

Forest Structure and Tree Species Diversity along an Altitudinal Gradient in Doi Inthanon National Park, Northern Thailand

Sakhan TEEJUNTUK¹⁾, Pongsak SAHUNALU¹⁾, Katsutoshi SAKURAI²⁾, and Witchaphart SUNGPALEE¹⁾

¹⁾ Faculty of Forestry, Kasetsart University, Chatuchak, Bangkok 10900, Thailand

²⁾ Faculty of Agriculture, Kochi University, Nankoku, Kochi 708-8502, Japan

ABSTRACT A study on forest vegetation along an altitudinal gradient was conducted in Doi Inthanon National Park, Chiangmai, Thailand. The purpose of the study was to elucidate how community characteristics change from lowland to mountain vegetation in the tropical monsoon climatic zone in mainland Southeast Asia by using floristic composition and species abundance data collected from forty five plots at different altitudes and forest types.

Community classification by cluster analysis suggested 45 sample stands to be classified floristically into three forest zones along an altitudinal gradient: (1) lowland forest (400-850 m asl) composed of 2 forest groups: (a) deciduous dipterocarp forest group dominated by *Shorea siamensis*, *Canarium subulatum*, and *Shorea obtusa* and (b) mixed deciduous forest group dominated by *Tectona grandis*, *Xylia xylocarpa*, *Lagerstroemia calyculata*, and *Millettia leucantha*. (2) Transition forest (850-1,400 m asl), in the intermediate zone between the lowland and montane zones composed of 2 forest groups: (a) pine-dipterocarp forest and pine-oak forest groups dominated by *Pinus kesiya*, *Dipterocarpus tuberculatus*, *Aporosa villosa*, *Wendlandia tinctoria*, *Schima wallichii*, and *Helicia nilagirica* and (b) lower montane forest group dominated by *Schima wallichii*, *Castanopsis ferox*, *Castanopsis tribuloides*, and *Helicia nilagirica*. And, (3) montane forest (1,400-2,500 m asl), in the uppermost zone composed of 2 forest groups of both montane forest dominated by (a) *Mastixia euonymoides*, *Castanopsis calathiformis*, and *Drypetes indica* and (b) *Neolitsea pallens*, *Actinodaphne henryi*, and *Rapanea yunnanensis*.

Tree density and basal area increases with rising altitude. Diversity of trees sharply increases from the lowland zone to an altitude of 1,800 m asl and gradually decreases at an altitude above 1,800 m asl shown by low species richness indices at high altitudes. In contrast, evenness indices were not greatly different along the altitudinal gradient.

Key words: altitudinal gradient, cluster analysis, diversity, dominance, forest vegetation composition

Tropical forests are the most species-rich and structurally complex plant communities on the earth (Ashton, 1964; Hubbell and Foster, 1985; Whitmore, 1990; Ashton and Hall, 1992; Gentry, 1992; Phillips and Gentry, 1994 and Condit *et al.*, 1996). Detailed studies have focused on trends in the composition, structure, and diversity of forest communities along the various ecological gradients, such as rainfall (Hall and Swaine, 1976; Gentry, 1982; 1988; Swaine, 1996), edaphic conditions (Newbery and Proctor, 1984; Baillie *et al.*, 1987) and topography (Day and Monk, 1974; Proctor *et al.*, 1983; Lieberman *et al.*, 1996). Numerous studies have quantitatively analyzed forest community properties along altitudinal gradients (Beals, 1969; Gentry, 1988; Bearman and Bearman, 1990; Kitayama, 1992; Nakashizuka *et al.*, 1992; Kitayama and Mueller-Dombois, 1994; Lieberman *et al.*, 1996). However, no

studies have, using quantitative methods, detailed community characteristics along a broad range of altitudes from lowlands to summits in the mountain ranges of monsoon Asia. Only a few have examined the transition from seasonal dry forests to montane forests (Ogawa *et al.*, 1961; Robbins and Smitinand, 1966; Santituk, 1988; Vazquez and Givnish, 1998). These papers mostly emphasized and qualitatively described the forest structure and species composition in general and did not include a numerical analysis classifying the hierarchical structure of forest communities, particularly in Southeast Asia.

This paper describes the results of an extensive investigation on forest structure and species composition, and proposes a classification system of tree community types and their species diversity and richness in the vegetation complex along an altitudinal gradient ranging between 450 and 2,500 m asl in Doi Inthanon National Park, Chiangmai Province, Northern Thailand, based on cluster analysis and various species diversity indices.

STUDY SITE

Doi Inthanon was established as a National Park in 1972 (Faculty of Forestry, 1992) and Doi Inthanon itself has been called the "summit" of the country. It is representative of the mountain complex forming part of the Thanon Thongchai Range, the southern extension of the Shan Hills of Myanmar which is the southernmost part of the Himalayan foothills. It is located at 18°24'N to 18°40'N latitude and 98°24'E to 98°24'E longitude. The park covers an area of 482.4 km² and its altitude ranges from 400 m at the southern entrance of the park up to 2,565 m at the summit in the north of the park.

According to Pendelton's reconnaissance geologic map (Pendelton, 1962), Doi Inthanon is a huge granite massive, underlain by three major rock types found in the highlands of Thailand. From Ban Mae Hoi, in the eastern part of the park, to Pha Mawn, in the central part of the park, it traverses the band of gneiss that connects in the northwest with Doi Suthep. This parent material produces the Sithammarat coarse sandy loams which Pendelton (1962) described as miserably poor and of little agricultural value. At Pha Mawn there is a narrow pocket of clastic sediments, the Kanchanaburi series consisting of shales, siliceous sandstone and in places, quartzites and slates. These parent materials produce poor soils, shallow and stony and of scant agricultural value. Doi Inthanon itself is a granitic massive generally giving rise to the Kuantan sandy loams of shallow coarse and stony soils.

Preliminary ecological study of forest formation in the northwest highlands, especially in Doi Inthanon, was initiated by Ogawa *et al.* (1961) followed by Robbins and Smitinand (1966) and Faculty of Forestry (1992). However, Santisuk (1988) presented an account of forest vegetation of northern Thailand which also included the forest formation of Doi Inthanon and Pengklai (1996) reported on the plant species richness in this area. According to the most recent preliminary study conducted by the Faculty of Forestry (1992), Doi Inthanon's vegetation is composed of six forest community types: dry dipterocarp (9.84 %), mixed deciduous (15.93 %), dry evergreen (0.75 %), pine-dipterocarp (7.49 %), pine-oak (1.21 %) and montane forests (41.50 %).

The area has a monsoon climate with a strong alternation of wet and dry seasons. Based on this seasonality, Sternstein (1962) recognized seven rainfall regions in Thailand. Doi Inthanon falls in the center of the North Region. This region has a uniform monsoon climate with the heaviest rains coinciding with the moist southwest monsoon during August to September and the driest month in

January coinciding with the dry northeast monsoon. Three sets of meteorological data are available for Doi Inthanon National Park. First is from the meteorological station at Chiangmai City (310 m asl), second from the Royal Project Doi Inthanon Station located near the Doi Inthanon National Park headquarters (1,300 m asl) and the other from a radar station base of the Royal Thai Air Force located at the summit (2,565 m asl). The climatic data sets are shown in Figure 1 as pluviothermic graphs drawn according to Walter's method.

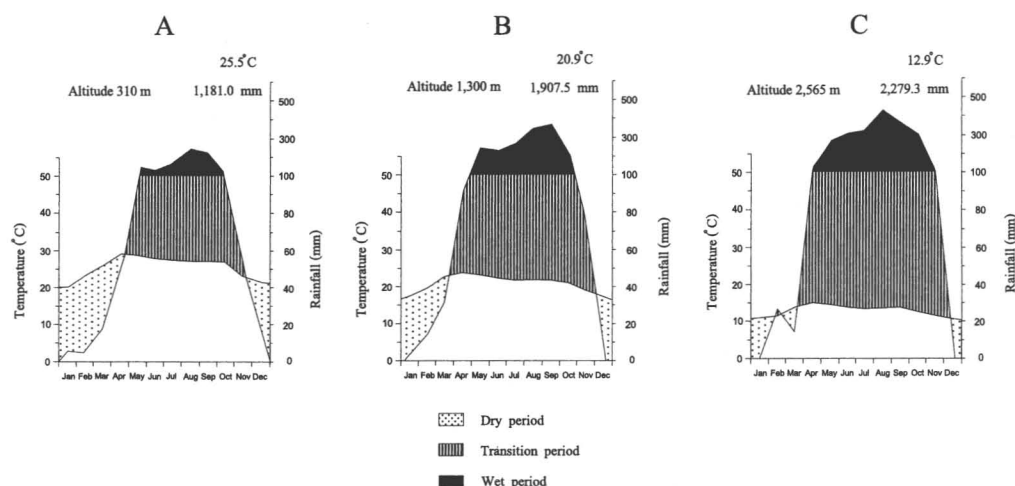


Figure 1. Walter's climatic diagram of three weather stations at various locations in the proximity and inside Doi Inthanon National Park, Chiangmai, Northern Thailand. (A: at the station at about 300 m asl from 1969 to 1999, B: at the station at 1,300 m asl from 1982 to 1999, C: at the station at 2,565 m asl from 1993 to 1999)

MATERIALS AND METHODS

Using a vegetation map, five forest types, excluding the dry evergreen forest due to its small area, were selected for this study. These forest types include: dry dipterocarp forest, mixed deciduous forest, pine-dipterocarp forest, pine-oak forest and montane forest. Three study sites were selected within each forest type. Three sample plots with different topography at three slope positions: upper (1), middle (2) and lower (3) were chosen. Plots varying in altitude were deliberately selected in order to represent the entire altitudinal gradient of the study area. There were a total of forty five sample plots (Figure 2) and field work was conducted in November 1999.

Each 0.16 ha (40 x 40 m²) sample plot was divided into sixteen 10x10 m² quadrats using a field surveying instrument set (field compass and measuring tape). In every quadrat, all living trees with a diameter at breast height (DBH) equal or exceeding 4.5 cm were measured with a diameter tape and as many as possible were identified to the species level. Plant specimens were collected and dried for identification at the Royal Forest Department Herbarium, Bangkok. Altitude, slope and aspect were determined using an altimeter and a pocket compass. Species abundance and presence/absence data were collected in each of the forty five sample stands and entered into a database for further analysis.

Relative basal area, relative density, relative frequency and importance value index (Brown and

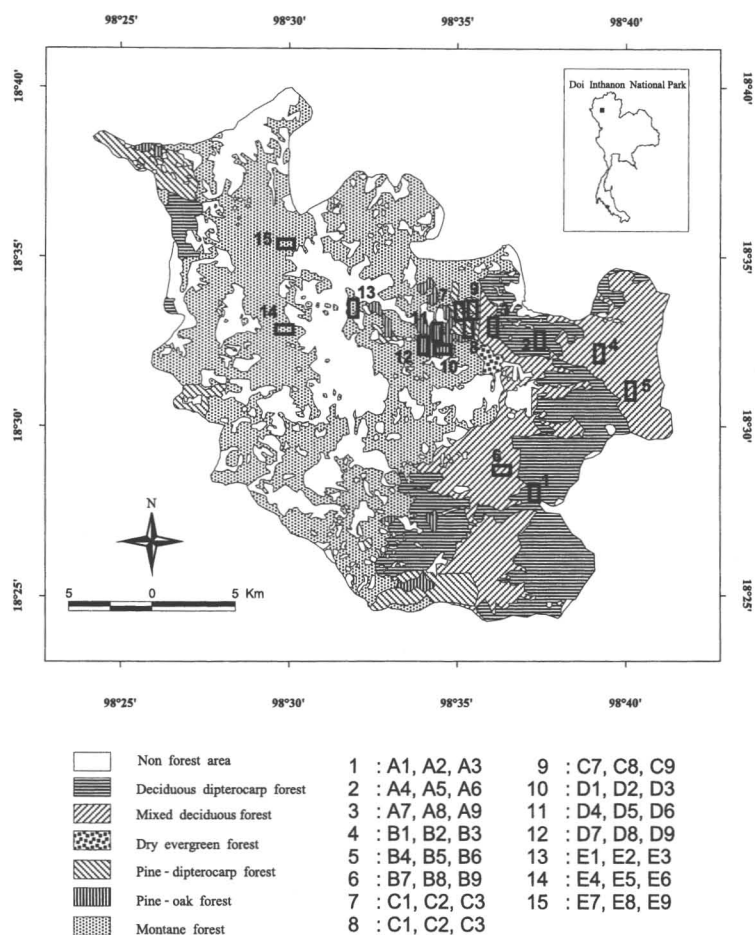


Figure 2. Vegetation map and location of study plots in Doi Inthanon National Park;

A1 to A9: dry dipterocarp forest, B1 to B9: mixed deciduous forest, C1 to C9: pine-dipterocarp forest, D1 to D9: pine-oak forest, E1 to E9: montane forest.

Curtis, 1952) for each tree species were calculated. A primary matrix of leading species having an importance value index exceeding 2.00 in the 45 stands (160 species x 45 stands) was developed. The data on abundance of trees were subjected to cluster analysis using Sorensen's distance (Bray and Curtis coefficient) for determining the similarity (Bray and Curtis, 1957) among forest stands. The group average by the pair-grouping method was adopted as a clustering strategy (Ludwig and Reynolds, 1988). The cluster analysis was processed by PC-OR statistical package. All stands were classified into stand groups and forest zones and detailed community characteristics of each forest group were summarized. Species diversity was expressed in the forms of Shannon-Wiener's H , Simpson's λ , Fisher's α , Hill's diversity $N1$ and $N2$, Margalef and Menhinick's richness $R1$ and $R2$ (Margalef, 1958; Menhinick, 1964) and evenness indices $E1$, $E3$, and $E5$ (Pielou, 1969).

The significant differences of forest community indices among the groups classified by cluster analysis were further determined by using the Kruskal-Wallis tests and the significant difference of

each index was compared between those groups by using a nonparametric multiple comparison method.

RESULTS

Floristic composition

A total of 306 tree species with a DBH equal to or exceeding 4.5 cm in 161 genera and 73 families were identified in the 45 forest stands. The number of species in each stand (0.16 ha) varied from 10 to 44 (mean = 27). The number of trees varied from 37 to 365 trees/stand (mean = 175).

Forest classification

Cluster analysis demonstrated that the 45 forest stands in Doi Inthanon National Park could be classified into six forest groups along the altitudinal gradient using the arbitrary criterion of Sorensen's distance of 6.40 (Figure 3). Species composition of each group is summarized in Table 1. The

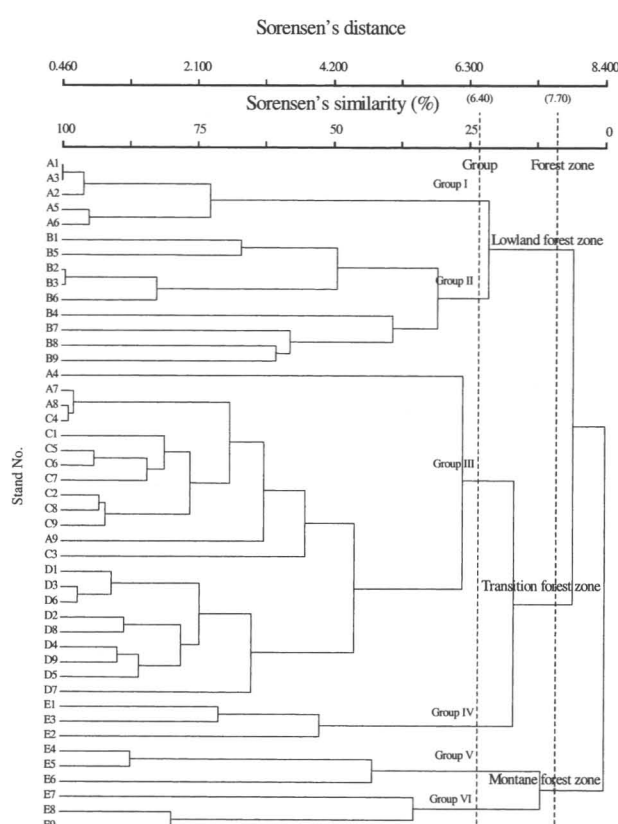


Figure 3. Dendrogram obtained by cluster analysis based on Sorensen's distance using importance value index.

Five clusters obtained by truncating the dendrogram at 6.40 distance were named forest Groups I, II, III, IV, V, and VI. These forest groups formed three clusters named lowland, transition, and montane forest zones at 7.70 distance.

nomenclature of each group was done by using the various numbers of important leading species depending on the importance value index in the forest group. Brief descriptions of their species composition are as follows:

Table 1. Relative basal area of the leading species in each group clustered by Sorensen's similarity coefficient.

	Zones					
	Lowland		Transition		Montane	
	Group					
	I	II	III	IV	V	VI
	Sub group					
	I		II			
Altitude range (m asl)	450-720	490-730	980-1120	1340-1440	1650-1710	2220-2320
No. of plot in group	5	9	12	9	3	3
Leading species	Average relative basal area (%)					
<i>Shorea siamensis</i>	49.87	-	1.56	-	-	-
<i>Canarium subulatum</i>	6.81	2.10	-	-	-	-
<i>Lannea coromandelica</i>	4.97	-	-	-	-	-
<i>Dalbergia dongnaiensis</i>	4.48	2.12	-	-	-	-
<i>Terminalia triptera</i>	4.17	1.11	-	-	-	-
<i>Cratoxylum formosum</i>	3.64	2.27	-	-	-	-
<i>Millettia leucantha</i>	3.10	8.07	-	-	-	-
<i>Lagerstroemia calyculata</i>	3.01	10.89	-	-	-	-
<i>Shorea obtusa</i>	2.53	-	0.58	-	-	-
<i>Vitex pinnata</i>	2.30	1.15	-	-	-	-
<i>Pterocarpus macrocarpus</i>	1.78	4.48	-	-	-	-
<i>Lagerstroemia macrocarpa</i>	1.31	-	-	-	-	-
<i>Bombax ceiba</i>	1.31	-	-	-	-	-
<i>Tectona grandis</i>	-	17.58	-	-	-	-
<i>Xylia xylocarpa</i>	-	13.86	-	-	-	-
<i>Anogeisus acuminata</i>	-	4.26	-	-	-	-
<i>Zollingeria acuminata</i>	-	2.57	-	-	-	-
<i>Antidesma acidum</i>	-	2.36	-	-	-	-
<i>Cordia sp.</i>	-	1.96	-	-	-	-
<i>Grewia eriocarpa</i>	-	1.73	-	-	-	-
<i>Terminalia sp.</i>	-	1.61	-	-	-	-
<i>Garuga pinnata</i>	-	1.28	-	-	-	-
<i>Dalbergia nigrescens</i>	-	1.27	-	-	-	-
<i>Spondias pinnata</i>	-	1.22	-	-	-	-
<i>Gmelina arborea</i>	-	1.17	-	-	-	-
<i>Pinus kesiya</i>	-	-	19.39	57.98	-	-
<i>Dipterocarpus tuberculatus</i>	-	-	11.83	-	-	-

<i>Quercus ramsbottomii</i>	-	-	6.16	-	-	-	-
<i>Schima wallichii</i>	-	-	1.08	7.86	17.63	-	-
<i>Aporosa villosa</i>	-	-	1.50	4.92	-	-	-
<i>Wendlandia tinctoria</i>	-	-	1.69	2.49	-	-	-
<i>Tristania rufescens</i>	-	-	1.74	1.26	-	-	-
<i>Lithocarpus elegans</i>	-	-	-	4.99	2.59	-	-
<i>Gluta usitata</i>	-	-	2.08	-	-	-	-
<i>Quercus kerrii</i>	-	-	1.60	-	-	-	-
<i>Anneslea fragrans</i>	-	-	1.10	-	-	-	-
<i>Dalbergia fusca</i>	-	-	-	1.70	-	-	-
<i>Lithocarpus polystachyus</i>	-	-	1.19	-	-	-	-
<i>Buchanania lanzan</i>	-	-	-	1.26	-	-	-
<i>Castanopsis armata</i>	-	-	-	1.47	-	-	-
<i>Syzygium angkai</i>	-	-	-	-	10.67	-	-
<i>Castanopsis tribuloides</i>	-	-	-	1.10	9.66	-	-
<i>Helicia nilagirica</i>	-	-	-	-	6.70	-	-
<i>Castanopsis ferox</i>	-	-	-	-	6.01	-	14.39
<i>Lithocarpus triboides</i>	-	-	-	-	5.29	-	-
<i>Castanopsis calathiformis</i>	-	-	-	-	4.53	3.35	-
<i>Ternstroemia gymnanthera</i>	-	-	-	1.14	3.94	-	-
<i>Xantolis sp.</i>	-	-	-	-	2.89	-	-
<i>Stereospermum neuranthum</i>	-	-	-	-	2.77	-	-
<i>Lindera missneri</i>	-	-	-	-	2.48	-	-
<i>Artocarpus chaplasha</i>	-	-	-	-	2.22	-	-
<i>Lithocarpus dealbatus</i>	-	-	-	-	2.22	-	-
<i>Quercus glabricupula</i>	-	-	-	-	1.51	-	-
<i>Cinnamomum glaucescens</i>	-	-	-	-	1.39	-	-
<i>Homalium ceylanicum</i>	-	-	-	-	1.31	-	-
<i>Protium serratum</i>	-	-	-	-	1.22	-	-
<i>Elaeocarpus floribundus</i>	-	-	-	-	1.10	-	-
<i>Syrax benzoides</i>	-	-	-	-	1.08	-	-
<i>Mastixia euonymoides</i>	-	-	-	-	-	16.58	-
<i>Mangleitia garrettii</i>	-	-	-	-	-	10.73	-
<i>Drypetes indica</i>	-	-	-	-	-	9.29	-
<i>Quercus lenticellata</i>	-	-	-	-	-	7.77	2.14
<i>Calophyllum polyanthum</i>	-	-	-	-	-	6.62	-
<i>Nyssa javanica</i>	-	-	-	-	-	5.97	-
<i>Cryptocarya dencifolia</i>	-	-	-	-	-	3.88	-
<i>Aidia yunnanensis</i>	-	-	-	-	-	3.29	-
<i>Lithocarpus aggregatus</i>	-	-	-	-	-	2.51	1.79
<i>Ostodes paniculata</i>	-	-	-	-	-	2.39	-
<i>Acer laurinum</i>	-	-	-	-	-	2.10	4.25

<i>Lindera sp.</i>	-	-	-	-	-	2.04	-
<i>Lindera metacafaena</i>	-	-	-	-	-	1.89	-
<i>Ilex triflora</i>	-	-	-	-	-	1.67	1.03
<i>Syzygium balsamea</i>	-	-	-	-	-	1.60	-
<i>Sarcosperma arboreum</i>	-	-	-	-	-	1.58	-
<i>Tarenna disperma</i>	-	-	-	-	-	1.53	-
<i>Litsea spl.</i>	-	-	-	-	-	1.39	-
<i>Rapanea yunnanensis</i>	-	-	-	-	-	1.31	2.60
<i>Chionanthus ramiflorus</i>	-	-	-	-	-	1.02	4.36
<i>Neolitsea pallens</i>	-	-	-	-	-	-	14.46
<i>Actinodaphne henryi</i>	-	-	-	-	-	-	13.95
<i>Beilschmiedia globularia</i>	-	-	-	-	-	-	11.55
<i>Litsea dubele</i>	-	-	-	-	-	-	5.83
<i>Camellia siamensis</i>	-	-	-	-	-	-	4.84
<i>Beilschmiedia roxburghiana</i>	-	-	-	-	-	-	3.46
<i>Glochidion acuminatum</i>	-	-	-	-	-	-	2.70
<i>Syzygium angkai</i>	-	-	-	-	-	-	2.22
<i>Symplocos longifolia</i>	-	-	-	-	-	-	1.33
<i>Helicia formosana</i>	-	-	-	-	-	-	1.29

Group I: Shorea siamensis, Canarium subulatum, Shorea obtusa

This group included five dry dipterocarp forest stands (A1, A2, A3, A5, and A6) located between 450 and 720 m asl. *Shorea siamensis* is the dominant species in every stand. Stands A1, A2, and A3, are represented by other co-dominant species such as *Canarium subulatum*, *Lannea coromandelica*, *Terminalia triptera*, *Cratogeomys formosum*, and some other minor species. In stands A5 and A6, there are *Shorea obtusa*, *Canthium parvifolium*, *Dalbergia dongnaiensis* and a few more underrepresented species. The most obvious characteristics of this group are an open canopy, low density, and the small diameter and short stature of most trees. These stands have a conspicuous layer of graminoid, dwarf bamboo, or other undergrowth.

Group II: Tectona grandis, Xylia xylocarpa, Lagerstroemia calyculata, Millettia leucantha

Nine stands of mixed deciduous forest are clustered in this group including B1, B2, B3, B4, B5, B6, B7, B8, and B9. This group can be further divided into two sub-groups, one with *Tectona grandis* as the dominant species, the other without its presence. The canopy strata of this forest are evenly mixed among almost all the deciduous tree species, lacking any single-species dominance. One of the sub-groups, which features *Tectona grandis* and *Xylia kerrii* as the dominant tree species, mixed with other species such as *Millettia leucantha*, *Dalbergia oliveri*, *Strychnos nux-vomica* and *Grewia eriocarpa*. These sub-group species are represented in stands B1, B2, B3, B5, and B6. Other sub-groups represented by stands B4, B7, B8, and B9 are characterized by the complete absence of *Tectona grandis*. Here the

dominant species are represented by *Millettia leucantha*, *Lagerstroemia calyculata* and *Pterocarpus macrocarpus* mixed with other species such as *Dalbergia dongnaiensis*, *Cratoxylum formosum*, *Garuga pinnata* and *Cananga latifolia*. This group is associated with bamboo in every stand.

Group III: Pinus kesiya, Dipterocarpus tuberculatus, Aporosa villosa, Wendlandia tinctoria, Schima wallichii, Helicia nilagirica

Pinus kesiya is the dominant species in this group and the main canopy tree species. The stands having *Pinus kesiya* as a dominant tree can be classified into two sub-groups: 1) those also including *Dipterocarpus tuberculatus*, *Quercus ramsbottomii* (C1, C2, C3, C4, C5, C6, C7, C8, C9) and, 2) those also including *Schima wallichii*, *Aporosa villosa*, and *Wendlandia tinctoria* (D1, D2, D3, D4, D5, D6, D7, D8, D9). Sub-group 1 occurs in habitats drier than sub-group 2. During the dry season, soils of this sub-group are often very dry, and therefore, some species shed their leaves. Normally this group is restricted to upper slopes or on mountain ridges at altitudes between 850 and 1,150 m asl. Furthermore stands A7, A8, and A9 are clearly associated with sub-group 1 (Figure 3) because there are many similar tree species in other stands of this sub-group which are dominated by *Dipterocarpus tuberculatus* and *Quercus ramsbottomii*. Only stand A4 was separated from the stands in the A4-A6 transect (Group II).

Group IV: Schima wallichii, Castanopsis ferox, Castanopsis tribuloides, Helicia nilagirica

This group is represented by three stands located between 1,340 and 1,440 m asl, E1, E2, and E3. Stands of this group is characterized by a tall and closed canopy. The canopy trees of this group are those belonging to the family Fagaceae, such as *Castanopsis ferox* and *Castanopsis tribuloides*, well mixed with *Schima wallichii*. Those species with lower statures, especially *Helicia nilagirica*, *Ternstroemia gymnanthera*, *Syzygium angkae* and *Wendlandia tinctoria*, are the main co-dominant trees.

Group V: Mastixia euonymoides, Castanopsis calathiformis, Drypetes indica

This group is located between 1,650 and 1,710 m asl. The essential characteristics of these stands are high density and a tall, closed canopy. In stands on the lower and middle slopes (E4, E5), *Mastixia euonymoides* is the dominant canopy tree mixed with other species such as *Manglietia garrettii*, *Lithocarpus aggregatus* and *Calophyllum polyanthum*. In the sub-canopy layer, *Drypetes indica*, *Mallotus khasianus*, *Ostodes paniculata* are abundant. In contrast, in stands on the upper slopes (E6), *Castanopsis calathiformis* is dominant, mixed with *Quercus lenticellata*, *Tarenna disperma*, and *Lindera metacafaena*. This group may be considered a cloud forest and mosses grow abundantly on tree trunks.

Group VI: Neolitsea pallens, Actinodaphne henryi, Rapanea yunnanensis

This group occurs at the highest altitudes in Doi Inthanon National Park, located between 2,220 and 2,320 m asl. The characteristics of the canopy layer are the same as those of group V, however the dominant trees are different. In this case, *Neolitsea pallens*, *Castanopsis ferox* and *Quercus lenticellata*

are the main canopy trees mixed with *Rapanea yunnanensis*, *Symplocos longifolia* in the sub-canopy.

Forest zones

If Sorensen's distance is arbitrarily set at 7.70 (Figure 3) then the forest stands can be divided into three forest zones: lowland, transitional and montane. The lowland forest zone is a combination of groups I and II and is located between the altitudes of 400 and 850 m asl. The forests distributed in this zone are deciduous forest and low density (Table 2). The transitional forest zone, which is composed of groups III and IV, occurs in a band between the altitudes of 850 and 1,400 m asl. The forest in this zone has changed to be an evergreen forest and density of tree gradually increases with altitude. Groups V and VI are therefore considered to be a montane forest zone, occurring between the altitudes of 1,400 and 2,500 m asl. The forest of this zone is tall, dense and forms a single storey. The crowns are typically dome shaped supported by crooked branches on which epiphytic flowering plants are

Table 2. Community characteristics (mean \pm S.D.) with the different superscripts a, b, c to compare zones by using a nonparametric rank test (Kruskal-Wallis' method at $p < 0.05$). ns indicates non-significant differences of different groups of forest trees as classified by cluster analysis. (N1, N2 = Hill's diversity indices, H = Shannon-Wiener's index, λ = Simpson's index, α = Fisher's index, R1, R2 = Margalef & Menhinick's richness indices, E1, E3 and E5 = Pielou's evenness indices)

Zone	Lowland forest zone	Transition forest zone	Montane forest zone
No. of plots/area (ha)	14 / 2.24	25 / 4.0	6 / 0.96
Mean no. of trees (indiv./0.16 ha)	112.64 \pm 54.35 ^b	196.92 \pm 66.83 ^a	236.50 \pm 76.74 ^a
Basal area (m ² /ha)	15.33 \pm 4.52 ^c	35.18 \pm 10.46 ^b	66.36 \pm 18.63 ^a
Density (stem/ha)	704 \pm 340 ^b	1231 \pm 418 ^a	1478 \pm 437 ^a
Diversity indices:			
N1	10.70 \pm 4.82 ^b	14.97 \pm 4.45 ^{ab}	17.16 \pm 6.68 ^a
N2	7.67 \pm 4.58 ^b	10.64 \pm 3.46 ^{ab}	12.98 \pm 6.32 ^a
H	2.27 \pm 0.49 ^b	2.65 \pm 0.38 ^{ab}	2.78 \pm 0.39 ^a
λ	0.17 \pm 0.10 ^a	0.11 \pm 0.06 ^{ab}	0.09 \pm 0.03 ^b
α	8.43 \pm 2.98 ^{ns}	10.37 \pm 4.16 ^{ns}	12.39 \pm 9.56 ^{ns}
Richness indices:			
Mean no. of species (/ 0.16 ha)	21.1 \pm 6.1 ^b	29.6 \pm 8.7 ^{ab}	30.3 \pm 10.9 ^a
R1	4.34 \pm 1.09 ^{ns}	5.48 \pm 1.59 ^{ns}	5.39 \pm 1.94 ^{ns}
R2	2.08 \pm 0.53 ^{ns}	2.18 \pm 0.63 ^{ns}	1.99 \pm 0.69 ^{ns}
Evenness indices:			
E1	0.75 \pm 0.12 ^{ns}	0.79 \pm 0.08 ^{ns}	0.83 \pm 0.06 ^{ns}
E3	0.47 \pm 0.17 ^{ns}	0.49 \pm 0.11 ^{ns}	0.56 \pm 0.12 ^{ns}
E5	0.64 \pm 0.14 ^{ns}	0.69 \pm 0.11 ^{ns}	0.73 \pm 0.17 ^{ns}

luxuriantly developed. The result from Table 2 shows that the tree basal area is significantly different among the forest zones, while tree density in the lowland zone is clearly lower than in the transitional and montane zones. Diversity indices are significantly different between the lowland and montane zones, however, the indices of the transition zone are between these zones. Fisher's(α), richness (R1 and R2) and evenness (E1, E3 and E5) indices are not significantly different among the forest zones.

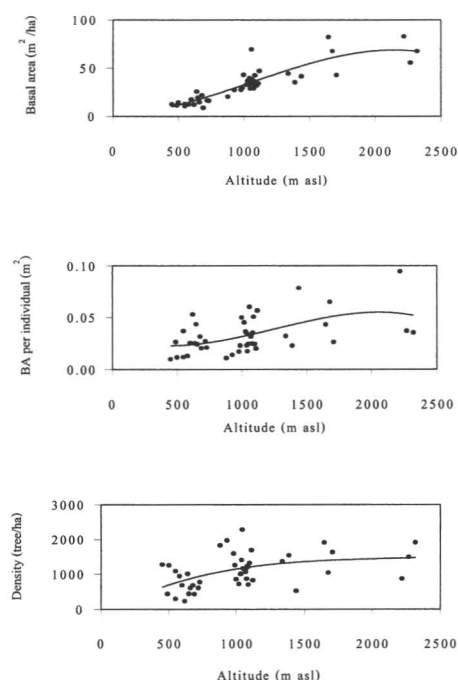


Figure 4. Stand structure of forest along the altitudinal gradient in Doi Inthanon National Park.

Forest structure and species diversity

Forest communities in Doi Inthanon National Park vary greatly in species composition as shown by the classification above. The number of trees and species richness, diversity, and evenness indices of each group are shown in Table 3. Forest stands of Group II show the lowest tree density and basal area. Stands of Group V are highest in tree density, and stands of Group VI, in basal area. The mean species number of Group II is the lowest and increases in the following order: Group VI, I, III, IV and V. Diversity indices of all stands, as determined by N1, N2 and H, indicate that group I has significantly lower diversity than the other groups followed in order using N1 and N2, by Groups VI, II, III, IV and V, and, using H, by Groups II, VI, III, IV and V. Moreover, Fisher's index is associated with other indices. This diversity index of Group V is the highest and decreases, in the following order, by Groups IV, III, II, I and VI. The Simpson's index is an inversion value unlike the other indices. The result from Table 3 shows that group I has the highest value, expressing the lowest diversity, followed by Groups II, VI, III, IV and V. Richness value trends are closely related to diversity indices therefore, group VI shows the lowest richness increasing, using R1, in the following order: Groups II, I, III, IV and V, and, using

Table 3. Community characteristics (mean \pm S.D.) with the different superscripts a, b, c to compare groups by using a nonparametric rank test (Kruskal-Wallis' method at $p < 0.05$). ns indicates non-significant differences of different groups of forest trees as classified by cluster analysis. (N1, N2 = Hill's diversity indices, H = Shannon-Wiener's index, λ = Simpson's index, α = Fisher's index, R1, R2 = Margalef & Menhinick's richness indices, E1, E3 and E5 = Pielou's evenness indices)

Zone	Lowland forest zone		Transition forest zone		Montane forest zone	
Group	I	II	III	IV	V	VI
No. of plots/area (ha)	5 / 0.80	9 / 1.44	22 / 3.52	3 / 0.48	3 / 0.48	3 / 0.48
Mean no. of trees (indiv./0.16 ha)	168.0 \pm 12.9 ^{ab}	81.9 \pm 30.0 ^b	198.7 \pm 66 ^a	184.0 \pm 86.8 ^{ab}	244.0 \pm 70.9 ^a	228.3 \pm 83.5 ^a
Basal area (m ² /ha)	16.36 \pm 5.35 ^{bc}	14.75 \pm 4.23 ^c	34.47 \pm 10.89 ^{abc}	40.38 \pm 4.63 ^{bc}	64.15 \pm 20.03 ^a	68.58 \pm 13.69 ^a
Density (stem/ha)	1050 \pm 268 ^{ab}	511 \pm 187 ^b	1241 \pm 412 ^a	1150 \pm 542 ^{ab}	1529 \pm 443 ^a	1427 \pm 521 ^a
Diversity indices:						
N1	6.44 \pm 3.39 ^c	11.88 \pm 5.70 ^{bc}	14.58 \pm 4.53 ^{abc}	17.84 \pm 2.76 ^{ab}	22.63 \pm 4.45 ^a	11.69 \pm 1.39 ^{bc}
N2	4.98 \pm 0.92 ^b	10.10 \pm 6.38 ^{ab}	10.40 \pm 3.33 ^a	12.40 \pm 4.67 ^a	16.60 \pm 7.44 ^a	9.35 \pm 2.23 ^{ab}
H	1.70 \pm 0.69 ^b	2.34 \pm 0.60 ^{ab}	2.62 \pm 0.39 ^a	2.87 \pm 0.15 ^a	3.11 \pm 0.21 ^a	2.45 \pm 0.12 ^{ab}
λ	0.21 \pm 0.04 ^a	0.16 \pm 0.13 ^{abc}	0.11 \pm 0.06 ^{bc}	0.09 \pm 0.03 ^{bc}	0.07 \pm 0.04 ^b	0.11 \pm 0.03 ^{abc}
α	7.49 \pm 1.29 ^{bc}	8.95 \pm 3.58 ^{abc}	9.76 \pm 4.07 ^{abc}	14.82 \pm 0.24 ^{ab}	19.20 \pm 9.43 ^a	5.57 \pm 0.52 ^b
Richness indices:						
Mean no. of species (/ 0.16 ha)	23.4 \pm 3.9 ^{ab}	19.8 \pm 6.9 ^b	28.6 \pm 8.4 ^a	37.3 \pm 8.1 ^a	40.0 \pm 2.0 ^a	20.7 \pm 3.5 ^{ab}
R1	4.39 \pm 0.62 ^{bc}	4.31 \pm 1.32 ^{bc}	5.27 \pm 1.55 ^{ab}	7.04 \pm 0.84 ^a	7.14 \pm 0.29 ^a	3.64 \pm 0.39 ^c
R2	1.82 \pm 0.21 ^{ab}	2.22 \pm 0.61 ^{ab}	2.09 \pm 0.62 ^{ab}	2.85 \pm 0.17 ^a	2.61 \pm 0.33 ^{ab}	1.39 \pm 0.04 ^b
Evenness indices:						
E1	0.54 \pm 0.21 ^b	0.79 \pm 0.13 ^a	0.79 \pm 0.08 ^a	0.80 \pm 0.10 ^a	0.84 \pm 0.07 ^a	0.81 \pm 0.06 ^a
E3	0.24 \pm 0.14 ^b	0.55 \pm 0.18 ^a	0.49 \pm 0.10 ^a	0.49 \pm 0.21 ^a	0.56 \pm 0.14 ^a	0.56 \pm 0.12 ^a
E5	1.40 \pm 1.63 ^{ns}	0.77 \pm 0.23 ^{ns}	0.69 \pm 0.10 ^{ns}	0.66 \pm 0.16 ^{ns}	0.69 \pm 0.22 ^{ns}	0.77 \pm 0.14 ^{ns}

R2, Groups I, III, II, V and IV. However, evenness values are not closely related to diversity indices. Evenness values, such as E1 and E3, indicate that forest stands of Group I are significantly lower in evenness than those of other groups, while using E5 demonstrates no significant difference.

Total tree basal area, tree density, as well as average basal area along the altitudinal gradient, display an increasing trend with altitude, and can all be explained by the cubic polynomial form (Figure 4). Compared to basal area, density exhibits relatively little variation with altitude. The co-occurrence of low basal area per individual, low total basal area and low tree density are remarkable at low altitudes. Therefore, longer drought periods (Figure 1) or a sporadic disturbances by humans (as is usual for most deciduous type forests located at lower altitudes close to human settlements (e.g. forest fire, tree cutting and firewood extraction)) may be more or less the main factors affecting the species composition and physiognomy of these forest stands.

The results from Figure 5 show that the explicit trends of number of species, diversity indices such as N1, N2, Shannon-Wiener's, and Simpson's indices, as well as richness index (R1), can be well described by the cubic polynomial forms with altitude, but by the quadratic polynomial forms with altitude when using N1 and N2. The trends of these indices along the altitudinal gradient show gradually increasing species diversity from 450 m asl reaching a maximum at around 1,800 m asl and then decreasing species diversity at altitudes above that. However, the Simpson's index trend is the inverse of the others. It also follows the quadratic polynomial form while evenness (E5) values are not clearly differentiated along the altitudinal gradient (Figure 5).

DISCUSSION

Forest zonation along an altitudinal gradient in Doi Inthanon National Park

The forests of Thailand located in the tropical monsoon climate zone are classified into two categories. First, evergreen forests whose trees are physiognomically characterized by maintaining their green leaves throughout the year. Second, deciduous forests whose trees usually shed their leaves in the dry seasons (January to April). Santisuk (1988) suggested that the ecological distribution of vegetation types in Northern Thailand is fundamentally governed by two paramount factors: the availability of moisture in the soil and elevation. The results of studies suggest that the forest stands investigated in Doi Inthanon National Park can be classified into six forest groups and three forest zones. The lowland forest zone (400-850 m asl) is composed of two forest groups as described earlier by which forest Group I refers to the deciduous dipterocarp forest (Faculty of Forestry, 1992; Santisuk, 1988) and forest Group II is classified as a mixed deciduous forest (Faculty of Forestry, 1992) or tropical mixed deciduous forest (Santisuk, 1988) in which a few evergreen tree species are well mixed with the predominant deciduous tree species and has been defined by Ogawa *et al.* (1961) as a monsoon forest. These stands obviously show a distinctive structure and species diversity as compared to other forest stands at higher altitudes (Table 3). However, there are some tree species that this zone has in common with the transitional forest zone (Table 1). The characteristics of this zone are different from those found elsewhere in the tropical wet zone e.g.; van Steenis (1984), Kitayama (1992), Pendry and Proctor (1997). Basal area and tree density in this study are lower than those reported in studies of in other climatic regions. The distribution of vegetation in Doi Inthanon National Park is typical of the ecological zonation in the monsoon climate zone where the distinctive dry period always prevails alternately with the wet period (Figure 1). Logging and human disturbances are probably the main causes of the damage of this forest type as it contains many valuable timbers (e.g. teak; *T. grandis*) that might have been subjected to severe harvesting prior to the establishment of the National Park. Much of this land is highly fertile, and its suitability for agriculture is another factor that has contributed to forest destruction. The transitional forest zone (850-1,400 m asl) is an intermediate zone between lowland and montane zones composed of upper dry dipterocarp forest, pine-dipterocarp forest, pine-oak forest, and partly overlapping with the montane forest which may be referred to as lower montane forest as proposed by Santisuk (1988). *Pinus kesiya*, *Schima wallichii* and some species belonging to the Fagaceae family are dominant. In the canopy, *Pinus kesiya* is often found as an emergent tree in these forest stands. The characteristics of this zone are higher tree density and basal area than the lowland forest zone, resulting in a closed canopy and high stand density (Table 2). Nakashizuka *et al.*

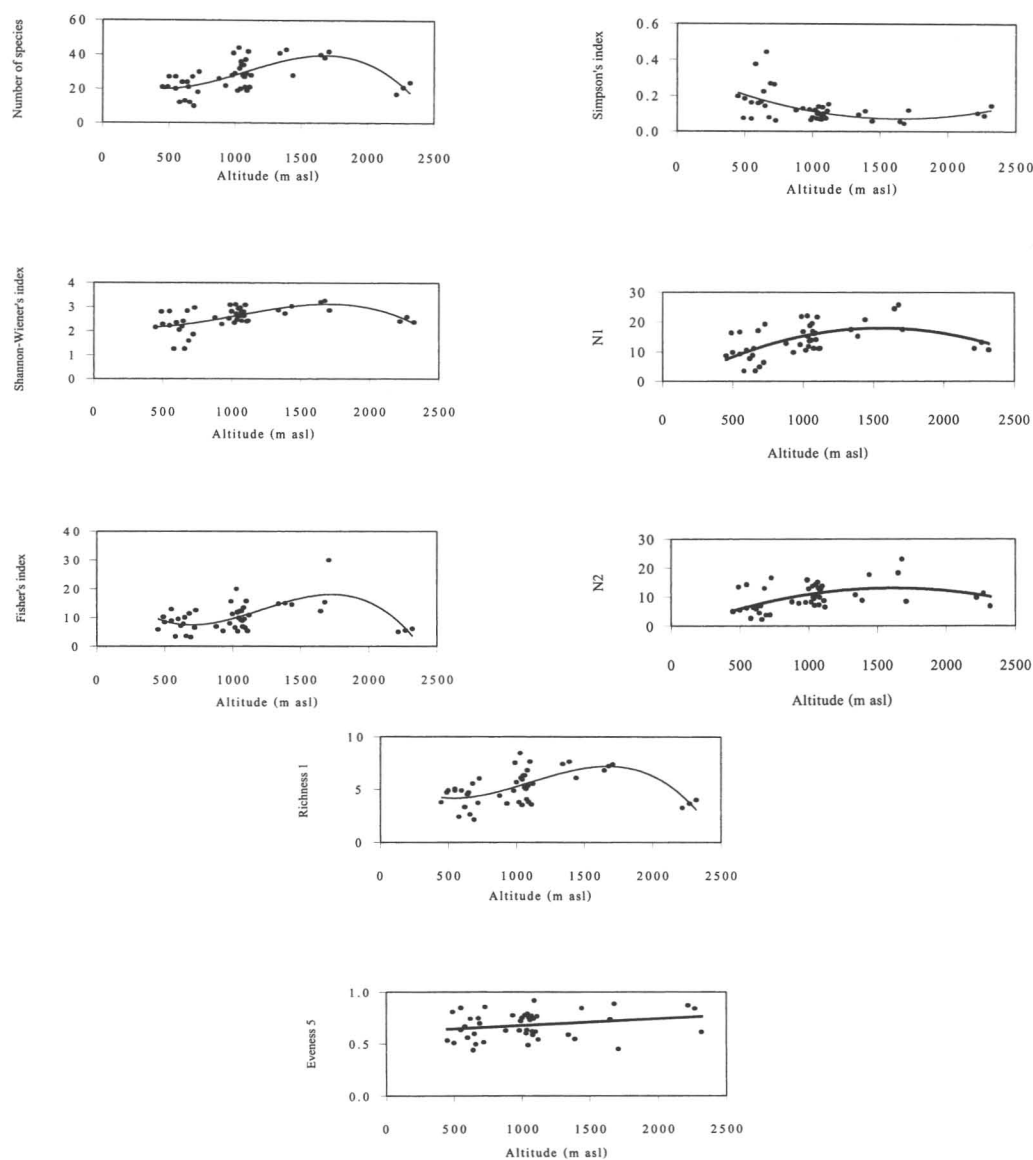


Figure 5. Species richness and diversity of tree species along the altitudinal gradient in Doi Inthanon National Park.

(1992) classified a transition zone between the lowland forest zone and the montane forest zone in Malaysia using the genera of plant to form the cluster of the forest community. The altitude of transition zone (Nakashizuka *et al.*, 1992) ranged between 700 and 1,100 m asl, which is a narrow range in comparison with that found in this study in the Doi Inthanon mountain range. In Doi Inthanon, changes in vegetation are less continuous than in the Malaysian forest studied by Nakashizuka *et al.* (1992), due to the extreme contrast between the lowland forest zone and the montane forest zone in Doi Inthanon. The lowland zone is characterized by periodic droughts, low soil moisture during the dry

season, and low humidity. In contrast, the montane forest zone is characterized by relatively uniform soil moisture, due to high humidity and condensation from low clouds that are always present in this zone. Consequently, in this region, the transitional forest zone occurs over a wider altitudinal range. Montane forest zone (1,400-2,500 m asl), the uppermost zone, is composed of two groups. This zone seems to be correspondent to those found by previous studies located in the more humid tropical regions (Richards, 1964; Vazquez and Givnish, 1998; Kitayama, 1992; Ohsawa *et al.*, 1985). The structure of forest stands in this zone can be separated into two groups as shown by Figure 3. The forest located between 1,500 and 1,800 m asl shows high tree density and basal area (Table 3), especially on the lower slopes. *Mastixia euonymoides* is the dominant and canopy tree species and is found only in this area. The floristic characteristics of this high altitude plant community are not likely to be representative of the main species composition of the typical montane forest as their dominant tree families are not only Lauraceae and Fagaceae, but others as well. However, forest stands located between 1,800 and 2,500 m asl are floristically dominated by those belonging to the families Lauraceae and Fagaceae.

The basal area and density of trees along the altitudinal gradient in Doi Inthanon tend to increase with altitude (Figure 4). The forests in the lowland zone have a low tree basal area and density that can be attributed to some limiting factors. Low soil moisture in the dry season is considered to be the most significant factor affecting growth and development of trees in this zone. As shown in Figure 4, basal area and tree density increase with increasing altitude through the transitional and montane forest zones. These forest stands always obtain sufficient water via both the soil and the atmosphere, making it possible for the trees in these stands to maintain their physiological activities even in the dry season. This is particularly true of the montane forest zone, which is normally dominated by evergreen tree species.

Diversity of tree species

Diversity indices of tree species having a DBH equal to, or more than, 4.5 cm have somewhat lower values in the lowland forest zone and increase continuously from an altitude of about 850 m asl in the transitional forest zone to an altitude of around 1,800 m asl in the montane forest zone. Above this altitude they tend to decrease, as is clearly demonstrated by Shannon-Wiener's, Hill's and Fisher's diversity indices, as well as richness indices (Figure 5). However, evenness indices do not vary much along the altitudinal gradient. In the lowland forest zone, there are differences between the two groups of forest stands. The number of species in the 0.16 ha plots are not found to vary much among the two forest groups, but the number of main species, as determined by N1 and N2 (Table 3), is less in Group I than Group II. This result is attributable to the fact that the site capacity of forest Group II is higher than Group I. Therefore, several more species are found in forest Group II than in Group I. Furthermore, the number of tree species of Group II is greater than Group I, because the habitat of the forest stands of Group I are more limiting. Disturbance is also an important factor in determining the success or failure of forest establishment and growth in this forest zone. Forest fires, which occur almost every year, may cause accelerated soil erosion during the early rainy season (e.g., Sakurai *et al.* (1998)). Therefore, forests of Group I are more affected by these disturbances than forests of Group II. The other reason is the nutrient availability in the soil. A higher amount of nutrients are available to the forest stands of Group II. So, soil in forest Group II are more fertile than in Group I thus, a greater

number of tree species can survive in Group II than Group I. This reason is supported by the studies of Khemnark *et al.* (1972), Kutintara (1975) and Bunyavejchewin (1983). Adequate soil moisture content during the dry season and less disturbance are probably the main cause of the greater species diversity in transitional and montane forest zones, with diversity of tree species increasing up to an altitude of about 1,800 m asl. Diversity tends to decrease again at an altitude above 1,800 m asl, probably due to the decrease of temperature with increasing altitude. Temperature at an altitude of 1,800 m asl and above is always cooler, as shown in the pluviothermic diagram in Figure 1. Only some tree species can tolerate these temperatures and survive in this zone successfully. The other factors, such as nutrient availability, particularly nitrogen available (Marr *et al.*, 1988), radiation concentration, and humidity (Cavelier, 1996) also affect species diversity in montane forests. Moreover, a study of Vazquez and Givnish (1998) in a tropical seasonal dry forest in Jalisco, Mexico suggested that the decline in plant species richness in tropical forests might have four reasons. The first is based on the theory of island biogeography. Local regions at high altitude are smaller in area and more isolated from similar habitats than those in low altitudes, and should thus support a lower equilibrium number of species. The second is based on the theory of equal species packing along gradients (Terborgh, 1973). A third explanation is structure due to altitudinal differences in nutrient availability, forest stratification and plant speciation. The greater availability of nutrients at lower altitudes and moisture on rainier sites should reduce whole-plant compensation points. The fourth cause may be related to altitudinal declines in the rate of plant growth and forest turnover.

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REFERENCES

- Ashton, P. 1964. Ecological studies in the mixed dipterocarp forests of Brunei State. *Oxford Forestry Memoirs* **25**: 1–75.
- Ashton, P.S. & Hall, P. 1992. Comparisons of structure among mixed dipterocarp forests of northwestern Borneo. *Ecology* **80**: 459–481.
- Baillie, I.C., Ashton, P.S., Court, M.N., Anderson, J.A.R., Fitzpatrick, E.A. & Tinsley, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* **3**: 201–220.
- Beals, E.W. 1969. Vegetation change along altitudinal gradients. *Science* **165**: 981–985.
- Beaman, J.H. & Beaman, R.S. 1990. Diversity and distribution patterns in the flora of Mount Kinabalu. pp. 147–160. *In*: Baas, P., Kalkman, K. & Geesink, R. (eds.). *The Plant Diversity of Malaysia*. Kluwer Academic Publisher.
- Bray, J.R. & Curtis, J.T. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* **27**: 325–349.

- Brown, R.T. & Curtis, J.T. 1952. The upland conifer-hardwood forests of northern Wisconsin. *Ecological Monograph* **22**: 217–234.
- Bunyavejchewin, S. 1983. Analysis of the topical dry deciduous forest of Thailand, I. Characteristics of the dominant types. *Natural History Bulletin of the Siam Society* **31**(2): 109–112.
- Cavelier, J. 1996. Environmental factors and ecophysiological processes along altitudinal gradients in wet tropical mountains. pp. 399–439. In: Mulkey, S.S., Chazdon, R.L. & Smith, A.P. (eds.). Tropical Forest Plant Ecophysiology. An International Thomson Publishing Company, New York.
- Condit, R., Hubbell, S.P., LaFrankie, J.V., Sukumar, R., Manokaran, H., Foster, R.B. & Ashton, P.S. 1996. Species-area and species-individual relationships for tropical trees: a comparison of 3, 50 ha plots. *Journal of Ecology* **84**: 549–562.
- Day, F.P.Jr. & Monk, C.D. 1974. Vegetation patterns on a southern Appalachian watershed. *Ecology* **55**: 1064–1074.
- Faculty of Forestry. 1992. Master plan for management Doi Inthanon National Park, Chiangmai. Kasetsart University, Bangkok (mimeographed in Thai).
- Gentry, A.H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* **15**: 1–84.
- Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* **75**: 1–34.
- Gentry, A.H. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos* **63**: 19–28.
- Hall, J.B. & Swaine, M.D. 1976. Classification and ecology of close-canopy forest in Ghana. *Journal of Ecology* **64**: 913–951.
- Hubbell, S.P. & Foster, R.B. 1985. Biology, chance, history and the structure of tropical rain forest tree communities. pp. 314–329. In: Diamond, J. & Case, T.J. (eds.). *Community Ecology*. Harper and Row, New York.
- Khemnark, C., Wacharakitti, S., Aksornkoae, S. & Kaewla-iad, T. 1972. Forest production and soil fertility at nikhom Doi Chiangdoa, Chiangmai province. For. Res. Bull. No.22. Faculty of Forestry, Kasetsart University.
- Kitayama, K. 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* **102**: 146–171.
- Kitayama, K. & Mueller-Dombois, D. 1994. An altitudinal transect analysis of the windward vegetation on Haleakala, a Hawaiian island mountain. 2. Vegetation zonation. *Phytocoenologia* **24**: 135–154.
- Kutintara, U. 1975. Structure of the dry dipterocarp forest. Ph. D. Dissertation. Colorado State University. Fort Collins. 242 p.
- Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradients in Costa Rica. *Journal of Ecology* **84**: 137–152.
- Ludwig, J.A. & Reynolds, J.F. 1988. Statistical Ecology, A primer on methods and computing. John Wiley & Sons, Inc., New York.
- Margalef, R. 1958. Information theory in ecology. *General Systematics* **3**: 36–71.
- Marrs, R.H., Proctor, J., Heaney, A. & Mountford, M.D. 1988. Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *Journal of Ecology* **76**: 466–482.
- Menhinick, E.F. 1964. A comparison of some species-individuals diversity indices applied to samples
-

- of field insects. *Ecology* **45**: 859–861.
- Nakashizuka, T., Zulkifli Yusop & Abdul Rahim Nik. 1992. Altitudinal zonation of forest communities in Selangor, peninsular Malaysia. *Journal of Tropical Forest Science* **4**(3): 233–244.
- Newbery, D. Mc. & Proctor, J. 1984. Ecology studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. IV. Associations between tree distribution and soil factors. *Journal of Ecology* **72**: 475–493.
- Ogawa, H., Yoda, K. & Kira, T. 1961. A preliminary survey of the vegetation of Thailand. *Nature and Life in Southeast Asia* **1**: 21–157.
- Ohsawa, M., Nainggolan, P.H.J., Tanaka, N. & Anwar, C. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra with comparisons to zonation in the temperate region of East Asia. *Journal of Tropical Ecology* **1**: 193–216.
- Pendelton, L. 1962. Thailand, aspects of landscape and life. Duell, New York.
- Pendry, C.A. & Proctor, J. 1997. Altitudinal zonation of rain forest on Bukit Belalong, Brunei: soils, forest structure and floristic. *Journal of Tropical Ecology* **13**: 221–241.
- Pengkla, C. 1996. A preliminary survey of plant diversity at Doi Inthanon. A paper presented to symposium on plant resources of the Himalayan foothills, Queen Sirikit Botanical Gardens, Chiangmai. (mimeographed in Thai).
- Phillips, O.L. & Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* **263**: 954–968.
- Pielou, C.E. 1969. An Introduction to Mathematical Ecology. John Wiley & Sons, Inc., New York.
- Proctor, J., Anderson, J.M. & Vallack, H.W. 1983. Comparative studies on forests, soils and litterfall at four altitudes on Gunung Mulu, Sarawak. *The Malaysian Forester* **46**(1): 60–76.
- Richards, P.W. 1964. The Tropical Rain Forest. The University Press, Cambridge.
- Robbins, R.G. & Smitinand, T. 1966. A botanical ascent of Doi Inthanon. *Natural History Bulletin of the Siam Society* **21**: 205–227.
- Sakurai, K., Tanaka, S., Ishizuka, S., & Kanzaki, M. 1998. Differences in soil properties of dry evergreen and dry deciduous forests in the Sakaerat Environmental Research Station. *TROPICS* **8**: 61–80.
- Santisuk, T. 1988. An Account of the Vegetation of Northern Thailand. Geocological Research. 5 (ed. by Ulrich Schweingurth). Franz Steiner Verlag Weisbaden GMB H, Stuttgart.
- Sternstein, L. 1962. The rainfall of Thailand. Monograph of Indiana University Research Division.
- Swaine, M.D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* **84**: 419–428.
- Terborgh, J. 1973. On the notion of favorableness in plant ecology. *American Naturalist* **107**: 481–501.
- van Steenis, C.G.G.J. 1984. Floristic altitudinal zones in Malaysia. *Botanical Journal of Linnean Society* **89**: 289–292.
- Vazquez, G. & Givnish, T.J. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* **86**: 999–1020.
- Whitmore, T.C. 1990. An Introduction to Tropical Rain Forests. Clarendon Press, Oxford.

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