Structural dynamics of a natural mixed deciduous forest in western Thailand

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Abstract. Structural dynamics of a natural tropical seasonal – mixed deciduous – forest were studied over a 4-yr period at Mae Klong Watershed Research Station, Kanchanaburi Province, western Thailand, with particular reference to the role of forest fires and undergrowth bamboos. All trees > 5 cm DBH in a permanent plot of 200 m × 200 m were censused every two years from 1992 to 1996. The forest was characterized by a low stem density and basal area and relatively high species diversity. Both the bamboo undergrowth and frequent forest fires could be dominant factors that prevent continuous regeneration. Recruitment, mortality, gain (growth of survival tree plus ingrowth) and loss in basal area (by tree death) during the four years were 6.70 %/yr, 2.91 %/yr, 1.22 %/yr and 1.34 %/yr, respectively. Mortality was size dependent; middle size trees (30 - 50 cm) had the lowest mortality, while the smallest (5 - 10 cm) had the highest mortality. Tree recruitment was observed particularly in the first two years, mostly in the area where die-back of undergrowth bamboo occurred. The bias of the spatial distribution of recruitment to the area of bamboo die-back was significant and stronger than that to the forest canopy gaps. Successful regeneration of trees which survive competition with other herbs and trees after dieback of bamboo could occur when repeated forest fires did not occur in subsequent years. It is suggested that both the fire disturbance regime and bamboo life-cycle greatly influence the structure and dynamics of this seasonal tropical forest.

Keywords: Bamboo; Canopy gap; Forest fire; Kanchanaburi; Mortality; Recruitment; Spatial pattern.

Nomenclature: Smitinand (1980).

Introduction

Seasonally dry tropical forests occur in areas with several months of severe drought each year and cover larger areas of tropical and subtropical landscapes than wet rain forests (Murphy & Lugo 1986; Mooney et al. 1995).

Their ecological characteristics, structure and dynamics may differ largely from those of tropical rain forests (Murphy & Lugo 1986; Mooney et al. 1995; Gerhardt & Hytteborn 1992). In addition, they have a long history of disturbance from frequent fires and human activities (Mueller-Dombois & Goldammer 1990; Murphy & Lugo 1986). Despite the large areas covered and uniqueness of the forest, little attention has been given to this diverse ecosystem compared to tropical rain forests and savannas (Mooney et al. 1995). In particular, the dynamics and regeneration of these forests have not been investigated (Gerhardt & Hytteborn 1992). Considering the importance of these forests, both locally and nationally, information regarding their dynamics and maintenance mechanisms is urgently needed to facilitate their conservation and management.

Mixed deciduous forest is a type of tropical seasonal forest found in Thailand (Anon. 1962; Ashton 1995; Blasco et al. 1996), it covers large areas and shows much variation in composition and structure (Bunya-vejchewin 1983, 1985; Rundel & Boonpragob 1995). In the northern parts of the country, this forest type occupies riparian areas and gentle slopes below 500 m a.s.l. (meters above mean sea level) (Kutintara 1975; Smitinand 1977). It is dominant on deep-toned red and brown latosols which usually have a deep top soil. The characteristic tree species are *Tectona grandis*, *Pterocarpus macrocarpus*, *Xylia xylocarpa* var. *kerrii*, *Afzelia xylocarpa*, *Lagerstroemia calyculata*, *Terminalia* spp. and *Vitex peduncularis*. *Tectona grandis* (Teak) is usually the most important species although it can be absent from the mixed deciduous forest (Ogawa et al. 1961; Smitinand 1996; Ashton 1995). The middle layer is dominated by bamboos (Ogawa et al. 1961; Whitmore 1984; Ahston 1995), with *Gigantochloa albociliata, Bambusa tulda* and *B. nutans* the most common species (Kutintara 1994). During the dry season forest fires occur.

The suppression of tree regeneration by undergrowth bamboos has been reported from several types of forests (Veblen et al. 1980; Nakashizuka 1988; Taylor & Zisheng 1992). Bamboos grow rapidly, intercept the light efficiently and cast a deep shade on the forest floor. Thus, once established, they prevent tree regeneration. In Thailand they usually form large clumps and cover the forest floor at high densities, especially in natural mixed deciduous forests (Smitinand & Chumsri 1985). They have long life spans of up to 40 yr (Janzen 1976; Taylor et al. 1991; Numata 1970), but their simultaneous death after gregarious flowering can episodically provide a large vacant space which is then available for tree regeneration (Veblen et al. 1980; Nakashizuka 1987, 1988, 1991; Taylor & Zisheng 1988, 1992).

Fire is known to be an important ecological factor that helps to maintain certain types of plant communities and populations in seasonally dry regions of the world (Phillips 1974; Gill et al. 1970; Tyler 1995; Mueller-Dombois & Goldammer 1990). Adaptations of plants in fire-prone communities, including life form and regeneration strategies, promote their survival following fire (Gill 1981). In Thailand forest fires occur frequently in dry dipterocarp forests and mixed deciduous forests, usually as ground fires during the dry season (Sukwong & Dhamanittakul 1977; Bunyavejchewin 1983). Fire may have a strong influence upon these forest types and help to maintain them (Stott 1988; Stott et al. 1990) but the role of fire in the dynamics of these forests is not yet clear.

In this paper, the structure and dynamics of a mixed deciduous forest in Thailand is investigated. The flowering of bamboo, which occurred in part of the forest gave an opportunity to study the effects of bamboo dieback on forest regeneration. Thus, this paper focuses on the effects of the two factors most likely to control the regeneration dynamics and tree diversity of the mixed deciduous forest; forest fire and undergrowth bamboos.

Study site

The study was conducted in a natural mixed deciduous forest, with a bamboo undergrowth, where teak was absent (Kutintara et al. 1995) at the Mae Klong Watershed Research Station, Thong Pha Phoom District (14° 30' - 14° 45' N, 98° 45' - 99° E), Kanchanaburi Province, western Thailand, 250 km west of Bangkok. The watershed is ca. 109 km^2 in area and is located at a branch of the Kwai Noi River; it ranges from 100 to 900 m a.s.l. The climate is subtropical with a long wet season which alternates with a short, cool dry season and a subsequent hot dry season. Annual rainfall normally exceeds 1650 mm and is concentrated from late April to October. Mean monthly temperature is ca. 27.5 °C with a

maximum of 39.1 °C in April and a minimum of 14.6 °C in December. Geologically, the area is underlain by parent material of the Rachaburi and the Kanchanaburi series. The Rachaburi series is present in the middle area of the watershed and is composed of granite, limestone and shale. The Kanchanaburi series is found in the western part of the watershed and is composed of shale and limestone. Some rocks have been metamorphosed and phyllite and quartzite are found. The soils are a reddish brown lateritic soil weathered from parent materials of alluvium with residuals of sandstone, limestone and quartzite (Suksawang 1993).

The prevailing forest type is a mixed deciduous forest, with some dry dipterocarp forest on the mountain ridges and dry evergreen forest along the creeks (Kutintara et al. 1995). Four bamboo species: *Bambusa tulda, Cephalostachyum pergracile, Gigantochloa albociliata* and *G. hasskarliana* are dominant in the understorey. Most of the forest understorey was dominated by one or two of these species. Some undergrowth bamboos (most *Gigantochloa hasskarliana* and part of the *G. albociliata* populations) had flowered and died in part of the plot in 1990. A forest fire had also occurred prior to 1992 following the death of bamboos, but did not occur again until 1995. The dead culms of bamboo were burnt by fire. Wild banana was mainly found at the mesic site along the valley, where previously *Gigantochloa hasskarliana* once dominated. There were no records or evidence of logging within the plot. However, the activities of local people such as selective felling of particular species or burning may have affected the forests surrounding the plot. Within the area severe forest fires may have occurred repeatedly over hundreds of years in the past (Rundel & Boonpragob 1995).

Methods

A 4 ha (200 m × 200 m) permanent plot to monitor forest dynamics was established in May 1992 on the south-facing slope of the mountain. All the trees > 5 cm DBH (diameter at breast height, 1.3 m) were tagged, identified and their girth measured to the nearest mm in December, 1992. The plot was divided into 10 m × 10 m subquadrats and the position of each tree was recorded in each subquadrat. A crown projection diagram for the tagged trees was also drawn. The distribution of the four bamboo species in the plot was mapped and the area where the bamboo population was still in the recovering phase after the dieback was specified. Tree censuses and measurements were conducted every two years in December. Trees > 2 cm DBH were also included in 1994 and thereafter, though only the data for trees > 5 cm DBH were used for the analysis in this paper. At each

census, the mortality pattern of the dead trees (standing dead, trunk breakage, uprooting) was also recorded.

Multidimensional contingency table analysis (log linear model analysis) (Sokal & Rohlf 1995) was conducted to analyse the statistical significance of the relationship between the spatial distribution of recruitment and mortality and the distribution of bamboo dieback and forest canopy gaps. Each 10 m × 10 m subquadrat was characterized as (1) under canopy or canopy gap, (2) in an area with bamboo, dead or still alive. A gap was defined as a 10 m × 10 m quadrat with less than 50 % cover of tree crown higher than bamboo canopy in the crown projection diagrams. Newly recruited and recently dead trees were counted for each 10 m × 10 m subquadrat. Distributional patterns of recruited and dead trees were analysed by two-way contingency table using canopy and bamboo as factors. 'STATISTICA version 5.1' (Anon. 1995) was used for computer analyses.

Results

Species composition

Within the mixed deciduous forest 93 tree species were identified in 1992; Table 1 presents some data on the 34 most dominant species. The diversity of the *Dipterocarpaceae* was much lower than their diversity in the tropical rain forests of Peninsular Malaysia (Pasoh) and Sarawak (Ashton 1998). Only four species from the genera *Shorea* and *Dipterocarpus* occurred, however, *Shorea siamensis* was the dominant species. This species constituted 18.3 % of the total basal area, it occurred mainly on ridges and is usually dominant in dry dipterocarp forests (Sukwong & Dhamanittakul 1977). Other major species of mixed deciduous forest such as *Xylia xylocarpa* var. *kerrii*, *Dillenia parviflora* var. *kerrii*, *Vitex peduncularis*, *Mangifera caloneura*, *Schleichera oleosa* and *Pterocarpus macrocarpus* were also important in the

Table 1. Some major tree species occurring in a mixed deciduous forest at the Mae Klong Watershed Research Station, western Thailand, in 1992. Density (D), frequency (F), basal area (BA) and relative basal area (RBA) are shown.

| Species	D (stems/ha)	F (%)	BA (m²/ha)	RBA (%)
Shorea siamensis	7.00	6.50	3.11	8.32
Dillenia parviflora var. *kerrii*	4.25	4.00	1.19	6.90
Xylia xylocarpa var. *kerrii*	6.50	6.25	0.73	4.23
Vitex peduncularis	3.50	3.75	0.72	4.17
Mangifera caloneura	1.00	1.00	0.67	3.88
Schleichera oleosa	3.25	3.50	0.65	3.77
Dipterocarpus alatus	0.50	0.50	0.63	3.65
Pterocarpus macrocarpus	1.50	1.50	0.54	3.13
Gmelina arborea	1.75	1.50	0.45	2.61
Bombax anceps	8.00	7.50	0.33	1.91
Canrium subulatum	2.75	2.75	0.33	1.91
Millettia brandisiana	6.75	4.75	0.13	0.75
Careya arborea	3.25	3.25	0.24	1.39
Vitex canescens	3.25	3.25	0.12	0.70
Terminalia nigrovenulosa	3.00	3.00	0.15	0.87
Cassia fistula	3.00	2.75	0.13	0.75
Lagerstroemia venusta	3.25	3.00	0.05	0.29
Aporusa wallichii	3.50	2.75	0.05	0.29
Protium serratum	1.75	1.75	0.32	1.86
Cassia garrettiana	2.75	2.50	0.12	0.70
Cratoxylum formosum	2.25	2.25	0.16	0.93
Mitragyna brunonis	2.25	2.00	0.16	0.93
Premna latifolia	2.25	2.00	0.18	1.04
Sterculia macrophylla	7.50	5.00	0.28	1.62
Lagerstroemia calyculata	1.50	1.50	0.25	1.45
Colona javanica	2.25	2.25	0.08	0.46
Garuga pinnata	1.00	1.00	0.17	0.99
Eugenia cumini	0.75	0.75	0.28	1.62
Homalium tomentosum	1.00	1.00	0.10	0.58
Phyllanthus emblica	2.25	2.25	0.08	0.46
Diospyros ehretioides	0.75	0.75	0.11	0.64
Antidesma bunius	1.25	1.00	0.02	0.12
Artocarpus lakoocha	0.50	0.50	0.12	0.70
Annogeissus acuminata	0.50	0.50	0.12	0.70
Other species (65)	74.25	66.00	4.43	25.68
Total	170.50	154.50	17.25	100.00

plot. Thus, considering species composition, this forest could be characterized as a dry mixed deciduous forest with a portion of dry dipterocarp forest on the ridge.

Forest structure and changes in stem density and basal area

The values for tree density and basal area (171/ha and 17.2 m²/ha, respectively, see Table 2) were much lower than those reported for many other forests in the tropics; density values in these forests ranged from 170 - 590/ha and basal area values from 13 - 63 m²/ha (Sukwong 1977; Bunyavejchewin 1983). Low tree density has been reported as a unique characteristic of mixed deciduous forests in Thailand (Bunyavejchewin 1983). Over the 4-yr observation period the change in basal area was small whilst the change in tree density was fairly large (Table 2).

The tree canopy covered only 46.3 % of the plot while the remainder (53.7 %) was classified as gaps. Bamboo undergrowth covered 87.5 % of the plot and the remainder (12.5 %) was classified as bamboo dieback area where bamboos were regenerating.

The mortality rate was dependent upon tree size (Fig. 1); size-dependent mortality has been reported for several forests (Nakashizuka 1991; Nakashizuka et al. 1992; Platt et al. 1988; Swaine 1992), although not all forests display this characteristic (Swaine et al. 1987). The medium size-class (30-60 cm) had a lower mortality than the smallest size-class (5-10 cm) ($\chi^2 = 45.5$; df = 3; p < 0.001). Most of the dead trees in the small size-classes were standing dead, this suggests that mortality may have resulted from suppression or competition
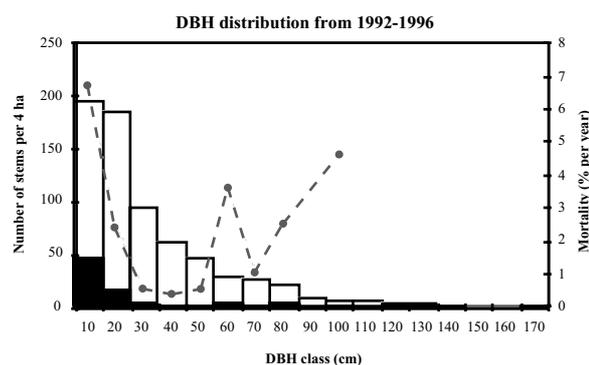
Fig. 1. DBH-distribution and size-specific mortality from 1992-1996. The dots and broken line show the mortality rate in each class. White and black columns show DBH distribution and mortality, respectively.

from larger trees. Mortality among trees in the large size class was mainly due to uprooting by strong winds during the rainy season. The death of large trees through blowdown also resulted in the occasional death of nearby smaller trees.

Mortality during the third and fourth years of study was higher than in the first two years. This higher mortality was mainly due to increased mortality in the smallest size class. Mortality within this class doubled in the latter half of the study. Spatially, the dead trees were concentrated within the area where high recruitment had occurred during the first two years (Fig. 2). This indicates that a thinning process among recently recruited trees began during the third year.

A forest fire occurred in 1995 although this was not considered to be a direct cause of mortality (Marod

Table 2. Summary data of dynamics and number of species (± standard deviation) in the mixed deciduous forest (see Table 1).

	1992		1994		1996		1992-1996
BA (m²/ha)	17.25		16.89		17.16		
Loss (m²/ha)		0.51		0.46			0.92
Gain (m²/ha)		0.15		0.73			0.83
Stem density* (/ha)	170.50		199.25		197.75		
Mortality rate (%/yr)		2.32		4.53			2.90
Recruitment rate (%/yr)		10.61		3.95			6.70
No. of species							
D > 5 cm							
(per 4 ha)	99		107		107		
(per 1 ha)	54 ± 7.97		58 ± 9.03		57 ± 9.65		
D > 10 cm							
(per 4 ha)	92		91		93		
(per 1 ha)	49.7 ± 6.89		51.5 ± 6.52		49 ± 5.83		

* The minimum stem diameter for density is > 5 cm.
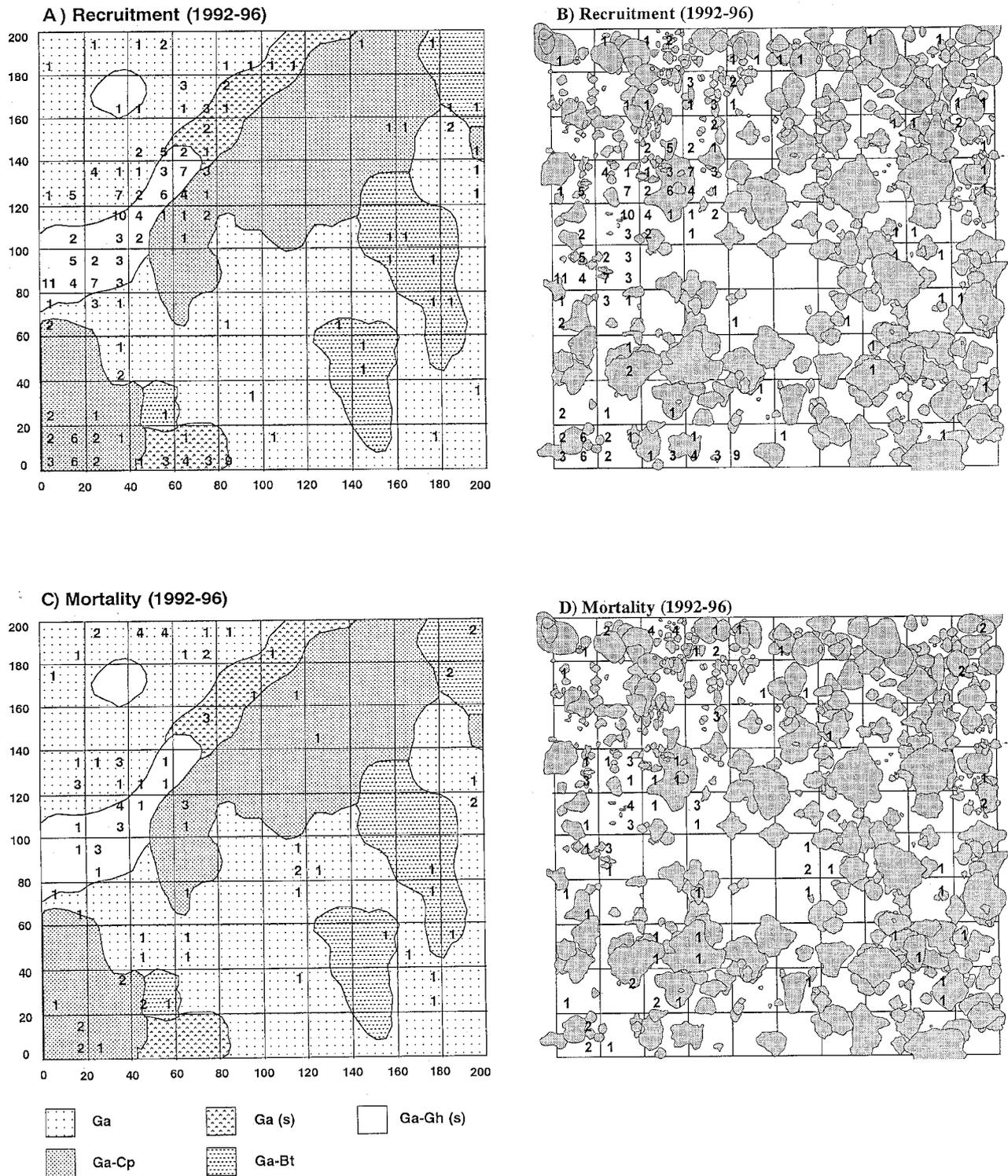
Fig. 2. The spatial pattern of recruitment and mortality from 1992 to 1996. **A** and **B**: relationships between the recruitment and distribution of undergrowth bamboos and canopy conditions, respectively. **C** and **D**: relationships between the mortality and distribution of undergrowth bamboos and canopy conditions, respectively. The different hatched patterns show the distributions of bamboo species. Bt =*Bambusa tulda*; Cp = *Cephalostachyum pergracile*; Ga =*Gigantochloa albociliata*; Gh =*G. hasskarliana*. The abbreviations with (s) show the recovering populations after die-back. The number in each subquadrant indicates recruitment in A and B, and dead trees in C and D in each 100-m² subquadrant during the 4-yr period.

Table 3. Summary of the results of a multi-dimensional contingency table analysis (log-linear model analysis).

| | | 1992 - 1994 | | | 1994 - 1996 | | | 1992 - 1996 | |
Factors	df	χ^2	p	df	χ^2	p	df	χ^2	p
Recruitment									
Canopy (C)	1	1.57	0.208	1	3.21	0.073	1	2.95	0.086
Bamboos (B)	1	36.37	<0.001	1	37.69	<0.001	1	46.28	<0.001
C × B	1	0.78	0.376	1	0.15	0.693	1	0.13	0.715
Mortality									
Canopy (C)	1	0.86	0.354	1	0.08	0.770	1	0.18	0.667
Bamboos (B)	1	0.36	0.548	1	6.37	0.011	1	7.37	0.006
C × B	1	0.02	0.877	1	0.16	0.687	1	0.76	0.382

pers. obs.), probably because the recruited trees had already reached a size large enough to persist during a ground fire.

The spatial pattern of recruitment and mortality

During the 4-yr observation period recruitment was more spatially concentrated than mortality (Fig. 2). Recruitment was significantly concentrated within areas of bamboo dieback (Table 3), rather than canopy gaps. The net recruitment for the 4-yr period only had a significant relationship with bamboo dieback. An interacting effect between canopy gap and bamboo dieback on tree recruitment was not significant.

The spatial distributions of dead trees also showed a relationship to bamboo dieback (Table 3). During the first 2-yr period, neither the area of bamboo dieback nor canopy gaps showed a significant relationship with mortality. However, during the second 2-yr period the former showed a highly significant relationship. An interacting effect of canopy gap and bamboo dieback on tree recruitment was not detected. Net recruitment during the four years only showed a significant relationship to bamboo dieback (Table 3).

In summary, spatially and temporally concentrated recruitment and mortality patterns were observed. Most recruitment occurred only in the areas of bamboo dieback. In the second half of the study period, the high mortality of small trees occurred mostly in places of bamboo dieback where the overcrowded population started to suffer from natural thinning. The effect of canopy gaps (with a high proportion i.e. 46.3 %), was not significant.

Recruitment and mortality pattern of tree populations

Eight species were newly recruited during the four years, while recruitment occurred intermittently. During the first two years (1992-1994) the number of species for trees >5 cm DBH increased while little change occurred during the next two years. For trees >10 cm DBH, the number of species hardly changed over the four years (Table 2).
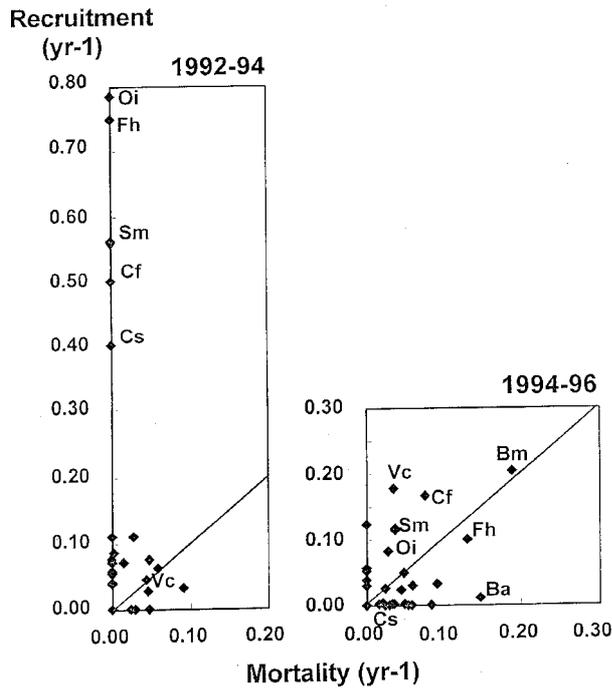
The relationship between mortality and recruitment of tree populations with more than 10 stems differed among the species (Fig. 3). During the first two years, some species showed disproportionately high recruitment and quite low mortality. Most of these species were pioneer species such as *Colona floribuda*, *Ficus hispida* and *Sterculia macrophylla*. During the second two years, recruitment and mortality of these species were almost balanced, due to a decrease in recruitment and an increase in mortality (Fig. 3). There were extreme cases e.g. *Bauhinia malabarica* which was not represented in 1992 and *Ficus hispida* (both are pioneer species) where populations expanded rapidly by 1994, but began to decrease during 1994-1996. Thus, the compositional change that occurred during the four years was mainly due to recruitment of the short-lived pioneer species in the first two years. Some of the late successional trees, *Vitex canescens* and *Oroxylum indicum*, were also recruited between 1992 and 1994, though the mortality did not increase from 1994 to 1996 (Fig. 3).

Discussion

Structure and dynamics of the forest

Low stem density and basal area with relatively discontinuous canopy layer and large canopy gap proportion characterized the forest (Table 2, Fig. 2). Tree density and basal area were much lower than those reported for other forest types in tropical areas (Swaine et al. 1987). A relatively low tree density and basal area is a common structural feature among seasonally dry forests (Murphy & Lugo 1986; Gerhardt & Hytteborn 1992); however, these values are particularly low (see Menaut et al. 1995; Sukwong 1977; Bunyavejchewin 1983). Within mixed deciduous forests very low tree density

Fig. 3. Relationships between the recruitment and mortality of trees over 10 stems in 4 ha during 4 yr. Species abbreviations are: Ba: *Berrya ammonilla*; Bm: *Bauhinia malabalica*; Cs: *Canarium subulatum*; Cf: *Colona floribunda*; Fh: *Ficus hispida*; Oi: *Oroxylum indicum*; Sm: *Sterculia macrophylla*; Vc: *Vitex canescens*.

and basal area occur under the influence of severe seasonal water stress; two other factors may also be important, e.g. the dominance of undergrowth bamboos and the frequent occurrence of fire. Short-term dynamics of this forest after the local dieback of bamboos clearly showed the importance of the life history of bamboo for the dynamics and structure of the mixed deciduous forest. The fire occurred just after the bamboo dieback in 1995 and indicates the complexities of forest dynamics.

The role of undergrowth bamboos

The inhibitory effect of undergrowth bamboos on tree recruitment is common in temperate zone forests (Veblen et al. 1980; Nakashizuka 1987, 1988; Taylor & Zisheng 1992). The low tree density of the natural mixed deciduous forest may be partly due to the effects of the deep shade from the bamboos. Low tree density and large canopy gap proportion due to the persistence of undergrowth bamboos were also reported for Japanese beech forests (Nakashizuka 1987; Peters et al. 1992). As the cover of bamboo becomes more dense in

the canopy gaps, the regeneration of tree seedlings will be prevented and the canopy tends to become more discontinuous (Marod unpubl.). In this forest, recruitment of trees hardly occurred in the area covered by the undergrowth bamboos and canopy gaps themselves had little effect upon tree recruitment (Fig. 2). Without episodic death of bamboos and consequent tree recruitment, the canopy would become more discontinuous and tree density would also gradually decrease. Human disturbances such as harvesting would accelerate such a process.

The long life-span of undergrowth bamboo makes the continuous recruitment of trees difficult and greatly affects the regeneration pattern of the forest. The longevity of bamboo differs among species, but usually extends to 40 yr; flowering intervals were reported as ca. 25 - 100 yr for *Dendrocalamus strictus* in India (Gupta 1972; Dwivedi 1988), ca. 42 - 51yr for *Melocanna bambusoides* in Bangladesh (Hossain 1962). However, after they have flowered and died simultaneously, light conditions on the forest floor are greatly improved and forest regeneration is facilitated (Fig. 2), particularly within the canopy gaps. The lengthy period of bamboo dieback offers several opportunities for tree seedlings to regenerate.

The regeneration process after the dieback of the undergrowth bamboo is affected by many factors, such as the size of the area of bamboo dieback, the recovery rate of bamboo (a new cohort from the seeds produced by the dying cohort), the abundance and composition of the colonized tree populations (via seed bank, seed rain and advanced regeneration) and competition among them and with several colonizing herbs. A large amount of fuel supplied by the bamboo dieback (dead culms and leaves) will be readily burnt during any subsequent forest fires. This will also affect the colonization process. In this forest, wild bananas (*Musa acuminata*) quickly colonized and dominated after the bamboo dieback and a subsequent fire (Takahashi et al. 1995), because the area where the bamboo dieback occurred was relatively moist. Since the dormancy of long-lived buried seeds of wild banana are broken by fire (Kobayashi et al. 1995), this large perennial plant can be a strong competitor in the early phase of regeneration. Six years after bamboo dieback, the regenerating tree populations had become very dense and self-thinning was occurring. Both recruitment and mortality were high for pioneer species, thus the composition would gradually become biased to more shade-tolerant species.

The role of fire

Forest fires occur during the dry season in mixed deciduous forests, and typically burn only the surface of the forest floor. The common or dominant species in this forest may be adapted to this type of fire, but frequent surface fires will inhibit continuous regeneration. Fire tends to selectively attack younger and smaller individuals in a population, and species with thinner bark in a community (Uhl & Kauffman 1990). In this natural forest, fire occurred in 1995 and killed only a small number of tree saplings; this differs from tree mortality in grassland fires. Because of their high fuel load, grassland fires can occur as crown fires. Approximately half (46.9 %) of young trees (> 5 cm) were killed by a fire which occurred in grassland near to the plot (Takahashi et al. 1995). Frequent fires burn only small amounts of litter on the forest floor and do not cause severe damage to trees which are resistant or large (Heinselman 1975; Goldammer & Seibert 1990). However, seedlings and small saplings are killed or suffer from dieback when such fires occur repeatedly (Marod unpubl.). If forest fires occur less frequently, e.g. with intervals of 3 - 4 yr, seedlings can become large enough to tolerate fire. The trees which regenerated after bamboo dieback were little affected by the fire of 1995. However, if fire is rare and occurs after the accumulation of large amounts of litter on the ground, it can cause severe damage to the whole forest (Stott et al. 1990). Frequency and intensity of fires will critically affect the dynamics of this forest. There could be an optimal fire frequency for forest maintenance; frequent enough not to accumulate too much fuel on the forest floor, but infrequent enough to allow regenerated seedlings to achieve a tolerant size. To understand the fire regime which formed and maintained this type of forest, much more information about the species-specific response to the variable types of fire is necessary.

The data presented here are based on only four years of observations which is not sufficient to understand the role of rare events such as bamboo dieback, the effect of fire disturbance regime and their interaction with forest community dynamics. Dieback of one bamboo species (*G. hasskaliana*) affected only a small portion of the forest. Continuous long-term observations and additional experimental studies involving manipulation of these critical factors are necessary. Forest dynamics is a slow process with a large heterogeneity in time and space (Nakashizuka et al. 1992). To obtain the baseline data for the prediction of vegetation change in this unique ecosystem, networking and comparison of the long-term studies in various permanent plots are essential (Murphy & Lugo 1986; Mueller-Dombois & Goldammer 1990).

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