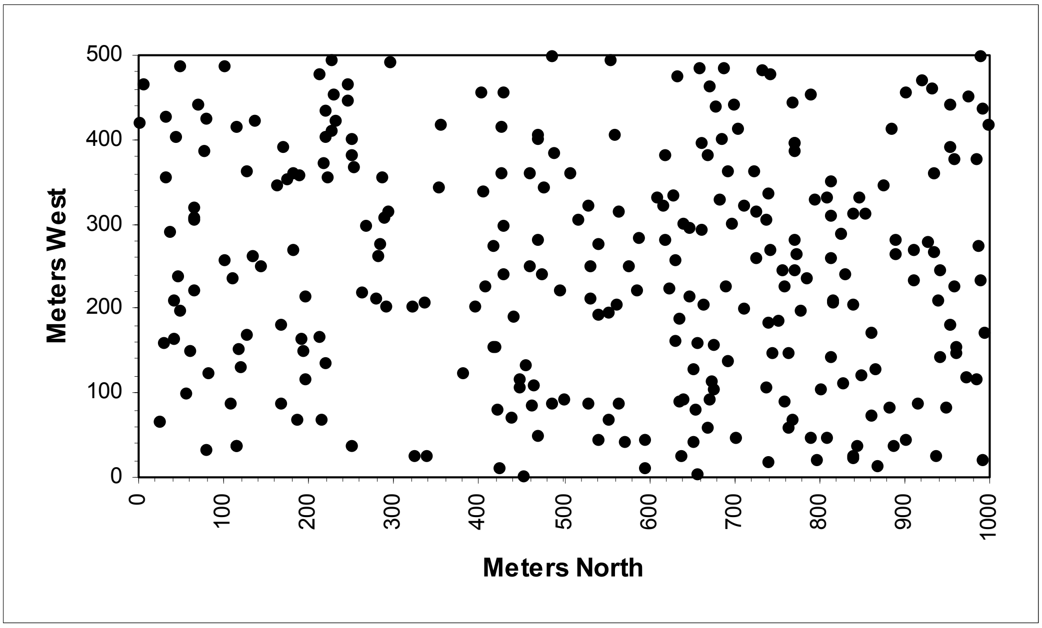


Figure 9. Distribution map of all trees ≥100 cm dbh in the 50-ha plot, Huai Kha Khaeng WS, Thailand.

The distribution of the smallest trees (1-2 cm dbh) is shown in Figure 10. The small trees are highly aggregated but well distributed across the plot. The southeastern corner of the plot has the lowest density of small trees. This is most likely the consequence of a fire that burned through that part of the plot in 1992, just before the initial plot census began. Such low-intensity surface fires typically result in widespread mortality of the smallest size classes of trees (<5 cm dbh; P.J. Baker, unpublished data). While many saplings in the seasonal evergreen killed by the fire subsequently re-sprout (S. Bunyavejchewin, unpublished data), few would have reached 1 cm dbh sufficiently quickly to be included in the census.

DISCUSSION

Is the forest of the HKK FDP representative of seasonal evergreen forests of continental southeast Asia?

There exist two quantitative studies of seasonal evergreen forest in Thailand and one from southern Vietnam for comparison with the HKK dataset. The first study in Thailand was conducted by the Osaka City University Biological Expedition to Southeast Asia 1957-1958 (Ogawa *et al.* 1961, 1965). However, the data from their reports that are comparable to the HKK FDP are extremely limited. They established study plots in several sites in Thailand to obtain representative descriptions of as many Thai forest types as possible. One of the 8 study plots was situated in evergreen gallery forest southeast of Doi Inthanon, Chiang Mai Province. The plot was 10 m x 10 m and included all individuals ≥1.4 m tall. The total number of individuals was 162 (16,200 ha^{-1}). While the density of individuals in the gallery forest plot was an order of magnitude greater than at the HKK FDP, the results are not directly comparable because the HKK FDP does not include individuals <1 cm dbh, which may be numerous. Among the larger size classes approximately 32 individuals were ≥10 cm dbh (320 ha^{-1})—somewhat less than the density of the HKK FDP—although Ogawa *et al.* (1961) noted that the gallery forest plot in their study appeared immature based on total canopy height and the vertical distributions of particular species.

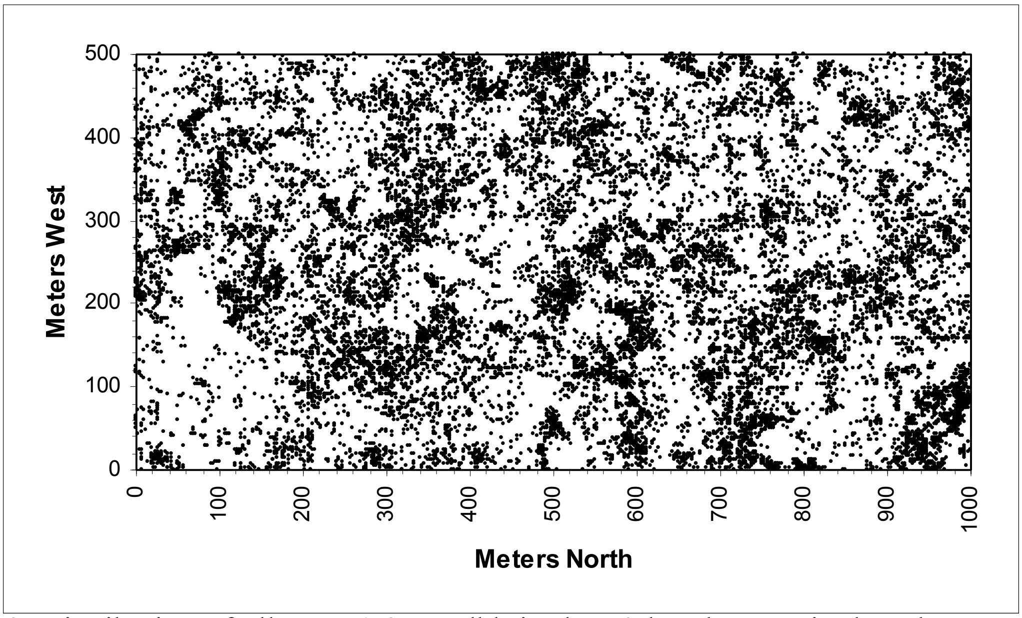


Figure 10. Distribution of all trees 1-2 cm dbh in the 50-ha plot, Huai Kha Khaeng WS, Thailand

In a much more detailed study Bunyavejchewin (1986, 1999) enumerated all trees ≥ 4.5 cm dbh in two 1-ha plots of seasonal evergreen forest in Sakaerat, Nakhon Ratchasima. The two Sakaerat plots were floristically distinct, principally with respect to the primary dipterocarp canopy species: one plot was dominated by *Hopea ferrea* Pierre, while the other was dominated by *Shorea henryana* Pierre. Structurally, the stands were relatively similar to each other and to the HKK FDP. The *Hopea ferrea* plot had 1168 stems ha^{-1} and 29.1 m^2 ha^{-1} of basal area, while seasonal evergreen forest dominated by *Shorea henryana* had 1356 stems ha^{-1} and 29.8 m^2 ha^{-1} of basal area (Bunyavejchewin, 1999). However, both of the Sakaerat plots only included trees ≥4.5 cm dbh, compared to the minimum diameter of 1 cm at the HKK FDP. When trees <4.5 cm were excluded from the HKK dataset, stem density was 811 stems ha^{-1} (SD = 107.0) and basal area decreased slightly to 30.11 m^2 ha^{-1} (SD = 5.63). For trees ≥10 cm dbh the Sakaerat plots had densities of 562 and 514 trees ha^{-1} and basal areas of 30.01 and 26.88 m^2 ha^{-1} for the *H. ferrea* and *S. henryana* sub-types, respectively. The pattern at HKK was similar with 439 trees ha^{-1} ≥10 cm dbh accounting for 28.69 m^2 ha^{-1} of basal area.

In a recent study in southern Vietnam, Blanc *et al.* (2000) established five 100 m x 100 m (1 ha) study plots in the Cat Tien National Park. All trees ≥10 cm dbh were measured, mapped and identified. While the study area receives nearly 1000 mm more rainfall than the HKK FDP, the floristic composition, at both the level of genera and species, is remarkably similar to HKK. The patterns of species dominance are somewhat different: at Cat Tien *Lagerstroemia calyculata* Kurz. is the dominant overstory tree, whereas at the HKK FDP *Hopea odorata* is the dominant species. [It is worth noting that there are stands near the HKK FDP that are dominated by *Lagerstroemia calyculata* that are almost identical to the Cat Tien stands in terms of dominance, density, and basal area patterns (S. Bunyavejchewin, unpublished data).] The density of trees in the five Cat Tien study plots was 419, 389, 540, 195, 469 individuals ha^{-1}. Only the fourth plot (195 individuals ha^{-1}) is not directly comparable to the HKK FDP but the authors suggest that it may have been disturbed in recent history. The basal area of the Cat Tien study plots was 69.4, 31.7, 54.9, 29.3, 31.3 m^2 ha^{-1}. The first and third plots had extremely high basal areas. The authors describe both of these plots as recently disturbed; however, many large trees survived the disturbance and contribute the majority of the stand basal area (*e.g.*, in the third plot the 20 trees in the largest diameter class, which account for 3.7% of the total number of individuals on the plot, contribute 71.4% of the total basal area). The other plots have basal areas that are almost identical to the HKK FDP.

While there are relatively few studies documenting forest structure in Thailand and continental southeast Asia it appears that the stand structure at the HKK FDP is consistent with the existing studies and can be taken as broadly representative of seasonal dry evergreen forests in the region.

How does the structure of the seasonal evergreen forest differ from other lowland tropical forest types?

While there are slight differences between the results from the HKK and Sakaerat studies, they are minor when compared to other lowland tropical forests (Table 1). For example, the density of trees ≥1 cm dbh in lowland rain forest at the Pasoh Forest in peninsular Malaysia is 6769 trees ha^{-1} (Manokaran & LaFrankie 1990), more than four times the density of stems at the HKK FDP. Another lowland rain forest, that of Lambir Hills

National Park in Sarawak, is nearly identical to Pasoh in density of trees ≥1 cm dbh with 6687 trees ha^{-1}. At Barro Colorado Island (BCI) in Panama in a 50-ha plot identical in layout to the HKK FDP the density of trees was 4882 trees ha^{-1} ≥1 cm dbh, approximately three times the density at HKK (Condit *et al.* 1996). At the other extreme, a 50-ha FDP of mixed deciduous forest in southern India had 514 trees ha^{-1} ≥1cm dbh (Condit *et al.* 1996)—one-third the density of the HKK FDP.

A closer examination of the patterns of stem density among these plots shows that the differences are principally restricted to the smallest size classes (<10 cm dbh). For trees ≥10 cm dbh the density of individuals in the seasonal evergreen forest at HKK is similar to that of the Malaysian and Panamanian lowland evergreen forest plots as well as the mixed deciduous forest plot in India (Table 1). In the largest size classes (≥100 cm dbh) the density of trees at HKK (5.6 trees ha^{-1}) was high compared to that at Pasoh (1.6 ha^{-1}) and BCI (3.4 ha^{-1}). However, in other tropical lowland rain forests the density of large trees may be as great or greater than that of HKK. Thus, the major structural difference between seasonal dry evergreen forest in Thailand as exemplified by the HKK FDP and lowland tropical forest appears to be a paucity of saplings in the former.

A mechanism that could contribute to the low density of saplings in the seasonal evergreen forest is forest fire. Low-intensity surface fires have occurred within the sanctuary repeatedly. While no data exist on point-return fire intervals at HKK, in the past decade there have been two fires that burned through the entire plot (1993, 1998) and one fire that burned approximately 4 ha in the southeast corner of the plot (1991). Similarly, there is a lack of published data on the effects of the fires on the forest. However, following the 1998 fires we observed widespread mortality among trees <5 cm dbh, although many of the seedlings and saplings that appeared to have been killed in the fires resprouted vigorously over the ensuing weeks and months (Baker & Bunyavejchewin, unpublished data).

The seasonal nature of the monsoon climate that prevails at HKK and across much of Thailand may also contribute to the low sapling density in the seasonal evergreen forest. During the 5-6 month dry season at HKK available soil moisture levels drop significantly, particularly in the uppermost portion of the soil column, contributing to high levels of mortality among seedlings and saplings in most years (Baker, 1997). Successful recruitment of seedlings and saplings may depend on one or more years of unusually mild (*i.e.*, wet) dry seasons.

HKK supports a diverse fauna of mammalian herbivores that includes Asian elephants, gaur, banteng, wild buffalo, tapir, wild pig, sambar deer, and barking deer (Srikosamatara, 1993). While the impact of large herbivores on forests, especially forest regeneration, has been well-documented in tropical forests (*e.g.*, Sukumar, 1989; Ickes *et al.* 2001), there is little evidence that the mammalian herbivore community at HKK has had a significant impact on the forest vegetation (Baker & Bunyavejchewin, personal observation). Wild pigs, which can significantly reduce local sapling density, appear to be much more destructive at the Pasoh FDP than at HKK (K. Ickes, personal communication). At the Mudumalai FDP in southern India elephants play a major role in structuring the forest vegetation by knocking over and pulling up saplings and small trees (Sukumar *et al.*, 1992). However, the density of elephants at Mudumalai is nearly 40 times greater than at HKK (~3 elephants km^{-2} vs. 0.08 elephants km^{-2}, respectively); and, aside from occasionally debarking individuals of certain tree species, the HKK elephants have had little overt impact on the forest at the HKK FDP.

Is there evidence that the stand has experienced severe disturbance in the past?

Using stand-wide diameter distributions to infer historic stand development patterns is problematic because of the interspecific variation in life-history traits such as maximum diameter and shade tolerance. In contrast, individual species' diameter distributions may be informative, particularly when the species' relative shade tolerances and establishment patterns are known. For example, in long-lived shade-intolerant and mid-tolerant species unimodal diameter distributions are often indicative of even-aged (*i.e.*, single age cohort) populations (Harcombe & Marks, 1978; Lorimer & Krug, 1983). In contrast, size distributions of shade tolerant species are much more plastic. Even-aged stands of shade-tolerant species may have negative exponential distributions or unimodal distributions depending upon the species composition of the stand (Lorimer & Krug, 1983), whereas multiple-cohort (uneven-aged) stands typically have negative exponential or multi-modal distributions.

Most primary tropical forest stands are presumed to be uneven-aged. Two factors contribute to this belief. First, the most widely documented pattern of tropical forest development is gap dynamics (Hartshorn, 1978; Whitmore, 1978), which, if extrapolated across time and space, predicts an uneven-aged or all-aged structure. Second, there are almost no data on the age structure of tropical forests due to the lack of annual growth rings in most tropical tree species. Therefore, the expectation is that the majority of individual tree species' diameter distributions should be more or less negative exponential in form. This is clearly not the case among the species at the HKK FDP. Unimodal and compound diameter distributions were more common than negative exponential distributions among the 20 most common species. In addition, *Hopea odorata*, a fast-growing, shade-intolerant dipterocarp, which had the greatest basal area of the 248 plot species and is the major structural component of the forest canopy, had a positively skewed unimodal diameter distribution with a large peak in the 70-100 cm dbh class. In addition, many species, especially those typically associated with the mixed deciduous and deciduous dipterocarp forest, have irregular populations consisting of a few large scattered individuals. Taken together these results suggest that the seasonal evergreen forest at the HKK FDP may have been subject to a catastrophic disturbance in the past.

While large-scale catastrophic disturbances have not been historically associated with tropical forests, there is increasing recognition of the role that such disturbances play in structuring tropical forests (see Whitmore & Burslem (1997) for an extensive review).

What type of disturbance might have destroyed 200-300 ha of forest (the area dominated by *Hopea odorata* in and around the FDP)? One likely disturbance agent is a catastrophic windstorm. Within HKK a windstorm knocked down an area of mixed deciduous forest ~30 m wide and ~3-4 km long (Theerapat Prayurasiddhi, *personal communication*). Violent windstorms that leveled several square kilometers of forest in areas of Myanmar <100 km from the HKK FDP have been documented within the past century (Anonymous, 1929, 1932). In 1880 a typhoon flattened large areas of lowland tropical forest in Kelantan, northeastern Malaysia (Browne, 1949; Wyatt-Smith, 1954). Nelson *et al.* (1994) showed that sudden localized convectional downdrafts could generate large-scale blowdowns (>30 ha) in tropical forests in the Brazilian Amazon.

Other natural and human-induced disturbances such as logging or agriculture could lead to the conditions necessary for establishment of the Hopea stand. Due to the lack of anthropological and archaeological evidence in the area it is difficult to assess the potential influence of human-induced disturbance during the past 100-400 y. However, the mass movements of Burmese and Thai military troops in the region during the late 1500s and the 1760s have been well documented. While it is possible that the armies may have cleared large areas of forest for timber or temporary rice cultivation, the main routes traveled by the invading armies were to the south (Three Pagodas Pass, Kanchanaburi Province) and north (Mae Sot, Tak Province) of HKK.

Fire is unlikely to have directly contributed to the establishment of the *Hopea* stand, as forest fires at HKK are characteristically low-intensity surface fires. It is unknown what climatic and stand structural conditions would be required to generate a catastrophic stand-replacing fire at HKK. However, low-intensity fires may facilitate establishment among some species by creating gaps in the forest canopy or by improving germination conditions. During the mast fruiting of *Hopea odorata* in 1994 seed germination was strongly inhibited by the presence of undecomposed organic matter on the forest floor (P.J. Baker & S. Bunyavejchewin, *personal observations*). Low-intensity fires would remove the leaf litter layer, enabling *Hopea odorata* seedlings to germinate with greater success.

While the evidence from the HKK FDP suggests that a catastrophic disturbance may have initiated the current stand, there is also ample evidence for gap dynamics. The death of individual trees or small groups of trees that create gaps in the forest canopy increases the amount of direct sunlight available to the lower strata of the forest (Denslow, 1987), as well as decreasing root competition for water and nutrients. The distribution of small trees at HKK is highly aggregated (Figure 10) and appears to be closely linked to the presence of recent or former canopy gaps (S. Bunyavejchewin, unpublished data). In addition, many tree species, such as *Tetrameles nudiflora* R.Br. (Datiscaceae) and *Macaranga* sp. nov. (Euphorbiacae), have compound diameter distributions with hundreds or thousands of individuals <5 cm dbh, few individuals in the middle size classes and then a group of large diameter trees, suggesting a pattern of gap-phase recruitment.

CONCLUSIONS

(1) The stand structure within the large-scale permanent forest dynamics plot at HKK is representative of seasonal dry evergreen forest in Thailand and continental southeast Asia.

(2) The structure of the seasonal dry evergreen forest at HKK differs from lowland evergreen forest only in its low density of trees in the smallest size classes.

(3) Disturbances at the HKK FDP appear to operate at several temporal and spatial scales. There is strong evidence of a large-scale catastrophic disturbance based on size class distributions and species' life histories. More recently, small-scale disturbances such as tree falls appear to have dominated the forest dynamics within the plot.

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