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LOCAL DISTRIBUTION AND COEXISTENCE OF PREVALENT TREE SPECIES IN PEAT SWAMP FORESTS OF CENTRAL KALIMANTAN

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ABSTRACT

SIMBOLON, H. 2009. Local Distribution and coexistence of prevalent tree species in peat swamp forests of Central Kalimantan. *Reinwardtia* 12(5): 373–382. — A study on the distribution and coexistence of prevalent tree species in peat swamp forests was conducted at Lahei and Kelampangan, Central Kalimantan. The prevalent species in both sites were *Calophyllum canum*, *Combretocarpus rotundatus*, *Cratoxylum glaucum*, *Ctenolophon parvifolius*, *Elaeocarpus petiolatus,* with *Palaquium cochleariifolium* at Kelampangan, and *Buchanania sessifolia*, *Madhuca sericea*, *Semecarpus* sp., *Shorea balangeran*, *Tetractomia obovata* and *Vatica oblongifolia* at Lahei plot. The prevalent species were randomly distributed, however, when individuals were grouped into mature *vs* juvenile, the mature individuals of *C. parvifolius* tended to be clumped and the juvenile were randomly distributed; while in *C. rotundatus*, the mature individuals were randomly distributed and the juvenile were clumped. Pattern of the coexistence among the prevalent species in the study site were associated, and independent relationships, and almost no exclusion relationship was found. Independent and associated relationships among the coexisting species may be one of the explanations of the mechanism which maintain relatively high diversity of plant species in the tropical peat swamp forests, which has extreme habitat conditions and narrow habitat heterogeneity. Pattern of the coexistence relationships among mature *vs* juvenile individuals of the same species varied.

Key words: peat swamp forest, prevalent species, local distribution, coexistence, Central Kalimantan

ABSTRAK

SIMBOLON, H. 2009. Persebaran lokal dan kebersamaan jenis pohon utama di hutan rawa gambut Kalimantan Tengah**.** *Reinwardtia* 12(5): 373–382. — Penelitian terhadap pola persebaran dan hubungan kerbersamaan jenis-jenis pohon utama hutan rawa gambut telah dipelajari di Lahei dan Kelampangan, Kalimantan Tengah. Jenis-jenis dominan di kedua petak penelitian adalah: *Calophyllum canum*, *Combretocarpus rotundatus, Cratoxylum glaucum*, *Ctenolophon parvifolius*, *Elaeocarpus petiolatus* dan *Palaquium cochleariifolium* di Kelampangan; dan *Buchanania sessifolia*, *Madhuca sericea*, *Semecarpus* sp., *Shorea balangeran*, *Tetractomia obovata* dan *Vatica oblongifolia* di Lahei. Secara umum, persebaran lokal jenis-jenis utama di kedua petak penelitian umumnya adalah acak. Akan tetapi, pada pengelompokan individu antara induk *vs* juvenil, induk *C. parvifolius* memperlihatkan kecenderungan persebaran yang mengelompok sedangkan juvenilnya acak; sebaliknya induk jenis *C. rotundatus* tersebar secara acak sedang juvenilnya mengelompok. Pola hubungan kebersamaan antar jenis di dalam petak penelitian umumnya adalah asosiasi tumpang tindih, dan tidak saling tergantung; kecenderungan pola hubungan bersaing yang saling meniadakan hampir tidak ada. Pola hubungan tidak tergantung dan saling berasosiasi antar sesama jenis utama adalah merupakan salah satu penjelasan mengenai mekanisme yang menjaga keanekaragaman relatif tinggi di hutan gambut dengan keadaan lingkungan yang ekstrim. Pola hubungan induk *vs* juvenil dalam jenis yang sama terlihat berbeda antara satu jenis dan jenis lainnya.

Kata kunci: hutan rawa gambut, jenis utama, persebaran lokal, kebersamaan, Kalimantan Tengah

INTRODUCTION

Natural vegetation of many tropical areas contains many plant species (Richards 1952; Whitmore, 1984; Okuda *et al*., 1997). The number of tree species per ha in lowland of mixed dipterocarp forests, for example, ranges between 94–362 species, heath forests ranges between 121–151 species and peat swamp forests ranges between 72–81 species (see Kartawinata *et al.,* 2008; Simbolon, 2008). Tree species composition in tropical rain forest also varies with habitat (Richards, 1952) and tree distributions are often associated with environmental factors (Baillie *et al*., 1987; Cannon & Leighton, 2004; Clark *et al*., 1998; Lieberman *et al*., 1996; Miyamoto *et al*., 2003; Newbery & Proctor, 1984; Pendry & Proctor, 1997; Sollins, 1998; Swaine, 1996).

Coexistence of some species in a community may occur because habitats naturally vary and each species has its own morphological, niche and plasticity adaptations. The spatial pattern of distribution of each species in an ecosystem might be random or agregated, and the pattern may be related to the propagules, adaptations, agents of dispersal, patterns of relationships among coexisting species and its interaction with habitat and environments. The relationships among coexisting species might be spatial overlapping (associated), independent or exclusive (possibly as a result of competition). Naturally, if species live in different habitats, have different needs for resources and have no direct or indirect interactions with each other, or when habitats offer unlimited resources, they should have no difficulty coexisting in a region containing these separate habitats (Chesson, 2000b). However, species do not have to be strictly segregated in space for regional coexistence; resources are often limited, and species have direct and indirect competition for nutrients, space, light and others. As a result, species or individuals may reduce the access of other species or individuals to a necessary resource that is in limited supply; this is called competition (Palmer *et al*., 2003). Communities with many competitive species are ubiquitous in nature (Tilman, 1982; Shiyomi & Yoshimura, 2000). Species experience greater intraspecific than interspecific competition in favorable areas and vice versa in unfavorable areas (Chesson, 2000*a*, 2000*b*).

Both non-equilibrium and equilibrium theories have been proposed to account for species richness in tropical rain forests (Hubbell & Foster, 1986; Whittaker, 1975; Okuda *et al*., 1997). Further, Hubbell & Foster (1986) emphasized that it is impossible to explain species richness by niche differentiation, and treated non-equilibrium forces as the working mechanism of species richness. The pattern of relationships among coexisting species in a community have been also approached with mathematical models (see Iwao, 1977; Chesson, 2000a; 2000b; Nishimura *et al*., 2002; Amrasekare *et al*., 2004 and Palmer *et al*., 2003) studied the mechanisms that restrict and maintain diversity within mutualist guilds.

Relevant studies on the spatial distribution of tree species have been conducted in some areas in South and Southeast Asia. These include the spatial distribution of *Elatiospermum tapos* in West Kalimantan (Simbolon *et al.,* 2000), local and geographical distributions for a tropical tree genus *Scaphium* (Yamada & Suzuki, 1997, Yamada *et al*., 2000), tree species distributions across five habitats in a Bornean rain forest (Cannon & Leighton, 2004), tree distribution pattern and fate of juveniles in a lowland tropical rain forest, Malaysia (Okuda *et al*., 1997), spatial patterns in the distribution of tropical tree species (Condit *et al*., 2000), tree diversity and distribution in undisturbed and human-impacted sites of tropical wet evergreen forest in southern Western Ghats, India (Parthasarathy, 1999). The present paper intends to discuss the local distribution and pattern of relationship among coexisting of prevalent tree species in peat swamp forests of Kelampangan and Lahei, Central Kalimantan in relation to high tree diversity under extreme habitat conditions.

METHODS

Study sites

A 1-ha plot (100 m x 100 m) was established in two sites of peat swamp forest of Central Kalimantan, those are: P-L plot at Lahei and P-K at Kelampangan. The Lahei site is located in the area approximately 3–4 km east from Kampung Babugus, Desa Lahei, Kecamatan Mentagai, Central Kalimantan. The average annual precipitation (1993–1999) was about 2800 mm. Although the monthly rainfall was over 100 mm in most months, a few months especially July and August occasionally was less than 100 mm of rain. Most of the area is covered with heath forest, while patches of peat swamp forest (up to 7 m peat depth) occured along the Mangkutup River, a branch of Kapuas River (for detail see Miyamoto *et al*., 2003, Nishimura & Suzuki, 2001, Nishimura *et al*., 2007 and Haraguchi *et al.,* 2000).

P-K plot is located between Sebangau river and Kahayan river, with peat depth of 3-5 m. The Kelampangan area is a remnant of peat swamp forest selectively logged in the 1980s and also included in the 1990s mega rice project of Central Kalimantan, the so called *Proyek Lahan Gambut Satu Juta Hektar.* A man-made canal, 6–8 m wide, running from north to south about 200 m to the west of the P-K plot, to drain the water of peat swamp, was established during the project.

Field survey

After a reconnaissance study to explore the general conditions of the peat swamp forests, the 1-ha plots were set up. They were divided into 100 sub-plots of 10 x 10 m^2. All trees with stem girth at breast height (*gbh,* or at 130 cm above the ground) of more than 15 cm (or about 4.8 cm in diameter at breast height, DBH) were individually numbered with aluminum tags, their positions were mapped, and their *gbh* was measured. Voucher specimens were taken for further species identification in the Herbarium Bogoriense.

Based on these measurements, total basal areas, number of species, number of individuals of each species and diversity index in each plot were determined. Plant position within the plots were analyzed using Morisita's indices of dispersion, and Iwao's indices of association, for each prevalent species. The prevalent species in the P-K plots have been reported in Simbolon (2003), while those in the P-L plot have been reported in Nishimura *et al*., (2007) and Simbolon (2002, 2008). The prevalent species in this paper are the top five species for total basal area and number of individuals. The paper also deals with intraspecific relationships between juveniles (5–25 cm DBH) and mature individuals (> 25 cm DBH) of the prevalent species.

The local distribution pattern of individuals of the prevalent species within the plot was examined by the Morisita's index of dispersion, I_δ (see Morisita, 1959, 1962). The formulas for these indices have been translated by Suzuki (unpublish, pers. comm.) into a macro for Microsoft Excel. When the Morisita index is 1, individuals are randomly distributed, with aggregated individuals having a value larger than 1. The pattern of relationships among coexisting species within a plot was examined by Iwao's indices of association, $I\,\omega$ (see Iwao, 1977). When the index is +1, both spe-cies are overlapping (associated), when index is 0 both species are independently distributed, and both species are in complete exclusion (possibly due to competition) when the index is -1.

RESULTS

Prevalent Species

The density of trees in both studied plots of peat swamp forests were very high, especially at Kelampangan where the soil water level is getting progressively lower and lower due to the presence of man-made canals in the areas, which drain the water from peatland and flow to the sea. The tree density at Lahei plot was lower than that at Kelampangan, but the total basal area of trees at Lahei plot was higher than that at Kelampangan (Table 1), possibly indicating that forest succession at peat swamp of Lahei was more advanced than that at Kelampangan. This interpretation was also supported by the data on the diameter class distribution of tree trunks, and the largest trunk diameter of trees and the average numbers of individuals of each species in both study plots. *Calophyllum canum* had the highest density of 324 individuals per ha among the prevalent species in the 5–10 cm diameter class at the Kelampangan plot, but the species with the highest trunk diameter, of 65 cm, was *Combretocarpus rotundatus*. At Lahei, the most abundant species in the 5–10 cm diameter class was *Buchanania sessifolia,* having a density of only 14 individuals per ha; this was also the species with the biggest trunk diameter that reaching up to 105 cm.

Table 1. The number of individuals (TN) and total basal areas (BA, m^2/ha) of the top five most prevalent species within 1ha plot of peat swamp forest at Kelampangan and Lahei, Central Kalimantan.

No	Species	Family	Peat swamp forest			
			Kelampangan		Lahei	
			TN	BA	TN	BA
1	*Buchanania sessifolia*	*Anacardiaceae*			147	6.296
2	*Calophyllum canum*	*Guttiferae*	515	3.914		
3	*Combretocarpus rotundatus*	*Rhizophoraceae*	36	4.824		
4	*Cratoxylom glaucum*	*Hypericaceae*	125	2.107		
5	*Ctenolophon parvifolius*	*Olacaceae*	350	3.167	3	0.009
6	*Elaeocarpus petiolatus*	*Elaeocaroaceae*	183	1.221		
7	*Madhuca sericea*	*Sapotaceae*			127	4.574
8	*Palaquium cochleariifolium*	*Sapotaceae*	355	4.259		
9	*Semecarpus* sp. [umpa]	*Anacardiaceae*			161	8.903
10	*Shorea balangeran*	*Dipterocarpaceae*	2	0.216	24	8.321
11	*Tetractomia obovata*	*Rutaceae*	1	0.003	150	1.322
12	*Vatica oblongifolia*	*Dipterocarpaceae*			237	2.125
	Number of trees		3074		1590	
	Number of species		81		72	
	Number of trees / species		37.95		22.08	
	Basal area (m^2/ha)			34.14		45.58
	Fisher Diversity Index		15.02		15.25	
	Number of trees D>10cm		1084		700	
	Number of species D>10cm		54		52	

The trunk diameter class distribution of trees and some selected species at both study sites showed inverse *J*-shaped curves (Fig 1). The inverse *J*-shaped curve of the Kelampangan plot was much steeper than that of the Lahei plot for *Calophyllum canum*, indicating that the density of juvenile individuals at Kelampangan was higher than that at Lahei. The density of trees of 5-25 cm class diameter at Kelampangan was higher than that at Lahei, meanwhile the density of large trunks of more than 25 cm in diameter at Kelampangan was lower than that at Lahei, although the density of trees was much lower.

Table 1 shows the numbers of individuals and total basal areas of tree trunk of the top five prevalent species in each of the study plots. Beside the demography of composing species and stages of succession of the forests discussed above, the species composition of the study sites also shows a great difference. Among 145 species recorded in two 1-ha plots, only 8 species occurred in both plots, *i.e. Tetramerista glabra, Tetractomia obovata, Pternandra coerulescens, Nephelium maingayi, Lophopetalum beccarianum*, *Diospyros hermaphroditica*, *Ctenolophon parvifolius* and *Shorea balangeran*.

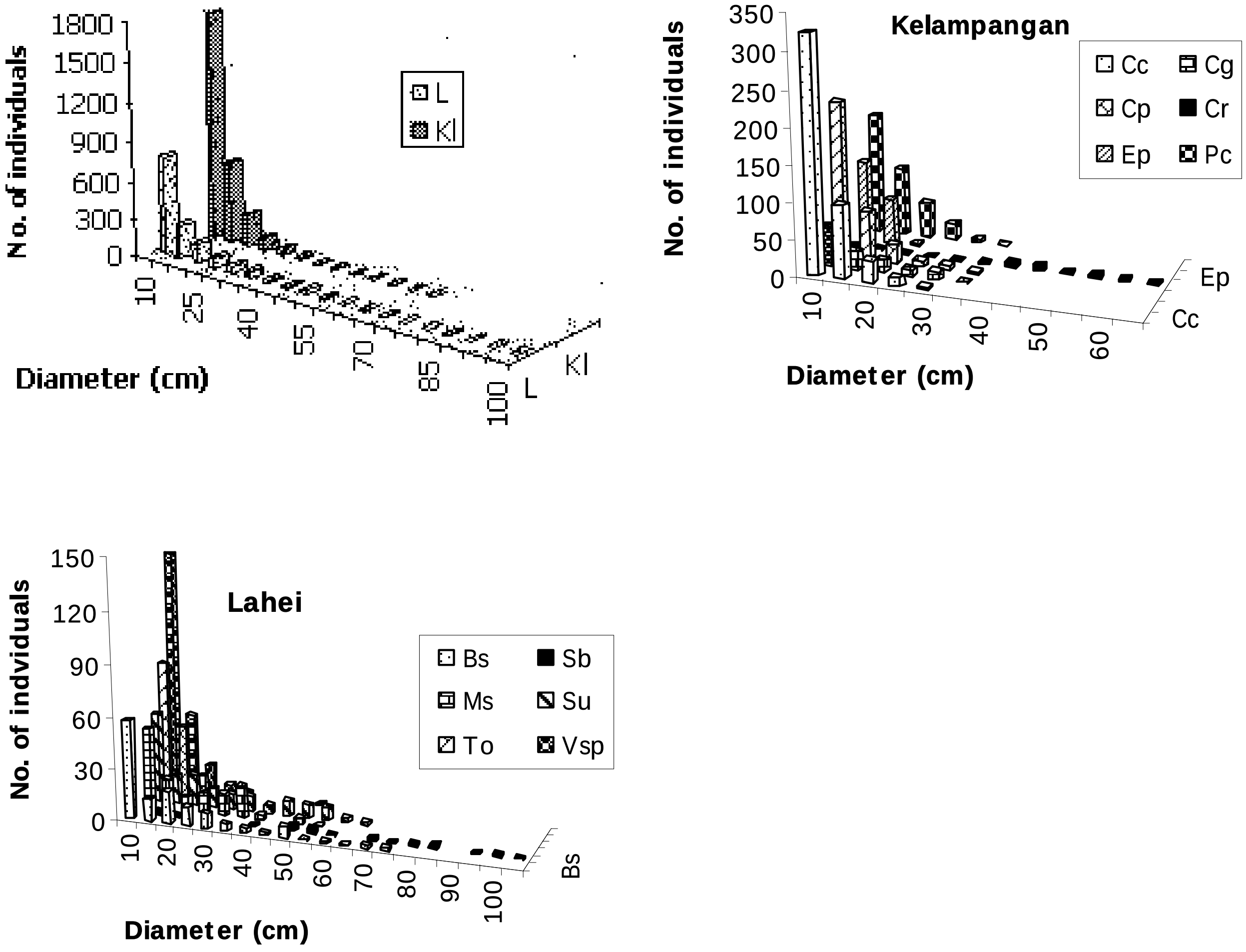

Fig. 1. Trunk diameter class distribution of all species in L: Lahei and Kl: Kelampangan (upper left), and prevalent species at Kelampangan: (Cc: *Calophyllum canum,* Cr: *Combretocarpus rotundatus*, Cg: *Cratoxylum glaucum*, Cp: *Ctenolophon parvifolius,* Ep: *Elaeocarpus petiolatus* and Pc: *Palaquium cochleariifolium*) and Lahei: (Bs: *Buchanania sessifolia,* Ms: *Madhuca sericea*, Su: *Semecarpus* sp. [umpa], Sb: *Shorea balangeran*, To: *Tetractomia obovata* and Vsp: *Vatica oblongifolia*).

Local distribution of prevalent species

Based on the Morisita's (1959, 1962) indices of dispersion, the distributional pattern of trees of prevalent species in peat swamp forest at Kelampangan was random, except for *C. rotundatus* which was slightly aggregated when the number of subplots was larger (50 subplots). Similarly the distributional pattern of prevalent trees in the peat swamp forest of Lahei was also random (Fig. 2).

Pattern of relationships among coexisting species

The results of analysis of the Iwao's (1977) indices show that the pattern of relationships among coexisted prevalent tree species in Kelampangan areas, some tended to be independent and some others were overlapping (associated), and almost no values indicated exclusion (competition) relationships (Fig. 3). *Calophyllum canum* showed an overlapping relationship with four other prevalent species, *i.e.*: *C. rotundatus*, *C. glaucum*, *C. parvifolius*, *E. petiolatus*, and the species performed an independent relationship with *P. cochleariifolium* (Fig. 3a). *C. rotundatus* had an overlapping relationship with *C. parvifolius* and *P. cochleariifolium,* but showed an independent relationship with *C. glaucum,* and slightly indicated a competitive (exclusion) relationship with *E. petiolatus*; meanwhile, *E. petiolatus* indicated an overlapping relationship with *P. cochleariifolium* (Fig. 3b). The relationship between *C. glaucum* and *E. petiolatus*; *C. glaucum* and *P. cochleariifolium*; *C. parvifolius* and *P. cochleariifolium,* and *C. parvifolius* and *E. petiolatus* was independent, *C. glaucum* and *C. parvifolius* were associated (Fig. 3c).

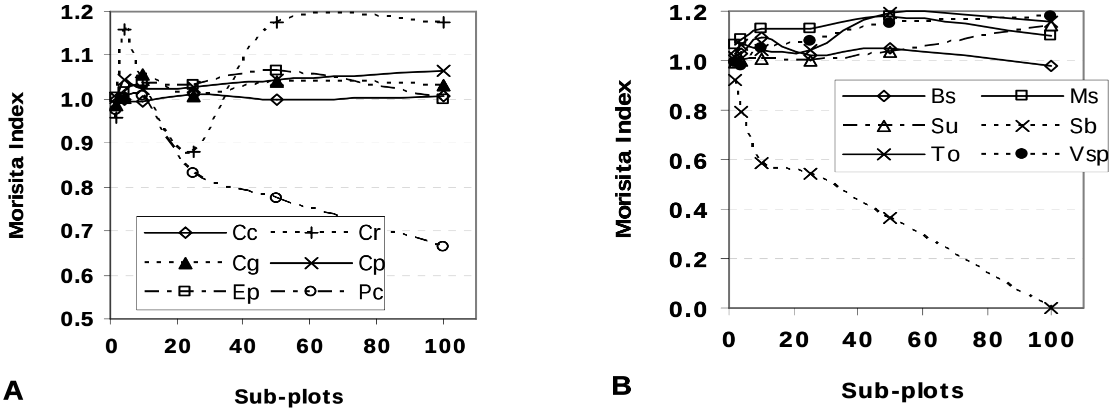

Fig. 2. Morisita's indices of dispersion versus spatial scale for tree prevalent species in peat swamp forest at Kelampangan **(A):** (Cc: *Calophyllum canum*, Cr: *Combretocarpus rotundatus*, Cg: *Cratoxylum glaucum*, Cp: *Ctenolophon parvifolius*, Ep: *Elaeocarpus petiolatus* and Pc: *Palaquium cochleariifolium*); and Lahei (**B**): (Bs: *Buchanania sessifolia*, Ms: *Madhuca sericea*, Su: *Semecarpus* sp[umpa], Sb: *Shorea balangeran*, To: *Tetractomia obovata* and Vsp: *Vatica oblongifolia*)

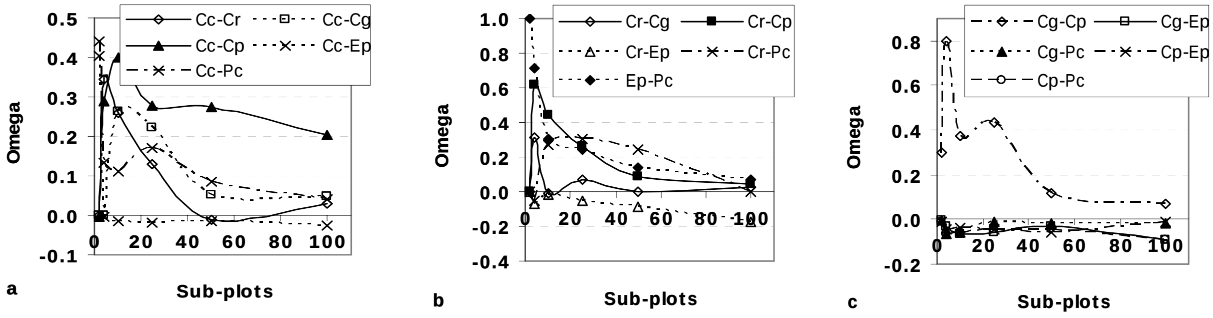

Fig. 3. Iwao's indices of association (Omega) between two species of coexisting species in peat swamp forest at Kelampangan**:** (Cc: *Calophyllum canum*, Cr: *Combretocarpus rotundatus*, Cg: *Cratoxylum glaucum*, Cp: *Ctenolophon parvifolius*, Ep: *Elaeocarpus petiolatus* and Pc: *Palaquium cochleariifolium*).

As in Kelampangan, Iwao's association indices of the coexisting prevalent tree species in peat swamp forests at Lahei site also indicated an independent or overlapping (association) relationship (Fig. 4). The pattern of overlapping relationships among two coexisting species was obvious between *B. sessifolia* and *T. obovata*; *B. sessifolia* and *S. balangeran* (Fig. 4a); *M. sericea* and *Vatica* oblongifolia (Fig. 4b); *Semecarpus* sp. [umpa] and *Vatica* oblongifolia; *Semecarpus* sp. [umpa] and *S. balangeran*; and *S. balangeran* and *T. obovata* (Fig. 4c). An independent relationship is shown by *B. sessifolia* and *M. sericea*; *B. sessifolia* and *Semecarpus* sp. [umpa]; *B. sessifolia* and *Vatica oblongifolia* (Fig. 4a); *M. sericea* and *Semecarpus* sp. [umpa]; *M. sericea* and *T. obovata*; *M. sericea* and *S. balangeran*; *T. obovata* and *V. oblongifolia* (Fig. 4b), and *Semecarpus* sp. [umpa] and *T. obovata,* and between two species of *Dipterocarpaceae,* between *S. balangeran* and *V. oblongifolia* (Fig. 4c).

Intraspecific relationship: mature vs *juvenile individuals*

When the individuals of each prevalent species were categorized into juvenile and mature stages for analysis of intraspecific relationships, some species had groups of less than 10 individuals and were excluded from analysis of Morisita's indices of dispersion and Iwao's indices of association. These excluded groups from Kelampangan site included: mature trees of *C. canum* and *E. petiolatus*; and from Lahei site were juvenile individuals of *S. balangeran*; and mature trees of *T. obovata* and *V. oblongifolia*.

Based on the Morisita's indices of dispersion, two prevalent species from Kelampangan site showed an different pattern of distribution between juvenile and mature individuals. The distribution pattern of the mature individuals of *C. parvifolius* were clumped while its juveniles were random; conversely, the mature individuals of *C. rotundatus* were random while its juvenile were clumped. The distributional pattern of the mature and juvenile individuals of other tree prevalent species were random. At the Lahei site, the distributional pattern of the juvenile and mature individuals of the prevalent species were random (Fig. 5).

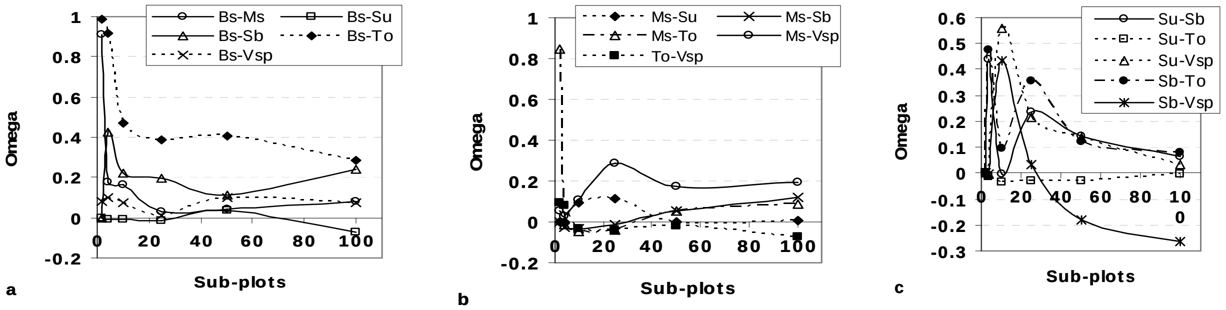

Fig. 4. Iwao's indices of association (Omega) between two species of coexisting species in peat swamp forest at Lahei**:** (Bs: *Buchanania sessifolia*, Ms: *Madhuca serices*, Su: *Semecarpus* sp. [umpa], Sb: *Shorea balangeran*, To: *Tetractomia obovata* and Vsp: *Vatica oblongifolia*)

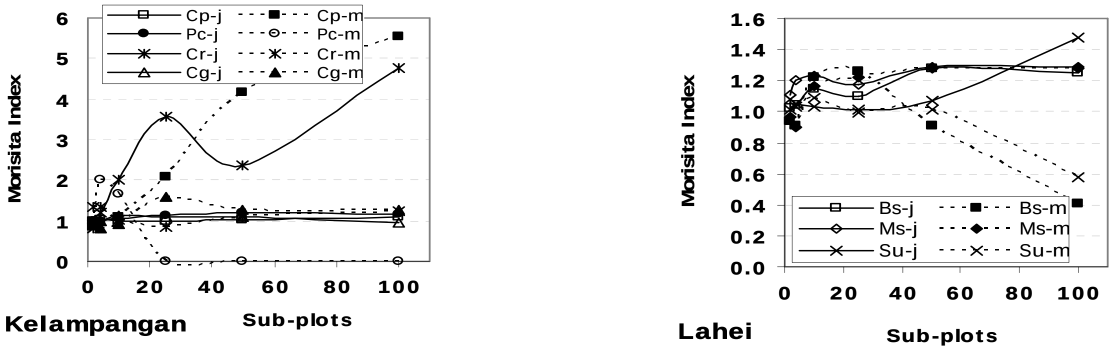

Fig. 5. Morisita's indices of dispersion versus spatial scale for mature (m) and juvenile (j) individuals of the same species in peat swamp forest at Kelampangan**:** (Cr: *Combretocarpus rotundatus*, Cg: *Cratoxylum glaucum*, Cp: *Ctenolophon parvifolius*, Pc: *Palaquium cochleariifolium*), and Lahei: (Bs: *Buchanania sessifolia*, Ms: *Madhuca serices*, Su: *Semecarpus* sp. [umpa]).

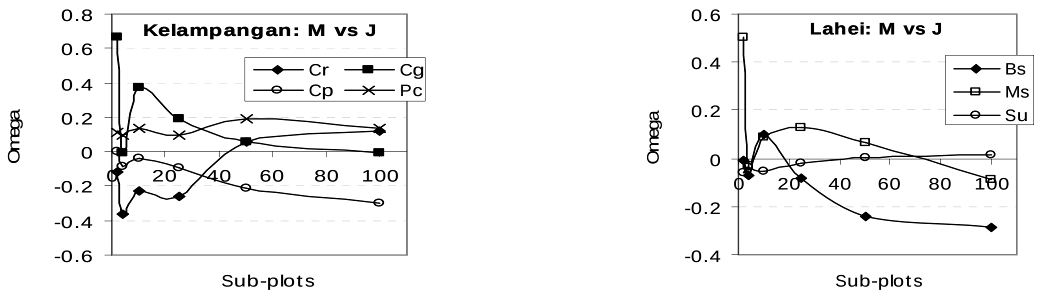

Fig. 6. Iwao's indices of association (Omega) versus spatial scale for mature (M) and juvenile (J) individulas in peat swamp forest at Kelampangan**:** (Cr: *Combretocarpus rotundatus*, Cg: *Cratoxylum glaucum*, Cp: *Ctenolophon parvifolius*, dan Pc: *Palaquium cochleariifolium*), and Lahei: (Bs: *Buchanania sessifolia*, Ms: *Madhuca sericea*, Su: *Semecarpus* sp. [umpa]).

Based on the Iwao's indices of association, the pattern of relationships between juvenile and mature individuals of the prevalent species varied. The pattern of relationships between juvenile and mature individuals of *C. glaucum* and *P. cochleariifolium* at Kelampangan site were overlapping (associated); and the patterns were exclusion (competitive) for *C. parvifolius* and *C. rotundatus* (Fig. 6). The pattern of relationship between mature and juvenile individuals of *Semecarpus* sp. [umpa] at Lahei site was independent, however, the pattern was associated for *B. sessifolia* and *M. sericea* (Fig. 6).

DISCUSSION

The densities of trees in the peat swamp forest studied were very high compared to that of other forest types in the lowlands of tropical areas. The range of densities of trees with dbh greater than 10 cm in tropical areas is 245–859 individuals per ha (Richards, 1952; Ashton,1964; Manokaran & LaFrankie, 1990; Campbell *et al.,* 1992; Condit *et al.,* 1996; Lieberman *et al.,* 1996; Kartawinata *et al.,* 2008). The great difference of tree densities between two study sites is mainly due to different ages of the forests, and to the selective logging conducted in 1980s in the peat swamp forest of Kelampangan (Simbolon, 2003). As the results, there are many small (juvenile) individuals, with the biggest trunk diameter in Kelampagan at present of only 65 cm, while in Lahei there are only few small individuals and the dbh of the biggest trunks reached up to 105 cm.

The number of species in the study sites is categorized as high (81 and 72 species per ha, respectively), although not as high as the mixed dipterocarps forest that may reached up to 94–362 species per ha (Kartawinata *et al*., 2008, Simbolon, 2008). This is attributed to the environmental conditions of the peat swamp forests of the study sites, whose soils are extremely acids, low in available nutrients, anaerobic and consisting mainly of organic materials. It is, however higher in comparison to the number of tree species of only 63 species in 50 ha deciduous forest of Mudumalai, Southern India, where the mineral soils are well drained (Condit *et al*., 1996).

The prevalent species in the study sites are commonly found in peat swamp forests of Kalimantan (Anderson, 1963, 1972; Simbolon & Mirmanto, 2000). However, only 3 out of 12 prevalent species were distributed in both study plots, indicating that the tree beta-diversity in the peat swamp of the study sites was relatively high, and the prevalent species in other site may be different. Anderson (1963) reported about 376 plant species in peat swamp forests of Sarawak and Brunei, and Simbolon & Mirmanto (2000) reported 310 plant species in peat swamp forests of Central Kalimantan. As have been mentioned above also, only 8 out of 145 species occurred in both plots. The results of the present study is in line with Richards (1952) and Okuda *et al*. (1997) who stated that species composition of tropical forest varies from site to site.

The pattern of local distribution of prevalent species in both study sites were mostly random. Observed distribution patterns were the result of responses of plants to the abiotic environment in combination with biotic interactions, such as seed dispersers, natural enemies and competitors (Kneitel & Chase, 2004; Russo *et al*., 2005). Aggregated tree distributions, for example, can also be established and maintained by niche segregation and dispersal limitation, *i.e.,* the failure of seeds to reach all possible recruitment sites, as well as intra- and inter-specific interactions, such as competition and pathogen-pressure (Janzen, 1970; Condit *et al*., 2000; Hubbell, 2001; Dalling, *et al*. 2002, Russo *et al*., 2005).

Some prevalent species, such as two species of *Dipterocarpaceae* (*S. balangeran* and *V. oblongifolia*) and *C. rotundatus* have fruits which are slightly adapted to wind dispersal. These fruits, however, could not be dispersed by wind quite far from the parent trees, but the adapted fruit parts and water may help the fruits to find suitable niches for growing, and to be randomly distributed. As for the other prevalent species which have fruits with dispersal limitation, the random distribution might be caused by the physical condition of peat swamp forest, such as flat topography and annual periodic inundation, especially during the rainy seasons. During the inundated periods in rainy season, the flat condition of the peat swamp forest ground makes it possible for water to transport and disperse fruits to any direction reaching suitable niches to grow. Again, the peat land with inundated conditions and homegenous organic materials may lead to the formation of a homogenous habitat, and less niche segregation compared to forests with well drained mineral soils. As has been mentioned above, niche segregation will contribute to the aggregated tree distribution (Condit *et al*., 2000; Hubbell, 2001; Dalling *et al*., 2002, Russo *et al*., 2005).

The pattern of relationships among the coexisting prevalent tree species in the study sites varied: some were independently distributed and some others were overlapping (associated) and almost none showed an exclusive (competitive) relationship. Independent and associated relationships among the coexisting species may help maintain relatively high diversity of plants in the tropical peat swamp forests, which have extreme habitat conditions and low habitat heterogenity. Some researchers have explained that the mechanisms which operated in the maintenance of high diversity in tropical forests include habitat heterogenity (*e.g.* Grubb, 1977; Nakashizuka *et al*., 1992; Rebertus and Veblen 1993; Manabe *et al*., 2000), specialization on narrow niches (Ashton, 1969; MacArthur, 1969; Tilman, 1982; Russo *et al*., 2005) but that most tropical tree species belong to a large habitat generalist guild (Hubbell & Foster, 1986).

The distributional patterns of juvenile and mature individuals of the same species on *C. parvifolius* and *C. rotundatus* are quite different with the distributional pattern of all individuals of the prevalent species in the study sites, which are randomly distributed. The mature individuals of *C. parvifolius* show an agregated distributional pattern while its juvenile individuals are random; conversely, the mature individuals of *C. rotundatus* show a random distributional pattern while its juvenile individuals are agregated. The pattern of intraspecific relationships between coexisting mature and juvenile individuals of both species show an exclusion relationships, which indicate that there may be competition between mature and juvenile individuals (Harada & Iwasa, 1994; Harada, 1999). As has been discussed above, seeds of *C. rotundatus* and *C. parvifolius* might be dispersed farther from the parent trees. Nakashizuka (2001) has summarized three important advantages of the long distance dispersal of seed, such as: avoiding high mortality near the parent plant due to specific enemies (escape or Janzen–Connell hypothesis); increasing the probability of finding a suitable (safe) site for establishment (colonization hypothesis), and reducing sibling competition (see also Janzen, 1970; Howe & Smallwood, 1982; Willson, 1993; Takeuchi *et al.*, 2005).

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