Reciprocal Interactions between Carbon Storage Function and Plant Species Diversity in a Tropical Peat Swamp Forest

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Abstract

Although carbon storage in ecosystems and biological diversity have been central issues of environmental and ecological sciences for a decade, a reciprocal relationship between diversity and productivity of ecosystems is still unknown. To reveal such the reciprocal relationship, we measured the microtopography around some tree groups, estimated flows and stocks of organic matters in soils in the form of litters and roots under three kinds of microtopographic conditions, measured decomposition rates, and detected the shift of distribution patterns of dominant species among growing stages in relation to locations of tree groups creating specific microtopographic conditions in a tropical peat swamp forest. The results suggest that heterogeneity of peat accumulation rate results in undulating peat surface. Such undulating peat surface contributes to habitat differentiation of tree species, because subtle difference in peat surface elevation determines the degree of flooding, which affects survival rates of plants differently according to species. Such the distribution of plant species formed through the above process determines local regime of organic matter dynamics that determines peat surface conditions of near futures. Thus, in tropical peat swamp forests diversity and productivity were closely interdependent to each other, although the diversity has attracted less attention than carbon storage function.

1. Introduction

Biological diversity and the ecosystem function of carbon storage have attracted considerable interest in relation to global environmental issues. Higher species and/or functional diversity of plants results in higher productivity [Hector *et al.* 1999; Tilman *et al.* 2001; Reich *et al.* 2004]. Recently, some studies have pointed out that other factors, such as the history of the community assemblage [Fukami and Morin 2003] and facilitative interactions among plant species [Mulder *et al.* 2001], affect diversity-productivity relationships. Facilitative interactions often include the carbon assimi-

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lation process. Through the carbon assimilation process, some influential plant species develop land cover. As a result, many species of smaller plants are protected from direct sunlight, winds, moving sands, waves, or predation [Pugnaire *et al*. 1996; Bruno and Kennedy 2000; Forseth *et al*. 2001; Quested *et al*. 2003; Tirado and Pugnaire 2003]. Growth of other plant species is also enhanced through the turnover of nutrient-rich leaves [Quested *et al*. 2003]. However, diversity-productivity relationships have been treated as one-sided interactions, with diversity as the causative factor and productivity as the result. Here, we introduce reciprocal relations between biodiversity and productivity as determining carbon storage abilities.

Tropical peat swamp forests contain important biodiversity [Dennis and Aldhous 2004] and play a significant role in carbon storage [Brady 1997; Page *et al*. 1999, 2002]. In tropical peat swamp forests, the peat surface is characterized by considerable topographic heterogeneity at various scales, ranging from tens of centimeters to several meters [Brady 1997; Page *et al*. 1999]. The large buttressed trees have large amounts of roots supporting the aboveground organs. The root architecture raises the peat surface around the buttresses and forms mounds. Some species have numerous pneumatphores that enable root respiration during flooding. Such species are found in non-mounded areas, whereas juveniles of other species are found on mounds.

Tropical peat swamp forests are appropriate ecosystems for studying the relationships between diversity and carbon storage for three reasons. First, plant activities regulate the conditions of the peat surface (mounded or non-mounded) at small scales. Peat that supports the terrestrial ecosystem originates from plant materials. The surface peat materials were deposited during the modern age (post 1950 AD) [Maloney and McCormac 1995; Brady 1997], and peat surface properties are vulnerable to organic matter input and decomposition. Organic matter dynamics at small scales (2-20 m) determine the conditions of peat surfaces, i.e., mounds and non-mounds. Where production exceeds decomposition, peat surfaces rise and mounds are created. Where the rate of decomposition exceeds production, peat surfaces sink. Production at small scales is greatly affected by large individuals of some tree species. Thus, large-tree distribution determines the conditions of the peat surfaces (mound or non-mound) at small scales. Here, one can assume a spatial association between specific microtopography and large individuals of specific trees. For example, huge-buttressed trees have mounded sites around them, whereas individuals without buttresses do not. Such differences in microtopography are caused by differences in production and decomposition regimes.

Second, the relative positions of the soil surface and the water table strongly regulate plant distribution [Keddy 1983; Huenneke and Sharitz 1986; Pollock *et al*. 1998; Denneler *et al*. 1999; Castelli *et al*. 2000], seedling survival [Budelsky and Galatowitsch 2000], and seedling germina-

tion [Seabloom *et al.* 1998; Smith *et al.* 1995], in wetlands. A similar phenomenon of the effect of humus depth on the spatial distribution of plant species at small scales is observed in tropical heath (*kerangas*) forests [Miyamoto *et al.* 2003]. Therefore, established individuals associated with specific microtopographies in tropical peat swamp forests affect the survival of younger individuals by modifying the conditions of the peat surface.

Third, effects of facilitative interactions through environmental modification are often documented in extreme habitats [Callaway 1994; Forseth *et al.* 2001; Quested *et al.* 2003] and lead to increased productivity [Mulder *et al.* 2001] because such effects are more important for plants as environmental stresses increase [Pugnaire and Luque 2001]. Tropical peat is characterized by low nutrient content and high acidity and the peat surface is inundated seasonally. Thus, locally mounded sites where the frequency of flooding is low can be regarded as examples of modified habitats in which facilitative interactions are observed.

Here, we hypothesized an important diversity-productivity relationship. The heterogeneity of peat surfaces enhance the co-existence of diverse plant species in wetlands, and also, plant species diversity increases heterogeneity in production, which leads to heterogeneity in the conditions of the peat surface. In this study, we present a reciprocal relationship between plant species diversity and carbon storage processes in a tropical peat swamp forest. To this end, we show how the activities of different plant functional groups regulate peat surface conditions, how the resulting peat surface conditions affect the regeneration of plants, and further, how such feedback between plant and soil contributes to species coexistence in a tropical peat swamp forest. We conducted studies on plant distribution patterns in relation to microtopographic heterogeneity and on organic matter dynamics, i.e., litter fall, root input, and decomposition processes, among different types of microtopography.

2. Study Site and Methods

2.1 *Study Sites and Plots*

The study was conducted in a tropical peat swamp forest in the Kerumutan Wildlife Sanctuary, Riau Province, Eastern Sumatra, Indonesia (0°7' N, 102°28' E). The Kerumutan River, a branch of the Kampar River, forms the northern boundary of the Kerumutan Wildlife Sanctuary. According to the local people and to our observations around the research site, illegal commercial logging by local people began in 1991, but the logging has not yet invaded the area of protected forest. A small amount of timber was logged for self-consumption before 1991, but the effects of this on the study site are very limited.

We laid out 1-ha (100-m square) study plots 800 m inland from the Kerumutan River. The plot was divided into 400 contiguous 5 × 5-m quadrats. Within each quadrat, the *x* and *y* coordinates, species, and diameter at breast height (dbh) of all living trees with dbh ≥ 1 cm were recorded. The dataset was obtained between August 2002 and March 2003. Details of the study plots are described by Momose and Shimamura [2002], Shimamura and Momose [2005] and Shimamura *et al*. [2006].

2.2 *Methods*

2.2.1 *Microtopography around Established Trees*

Elevation was defined as the distance between the ground surface and the water table on 14 February 2001, when the water table was high. We dug small holes to measure the elevation at a given point on the forest floor.

To study the relationships between microtopographic heterogeneity and organic matter dynamics, we defined some groups of established trees. We selected seven living and dead established, buttressed trees with dbh ≥ 40 cm and seven established individuals of *Madhuca motleyana* Macbride and *Stemonurus secundiflorus* Blume with dbh ≥ 15 cm. Established, buttressed trees reach the emergent stratum of the forest, which is over 40 cm in dbh, and are *Aglaia argentea* Blume, *Palaquium burckii* H. J. Lam, *Shorea teysmanniana* Dyer ex Brandis, *Shorea uliginosa* Foxworthy, and *Swintonia glauca* Engl. Established *M. motleyana* and *S. secundiflorus* trees reach the forest canopy, which is approximately 25 m in height, and have pneumatophores, but are not buttressed. Study trees were selected randomly from the tagged trees in the 1-ha plot, but dead buttressed trees were found in the plot and within 100 m of the boundary of the plot. To compare the microtopography around buttresses between dead and living individuals, we did not distinguish the species of living buttressed trees because it was difficult to identify the species by their rotten trunks and barks.

For each individual, we laid out four 6-m transect lines running toward each point of the compass from the center of the trunk. We measured the elevation at 12 points placed every 50 cm along the transects. At the same time, we took hemispherical photographs at 150 points (five individuals × two 5-m transects × five points (1-m intervals) × three tree groups) using a fish-eye camera (Cool Pix 900 with Fish-eye converter FC-E8, Nikon) at a height of 1.0 m above the ground, and we calculated the indirect site factor (ISF) using Hemiview software (Delta-T Device).

2.2.2 *Litter Fall, Root Production, Bulk Density, and Decomposition*

Gaps were defined as canopy openings exceeding 50 m² in this study. Mounds were defined as continuous areas exceeding 2 m in diameter where the elevation was higher than 15 cm, but such elevated sites in gaps were excluded. We use the term non-mounds to describe habitats that were

neither mounds nor gaps.

Litter fall, litter deposition, root production, bulk density of peat, and rates of leaf litter decomposition were measured on gaps, mounds, and non-mounds. Litter fall was collected monthly from the beginning of September 2001 to August 2002 using 10 litter traps for each type of habitat. Each litter trap was a basket 1 m in diameter made from 2-mm nylon mesh and suspended from a wire hoop. In December 2003 and March, June, and August 2004, litter deposits above the peat surface were collected. All recognizable aboveground litter was harvested from 30 quadrats of 50 × 50 cm located around the 30 litter traps.

Ingrowth cores (20 cm in length, 7 cm in diameter) made of 2-mm nylon mesh were filled with root-free peat soils and installed in the ground at a depth of 0-20 cm. In each type of habitat where litter traps were placed, four locations were randomly selected and a pair of ingrowth cores was inserted. In total, 24 ingrowth cores were buried in August 2001 and harvested 1 year later. However some cores were broken. The sample numbers became eight, six, and six for mounds, non-mounds, and gaps, respectively.

Volumetric samples of intact peat were extracted from the surface peat layer using open-ended coring tubes of pipe (1,061 cm^3, diameter 11.8 cm) in August 2003. In each type of habitat where litter traps were placed, five locations were randomly selected and a pair of volumetric samples was collected from nearby locations.

Leaf litter decomposition processes were studied using a litter-bag method. Leaf litter of *Swintonia glauca* measuring 10 g in dry weight was enclosed in a litter bag made of polypropylene cloth with a mesh size of 2 mm. Litterbags were deployed in August 2001. In each type of habitat where litter traps were placed, five locations were randomly selected and seven litterbags were placed at each selected point. Samples were collected seven times during 1 year: monthly for the first 2 months, then bimonthly until August 2002. Details of the above measurements are presented in Shimamura and Momose [2005].

2.3 *Analyses*

2.3.1 *Shift in Plant Distribution*

To investigate the relation between microtopographic types and plant species distribution, we conducted spatial point pattern analyses. For these analyses, we defined established, buttressed trees with dbh ≥ 40 cm as mound-forming trees and established trees of *Madhuca motleyana* and *Stemonurus secundiflorus* with dbh ≥ 15 cm as non-mound-forming trees. Living established, buttressed trees were always surrounded by mounds, whereas elevations around established trees of *Madhuca motleyana* and *Stemonurus secundiflorus* were mostly constant according to the distance

from the trunk.

We tested the spatial association of abundant species, i.e., the top 10 species in numbers of individuals, and *Shorea teysmanniana* as an important tree species that dominates at the emergent stratum (see Electronic Appendix part B in Shimamura and Momose [2005] for abundance) against mound-forming and non-mound-forming trees as indices of microtopography. For this purpose, distribution data obtained in the 1-ha plot were analyzed using the $L_{1,2}(t)$ function [Besag 1977; Ripley 1977; Lotwick and Silverman 1982]. Statistical significance of the function was calculated using 10,000 simulations of random toroidal shifts (mean ± 1.96 s.d.) for 95% confidence intervals. If the sample statistic remained within the bounds of the confidence intervals at any given t, the null hypothesis of spatial independence was not rejected; when it exceeded the upper (lower) boundaries, the sampled points were regarded as an attractive (repulsive) pattern [Diggle 1983].

We divided each tree species into two groups: large and small trees. Large trees were the top 30% of individuals in dbh within each species; small trees were the bottom 40%. Large trees of *Madhuca motleyana* and *Stemonurus secundiflorus* are non-mound-forming trees and *Swintonia glauca* and *Shorea teysmanniana* are mound-forming trees. Tests on the spatial associations of large *Madhuca motleyana* and *Stemonurus secundiflorus* trees with established non-mound-forming trees were conducted by omitting trees with dbh > 15 cm from the category of large trees. Also, spatial associations of large *Swintonia glauca* and *Shorea teysmanniana* trees with mound-forming trees were tested by omitting individuals with dbh > 40 cm from large trees.

2.3.2 *Modeling the Peat Accumulation Process*

We used models to evaluate carbon accumulation processes at small scales. Details of the models are described in Shimamura and Momose [2005]. In the model, tropical peat soils consist of three layers. The litter layer is made of undecomposed leaves and small woody debris above the peat layer. Similar to boreal and temperate peat, tropical peat is characterized by two horizons: the surface aerobic acrotelm and the deeper anaerobic catotelm. Differences in acrotelm thickness strongly contribute to differences in elevation. Because the depth of the catotelm layer is defined by the height of the water table and the bottom of the peat, there is no heterogeneity in the depth of catotelm within a relatively short distance. Thus, the net accumulation of peat is reflected by the mass of the acrotelm layer. In the model, the mass of the acrotelm (m_A) is expressed as follows:

$$m_A = A\exp(p_A/b \text{-} k_A)t + sk_L(p_L/k_L \text{-} m_{L0})\exp(\text{-} k_L t)/(k_L + (p_A/b \text{-} k_A)) \text{-} (sp_L \text{-} m_C k_C)/(p_A/b \text{-} k_A),$$

where A is an integral constant, t is time, p_A is root production per unit depth, b is the bulk density of the acrotelm, s is the portion of fragmented litter not lost from soils by respiration or leaching, k_L and k_A are Olson's decomposition constants [Olson 1963] for the litter and acrotelm layers,

respectively, m_{L0} is the initial mass of the acrotelm, p_L is the mass of litter fall, m_C is the mass of catotelm, and k_C is Olson's decomposition constant for catotelm.

Using the model, we also examined the effects of shifting habitat on the peat surface. We simulated shifts in habitat by exchanging variables. For example, to determine the effect of disturbance on mounds, we changed five variables, p_L, k_L, p_A, k_A, and s, for those of gaps. In this way, we simulated four types of shifting habitat: non-mound to mound, gap to non-mound, non-mound to gap, and mound to gap.

3. Results

3.1 *Microhabitat around Established Trees*

According to the measurements of elevation at transect lines around seven trees, mounds occurred around the living or dead established, buttressed trees. The mean elevation was 43.6 cm at points 0.5 m from the center of trunks of large living buttressed trees, and decreased gradually as the distance from tree trunks increased (Fig. 1). Flatter sites were found around the established *Madhuca motleyana* and *Stemonurus secundiflorus* trees than around living or dead established, buttressed trees.

There were significant differences ($p < 0.001$) in elevations within 3.5 m among the four types of established trees between all pairs of species, except *Madhuca motleyana* and *Stemonurus secundiflorus* trees ($p = 0.791$, ANOVA and Tamhane's T2). Thus, the microtopography around established tree groups can be categorized into three groups: highly mounded sites around living buttressed trees, moderately mounded sites around dead buttressed trees, and non-mounded sites
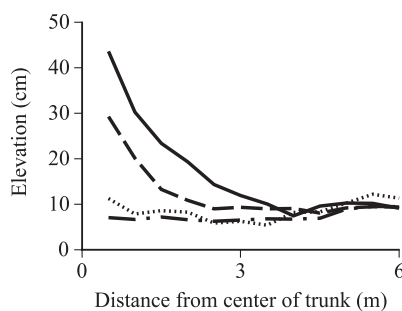

Fig. 1. Changes in Ground Surface Elevation with Distance from Living Established Buttressed Trees (dbh ≥ 40 cm; solid line), Dead Established Buttressed Trees (broken line), Established *Madhuca motleyana* Trees (dbh ≥ 15 cm; dotted line) and Established *Stemonurus secundiflorus* Trees (dbh ≥ 15 cm; broken-dotted line)
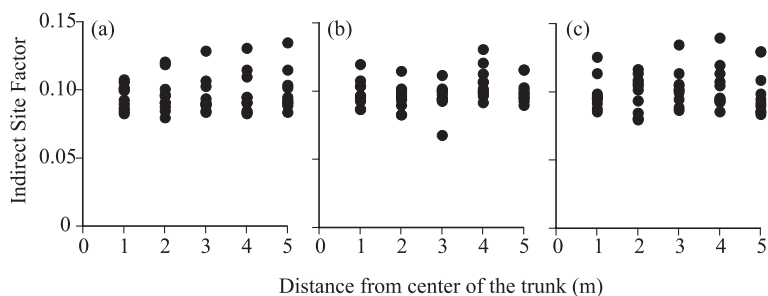This figure was reproduced using data from Shimamura and Momose [2005].

Fig. 2. **Changes in the Indirect Site Factor with Distance from (a) Established Buttressed Trees (dbh ≥ 40 cm), (b) Established *Madhuca motleyana* Trees (dbh ≥ 15 cm), and (c) Established *Stemonurus secundiflorus* Trees (dbh ≥ 15 cm)**

around *Madhuca motleyana* and *Stemonurus secundiflorus* trees (Fig. 1).

Mean values (s.d.) of indirect site factor (ISF), an indicator of light conditions, around established buttressed, *Maduca motoleyana*, and *Stemonurus secundiflorus* trees were 0.0963 (0.0131), 0.0987 (0.0107), and 0.100 (0.0143), respectively. There was no significant differences in light conditions between the three groups (χ^2 = 4.55; p = 0.103, Kruskal-Wallis test). ISF was not significantly regressed to distance from the center of the trunk of established buttressed trees ($F_{1,48}$ = 0.526, p=0.472), established *Maduca motleyana* trees ($F_{1,48}$=1.72, p=0.196), or established *Stemonurus secundiflorus* trees ($F_{1,48}$=0.301, p=0.586; Fig. 2).

3.2 *Litter Fall, Root Production, Bulk Density, and Decomposition*

There were consistent seasonal patterns of litter fall among mounds, non-mounds, and gaps. There was an increase in litter fall during November and December 2001, when precipitation
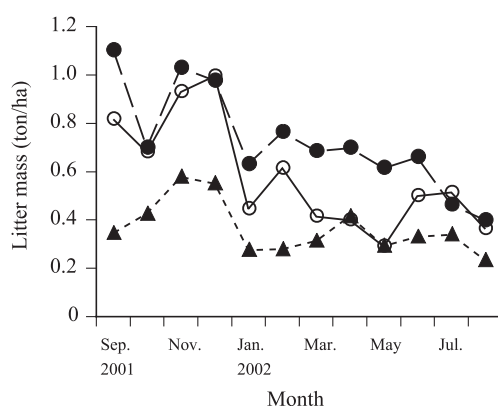

Fig. 3. **Monthly Litter Fall for Mounds (shaded circles), Non-mounds (open circles), and Gaps (shaded triangles)**

was relatively high. Litter production between January and June 2002 was constant in all three types of sites (Fig. 3). Mean (s.d.) litter fall was highest on mounds and lowest in gaps, at 9.43 (1.94), 6.96 (0.770), and 4.20 (1.64) ton ha^{-1} year^{-1}, respectively. The rank of fine root production among the three types of habitat was mounds>non-mounds>gaps. Mean (s.d.) estimated fine root production was 1.99 (1.55), 1.14 (1.15), and 0.307 (0.222) ton ha^{-1} year^{-1}, respectively (Fig. 4). The rank in mass of litter deposits on the peat surface among the three habitats was mounds>non-mounds>gaps, at means (s.d.) of 9.62 (4.35), 7.41 (4.05), and 4.98 (4.32) ton ha^{-1}, respectively. There were significant effects of habitat ($F_{2,108}$ = 13.1, p < 0.001, ANOVA) and season ($F_{3,108}$ = 5.86, p < 0.001, ANOVA) on the mass of litter deposition, but no significant interaction of habitat and season was found (Fig. 5). The mean peat bulk density of non-mounds and gaps was similar; that of peat on mounds was lower (Fig. 6). The mean values (s.d.) peat bulk density of non-mounds,
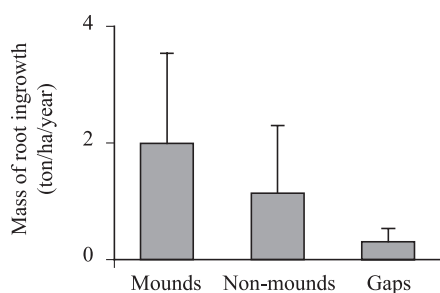

Fig. 4. Mean (s.d.) Estimated Annual Fine Root Production for Mounds, Non-mounds, and Gaps

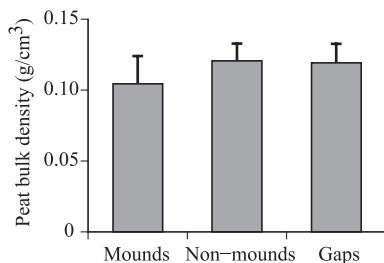This figure was reproduced using data from Shimamura and Momose [2005].

Fig. 5. Seasonal Changes in the Mass of Litter Deposition on the Forest Floor for Mounds, Non-mounds, and Gaps

Fig. 6. Mean (s.d.) Bulk Density for Mounds, Non-mounds, and Gaps

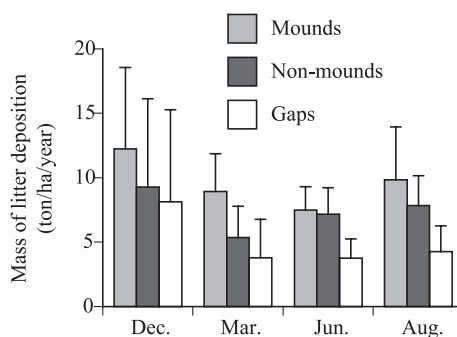This figure was reproduced using data from Shimamura and Momose [2005].
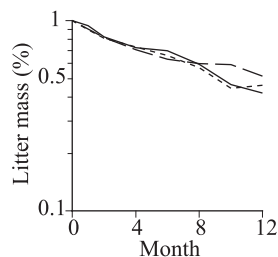

Fig. 7. Changes in the Dry Weight of *Swintonia glauca* Leaf Litter during Decomposition

Solid, dotted, and broken lines indicate the dry weight for mounds, non-mounds, and gaps, respectively.

gaps, and mounds was 0.121 (0.0121), 0.119 (0.0136), and 0.104 (0.0196) g cm^{-3}, respectively. The initial decomposition patterns among the three habitats were similar until the eighth month. After the eighth month, the decomposition process slowed in gaps (Fig. 7). The rank in leaf litter decomposition constants (Olson's k) among the three habitats was non-mounds>mounds>gaps at means (s.e.b) of 0.916 (0.0603, d.f. = 30), 0.891 (0.0410, d.f. = 29), and 0.760 (0.0394, d.f. = 30) year^{-1}, respectively.

3.3 *Spatial Associations among Tree Groups*

According to spatial point pattern analyses, small trees of *Knema intermedia* Warb were significantly attracted to mound-forming trees at 2-2.5 and 5-5.5 m, whereas small trees of other species showed no significant spatial associations with mound-forming trees (Fig. 8). In contrast to small trees, the large trees of five study species showed significant spatial associations with mound-forming trees. Large trees of *Eugenia rhizophora* Boerlage et Koorders showed significant repulsion from mound-forming trees at 2.5-3.5 and 5 m. Large trees of *E. lepidocarpa* were significantly repulsed at 6 m. Large *Shorea teysmanniana* trees showed significant repulsive distribution at 4.5-6 m (Fig. 9).

Small trees of three species showed significant spatial associations with non-mound-forming trees. Small *Madhuca motleyana* trees showed significant attraction at 3, 4-5, and 6 m to non-mound-forming trees, and small *Calophyllum rigidum* Miq. trees were significantly attracted to non-mound-forming trees at 0.5 m. Small *Swintonia glauca* trees showed significant repulsive distribution to non-mound-forming trees at 3.5 and 5.5 m (Fig. 10). Large trees of six species showed significant spatial associations with non-mound forming trees.

Large *Stemonurus secundiflorus* trees showed attractive distribution to non-mound-forming trees at 2-2.5 and 4 m. Large *Eugenia rhizophora* trees were significantly repulsed at 6 m. Large trees of *Knema intermedia* showed significant attraction to non-mound-forming trees at 0.5-3 m. Large *Tetractomia tetrandra* Craib. and *Eugenia lepidocarpa* trees were significantly attracted at 6 and 2 m, respectively. Large trees of *Shorea teysmanniana* showed significant repulsive distribution to non-mound forming trees at 3-3.5 and 4.5-6 m (Fig. 11).

3.4 *Modeling Peat Surface Accumulation*

To simulate peat surface dynamics, we used variables obtained from our measurements. Variables that we did not measure here, such as k_C, were obtained from Brady [1997]. At the study site, the mean water table was -30.3 cm and the mean height of mounds was 34.1 cm [Shimamura *et al*. 2006]. We used 0.30 m as the initial thickness of the acrotelm layer for non-mounds and gaps, and 0.60 m as the initial thickness for mounds. According to the model, the thickness of the acrotelm layer will rise at mounds, non-mounds, and gaps. The rank in degree of surface rising was
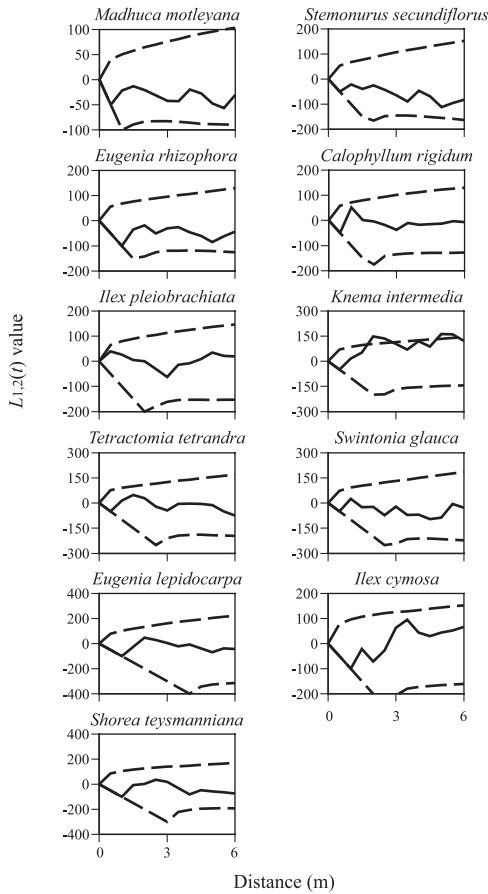
Fig. 8. $L_{1,2}(t)$ **Values of the Bivariate Distribution of Mound-forming Trees vs. Small Trees of Each Tree Species**

The solid line shows actual $L_{1,2}(t)$ values for extant plants, broken line shows 95% confidence limits for the pattern expected from an independent distribution of plant locations.
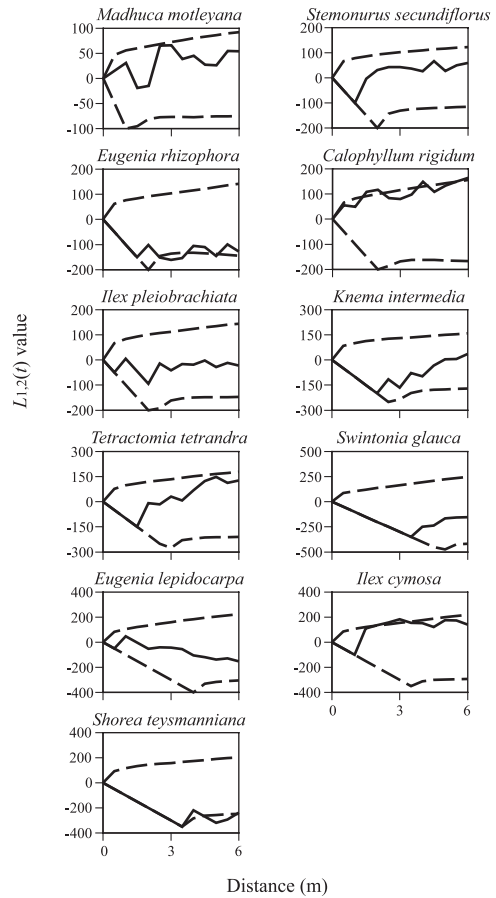
Fig. 9. $L_{1,2}(t)$ **Values of the Bivariate Distribution of Mound-forming Trees vs. Large Trees of Each Tree Species**

The solid line shows actual $L_{1,2}(t)$ values for extant plants, broken line shows 95% confidence limits for the pattern expected from an independent distribution of plant locations.

mounds>non-mounds>gaps, and peat accumulation after 5 years was 56.8, 28.5, and 3.57 ton ha^{-1}, respectively (Fig. 12). These values are equivalent to 5.46-, 2.35-, and 0.300-cm increases in the peat surface, respectively [Shimamura and Momose 2005]. The results of the simulation indicate that the establishment of non-mound-forming trees in gaps results in an increase of 22.6 ton ha^{-1} in Δm_A after 5 years. Similarly, establishment of mound-forming trees on non-mounds causes an increase of 15.2 ton ha^{-1} in Δm_A. In contrast, the death of mound- and non-mound-forming trees
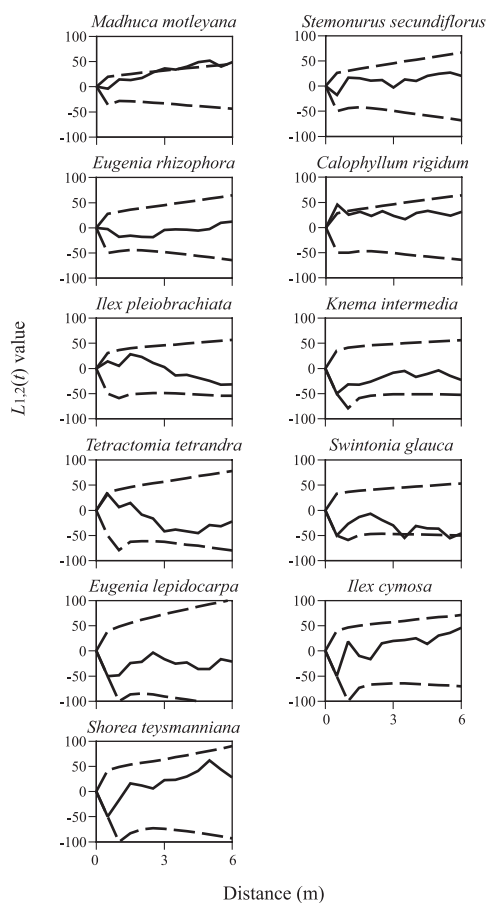
Fig. 10. $L_{1,2}(t)$ **Values of the Bivariate Distribution of Non-mound-forming Trees vs. Small Trees of Each Tree Species**

The solid line shows actual $L_{1,2}(t)$ values for extant plants, broken line shows 95% confidence limits for the pattern expected from an independent distribution of plant locations.
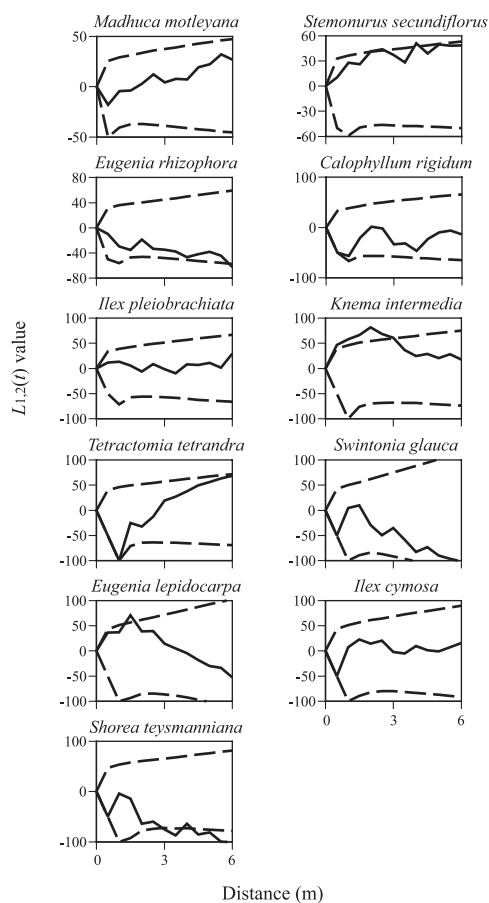
Fig. 11. $L_{1,2}(t)$ **Values of the Bivariate Distribution of Non-mound-forming Trees vs. Large Trees of Each Tree Species**

The solid line shows actual $L_{1,2}(t)$ values for extant plants, broken line shows 95% confidence limits for the pattern expected from an independent distribution of plant locations.

causes decreases of 54.7 and 22.7 ton ha^{-1} in Δm_{A}, respectively (Fig. 12).

4. Discussion

4.1 *Shifts in Plant Distribution and Flooding Tolerance*

Microtopography contributes to plant species distributions in wetlands [Huenneke and Sharitz 1986]. The distribution of plant species is arranged along the elevation according to flood tolerance
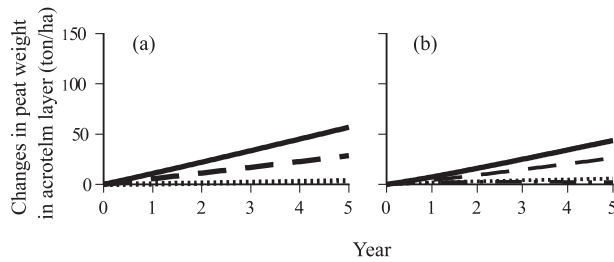
Fig. 12. Changes in Peat Deposition in the Acrotelm within 5 Years as Simulated by the Model

The solid, broken, and dotted lines in (a) indicate mounds, non-mounds, and gaps, respectively. In (b), shifts in habitat from non-mound to mound, gap to non-mound, non-mound to gap, and mound to gap are indicated by the solid, broken, dotted, and dotted-broken lines, respectively.

[Robertson *et al*. 1978; Jeglum and He 1995] because elevation reflects the frequency of inundation. The light environment also affects plant species distributions. Because there were no differences in the light environment between the two categories of established trees [Shimamura and Momose 2005], the differences in distributions of tree species in relation to mound-forming trees and non-mound-forming trees were mainly attributed to the effects of microtopography.

Stress-tolerant and stress-intolerant species are arranged along the gradient of inundation frequency. Stress-tolerant species often require stressful habitats where competitive species are excluded. In contrast, stress-intolerant species require a comparatively less stressful habitat. The mounds that occurred around the mound-forming trees represented less stressful habitats without frequent inundation, whereas stressful habitats occurred around the non-mound-forming trees. Thus, the tree species attracted to the mound-forming trees or repulsed from the non-mound-forming trees are flood-intolerant species, and those attracted to non-mound-forming trees or repulsed from mound-forming trees are flood-tolerant species.

It has often been documented that plant distributions, especially for juveniles and seedlings, are strongly affected by the means of dispersal [Hubbell 1979; Briggs and Gibson 1992]. Short dispersal distances [Prentice and Werger 1985; Sterner *et al*. 1986; Hatton 1989] explain the clumped distribution of small trees. The distribution of parent plants also affects the spatial heterogeneity of small plants [Nanami *et al*. 1999]. It is difficult to distinguish whether the observed pattern of distribution of small trees was caused by the dispersal or habitat preferences of each species. However, a comparison of the patterns of distribution between small and large conspecific trees offsets the effect of methods of seed dispersal. The difference in distributions reflects post-dispersal events. Thus, such a comparison is very informative in an analysis of habitat preferences. We here

focused on shifts in distribution between small and large trees to explain the habitat preferences of tree species. Because the mean size of mounds around mound-forming trees was 3.5 m in radius, we paid particular attention to significant spatial associations within 3.5 m.

The distribution patterns of *Calophyllum rigidum* and *Ilex cymosa* Blume trees shifted from random to closer to mound-forming trees with increasing size class. This indicates that they are flood-intolerant species. Similarly the shifts in distribution patterns of *Eugenia rhizophora* trees indicate that this species is flood-tolerant (Figs. 8, 9). The spatial associations of tree species to non-mound-forming trees indicate that *Stemonurus secundiflorus*, *Knema intermedia*, and *Eugenia lepidocarpa* trees are flood-tolerant (Figs. 10, 11).

4.2 *Proposed Four-phase Dynamics of Tropical Peat Swamp Forest*

Our results suggest that the microtopographic heterogeneity of the peat surface provides an axis of habitat partitioning for plant species, and that rising and sinking of the peat surface (elevation dynamics) occurs in the peat swamp forest. The establishment and death of huge buttressed trees causes the rise and sink of the peat surface, respectively, and results in an undulating peat surface. Mounds formed around huge buttressed trees are suitable habitats for regeneration of flood-intolerant species. After established buttressed trees die, mounds become lower and finally disappear (Fig. 12). As a result, habitats suitable for flood-tolerant species appear. Thus, plant species coexistence in the forest can be explained by the mosaic-like dynamics of mounds and non-mounds, although we do not know whether this forest is in kinetic equilibrium over a long time scale. Even if this forest is not in kinetic equilibrium, succession of the forest will gradually occur through fluctuations of the following mosaic-like dynamics.

We propose a dynamic model that allows us to explain the coexistence of tree species in tropical peat swamp forests (Fig. 13). The model is based on the following assumptions: (i) mounds are created around buttressed trees as they grow; (ii) after large buttressed trees die, the surrounding mounds sink; (iii) there are flood-tolerant and -intolerant tree species; and (iv) there are shade-tolerant and -intolerant tree species.

Peat swamp forests are composed of areas categorized as one of four phases based on the conditions of canopy coverage and microtopography; mounds under canopy: MU-phase; non-mounds under canopy: NU-phase; mounds in gaps: MG-phase; and non-mounds in gaps: NG-phase. Of the four phases MU-phase can be divided into two phase: mounds under canopy with an established mound-forming tree: MUa-phase; and mounds under canopy without any established mound-forming trees: MUb-phase.

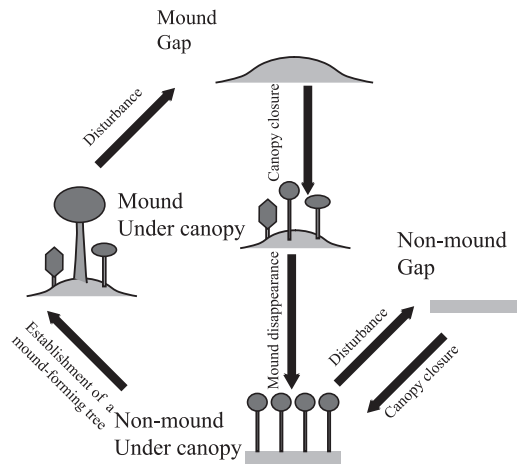In the NG-phase, individuals of flood-tolerant and shade-intolerant tree species dominate.

Fig. 13. Diagram of the Proposed Four-phase Dynamics Used to Explain Plant Species Coexistence in Tropical Peat Swamp Forests

Canopy gaps in tropical moist forests return to the pre-gap phase within 5 years in tropical moist forests [Fraver *et al*. 1998; Van der Meer 1997]. This time scale is less than that required for the establishment of large buttressed trees that form mounds. Thus, whether regenerating tree species are mound-forming or non-mound-forming, the NG-phase is replaced by the NU-phase. In the NU-phase, individuals of flood-tolerant and shade-intolerant species dominate. If a disturbance occurs, the NU-phase is replaced by the NG-phase. *Shorea teysmanniana* is one of the mound-forming tree species that can inhabit non-mounds. Once a large individual of a mound-forming tree species such as *S. teysmanniana* is established, this phase is replaced by the MUa-phase. In the MUa-phase, individuals of flood-intolerant and shade-tolerant species successfully regenerate. If a disturbance occurs in the MUa-phase, this phase is replaced by the MG-phase. As already mentioned above, canopy gaps in tropical forests return to pre-gap phase within 5 years [Fraver *et al*. 1998; Van der Meer 1997], and more than 5 years are needed for mounds to return non-mounded sites [Shimamura and Momose 2005]. Thus, canopy closure occurs faster than disappearance of the mound, and the MG-phase is replaced by the MUb-phase. Similar to the MUa-phase, individuals of flood-intolerant and shade-tolerant species successfully regenerate in the MUb-phase. In the MUb-phase, wheather mound- or non-mound-forming trees successfully regenerate, disappearance of the mound occurs faster than establishment of large trees, and the MUb-phase is replaced by NU-phase, because it takes longer term to establish a large tree than the disappearance of mounds.

The above model contains important suggestions. In tropical peat swamp forests, the carbon

storage function of tropical peat swamp forests is maintained by diverse plant species. The distribution of diverse plant species contributes to heterogeneity in carbon storage and results in an undulating peat surface. The undulating peat surface provides habitat for diverse plant species. Thus, the relation between diversity-maintaining mechanisms and carbon-storing functions of tropical peat swamp forests is reciprocal. The reciprocal relationship increases the importance of the diverse plant community in tropical peat swamp forests because they maintain carbon storage function, although the diversity in tropical peat swamp forests has been given less attention [Dennis and Aldhous 2004] than the carbon storage function.

Acknowledgements

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