Organic matter dynamics control plant species coexistence in a tropical peat swamp forest

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We studied the relationship between the coexistence of tree species and the dynamics of organic matter in forests. A tropical peat swamp forest was selected as a model ecosystem, where abiotic factors, such as geological topography or parent rock types, are homogeneous and only biological processes create habitat heterogeneity. The temporal or spatial variation of the ground elevation of peat soils is mainly caused by changes in the balance between organic matter inputs to soils and decomposition, which is affected by the growth and death of influential trees. To clarify the processes of elevation dynamics, we measured the microtopography around some tree groups, estimated organic matter (in the form of litter and roots) in soils under three kinds of microtopographic conditions, measured decomposition rates and detected dominant species' shifting distribution patterns in different stages of growth in relation to the locations of tree groups creating specific microtopographic conditions. We found that growth or death of buttressed trees has the greatest effects on the rising or sinking of ground surfaces through changes in litter supply and root production. We discuss here the possibility of extending our model to other forest types.

Keywords: tropical peat swamp forest; organic matter dynamics; elevation dynamics; species coexistence; heterogeneity

1. INTRODUCTION

Among the various factors causing habitat heterogeneity within forests, abiotic factors, such as geological topography or parent rock types, influence the composition of plant communities (Debski *et al.* 2000; Palmiotto *et al.* 2004) but are not directly associated with the forest dynamics that can explain species coexistence. On the other hand, habitat heterogeneity created by activities of plants themselves, for example, the creation of gaps, is closely associated with the forest dynamics as an important mechanism of species coexistence (Whitmore 1989). This is because biotic factors of each microhabitat change as influential plants establish, grow or die, while abiotic factors are almost static.

A more specific example of plant-caused heterogeneity is that conditions often become milder under relatively large plants in deserts, along coasts or in other severe habitats, which may protect smaller plants from direct sunlight, winds, moving sands, waves or predation (Pugnaire *et al.* 1996; Bruno & Kennedy 2000; Forseth *et al.* 2001; Quested *et al.* 2003; Tirado & Pugnaire 2003). In addition, the risk of diseases or predation varies according to distances from conspecific large plants (Janzen 1970; Connell 1971; Gavin & Peart 1997). In this paper, we introduce another example, the heterogeneity of organic matter dynamics, which has not been studied well.

Variables of organic matter dynamics are usually assumed to be constant within forests but they are expected to be strongly heterogeneous. For example, Ashton (1964)

observed a patchy accumulation of litter under crowns of two dipterocarp species in Borneo. Burghouts *et al.* (1998) revealed that spatial variations of litter fall within a forest are large.

Heterogeneity of organic matter dynamics is created by the activities of plants, including the growth and death of influential plant species, and it results in temporal and spatial fluctuations in the chemical and physical conditions of forest floors (Burghouts *et al.* 1998). Thus, we assume that heterogeneous organic matter dynamics cause forest dynamics that enable species coexistence, like the case of gap dynamics.

To determine the dynamics that can explain such heterogeneity, we focused on the ground elevation of peat swamp forests because elevation often determines the frequency of flooding. The frequency of flooding often affects the recruitment, survival, growth and mortality of plants and the resulting distribution of plants in wetlands (Pollock *et al.* 1998).

In a peat swamp forest in Riau, Eastern Sumatra, the ground surface is undulating and has mounds around tree trunks. Large mounds are especially prevalent around huge buttressed trees, which form an emergent stratum of the forest. Rich litter fall and root architecture supporting the aboveground organs raises the ground surface around buttresses, while common but smaller trees that have numerous pneumatophores seldom create mounds. Such microtopographic heterogeneity of the ground surface is also observed in other locations of Sumatra (Brady 1997) and Borneo (Page *et al.* 1999).

Suppose that a large buttressed tree falls down. Subsequently, the supply of litter and roots that have raised the ground surface is decreased and the litter and roots decompose. Thus, the mound becomes lower and finally disappears. Non-mounded sites are frequently

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inundated and dominated by flood-tolerant species. By contrast, the development of large buttresses forms mounds that less water-tolerant species can inhabit.

We hypothesize that such cyclic rising and sinking of the ground surface contributes to species coexistence in tropical peat swamp forests by providing an axis of habitat partitioning. To test the above assumption, we addressed whether microtopographic heterogeneity provides an axis of habitat partitioning and whether organic matter input and decomposition induce rising and sinking of the ground surface.

2. MATERIALS AND METHODS

(a) *Study site and plot design*

This study was conducted in the tropical peat swamp forest in Kermutan Wildlife Sanctuary, Riau Province, Sumatra, Indonesia. We laid out study plots approximately 1 km inland from the Kermutan River (0°7' N, 102°28' E). Bores indicated that the peat depth was 4–5 m. According to the residents near the study sites and our observation, logging has not yet invaded the area of protected forests, which can be regarded as virgin forests.

Precipitation was monitored between September 2000 and July 2002, using a tipping-bucket rain gauge located approximately 3 km away from the study site at our research station. Annual precipitation was 1906 mm in 2001. Maximum and minimum monthly precipitations during the monitoring were 305 mm in October 2001 and 27 mm in July 2001, respectively. The forest floor is patchily inundated when the water table is high especially in the rainy season. Maximum, minimum and mean levels of the water table as measured by water gauge beside the study site were 18.7 cm on 14th December 2001, –87.1 cm on 20th August 2001 and –30.3 cm, respectively.

We settled a square plot of 1 ha that was carefully delineated and subsequently divided into 400 contiguous quadrats of 5×5 m, using a pocket compass. Within each quadrat, the *x* and *y* coordination, the species and the diameter at breast height (dbh) of all living trees (dbh ≥ 1 cm) were recorded. The complete dataset used in analyses of this paper was obtained between August 2002 and March 2003, but establishment of the plots was begun in 2000. The identification of specimens was conducted in Herbarium Bogoriense, Bogor, Indonesia. Vouchers are deposited in the herbarium.

(b) *Microhabitats around established trees*

In this study, elevation is defined as the distance between the ground surface and the water table on 14 February 2001; at this time the water table was high since it was the middle of the rainy season. We dug small holes to measure the elevation at a given point on the forest floor. The water level in each hole rose with time. We waited until the water stopped rising and measured the distance between the ground surface and the water table. When there were huge obstacles such as dead trunks we did not measure elevation.

In February 2001, to study the microtopography around some groups of established trees, we selected seven living and dead established, buttressed trees (dbh ≥ 40 cm) and seven individuals of established *Madhuca motleyana* Macbride and *Stemonurus secundiflorus* Blume (dbh ≥ 15 cm). Established, buttressed trees reached the emergent stratum of the forest (over 40 m in height), and belonged to *Aglaiia argentea* Blume, *Palaquium burckii* H. J. Lam, *Shorea teysmanniana* Dyer ex

Brandis, *Shorea uliginosa* Foxworthy or *Swintonia glauca* Engl. Established *M. motleyana* and *S. secundiflorus* trees reached the forest canopy (ca. 25 m in height) and had pneumatophores, but were not buttressed.

Study trees were selected by random computation from the tagged trees in the 1 ha plot, but dead buttressed trees were found in and around the plot (within 100 m of the plot boundary).

We did not distinguish the species of living buttressed trees in our comparison of the microtopography around dead and living established, buttressed trees because it was not possible to confidently identify species of dead established, buttressed trees. For each individual, we laid out four 6 m transect lines running to each point of the compass from the centre of the trunk. We measured the elevation at 12 points placed every 50 cm along the transects and measured light conditions. The methods of measuring light conditions and those results are described in Electronic Appendix part A.

(c) *Litter fall, litter deposition, decomposition, root production and bulk density*

Gaps were defined as canopy openings exceeding 50 m². 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. In this paper we use the term non-mounds to describe habitats that were neither mounds nor gaps.

Litter was collected monthly from the beginning of September 2001 to August 2002 in three kinds of habitats, mounds, non-mounds and gaps, using ten litter traps per habitat. Each litter trap was a basket 1 m in diameter made from 2 mm nylon mesh and suspended from a wire hoop; the device was held 1 m above the ground. In mounds, traps were placed 1 m south of the trunks of 10 established, buttressed trees selected randomly by computation from tagged trees in the 1 ha plot. In non-mounds, traps were placed at intervals of 10 m along a transect line running north to south within the 1 ha plot. However, if the site was located in mounds or gaps, the location of the trap was moved 10 m to the east. Around the 1 ha plot (within 300 m of the plot boundary), 10 forest gaps were found. Traps were settled at the centre of these gaps. Only eight of the traps for mounds provided data because some litter traps were repeatedly stolen (nylon mesh baskets were useful for fishing). After collection, the litter samples were immediately dried in a self-made drying room to constant mass and weighed.

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. When traces of disturbance from the previous sampling were seen, samples were taken at the nearest intact site. After collection, the litter samples were immediately dried in a self-made drying room to constant mass and weighed.

Decomposition processes of leaf litter were studied by a litter bag method. To unify the litter samples, leaves of *S. glauca*, one of the dominant species, were used. The litter of 10 g in dry weight was enclosed in a litter bag (20×10 cm) made of polypropylene cloth with a mesh size of 2 mm. Litterbags were set in August 2001. From each type of habitat where litter traps had been placed, five locations were randomly selected and we placed seven litterbags at each selected point. Samples were collected seven times during one year: monthly for the first two months, then bimonthly until

August 2002. Although some bags had been lost or ripped, we successfully collected samples from 30 bags from mounds and 31 bags from non-mounds and gaps. Foreign plant remains and peat attached to the outsides of the bags were carefully removed with forceps. After transport to the laboratory, the losses of dry weight were determined by drying the samples to a constant mass at 80 °C.

Decomposition rates were estimated using Olson's k (Olson 1963) in the equation $W_t = W_0 \exp(-kt)$, where W_t is the litter weight after a given period, W_0 is the original litter weight, k is the decomposition rate and t is the time.

Ingrowth cores (20 cm length, 7 cm diameter), which were made of 2 mm nylon mesh, were filled with root-free soils and installed in the ground (depth of 0–20 cm). The soil used for this purpose was taken from a nearby location and care was taken to fill the cores so that bulk densities were similar to original levels. From each type of habitat where litter traps had been placed (mounds, non-mounds and gaps), 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 one year later.

We found at harvest time that four cores had been broken. Consequently, the sample numbers became eight, six and six for mounds, non-mounds and gaps, respectively. Living and dead fine roots were separated from soils. After transport to the laboratory, root samples of each core were dried at 80 °C until they reached constant mass and then weighed.

Volumetric samples of intact peat were extracted from the surface peat layer using open-ended coring tubes of pipe (1061 cm³, diameter 11.8 cm) in August 2003. From each type of habitat where litter traps had been placed, five locations were randomly selected and a pair of volumetric samples was collected from the nearby locations. The samples were dried in the self-made drying house to constant mass and then weighed. Dry bulk density was calculated as dried mass divided by the field volume of each sample.

(d) Shift of plant distribution

In order to detect the shift of plants' distributions in different stages of growth in relation to microhabitats, we conducted spatial point pattern analyses. For these analyses, we defined established, buttressed trees (dbh ≥ 40 cm) as mound-forming trees and established trees of *M. motleyana* and *S. secundiflorus* (dbh ≥ 15 cm) as non-mound-forming trees. As described in the result (figure 1), living established, buttressed trees were always surrounded by mounds, while elevations around established trees of *M. motleyana* and *S. secundiflorus* were mostly constant according to distances from trunks (they were always located in non-mounds).

We tested the spatial association of abundant species (the top ten species in individual number and *S. teysmanniana* as an important tree species that dominates at the emergent stratum (see Electronic Appendix part B)) against mound-forming and non-mound-forming trees as indices of the microtopography. For this purpose, distribution data obtained in the 1 ha plot was analysed using the $\hat{L}_{1,2}(t)$ function (Besag 1977; Ripley 1977; Lotwick & Silverman 1982).

The $\hat{L}_{1,2}(t)$ function indicates whether two groups are spatially independent at distance t . To examine statistical significance, we used simulated $\hat{L}_{1,2}(t)$ values at the limit of the 2.5% tails of 10 000 torus randomizations (mean ± 1.96 s.d.) for 95% confidence intervals. If the sample statistic

Figure 1. Changes in ground surface elevation with distance from (a) living established, buttressed trees (dbh ≥ 40 cm), (b) dead established, buttressed trees (dbh ≥ 40 cm), (c) established *Madhuca motleyana* trees (dbh ≥ 15 cm) and (d) *Stemonurus secundiflorus* trees (dbh ≥ 15 cm). Whiskers indicate estimated standard deviation for each group or species of trees.

remains within the bounds of the confidence interval at any given t , the null hypothesis of spatial independence is not rejected but when it exceeds the upper (lower) boundaries, the sampled points are regarded as an attractive (repulsive) pattern (Diggle 1983).

We divided each tree species into two groups, large and small trees, to detect the shifting distributions among growing stages. Large trees were the top 30% of individuals in dbh within each species and small trees were the bottom 40%. Large trees of *M. motleyana* and *S. secundiflorus* are the components of the non-mound-forming trees and *S. glauca* and *S. teysmanniana* are those of the mound-forming trees. Tests on spatial association of large *M. motleyana* and *S. secundiflorus* trees against the established non-mound-forming trees were conducted by omitting trees with a dbh greater than 15 cm from the category of large trees. Also, spatial associations of large *S. glauca* and *S. teysmanniana* trees against mound-forming trees were tested by omitting individuals with a dbh greater than 40 cm from large trees.

(e) Model of peat surface profile

We developed a model to understand the difference in the regimes of organic matter dynamics among the three habitats. 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 difference in elevation. On the other hand, because the depth of the catotelm layer is defined by the height of the water table and the bottom of the peat, there was no difference in the thickness of the catotelm layer among the three habitats. Thus, the model presented here simulates the depth of an acrotelm layer influenced by organic matter dynamics.

The change of the litter layer mass (m_L) is expressed as the difference between litter fall (p_L) and losses through decomposition

$$dm_L/dt = p_L - k_L m_L, \quad (2.1)$$

where the decomposition constant of litters is k_L . The above equation is solved as

$$m_L = p_L/k_L - A_2 \exp(-k_L t), \quad (2.2)$$

where A_2 is the integral constant. Litter decomposition processes include fragmentation, loss to the atmosphere through respiration and leaching. Fragmented litter moves to the acrotelm layer, while undecomposed litter remains in the litter layer. Let s be the portion of fragmented litter not lost from soils by respiration or leaching. Inputs to the acrotelm layer from the litter layer per unit time (i) equal the amount of fragmented litter

$$i = sk_L m_L. \quad (2.3)$$

The change of the acrotelm layer mass (m_A) is calculated from the inputs from the litter layer, root inputs and decomposition of the acrotelm materials as follows

$$dm_A/dt = i + p_A h_A - m_A k_A - l, \quad (2.4)$$

where p_A is the root input per unit depth, h_A is the thickness of the acrotelm layer, k_A is the rate of mass loss from the acrotelm materials through respiration and l is the mass of peat that is transported to the catotelm layer. Let b be the bulk density of the acrotelm layer; then h_A can be expressed as

$$h_A = m_A/b. \quad (2.5)$$

Mass loss of the catotelm layer is solely due to peat respiration and leaching. Let m_C and k_C be the mass and decomposition rate for the catotelm layer, respectively. Because the mass and thickness of the catotelm layer is determined by the height of the water table, mass loss from the catotelm layer is compensated for by peat materials from the bottom of the acrotelm layer. Then, it can be assumed that the catotelm mass is constant. Thus, output from the acrotelm is the same as input to the catotelm and is constant, as follows

$$l = m_C k_C. \quad (2.6)$$

Substituting equations (2.2), (2.3) and (2.6) into equation (2.4), we obtain

$$dm_A/dt = sp_L - sk_L(p_L/k_L - m_{L0}) \exp(-k_L t) + m_A(p_A/b - k_A) - m_C k_C. \quad (2.7)$$

This equation can be solved as

$$m_A = A_8 \exp(p_A/b - k_A)t + sk_L(p_L/k_L - m_{L0}) \exp(-k_L t) / (k_L + (p_A/b - k_A)) - (sp_L - m_C k_C) / (p_A/b - k_A), \quad (2.8)$$

where A_8 is integral constant for equation (2.8), which is

given as

$$A_8 = m_{A0} - sk_L(p_L/k_L - m_{L0}) / (k_L + (p_A/b - k_A))$$

$$+ (sp_L - m_C k_C) / (p_A/b - k_A), \quad (2.9)$$

where m_{A0} is the initial acrotelm layer mass and m_{L0} is the initial mass of litter layer. When t is large enough, $\exp(-k_L t)$ in equation (2.8) is ignorable

$$m_A = A_{10} \exp((p_A/b - k_A)t) - (sp_L - m_C k_C) / (p_A/b - k_A), \quad (2.10)$$

where A_{10} is the integral constant. The change in the thickness of acrotelm layers (Δh) is calculated as

$$\Delta h = (m_A - m_{A0})/b. \quad (2.11)$$

Concerning equations (2.8) and (2.10), if $p_A/b < k_A$, m_A has the equilibrium point, $(sp_L - m_C k_C) / (k_A - p_A/b)$. If $p_A/b \geq k_A$, m_A diverges to infinity. This is because root production, which is assumed to be constant per volume, exceeds the mass loss by respiration. However, root production per area has an upper limit (p_{Amax}), depending on the primary production and resource allocation to roots. If $p_A h_A$ exceeds p_{Amax} , $p_A h_A$ in equation (2.4) should be replaced by p_{Amax} . In this case, equation (2.7) should be rewritten as

$$dm_A/dt = sp_L + p_{Amax} - sk_L(p_L/k_L - m_{L0}) \times \exp(-k_L t) - m_A k_A - m_C k_C. \quad (2.12)$$

The equilibrium point of m_A is $(sp_L + p_{Amax} - m_C k_C) / k_A$.

Most variables in the model were estimated based on our study, but we applied data from the SE6 site in Brady (1997) for the variables k_A , s and k_C because the location used in that study was very close to our study site and the peat depth was similar. According to Brady, the mean respiration of mixed leaves from the litter layer incubated for 30 days under 50% moisture conditions was 20.47 mg CO₂ g⁻¹ per 30 days, from which s can be calculated. The mean respiration rate of peat samples incubated for 30 days under 50% moisture conditions was 1.00 and 1.86 mg CO₂ g⁻¹ per 30 days at 25 °C (representing the temperature condition under forest canopy) and 35 °C (representing gaps), respectively. The estimated mass loss rate of the catotelm layer was 0.000 22. We used 121 kg m⁻³ as the bulk density of the catotelm, which was the bulk density of a non-mounded site.

In addition to studying the regimes of organic matter dynamics among the three habitats, we examined the effects of shifting habitats on peat surface. We simulated shifts in habitat by exchanging variables. For example, to determine the effects of disturbance on mounded sites, we changed five variables, p_L , k_L , p_A , k_A and s for those of gaps.

We focused on Δh in a relatively short term (5 years) as an index of the initial slope of changes in peat thickness. We used equations (2.8) and (2.11) to simulate changes in elevation. We conducted sensitivity analyses to examine which variables are most important in determining the change of elevation (Δh). Variables tested in sensitive analyses were litter fall, root production, peat respiration and initial thickness of the acrotelm layer, because the former three variables showed relatively high fluctuation and the last variable was affected by fluctuating water table. The sensitivity of peat accumulation against variables was explored by varying each variable by multiplying it by 2 and 0.5.

3. RESULTS**(a) Microhabitats around established trees**

The mean elevation at points 0.5 m from the centre of trunks of living established, buttressed trees was 43.6 cm,

Table 1. Summary of organic matter dynamics and the values applied in the peat surface profiling model. (Means for different parameters followed by the same letter within a row are not significantly different at $p=0.05$ (pairwise Welch's t -test and Bonferroni's multiple comparison; see Electronic Appendix part C). *Data from Brady (1997), **calculated from: leaf litter respiration rate/litter decomposition constant, *** k_C (0.00 022) is data from Brady (1997) and m_C is determined arbitrarily (thickness: 4.7 m, bulk density: 121).)

	symbol	mound	non-mound	gap
litter fall (kg m^{-2} per year)	p_L	0.943 ^a	0.696 ^b	0.420 ^c
litter decomposition constant (kg kg^{-1} per year)	k_L	0.891 ^a	0.916 ^a	0.760 ^b
initial mass of litter layer (kg m^{-2} per year)	m_{L0}	0.962 ^a	0.741 ^a	0.498 ^b
fine root production (kg m^{-3} per year)	p_A	0.995 ^a	0.570 ^{ab}	0.150 ^b
bulk density (kg m^{-3})	b	104	121	119
leaf litter respiration rate (kg kg^{-1} per year)*	—	0.0681	0.0681	0.0681
peat respiration rate in acrotelm (kg kg^{-1} per year)*	k_A	0.00 332	0.00 332	0.00 617
proportion of fragmentation per mass loss of leaf litter**	s	0.924	0.926	0.910
initial acrotelm thickness (m)	h_{A0}	0.6	0.3	0.3
output to catotelm (kg m^{-2} per year)***	$m_C k_C$	0.125	0.125	0.125

and it decreased gradually as the distance from tree trunks increased ($F_{1,334}=181$, $p<0.001$; figure 1a). Mean elevations became mostly constant (6.75–12.2 cm) when the distance from tree trunks was 3.5 m or more. On average, the height of mounds around the established, buttressed trees was 34.1 cm (subtracting mean elevation at 3.5–6 m from that at 0.5 m), and the radius was between 3.5 and 4.0 m. Similarly, elevation around dead buttressed trees decreased gradually as the distance from tree trunks increased ($F_{1,323}=70.0$, $p<0.001$; figure 1b).

Elevations were lower around established *M. motleyana* and *S. secundiflorus* trees than those around living established, buttressed trees. Mean elevations were 11.3 and 7.2 cm at 0.5 m, respectively, and no explicit trend of decline or increment was found as the distance from tree trunks increased ($F_{1,333}=3.24$, $p=0.0728$ for *Madhuca*; $F_{1,331}=2.72$, $p=0.0999$ for *Stemonurus*; figure 1c,d).

Comparing elevations within 3.5 m among the types of established trees, we found that variances (Levene's test, $F_{3,768}=49.5$, $p<0.001$) and means (ANOVA, $F_{3,768}=80.2$, $p<0.001$) were unequal. According to the multiple comparisons of means (Tamhane's T2), all pairs among four groups showed a significant difference ($p<0.001$), except the pair between *M. motleyana* and *S. secundiflorus* trees ($p=0.791$). The significant difference of elevations within 3.5 m between living and dead, buttressed trees indicates that the ground surfaces are sinking after established, buttressed trees die.

(b) Litter fall, root production, bulk density and decomposition

The rank of annual litter fall among the three habitats was mounds, non-mounds and gaps in descending order, and the values (s.e.d.) were 9.43 (0.687), 6.96 (0.244) and 4.20 (0.547) ton ha^{-1} per year, respectively (table 1; see Electronic Appendix part C for statistical tests among habitats). Similarly, the rank of root production among the three habitats was mounds, non-mounds and gaps in descending order, and the values (s.e.d.) were 1.99 (0.585), 1.14 (0.517) and 0.307 (0.0985) ton ha^{-1} per year, respectively. The rank in mass of litter deposits on peat surface among the three habitats was mounds, non-mounds and gaps in descending order, and the values (s.e.d.) were 9.62 (0.688), 7.41 (0.641) and 4.98 (0.683) ton ha^{-1} , respectively. The rank in peat bulk density among the three habitats was non-mounds, gaps and mounds in descending

Figure 2. Changes in acrotelm thickness within 10 years as simulated by the model. The solid, broken and dotted lines in (a) indicate values for mounds, non-mounds and gaps, respectively. In (b), shifts in habitat from non-mound to mound, from gap to non-mound, from non-mound to gap and from mound to gap are indicated by the solid line, broken line, dotted line and dotted-broken line, respectively.

order, and the values (s.e.d.) were 121 (1.22), 119 (1.37) and 104 (1.96) kg m^{-3} , respectively. The rank in litter decomposition rates among the three habitats was non-mounds, mounds and gaps in descending order, and the values (s.e.b.) were 0.916 (0.0603, d.f. = 30), 0.891 (0.0410, d.f. = 29) and 0.760 (0.0394, d.f. = 30) per year, respectively (table 1; Electronic Appendix part C).

(c) Simulation and sensitive analyses

As the mean water table was -30.3 cm (study site) and the mean height of mounds was 34.1 cm, we used 0.30 m as an initial thickness of the acrotelm layer for non-mounds and gaps, and 0.60 m for mounds. According to the model, the thickness of the acrotelm layer will rise up to 5.46, 2.35 and 0.300 cm 5 years later in mounds, non-mounds and gaps, respectively (figure 2a). The result of simulation for shifts in habitat type showed that Δh in mounds and non-mounds 5 years later will decrease 5.26 and 1.88 cm after disturbance, respectively. The establishment of canopy trees in gaps will cause a 1.90 cm increase in Δh 5 years later and the establishment of buttressed trees in non-mounds will cause a 1.25 cm increase in Δh 5 years later (figure 2b).

According to the sensitive analyses, changes in litter fall had large positive effects on acrotelm depth for the three habitats and had the strongest effects on gaps (table 2). Changes in root production were positive for the three

Table 2. Sensitivity of changes in acrotelm thickness after 5 years at three habitats against changes of four model parameters. (The analyses were conducted by multiplying each parameter by 2 and 0.5; values in parentheses express the percentage of change in relation to simulated values based on the original estimation of parameters.)

variables changed	changes in thickness of acrotelm layer (cm) and % change			
	coefficient	mound	non-mound	gap
not changed	—	5.46	2.35	0.300
litter fall	2	8.68 (59)	4.40 (87)	1.44 (380)
	1/2	3.85 (−30)	1.33 (−44)	−0.271 (−190)
root production	2	8.58 (57)	3.10 (32)	0.488 (63)
	1/2	3.95 (−28)	1.99 (−16)	0.206 (−31)
acrotelm peat respiration rate	2	4.41 (−19)	1.84 (−22)	−0.605 (−300)
	1/2	5.99 (10)	2.61 (11)	0.763 (154)
initial thickness of acrotelm layer	2	7.36 (35)	2.56 (8.9)	−0.428 (−240)
	1/2	4.51 (−17)	2.25 (−4.5)	0.664 (121)

habitats and mounds were especially sensitive. Effects of peat respiration rates were negative and gaps were the most sensitive. Changes in initial acrotelm thickness had positive effects for mounds and non-mounds and had especially strong negative effects for gaps (table 2).

(d) Shift of plant distribution

Shifts of distribution between growing stages were detected in some species (tables 3 and 4). Small trees of *Calophyllum rigidum* Miquel, *Ilex cymosa* Blume and *Eugenia rhizophora* Boerlage et Koorders were independent against mound-forming trees, but large trees of the first two species were attracted to within, and those of the last species were repulsed from, 3.5 m of the trunks. Small trees of *S. secundiflorus*, *Knema intermedia* Warb. and *S. teysmanniana* were independent against non-mound-forming trees, but large trees of the first two species were attracted, and those of the last species were repulsed.

4. DISCUSSION

(a) Elevation dynamics

We hypothesized that the rising and falling of the ground surface contribute to species coexistence by providing an axis of habitat partitioning. We tested this hypothesis by analysing shifts in plant distribution patterns and modelling the ground surface dynamics.

Distribution patterns reflect dispersal processes, but shifts between growth stages are evidence of differences of mortality in relation to habitat conditions, including interactions among plants. Because population density and mortality after juvenile stages is low, we can detect the relation between mortality and habitat conditions only from long-term monitoring or by studying the distribution shifts. We detected habitat partitioning of some dominant species based on the latter method (tables 3 and 4). The habitat partitioning that we detected here was mainly due to differences in flood tolerance rather than responses to light environments, because there were no significant differences in light environment among the three habitats (figure 1; see Electronic Appendix part A).

We recognized three habitats: mounds, non-mounds and gaps. Mounds are formed around established, buttressed trees where p_L and p_A are high and k_A is low. Because $k_A < p_A/b$, the thickness of the acrotelm layer increases until the equilibrium point $(sp_L + p_{Amax} - m_C k_C)/k_A$. If established and buttressed trees die, the habitats shift to gaps.

In gaps, p_L and p_A decline, k_A increases and the thickness of the acrotelm layer changes towards the equilibrium point, $(sp_L - m_C k_C)/(k_A - p_A/b)$. If initial values of the thickness are large enough, the thickness declines, that is, the ground surfaces sink (figure 2b).

If flood-intolerant emergent species like *S. teysmanniana* (see Electronic Appendix part B for abundance) regenerate before mounds become too low, the habitat returns to the mound formation. Non-emergent and flood-intolerant species like *C. rigidum* and *I. cymosa* usually regenerate under mound-forming trees but have limited abilities to maintain or recreate mounds by themselves.

If flood-intolerant emergent species do not establish themselves before mounds disappear, flood-tolerant canopy and subcanopy species including *E. rhizophora*, *S. secundiflorus* and *Knema intermedia* become established and the habitats shift to non-mounds. Changes in the thickness of the acrotelm layer are very slow because $p_A/b \approx k_A$ at this stage. As non-mounds showed intermediate changes in the thickness of the acrotelm layer between mounds and gaps, the relative elevation fluctuates according to regenerating tree species.

Some other species can become established in both mounds and non-mounds, probably because they have intermediate flood tolerance. These species include buttressed trees that reach the emergent stratum, such as *S. glauca*. If buttressed trees with intermediate flood tolerance establish themselves, the habitats shift to mounds because the values of p and p_A increase.

(b) Characteristics of elevation dynamics and extension to other forest types

As explained above, the dynamics of the acrotelm layer (elevation dynamics) are closely related to gap dynamics. In gap dynamics, species coexistence is explained based on plants' responses to light conditions (Whitmore 1989). In wetlands, plants' responses to inundation frequency are also important factors of population dynamics. Light conditions are determined by canopy opening and closure being affected by the growth and death of trees. Inundation frequency is determined by the fluctuation of the ground surfaces that is mainly caused by the changing of p_L , p_A and k_A , which are also affected by the growth and death of trees.

We compared elevation dynamics with hummock-hollow cycles (Tallis 1983) in boreal peat lands, although some studies suggest that hummock-hollow cycles are unlikely to

Table 3. Significance of $L_{1,2}(t)$ values of bivariate distribution of mound-forming trees ($\text{dbh} \geq 40$ cm) versus small and large trees of each species. (A dot indicates that the trees are spatially independent of mound-forming trees at a distance t (m); R and A indicate that the trees showed significant ($p < 0.05$) repulsive (R) or attractive (A) distribution to mound-forming trees at a distance t (m).)

species	distance (m)											
	small trees						large trees					
	1	2	3	4	5	6	1	2	3	4	5	6
<i>Madhuca motleyana</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Stemonurus secundiflorus</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eugenia rhizophora</i>	•	•	•	•	•	•	•	•	R	•	R	•
<i>Calophyllum rigidum</i>	•	•	•	•	•	•	•	A	•	A	•	A
<i>Ilex pleiobrachiata</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Knema intermedia</i>	•	A	•	•	A	A	•	•	•	•	•	•
<i>Tetractomia terrandra</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Swintonia glauca</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Eugenia lepidocarpa</i>	•	•	•	•	•	•	•	•	A	•	•	R
<i>Ilex cymosa</i>	•	•	•	•	•	•	•	•	A	•	•	•
<i>Shorea teysmanniana</i>	•	•	•	•	•	•	•	•	•	•	R	R

Table 4. Significance of $L_{1,2}(t)$ values of bivariate distribution of non-mound-forming trees ($\text{dbh} \geq 15$ cm) versus small and large trees of each species. (A dot indicates that the trees are spatially independent of non-mound-forming trees at a distance t (m); R and A indicate that the trees showed significant ($p < 0.05$) repulsive (R) or attractive (A) distribution to non-mound-forming trees at a distance t (m).)

species	distance (m)											
	small trees						large trees					
	1	2	3	4	5	6	1	2	3	4	5	6
<i>Madhuca motleyana</i>	•	•	•	A	A	A	•	•	•	•	•	•
<i>Stemonurus secundiflorus</i>	•	•	•	•	•	•	•	A	•	•	•	•
<i>Eugenia rhizophora</i>	•	•	•	•	•	•	•	•	•	•	•	R
<i>Calophyllum rigidum</i>	A	•	•	•	•	•	•	•	•	•	•	•
<i>Ilex pleiobrachiata</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Knema intermedia</i>	•	•	•	•	•	•	A	A	A	•	•	•
<i>Tetractomia terrandra</i>	•	•	•	•	•	•	•	•	•	•	•	A
<i>Swintonia glauca</i>	•	•	•	R	•	R	•	•	•	•	•	•
<i>Eugenia lepidocarpa</i>	•	•	•	•	•	•	•	A	•	•	•	•
<i>Ilex cymosa</i>	•	•	•	•	•	•	•	•	•	•	•	•
<i>Shorea teysmanniana</i>	•	•	•	•	•	•	•	•	R	•	R	R

occur (Svensson 1988; Weltzin *et al.* 2001). In tropical peat swamps, mounds can be created within a single generation of buttressed trees, while mounds in boreal peat are created by the accumulation of bryophytes over many generations. The time-scale of habitat cycles is the same as the longevity of plant individuals in the former, whereas it is much longer than generations in the latter. Thus, population dynamics of plants in hummock-hollow cycles can be described separately from much longer habitat cycles.

The effects of heterogeneity of organic matter dynamics are most easily detected in peat swamp forests, where we focused on the dynamics of elevation. However, our model introduced in this paper can be modified to express conditions of A₀ and A layers of soils in non-swamp forests.

In our model, we described organic matter dynamics of the litter layer and the acrotelm layer. The materials suffering decomposition in mineral soils are similar between peat swamp forests and non-swamp forests. Thus, what occurs at the litter layer is mostly the same between peat swamps and non-swamps. In the case of non-swamp forests, fragmented organic matter in the litter layer is supplied to the A layer. The acrotelm layer of peat swamps should be replaced by the A layer of non-swamp forests. The only difference is that mineral soil particles are mixed with fragmented organic matter in the A layer. If we introduce variables expressing the mode of a mixture of mineral soil particles and fragmented organic matter, our model can be used to study non-swamp forests.

It is well known that some plant species can grow or establish themselves better on mull soils, while others do better on mor or moder soils. Previously, these soil types were treated as fixed at each habitat. However, such soil types may change because organic matter dynamics are heterogeneous (Ashton 1964; Burghouts *et al.* 1998; this study). The habitat dynamics can explain the coexistence of plant species that prefer different soil types. A slightly modified version of our model should supply the basic equations to describe this.

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