ELSEVIER

Forest Ecology and Management 175 (2003) 87–101

Forest Ecology and Management

www.elsevier.com/locate/foreco

Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand

Sarayudh Bunyavejchewin[a], James V. LaFrankie[b], Patrick J. Baker[c,*], Mamoru Kanzaki[d], Peter S. Ashton[e], Takuo Yamakura[f]

[a]*Royal Thai Forest Department, Silvicultural Research Division, Forest Research Office, Chatuchak, Bangkok 10900, Thailand*
[b]*Center for Tropical Forest Science, Smithsonian Tropical Research Institute, 469 Bukit Timah Road, Singapore 1025, Singapore*
[c]*College of Forest Resources, University of Washington, Seattle, WA 98195, USA*
[d]*Graduate School of Agriculture, Kyoto University, Kitashirakawa, Kyoto 606-8502, Japan*
[e]*Arnold Arboretum, Harvard University, One Eliot Street, Cambridge, MA 02138, USA*
[f]*Department of Biology, Faculty of Science, Osaka City University, Sumiyoshi-ku, Osaka 558-8585, Japan*

Received 2 October 2001; accepted 31 March 2002

Abstract

Population structure and spatial patterns were examined for four species of canopy dipterocarps (*Anisoptera costata*, *Dipterocarpus alatus*, *Hopea odorata*, *Vatica cinerea*) in a 50 ha plot in seasonal dry evergreen forest at the Huai Kha Khaeng Wildlife Sanctuary in western Thailand. Spatial dispersion was assessed with Morisita's index for quadrat sizes ranging from 61 m^2 to 25 ha; spatial attraction and repulsion between species and size classes were measured with Iwao's index. Only *Vatica* had a negative exponential diameter distribution suggesting continuous recruitment. The other species had either normal (*Hopea*) or irregular diameter distributions with peaks in the large size classes (*Anisoptera*, *Dipterocarpus*). All four species were significantly clumped at most quadrat sizes. At the local scale, saplings and poles of *Hopea* and *Anisoptera* were negatively associated with adults at quadrat sizes <1000–5000 m^2, while the distributions of *Dipterocarpus* and *Vatica* saplings and poles were independent of adult trees. In general, saplings and poles were always positively associated with each other. Spatial segregation among species may imply habitat specialization. A torus-translation analysis of habitat association for each of the dipterocarp species revealed both positive and negative species-specific associations. At HKK, most of the dipterocarps' spatial distributions were independent of each other and there was no evidence of strong spatial segregation among species. The irregular diameter distributions, clumping at large spatial scales, and lack of positive association between juvenile and adult stems suggest that many of the dipterocarps at the 50 ha plot may have established after a large-scale catastrophic disturbance. In the absence of catastrophic disturbance, we hypothesize that the *Hopea* and *Anisoptera* populations will eventually disappear from the plot because of a lack of suitable recruitment conditions.

Keywords: Spatial patterns; Dipterocarps; Thailand

1. Introduction

In recent decades much ecological research has focused on identifying potential mechanisms for the maintenance of diversity in species-rich communities

---

[*] Corresponding author. Present address: Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, 23 E. Kawili St., 967 20 Hilo, HI, USA.
E-mail address: patrickbaker@fs.fed.us (P.J. Baker).

PII: S0378-1127(02)00126-3

(Ashton, 1998). In the study of tropical forests two questions have received particular attention: (1) are tree species narrowly specialized for a certain habitat (e.g., Ashton, 1969; Hubbell, 1979)? and (2) is the distribution of juvenile trees a function of the distribution of adult trees (e.g., Janzen, 1970; Connell, 1971; Condit et al., 1992)?

The relationship between the local distribution of a species and topography in tropical forests has been studied in many regions (Hubbell and Foster, 1986; Basnet, 1992; Itoh, 1995; Yamada et al., 1997). Nonetheless, the relative importance of habitat specialization in structuring species-rich forest communities remains unclear. Some studies, particularly in the aseasonal evergreen forests of southeast Asia, have suggested that tree species may be habitat specialists for particular edaphic or topographic conditions (Ashton, 1964, 1976; Ashton and Hall, 1992; Richards, 1996; Yamada et al., 1997). Other studies have not found strong evidence of habitat specialization. For example, Hubbell and Foster (1986) found that the majority of species in a semi-evergreen neotropical forest were habitat generalists with respect to topography. However, studies in Asian forests have been mostly restricted to aseasonal forests; the relationship between spatial distribution and topography in seasonal forests in continental Asia has not yet been studied.

The spatial distribution of tropical tree populations has been a major source of interest among tropical ecologists because of its potential role in explaining the coexistence of tree species in species-rich forests. Janzen (1970) and Connell (1971) first proposed that the probability of mortality and survival of juveniles may be a function of the density of conspecific adults in the surrounding area. The intensity of predation by insects and other herbivores (Janzen, 1970; Burkey, 1994) and the probability of infection by fungal pathogens (Augspurger, 1983; Augspurger and Kelly, 1984) are expected to be higher where accumulations of seeds or seedlings are denser, and lower where seeds and seedlings are sparse. Given the dispersal limitations of most tropical forest tree species, seed and seedling density is typically highest directly below the crown of a mother tree and decreases exponentially with increasing distance from the mother tree. Yet, as with habitat specialization, the extent to which density-dependence influences community diversity patterns remains uncertain. For example, in an analysis of a large-scale permanent forest dynamics plot in Panama, Condit et al. (1992) found that few species showed signs of density-dependence. In a later paper (Condit et al., 1994), they suggested that the role of density-dependence may only be important among those species with the highest population densities. More recently, however, Wills et al. (1997), using more robust statistical techniques to reanalyze the Panama plot data, showed that density-dependence was much more common than originally believed. As with habitat specialization, most studies of spatial association among tropical forest species have been either in aseasonal or neotropical forests. No such studies exist for the seasonal forests of tropical southeast Asia.

An important factor that must be taken into consideration is the relative increase in disturbance intensity with increasing seasonality in tropical Asia. The occurrence of catastrophic drought, fire, and cyclones increases with increasing distance from the equator (Whitmore, 1984). Spatial patterns of tree species may provide indirect evidence of the relative influence of large- and small-scale disturbances in structuring forest communities (Duncan and Stewart, 1991).

Trees of the family Dipterocarpaceae dominate forests across much of south and southeast Asia (Wyatt-Smith, 1963; Champion and Seth, 1968; Ashton, 1982; Whitmore, 1984). Dipterocarps are typically canopy trees or emergents and reach considerable dimensions throughout forests of the region. Consequently, they are both ecologically and economically important. Developing a better understanding of how dipterocarp populations are maintained within a forest is critical to advancing forest management and silviculture in the seasonal tropics.

In this study, we examine patterns of spatial association and habitat specialization within and among four dominant dipterocarp species in a 50 ha permanent forest dynamics plot located in seasonal dry evergreen forest in western Thailand. Specifically, we test the following hypotheses:

1. Spatial dispersion of each species is random with respect to size class; that is, saplings and poles are neither positively or negatively associated with adult trees.
2. Spatial dispersion of each dipterocarp species is independent of all other dipterocarp species.

3. Spatial dispersion of each dipterocarp species is random with respect to habitat.

We evaluate the spatial patterns of each species within the context of the current stand structure and consider the processes that may have created these patterns and their role in forest development in the seasonal tropics of southeast Asia.

2. Study area and methods

2.1. Study area

The study area is located in the Huai Kha Khaeng Wildlife Sanctuary (15°40′N, 99°10′E) in Uthai Thani Province, western Thailand (Fig. 1). The sanctuary encompasses approximately 2780 km^2. Three main forest types, seasonal dry evergreen forest, deciduous dipterocarp forest and dry mixed deciduous forest, form a mosaic across most of the sanctuary, with a few high altitude sites (<5% of the total sanctuary area) occupied by lower montane forest. Rainfall is highly seasonal with a 4–6-month dry period (<100 mm per month) from November to April. Mean annual rainfall is approximately 1425 mm (1983–1995 average).

The study plot is located in the interior of the sanctuary in a stand of seasonal dry evergreen forest with no record of logging or other forest management activities. The topography of the plot is characterized by gentle slopes with a small stream in the northern

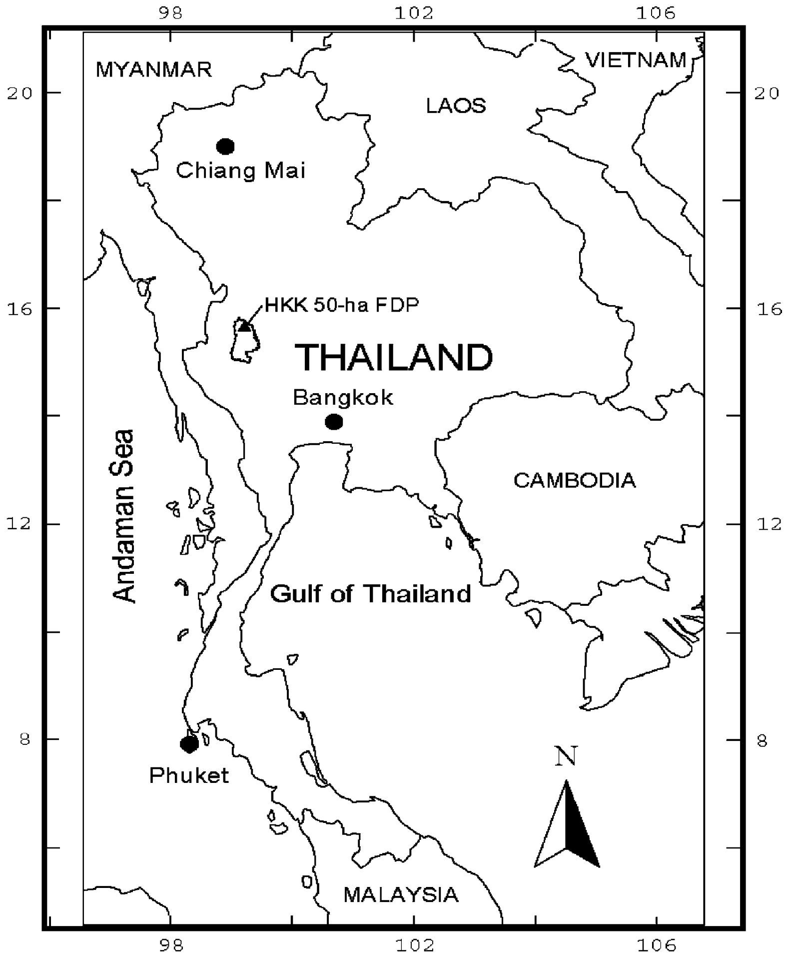

Fig. 1. Location of the study site at the HKK 50 ha forest dynamics plot in western Thailand.

section of the plot, two low hills that bisect the plot, and a minor swampy area. Details of the plot topography are described fully in Bunyavejchewin et al. (1998).

2.2. Tree census

The study plot is 1 km × 0.5 km (50 ha) and is divided into 1250 20 m × 20 m subquadrats. All woody plants 1 cm dbh (diameter at breast height, 1.30 m above ground) or larger within the plot were measured, tagged and mapped to the nearest 10 cm following a standard protocol (Manokaran et al., 1990). The total number of individuals in the first census was 80,640 (excluding climbers), consisting of 248 species, 164 genera and 61 families. The mean stand density was 1613 individuals ha^{-1}; mean basal area was 30.45 $\text{m}^2\,\text{ha}^{-1}$.

The family Dipterocarpaceae dominates the forest structure within the plot. The tallest dipterocarps are canopy emergents 55–60 m tall. Dipterocarpaceae also has the greatest basal area of all families on the plot (Bunyavejchewin et al., 2001). Seven dipterocarp species occur within the plot: *Anisoptera costata*, *Dipterocarpus alatus*, *D. obtusifolius*, *Hopea odorata*, *Shorea siamensis*, *S. roxburghii* and *Vatica cinerea*. Only *V. cinerea* is a subcanopy species, the rest are canopy or emergent species. The two *Shorea* species are represented by a single tree each and are not considered in the analyses presented here. For the sake of brevity each species is referred to by its generic name. Each species is divided into three general size classes: (1) saplings (≥1 to <5 cm dbh), (2) poles (≥5 to <20 cm dbh), and (3) adults (≥20 cm dbh). These divisions roughly correspond to trees that are in the understory, midstory, and canopy of the forest.

2.3. Habitat association

To quantify the effects of topography on species distributions we developed several measures describing various physiographic aspects of the plot. The surface of each of the one thousand two hundred and fifty 20 × 20 m^2 quadrats in the 50 ha plot was assumed to be a plane expressed by its X, Y and Z coordinates, where X and Y are plot coordinates and Z is elevation. Slope and aspect in each quadrat were defined by a regression plane using the least-squares method. Quadrat elevation was defined as the average elevation of the four corner posts. A landform shape index (i.e., an index of convexity or concavity of slope, IC; Yamakura et al., 1995) was obtained by comparing the mean elevation of a given quadrat with the mean elevation of the twelve surrounding corner posts. Each quadrat was classified as convex, concave or rectilinear. Based on a cluster analysis of slope, elevation, and convexity each 20 × 20 m^2 quadrat was classified into one of four habitat types: hilltop/ridge, slope, flat, or stream.

Traditional χ^2-tests are inappropriate for testing habitat association in many plant populations because the spatial pattern of the population is often autocorrelated due to poor dispersal. Recently, Harms et al. (2001) developed a torus-translation method that circumvents the problem of spatially autocorrelated populations. The spatial pattern of the trees is decoupled from the spatial distribution of habitats by moving the habitat map about a two-dimensional torus by 20 m increments in the four cardinal directions while maintaining the original tree coordinates. The 50 ha plot is 50 × 25 quadrats; thus there are 1250 possible habitat map positions available for analysis. To test for association between a tree species and a habitat type, the relative density of each species (density of the focal species divided by density of all species) in each habitat type was calculated. This was repeated for all 1250 habitat maps to generate a distribution of relative density estimates for each species in each habitat type. If the true relative density was higher than 97.5% of the simulated relative densities, then the species was considered to be positively associated with the habitat. A species was considered to be negatively associated with a habitat if 97.5% of the simulated relative densities were greater than the true relative density.

2.4. Spatial distribution and correlation

Spatial pattern in the distribution of saplings, poles, and adults of each species was described using Morisita's (1959) $I\delta$ index:

$$I\delta = \frac{\sum n_i(n_i - 1)}{N(N - 1)q}$$

where n_i is the number of individuals in each quadrat, N the total number of individuals in the 50 ha study plot, q the number of quadrats for a given quadrat size. The smallest quadrat size was obtained by subdividing the 50 ha plot into square quadrats with sides of $(0.5)^7 \times 1000$ m (i.e., x-axis length) and $(0.5)^6 \times 500$ m (i.e., y-axis length) yielding quadrats of 7.8125 m × 7.8125 m (61.04 m^2). Larger quadrat sizes were obtained by doubling the length of the quadrat sides. Quadrat sizes range from 61 m^2 to 25 ha. Morisita's $I\delta$ is 1 for a random distribution, >1 for a clumped distribution, and <1 for a regular distribution. An F-test was used to test for significance of departures from random for all quadrat sizes (spatial scales) at $P < 0.05$.

To evaluate patterns of spatial correlation between two populations, we calculated the index of Iwao (1977). The index is zero for spatially independent distributions, positive to a maximum of +1 for completely overlapping populations (i.e., attraction) and negative to a minimum of −1 for completely non-overlapping populations (i.e., repulsion). The index was calculated for all species pairs for the same quadrat sizes as Morisita's $I\delta$.

3. Results

3.1. Size structure

Vatica was the most abundant dipterocarp with 2085 individuals. *Hopea*, *Dipterocarpus*, and *Anisoptera* had 332, 297, and 155 trees, respectively. Of the four species all but *Vatica* had individuals with diameters >100 cm. The diameter distributions of the four dipterocarp species are shown in Fig. 2. Only one of the

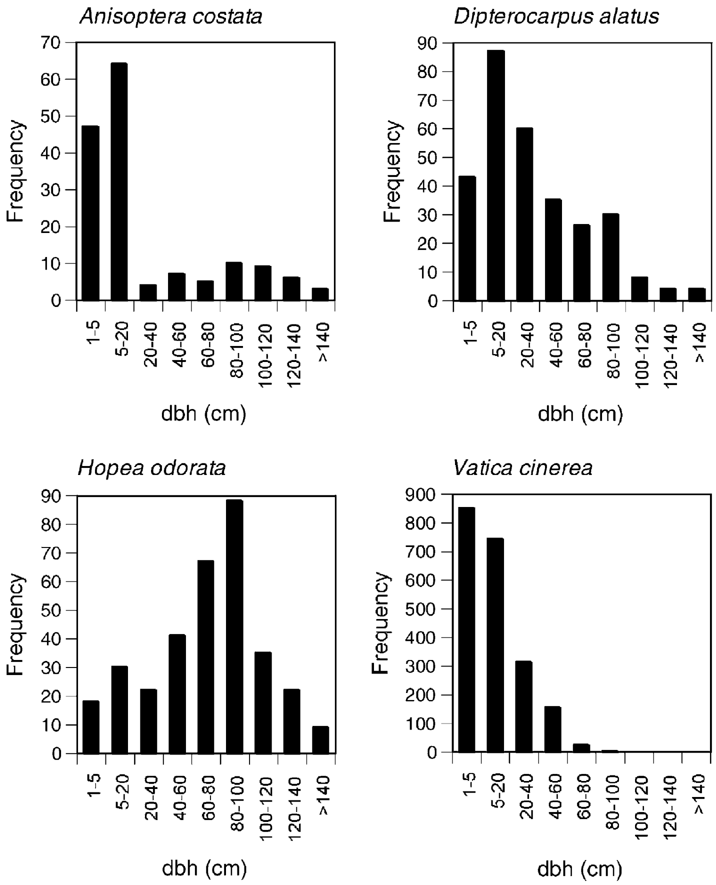

Fig. 2. Diameter distributions of the four dominant dipterocarp species in the HKK 50 ha plot.

four species, *Vatica*, is described by the reverse-J shaped frequency distribution expected of self-replacing populations. The frequency distribution for *Hopea* is approximately normal with a mean dbh of 71.4 cm. *Anisoptera* has a discontinuous diameter distribution with relatively high frequency of saplings and poles followed by a sharp decrease in the larger size classes; the frequency distribution of adult *Anisoptera*, taken separately, is normally distributed. *Dipterocarpus* had a right-skewed diameter distribution punctuated by occasional peaks in larger diameter classes.

3.2. Topographic and habitat specialization

Tree density of all species differed significantly among the five elevation classes, but was only significantly different among slope classes for *Dipterocarpus*, *Hopea*, and *Vatica* (Table 1). *Hopea* density and basal area were significantly higher in the lowest elevation and slope classes, decreasing in higher classes (Table 2). *Hopea* was principally associated with the low-lying areas around the stream in the northeastern portion of the plot. In contrast, the density of *Vatica* was highest in the second highest elevation class and also in the steepest slope class. *Vatica* mainly occurred on steep slopes at elevations ranging from 578 to 635 m. *Dipterocarpus* density was significantly different among elevation and slope classes, although no clear trend occurred for either variable. The distribution of basal area of the four species with respect to the topographic variables showed similar patterns to those of tree density.

Table 1
Summary of association of topographic variables with tree density for four dipterocarp species. IC is the index of convexity; see text for details

Species	Elevation	Slope	IC
A. costata	**	NS[a]	*
D. alatus	***	**	NS
H. odorata	***	***	**
V. cinerea	***	***	NS

[a] Not significant.

[*] Significance value of the Kruskal–Wallis non-parametric ANOVA is $P < 0.05$.

[**] Significance value of the Kruskal–Wallis non-parametric ANOVA is $P < 0.01$.

[***] Significance value of the Kruskal–Wallis non-parametric ANOVA is $P < 0.001$.

The dipterocarp species were non-randomly distributed with respect to habitat type (Tables 3 and 4). Distribution patterns of the dipterocarp species with respect to habitat type were consistent with the patterns for topographic variables. For example, density of *Hopea* was highest in the stream/swamp sites (lowest elevation class and flattest slope class) and lowest on hilltops and ridges (highest elevation class and steepest slope class). *Dipterocarpus*, although having highest densities on stream/swamp sites, was common on flat sites and slopes. *Vatica* was most common on slopes but was relatively well distributed among all habitat classes. *Anisoptera* occurred in all habitat types.

Table 2
Relative density ($N \times 1000$) per quadrat ($20 \times 20\ \mathrm{m}^2$) of four dipterocarp species for two topographic variables. Different letters indicate significantly different densities for each species among the topographic variable classes based on Mann–Whitney U-test ($P < 0.05$)

Topographic variable	*A. costata*	*D. alatus*	*H. odorata*	*V. cinerea*
Elevation (m a.s.l.)				
549–559 (lowest)	2.32 a	5.39 ab	8.34 a	15.6 a
560–567 (low)	2.24 a	3.03 ad	4.68 b	18.2 ab
568–577 (middle)	2.17 a	6.05 bc	4.08 bc	22.5 b
578–588 (high)	1.72 a	4.01 ac	1.95 cd	32.1 c
589–635 (highest)	0.64 b	1.37 d	1.33 d	26.92 bc
Slope (°)				
0.00–5.63 (flat)	2.73 a	6.04 a	6.88 a	22.5 a
5.64–7.62 (gentle)	1.67 a	5.30 a	3.45 b	19.0 a
7.63–10.21 (middle)	1.66 a	2.21 b	3.92 b	19.9 a
10.22–14.77 (steep)	1.76 a	3.70 ab	3.86 b	22.4 a
14.78–45.9 (steepest)	1.27 a	2.61 ab	2.23 b	31.3 b

Table 3
Habitat association based on two-tailed 95% significance test using the torus-translation method to generate random habitat maps

Species	Hilltops/ridges	Slopes	Flat	Stream
A. costata	–[a]	NA[b]	NA	NA
D. alatus	NA	NA	NA	NA
H. odorata	–	–	+[c]	NA
V. cinerea	NA	NA	NA	–

[a] Negative association between habitat type and dipterocarp species.

[b] No association.

[c] Positive association.

Table 4
Mean relative frequency ($N \times 10^6$) and relative basal area ($m^2 \times 10^8$) per quadrat (20 m × 20 m) by habitat type of four dipterocarp species in a 50 ha plot in seasonal dry evergreen forest in western Thailand

Species		Habitat types			
		Hilltops/ridges	Slopes	Flat	Stream
A. costata	Relative N	3.3	3.6	5.6	9.9
	Relative BA	5.5	3.3	6.5	1.1
D. alatus	Relative N	10.4	8.3	7.2	79.5
	Relative BA	12.3	8.75	6.57	96.6
H. odorata	Relative N	5.5	5.6	12.7	84.5
	Relative BA	13.8	12.3	32.9	276.0
V. cinerea	Relative N	185.0	65.3	41.8	99.4
	Relative BA	44.9	10.8	5.8	9.8

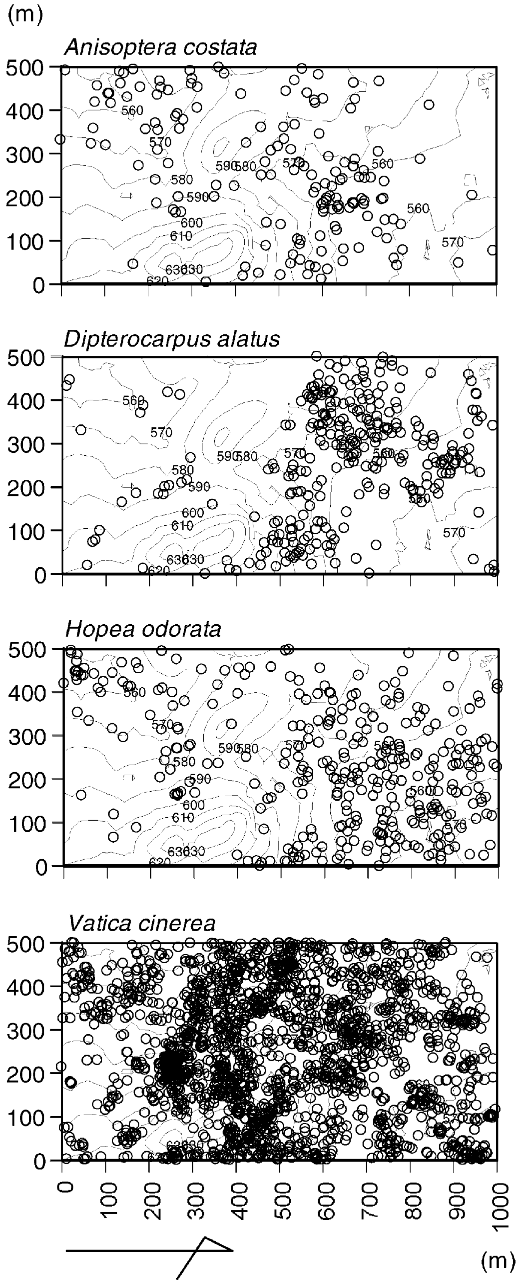

Fig. 3. Distribution patterns of the four dominant dipterocarp species in the HKK 50 ha plot.

3.3. Spatial distribution pattern

The spatial distribution patterns on the 50 ha plot for each of the study species are shown in Fig. 3. The distribution maps showed no evidence of clear spatial segregation among species. Most species overlapped at several spatial scales; however, the distribution centers of *Dipterocarpus* and *Hopea* were roughly non-overlapping. *Vatica* occurred across much of the plot but was particularly dense on the slopes of the eastern hill and upland sites in the northwestern quarter of the plot. *Hopea* had a broader distribution than the other three species. *Dipterocarpus* was distributed mainly in the northern half of the plot. *Anisoptera* was diffusely distributed from the northeast to southwest portion of the plot.

The spatial distributions of all four of the dominant dipterocarp species at HKK were clumped at most quadrat sizes (Fig. 4). All species except *Hopea* exhibited decreasing intensities of spatial aggregation with increasing quadrat size. The intensity of aggregation in *Hopea* was relatively constant across spatial

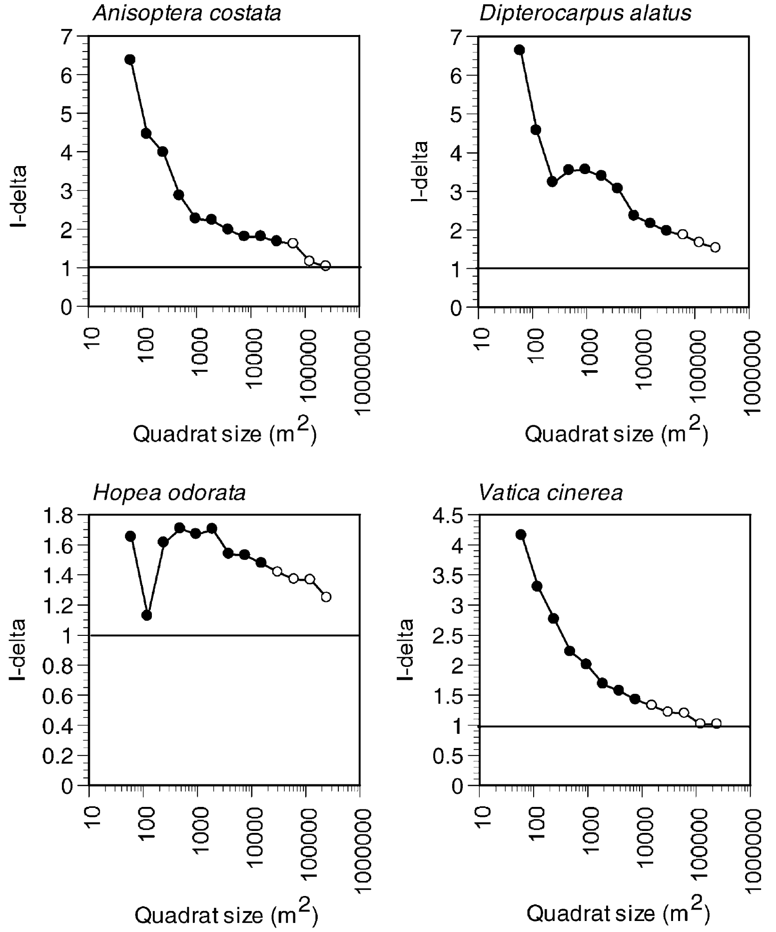

Fig. 4. Variation of dispersion index, $I\delta$, for all individuals of four dipterocarp species in the HKK 50 ha plot. $I\delta$ is 1 for a random distribution, >1 for a clumped distribution, and <1 for a regular distribution. Closed circles are significantly different from 1 at $P < 0.05$.

scales. *Vatica* was significantly aggregated at quadrat sizes <0.78 ha; at spatial scales >1 ha Morisita's $I\delta$ was not significantly different from unity. The other species were significantly aggregated at larger spatial scales. The largest quadrat size significantly greater than random—thus indicating spatial aggregation—was 1.56 ha for *Hopea*, and 3.12 ha for *Dipterocarpus* and *Anisoptera*.

When the species were analyzed by developmental classes, a variety of patterns emerged (Fig. 5). In general, saplings were more clumped than poles, which were more clumped than adult trees. However, at quadrat sizes <125 m^2 adults of *Anisoptera* and *Hopea* were randomly distributed. *Hopea* poles were clumped at all quadrat sizes except the largest, while saplings were clumped at <500 m^2 and randomly distributed at larger scales. *Anisoptera* saplings were clumped at all quadrat sizes; the distribution patterns of poles and adults were variable. At the smallest quadrat size adult *Anisoptera* were uniformly distributed.

3.4. Spatial association between developmental stages

There were several patterns of spatial association between developmental stages common to all four species: (1) at the local scale (five smallest quadrat sizes) saplings and poles were never positively associated with adults, (2) saplings and poles were

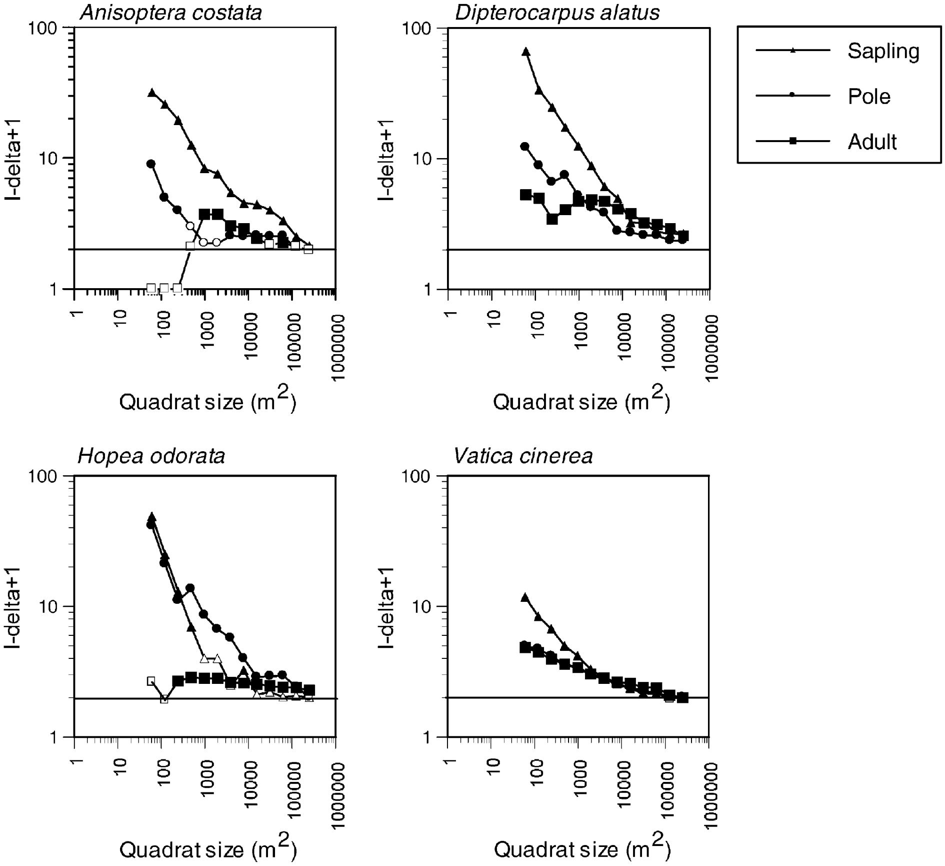

Fig. 5. Variation of dispersion index, *Iδ*, for developmental stages, saplings, poles and adults, of four dipterocarp species in the HKK 50 ha plot. *Iδ* is 1 for a random distribution, >1 for a clumped distribution, and <1 for a regular distribution. Closed circles are significantly different from 1 at $P < 0.05$.

positively associated at all but the two smallest quadrat sizes, (3) all developmental class pairs were increasingly positively associated with increasing quadrat size, and (4) all developmental class pairs showed positive spatial association at the largest quadrat sizes. However, the four species could be divided into two groups, exemplified by *Anisoptera* and *Dipterocarpus*, based on spatial association among developmental stages. *Anisoptera* saplings and poles had significant negative associations with adult trees at quadrat sizes <976 and <1464 m^2, respectively; only at the largest quadrat sizes was there a positive association between saplings/poles and adult trees (Fig. 6). *Anisoptera* saplings and poles were positively associated at all but the two smallest quadrat sizes. In contrast, spatial associations between all pairs of developmental stages in *Dipterocarpus* were independent at quadrat sizes <486 to 976 m^2 and positively associated at all larger quadrat sizes. *Vatica* exhibited spatial patterns between developmental stages similar to *Dipterocarpus*, while *Hopea* had patterns more similar to *Anisoptera*. *Hopea* saplings were negatively associated with adults up to quadrat sizes of ca. 4000 m^2.

3.5. Spatial association between species

Patterns of between species spatial associations are shown in Fig. 7. Two general patterns of association occurred: either (1) species pairs were spatially independent at small quadrat sizes but positively associated at larger quadrat sizes, or (2) species pairs were independent at all or most quadrat sizes. *Anisoptera*–

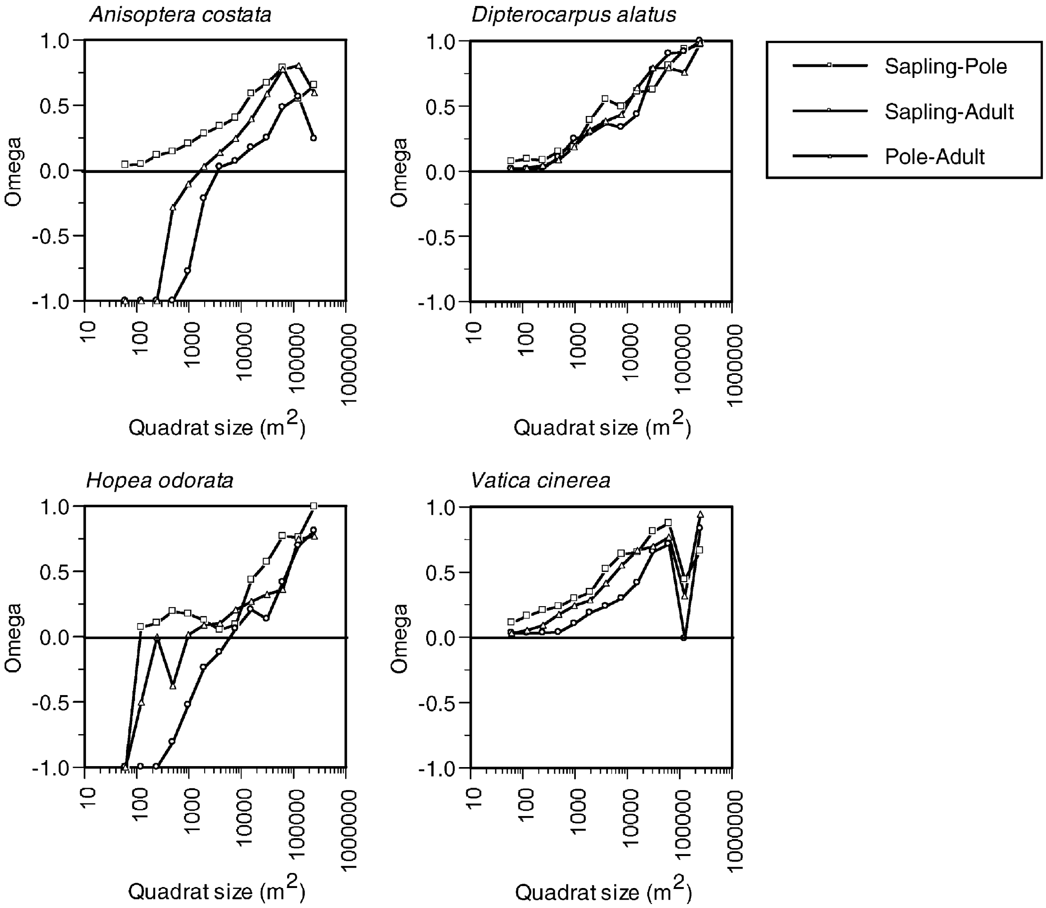

Fig. 6. Variation of Iwao's spatial association index, ω, between developmental stages (saplings, poles, and adults) of four dipterocarp species in the HKK 50 ha plot. Iwao's ω is zero for spatially independent distributions, positive to a maximum of $+1$ for overlapping populations (i.e., spatial attraction), and negative to -1 for non-overlapping populations (i.e., spatial repulsion).

Hopea, *Anisoptera–Dipterocarpus*, *Anisoptera–Vatica*, and *Dipterocarpus–Hopea*, showed the former pattern, although there was variation in the intensity of the association for different quadrat sizes specific to each species pair. *Vatica–Hopea*, and *Vatica–Dipterocarpus* exhibited the latter pattern.

4. Discussion

4.1. Size structure

Only *Vatica* exhibited a size structure with the reverse-J shape associated with continuously regenerating populations. Normally distributed diameter distributions, particularly for shade-intolerant species, have been used as indirect evidence of a single cohort age structure in temperate forests (Lorimer and Krug, 1983). The diameter distributions of *Hopea* and the adults of *Anisoptera* were consistent with the presence of a single age cohort. The cohorts of *Hopea* and adult *Anisoptera* may have established synchronously (see Section 4.3). In addition, *Dipterocarpus* had irregular peaks in the larger diameter classes that may represent historic pulses in recruitment. The diameter distribution of *Hopea* suggested that the species is not currently regenerating in situ and is therefore not in demographic equilibrium within this forest. The lack of *Hopea* regeneration may result from: (1) susceptibility of seedlings to occasional surface fires (return

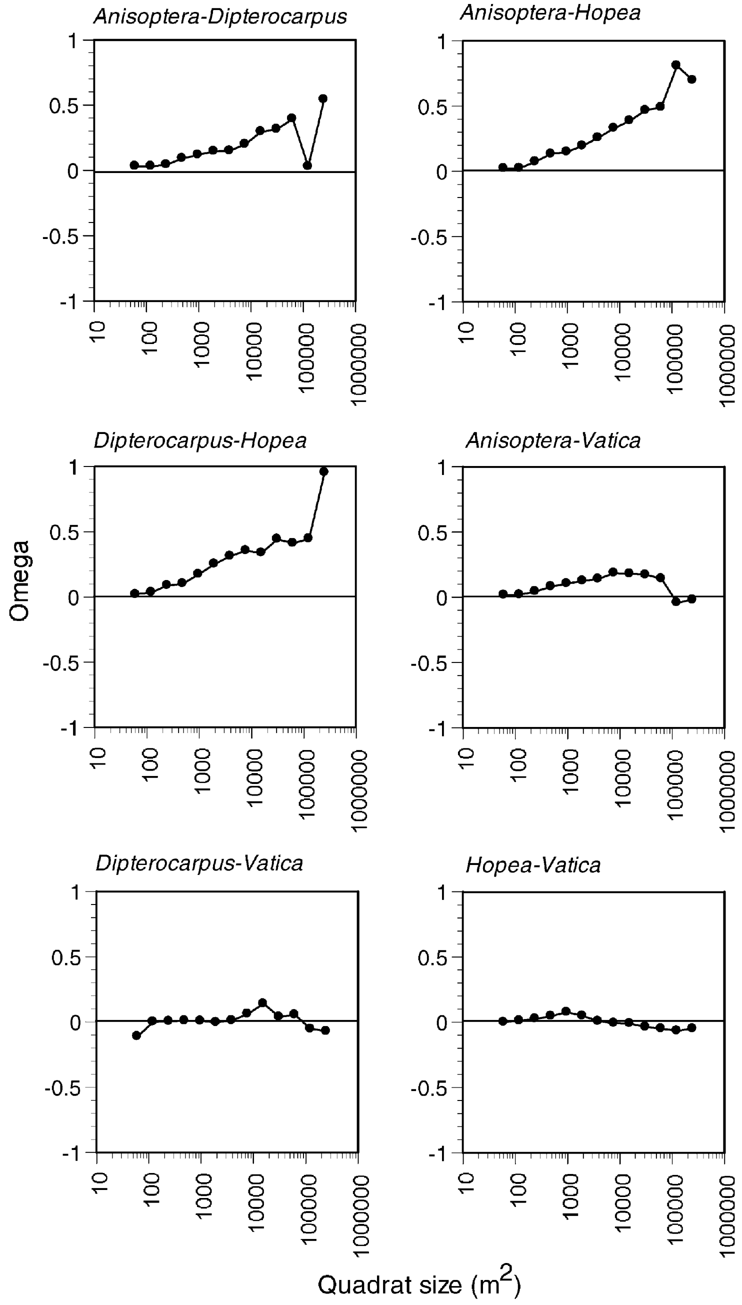

Fig. 7. Variation of Iwao's spatial association index, ω, between four dipterocarp species in the HKK 50 ha plot. Iwao's ω is zero for spatially independent distributions, positive to a maximum of $+1$ for overlapping populations (i.e., spatial attraction), and negative to -1 for non-overlapping populations (i.e., spatial repulsion).

interval ∼5 to 10 years) or (2) lack of suitable regeneration conditions, particularly with respect to available sunlight. Several pieces of evidence suggest that surface fires probably play only a minor role in limiting *Hopea* recruitment. First, all of the other dipterocarp species had a high proportion of individuals in the smallest size classes, suggesting that either *Hopea* is more susceptible to fire-induced mortality or that fire is not the determining factor in the regeneration gap for *Hopea*. Second, after a surface fire in 1998 that burned through ∼90% of the 50 ha plot, *Hopea* seedlings resprouted (P.J. Baker, personal observation). Third, fruiting events are highly supra-annual for *Hopea*. In 11 years of observations in and around the 50 ha plot, a general mast fruiting of *Hopea* occurred only twice (1994 and 2001; S. Bunyavejchewin and P.J. Baker, personal observation). In the other years fruiting was extremely rare. Such phenological observations suggest that recruitment limitation may be more a function of the rarity of reproductive events than fire-induced mortality.

In contrast to the population structure of *Hopea*, the other dipterocarps, *Anisoptera*, *Dipterocarpus* and *Vatica* have large numbers of juveniles. All three species grow well in small gaps (S. Bunyavejchewin and P.J. Baker, personal observation). The current disturbance regime, which is characterized by small gaps, provides ample opportunities for establishment and recruitment for these species.

4.2. Topographic and habitat specialization

The distribution of the four dipterocarps with respect to topographic variables such as elevation and slope, and habitat type is non-random. *Hopea* is positively associated with the lowest and flattest sites on the plot, most of which are located within a 100–200 m of the stream that passes through the northern section of the plot. *Vatica* is more common on slope sites than expected; the slope sites are restricted to the sides of the two hills in the center of the plot and are higher and steeper than other areas within the plot. *Dipterocarpus* is typically found on flat sites or sites with gentle slope and average elevation, although its distribution was not monotonically associated with any of the topographic variables.

Interpreting patterns of association between biotic and abiotic variables requires caution. While many studies have shown a strong correlation between a species and a topographic or edaphic variable, demonstrating causation requires controlled experiments in which the variable in question can be tested in isolation from other factors. In this study, species' distributions are highly correlated with elevation. However, environmental variables usually associated with elevation, such as ambient air temperature or partial pressure of oxygen, are unlikely to influence growth over the narrow range of elevations within the 50 ha plot. More likely, elevation is correlated with topographic and edaphic factors such as slope or proximity to the stream.

4.3. Spatial patterns

The ubiquity of clumped spatial distributions among tropical tree species is a well-established fact (Ashton, 1969; Richards, 1996; He et al., 1997; Condit et al., 2001). Poor dispersal of propagules and specialization for regeneration sites or establishment conditions may lead to such a pattern. The spatial scale of clumping for a given species is often related to the gap size at which the species is most likely to successfully regenerate. In tropical forests the vast majority of gaps are small—usually less than 500 m^2 (Brokaw, 1985). The spatial scale of clumping demonstrated in many studies is commensurate with the small gap sizes typical of gap-phase dynamics. Spatial pattern analysis of other 50 ha plots suggests that the relative frequency of spatial aggregation among tree species at HKK is comparable with other tropical forests, although the intensity of the aggregation may be greater at HKK than in more aseasonal forests (Condit et al., 2000). In this study, all four dipterocarp species were significantly clumped (Fig. 4); however, the scale at which clumping occurred was quite large when compared to other such studies. The smallest maximum clump size is 7800 m^2 (for *Vatica*), an order of magnitude larger than the largest gap size considered in most studies of gap dynamics (Brokaw, 1985). *Anisoptera*, *Dipterocarpus*, and *Hopea* are significantly clumped at scales from 1.5 to 3.1 ha. These results suggest that if disturbance structured the present forest community, it most likely occurred at larger spatial scales than would be expected from typical gap dynamics processes.

The relative proximity of juvenile trees to adult trees may be influenced by density- or distance-dependent patterns of mortality as well as the spatial distribution of suitable light levels required for germination and establishment (Hamill and Wright, 1986). Average crown projection of co-dominant and dominant dipterocarps is approximately 200 m^2 (P.J. Baker, unpublished data). At that scale none of the study species exhibit positive spatial association between juveniles and adults, implying recruitment limitation within the vicinity of conspecific adult trees. Juveniles (saplings and poles) of *Anisoptera* and *Hopea* are negatively associated (i.e., repulsion) with adults at scales less than 0.1–0.5 ha (Fig. 6). For *Dipterocarpus* and *Vatica* the distribution of juveniles is independent of adults at small scales. These results suggest that the stand conditions in the past that led to the recruitment of the current canopy trees were considerably different from the current stand condition.

Spatial repulsion between species provides indirect evidence of habitat segregation. In the present study none of the six species pairs exhibited repulsion. In general, the distribution of a given dipterocarp species was independent of other dipterocarp species at local scales and positively associated with other species at larger scales. The positive association between species may be an artifact of the relative paucity of dipterocarps in the southern half of the plot (Fig. 3).

It is not clear if the patterns of spatial dispersion and aggregation documented for the four dominant dipterocarp species at HKK are typical of other canopy tree species occurring in seasonal tropical forests in southeast Asia—no other studies have explicitly examined the spatial patterns of canopy species in continental southeast Asia.

However, the extent to which the patterns of spatial dispersion and association documented for the four dominant dipterocarp species occur in other forests in the region is unclear, as few studies have explicitly examined the spatial patterns of canopy species in the forests of southeast Asia. The only other such study demonstrated similar spatial patterns among canopy trees (i.e., prevalence of clumped populations, decreasing aggregation with tree size, decreasing aggregation with increasing spatial scale) in a 50 ha plot in aseasonal evergreen forest dominated by dipterocarps in peninsular Malaysia (He et al., 1997). Bunyavejchewin et al. (2001, in press) have shown that the seasonal dry evergreen forest at HKK is structurally and floristically representative of seasonal evergreen forests in continental southeast Asia, most of which are dominated by dipterocarp species. Further studies are needed to ascertain the generality of these results, but it is possible that they are common to southeast Asian forests dominated by dipterocarps.

4.4. Disturbance and forest structure

Based on an analysis of species composition and population structure in the study plot, Bunyavejchewin et al. (2001, in press) suggested that the current forest structure in the 50 ha plot may have arisen from a catastrophic disturbance and that prior to the disturbance the area may have been dominated by deciduous forest species, not evergreen forest species. The results of the spatial analyses support and extend this interpretation of the importance of historic disturbance in structuring the current forest community. Here, we describe a hypothesized scenario of stand development for the seasonal dry evergreen forest in the HKK 50 ha plot that is consistent with both previous results and the current analyses.

Based on the size and spatial structure of the dipterocarp populations in the 50 ha plot, we hypothesize that a catastrophic disturbance sometime in the past three centuries destroyed much of the forest canopy and allowed the broad-scale recruitment of a single age cohort of *Hopea* and *Anisoptera*, as well as scattered individuals of *Dipterocarpus* and *Vatica*. The forest that existed prior to the disturbance was most likely dominated by deciduous forest species in an association similar in composition to the current dry mixed deciduous forest at HKK (Bunyavejchewin et al., in press). Scattered individuals of *Dipterocarpus*, *Hopea*, and *Vatica* are known to occur in dry mixed deciduous forest at HKK (S. Bunyavejchewin, unpublished data from a 16 ha permanent forest dynamics plot in dry mixed deciduous forest located 4 km from the 50 ha plot). The short dispersal distance and lack of dormancy of dipterocarp seeds, combined with the abundance of the canopy dipterocarps in the present forest, suggest that several adult trees of each of the dipterocarp species must have survived the disturbance to provide viable seed sources for the post-disturbance cohort of dipterocarps.

Of the four study species, only *Hopea* is known to be restricted to a specific habitat, namely riparian fringes, in dry mixed deciduous forest in continental southeast Asia (Whitmore, 1984). Due to poor dispersal associated with large seeds, the majority of *Hopea* recruitment would have been limited to flat areas relatively close to the stream where adult trees would have occurred. The negative spatial association of *Hopea* with hilltops, ridges, and slope areas in the 50 ha plot is consistent with this pattern (Table 3 and Figs. 3 and 4). Individuals of *Anisoptera*, *Dipterocarpus*, and *Vatica* occurring in mixed deciduous forest are not typically associated with a specific habitat type (e.g., streams, slopes), but rather tend to occur as scattered individuals across the range of topographic sites (Smitinand et al., 1980). The general lack of positive associations with particular habitat types in the 50 ha plot is to be expected and the few negative habitat associations (e.g., *Anisoptera* on hilltops and ridges) are likely the consequence of the historical distribution of adult trees.

Stand development was dominated by the dipterocarps, particularly *Hopea* (see relative basal area by habitat type in Table 4) following the catastrophic disturbance. As the post-disturbance cohort grew to its full stature over the past century, mortality began to occur and single treefall gaps became more common. A second period of recruitment began for species capable of establishing and growing in the light conditions particular to small gaps. The population size structures of *Anisoptera*, *Dipterocarpus*, and *Vatica* all indicate that they have been able to establish new individuals under the regime of gap dynamics (Fig. 2). For *Dipterocarpus* and *Vatica*, the random or positive association of saplings and poles with respect to adults at spatial scales relevant to recruitment patterns of heavy seeded dipterocarps (<1 ha; Fig. 6) suggests a pattern of recruitment consistent with gap dynamics. In contrast, *Hopea*, which requires the high light conditions of large gaps to regenerate, has not established under the current disturbance regime of small gaps and has consequently developed an increasingly senescent population. Because the only successful *Hopea* recruitment in the 50 ha plot has occurred in a few relatively large gaps, the spatial distribution of saplings and poles is significantly clumped (Fig. 5) and negatively associated (i.e., repulsion) with adults at quadrat sizes <1000 m^2 (Fig. 6).

Based on analysis of the spatial patterns and population structures of the four dominant dipterocarp species we predict that in the absence of future catastrophic disturbance: (1) *Hopea* will gradually disappear from the plot due to senescence and fire-induced mortality of adults, (2) populations of *Vatica* and *Dipterocarpus*, which are capable of regenerating in small canopy gaps, will increase, (3) the future population structure of *Anisoptera* will depend on the ability of the current juveniles to recruit to the canopy.

Acknowledgements

The HKK FDP is a cooperative research project of the Royal Forest Department and the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute and has been funded in part through grants from the US National Science Foundation, the John D. and Catherine T. MacArthur Foundation, USAID/WWF, Conservation Food and Health, Inc., and the Merck Foundation. Many people have contributed to the success of the HKK FDP; to all of them we are deeply grateful. We wish to thank the staff of the HKK sanctuary for their support throughout. We would like to remember Dr. Tem Smitinand, one of the original principal investigators, and Mr. Pongsakorn Pattapong, who helped lay out the plot, both of whom passed away before the completion of the plot. We wish to thank E. Suzuki for permission to use the I-delta and Omega program, and S. Nanami for statistical advice.

References

Ashton, P.S., 1964. Ecological studies in mixed dipterocarp forests of Brunei state. Oxford Forestry Memories No. 25.

Ashton, P.S., 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. Biol. J. Linnean Soc. 1, 155–196.

Ashton, P.S., 1976. Mixed dipterocarp forest and its variation with habitat in the Malayan lowlands: a reevaluation at Pasoh. Malaysian For. 39, 56–72.

Ashton, P.S., 1982. Dipterocarpaceae. In: van Steenis, C.G.G.J. (Ed.), Flora Malesiana, Vol. 9, Series I. Martinus Nijhoff, The Hague, pp. 237–552.

Ashton, P.S., 1998. Niche specificity among tropical trees: a question of scales. In: Newbery, D.M., Brown, N.D., Prins, H.T.T. (Eds.), Dynamics of Tropical Communities. Blackwell Scientific Publications, Oxford, UK, pp. 491–514.

Ashton, P.S., Hall, P., 1992. Comparison of structure among mixed dipterocarp forest of northwest Borneo. J. Ecol. 80, 459–481.

Augspurger, C.K., 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. J. Ecol. 71, 759–771.

Augspurger, C.K., Kelly, C.K., 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. Oecologia 61, 211–217.

Basnet, K., 1992. Effect of topography on the pattern of trees in a tabonuco (*Dacryoides excelsa*) dominated forest of Puerto Rico. Biotropica 24, 31–42.

Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest. Ecology 66, 682–687.

Brokaw, N.V.L., 1985. Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbances and Patch Dynamics. Academic Press, New York, pp. 53–69.

Bunyavejchewin, S., LaFrankie, J.V., Pattapong, P., Kanzaki, M., Itoh, A., Yamakura, T., Ashton, P.S., 1998. Topographic analysis of a large-scale research plot in seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, Thailand. Tropics 8, 1–16.

Bunyavejchewin, S., Baker, P.J., LaFrankie, J.V., Ashton, P.S., 2001. Stand structure of a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. Nat. Hist. Bull. SIAM Soc. 49, 89–106.

Bunyavejchewin, S., Baker, P.J., LaFrankie, J.V., Ashton, P.S., in press. Floristic composition of a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. Nat. Hist. Bull. SIAM Soc.

Burkey, T.V., 1994. Tropical tree species: a test of the Janzen–Connell model. Oecologia 97, 533–540.

Champion, H.G., Seth, S.K., 1968. General silviculture for India. Government of India, Publication Branch, Department of Printing and Stationery, Delhi.

Condit, R., Hubbell, S.P., Foster, R.B., 1992. Recruitment near conspecific adults and the maintenance of tree shrub diversity in neotropical forest. Am. Nat. 140, 261–286.

Condit, R., Hubbell, S.P., Foster, R.B., 1994. Density dependence in two understory tree species in a neotropical forest. Ecology 75, 671–680.

Condit, R., Ashton, P.S., Baker, P.J., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., Hubbell, S.P., Foster, R.B., Itoh, A., LaFrankie, J.V., Hua Seng Lee, Losos, E., Manokoran, N., Sukumar, R., Yamakura, T., 2000. Spatial patterns in the distribution of tropical tree species. Science 288, 1414–1418.

Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer, P.J., Grandwell, G.R. (Eds.), Dynamics of Numbers in Populations. Center for Agricultural Publication and Documentation, Wageningen, pp. 298–312.

Duncan, R.P., Stewart, G.H., 1991. The temporal and spatial analysis of tree age. Can. J. For. Res. 21, 1703–1710.

Hamill, D.N., Wright, S.J., 1986. Testing the dispersion of juveniles relative to adults: a new analytic method. Ecology 67, 925–957.

Harms, K.E., Condit, R., Hubbell, S.P., Foster, R.B., 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. J. Ecol. 89, 947–959.

He, F., Legendre, P., LaFrankie, J.V., 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. J. Veg. Sci. 8, 105–114.

Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203, 1299–1309.

Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. In: Soule, M.E. (Ed.), Conservation Biology: The Science Scarcity and Diversity. Sinauer, Sunderland, MA, pp. 205–231.

Itoh, A., 1995. Regeneration processes and coexistence mechanisms of two Bornean emergent dipterocarp species. Ph.D. Dissertation. Kyoto University.

Iwao, S., 1977. Analysis of spatial association between two species based on the interspecies mean crowding. Res. Population Ecol. 18, 243–260.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528.

Lorimer, C.G., Krug, A.G., 1983. Diameter distributions in even-aged stands of shade-tolerant and midtolerant tree species. Am. Midland Nat. 109, 331–345.

Manokaran, N., LaFrankie, J.V., Kochummen, K.M., Quah, E.S., Klahn, J.E., Ashton, P.S., Hubbell, S.P., 1990. Methodology for the fifty hectare research plot at Pasoh Forest Reserve. Research Pamphlet No. 104. Forest Research Institute Malaysia, Kapong.

Morisita, M., 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. Mem. Fac. Sci. Kyushu Univ. Ser. E 2, 215–235.

Richards, P.W., 1996. The Tropical Rain Forest, 2nd Edition. Cambridge University Press, Cambridge.

Smitinand, T., Santisuk, T., Phengklai, C., 1980. The Manual of Dipterocarpaceae of Mainland Southeast Asia. Forest Herbarium, Bangkok, Thailand.

Whitmore, T.C., 1984. Tropical Rain Forests of the Far East. Clarendon Press, Oxford.

Wills, C., Condit, R., Foster, R.B., Hubbell, S.P., 1997. Strong density- and diversity-related effects helps to maintain tree species diversity in a neotropical forest. Proc. Natl. Acad. Sci. USA 49, 1252–1257.

Wyatt-Smith, J., 1963. Manual of Malaysian Silviculture for Inland Forests. Malayan Forest Records No. 23.

Yamada, T., Yamakura, T., Kanzaki, M., Itoh, A., Ohkubo, T., Ogino, K., Chai, E.O.K., Lee, H.S., Ashton, P.S., 1997. Topography dependent spatial pattern and habitat segregation of sympatric *Scaphium* species in a tropical rain forest at Lambir, Sarawak. Tropics 7, 57–66.

Yamakura, T., Kanzaki, M., Itoh, A., Ohkubo, T., Ogino, K., Chai, E.O.K., Lee, H.S., Ashton, P.S., 1995. Topography of a large scale research plot established within a tropical rain forest at Lambir, Sarawak. Tropics 5, 41–56.