Aboveground litter production, accumulation, decomposition, and tidal transportation of coral reef-type mangrove forest on Pohnpei Island, Federated States of Micronesia.

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ABSTRACT   Litter production, accumulation, and decomposition were examined on the seaward and landward sides of a long-term mangrove research site on Pohnpei Island, the Federated States of Micronesia, to estimate the contribution of litter deposited on the mangrove forest floor to carbon accumulation in mangrove forests. The annual litter production in the forest site was relatively high, 15 Mg ha^{-1} yr^{-1}. The litterfall was composed of leaves (55%), reproductive organs such as flowers and seeds (34%), and bark and small branches (11%). The seasonal fluctuation of the litter was small. The amounts of litter deposited on the floor were 0.51 Mg ha^{-1} on the seaward side and 0.76 Mg ha^{-1} on the landward side. Compared with the mangrove substratum, the litter deposited on the forest floor has an extremely low capacity to act as a carbon sink. During the first year of the leaf decomposition, the mangrove leaves decomposed markedly (k = 7.0 – 18.2) faster than the leaves of the terrestrial mahogany forest (k = 0.3). The mangrove leaves decomposed rapidly, losing more than 60% of their initial weight in the first month. This high rate might result from leaching of labile fraction from the leaves by the high frequency of immersion as well as by the high levels of activity of decomposers on the forest floor at high temperatures and humidity. Moreover, the effect of crab's feeding on the litter disappearance could not be disregarded. Tidal litter transportation rate was examined by collection of marked leaves along a tide level gradient. The transportation rate was greater as the highest tide level was higher. This study clarified that the disappearance of litter on the mangrove forest floor was strongly influenced by the tide, especially on the seaward side, as well as by the active microbial and faunal decomposability. We concluded that, despite the mangrove forest's high litter production, litter on the forest floor did not contribute much to carbon accumulation, especially on the seaward side, since litter was disappeared rapidly from forest floor by tidal exportation and strong microbial activity.

Key words: mangrove forest, forest floor dynamics, litterfall, deposited litter, leaf decomposition, Micronesia

INTRODUCTION

In recent years, the environments surrounding mangrove forests have been rapidly devastated on a global scale by artificial impacts such as the commercial cultivation of shrimp and fish and the felling of trees. More than half of all Southeast Asian mangrove forests have been lost since the 1960s (Miyagi et al., 2003). In contrast, most mangrove forests in Micronesia have been maintained as natural forests, and the country is home to the most intact examples of mangrove environments found in the world today (Cole et al., 1999).

Since 1994, we have been conducting an ongoing study of the stand structure and nutrient dynamics of mangrove forests at several long-term research sites on Pohnpei Island in Micronesia in order to establish an appropriate and sustainable mangrove forest management system (Fujimoto et al., 1995, 1999, 2000; Tabuchi et al., 1997, 2000; Utsugi et al., 2000). In our previous studies, the dry weight of the aboveground biomass in the mangrove forests on Pohnpei Island was estimated to be 482 Mg ha^{-1} to 693 Mg ha^{-1} (Tabuchi et al., 1997, 2000). The weight of carbon stored belowground to a depth of 2 m, a typical depth of mangrove peat in

Pohnpei, was estimated to be 1300 Mg ha^{-1} (Fujimoto *et al*. 1999). These results indicate that the carbon stocks in the mangrove forests on Pohnpei Island, including not only the aboveground biomass but the mangrove forest substrata, are extremely large compared with those of other terrestrial ecosystems. A thick, organic peat layer contributes to the large carbon stocks in mangrove forests.

The large carbon stocks in the mangrove forest on Pohnpei Island are the result of various processes such as forest growth, litter production, litter decomposition, organic substance accumulation on the substrata, and litter tidal exportation to the ocean, all of which have been occurring for a long time. To understand carbon and nutrient cycling in mangrove forests, it is essential to understand litter production in mangrove forests and litter disappearance on the forest floor. The litterfall rate is a major component of the organic material supply in forest ecosystems, and litter decomposition and tidal litter transportation are needed to estimate the contribution of mangrove forests to carbon accumulation in those forests. Litter production and decomposition studies in mangrove forests have been carried out in several parts of the world, such as Rookery Bay and Estero Bay in Southwest Florida (Twilley *et al*., 1986), Ohura Bay in Okinawa, Japan (Hardiwinoto *et al*., 1989), on Oahu Island in Hawaii (Cox & Allen, 1999), and on Iriomote Island in Okinawa, Japan (Kishimoto *et al*., 1987; Angsupanish *et al*., 1989). The forest biomass and the environmental conditions of these studies, however, are much different from those found on Pohnpei Island.

In the present study, we investigated aboveground litter dynamics by measuring on the mangrove forest floor on Pohnpei Island; specifically, the annual litterfall rate, the amount of litter deposited on the forest floor, the leaf decomposition rate, and tidal litter transportation. The major aims of this study were to evaluate how the litter deposited on the mangrove forest floor contributes to carbon accumulation in mangrove forests and to clarify what determines the amount of litter deposited on the forest floor. We defined litter decomposition as the biological and chemical denaturation and fragmentation processes. We characterized litter disappearance as both litter decomposition and tidal litter transportation.

METHODS

Site description

This study was conducted in a 1 ha (200 m × 50 m) long-term research site (PC-1) established in a coral-reef-type mangrove forest in 1994 (6° 52' 32" N, 158° 20' 02" E, Fig. 1). The stand structure in PC-1 was reported in detail in previous studies (Fujimoto *et al*., 1995; Tabuchi *et al*., 1997; 2000). This stand, which is dominated by *Rhizophora apiculata*, developed on a 0.7–1.2 m thick mangrove peat (Fujimoto *et al*., 1995). The total aboveground biomass in this plot was 546 Mg ha^{-1}. The aboveground biomass in *R. apiculata* was 418 Mg ha^{-1}, accounting for 77% of the total aboveground biomass in this plot (Tabuchi *et al*., 1997, 2000). The belowground carbon storage as mangrove peat and dead roots in this plot was estimated at 750 Mg ha^{-1} to a depth of 1.1 m (Fujimoto *et al*., 1997, 1999).

The mean air temperature from September 2003 to August 2004 was 26.8 °C; the coldest monthly mean air temperature was in September (26.0 °C) and the warmest was in January (27.3 °C) (Data not shown). The average annual rainfall from 1961 to 1990 was 4726 mm (National Astronomical Observatory, 2000). The rainy and dry seasons is not clearly distinguished; the relatively rainy period is from May – July, when monthly rainfall is over 430 mm, and the relatively dry period is from January – March, when less than 350 mm falls monthly.

Two subplots (2 m × 2 m) were established in PC-1, one on the seaward side and the other on the landward side. The ground level of each subplot was 0.1 and 0.3 m above mean sea level on the seaward and landward side, respectively. The tidal submergence frequencies to all high tides in a year were over 80% at the seaward side and under 40% at the landward side (Fujimoto *et al*., 1995). We investigated the annual litterfall rate, the amount of litter deposited, the leaf decomposition rate on the forest floor, and tidal litter transportation.

We established a contrastive plot (30 m × 30 m) in a mahogany plantation near PC-1, on Pohnlaungas, Pohnpei Island, Micronesia, to assess the leaf decomposition rate in a tropical terrestrial ecosystem (6° 50' 17" N, 158° 17' 56" E, altitude: 70 m, Fig. 1). This stand was dominated by mahogany (*Swietenia mahogani*) trees, 40–50 years old with an average height of 30 m, an average diameter at breast height (D. B. H.) of 45 cm, a tree stand density of 587 trees ha^{-1}, and a basal area of 98 m^2 ha^{-1}. The understory vegetation was composed of herbs, shrubs, and mahogany seedlings. The soil in this mahogany stand originated as basalt.

Litterfall rate and amount of litter deposited on the forest floor

We analyzed the annual litterfall rate and amount of litter deposited on the forest floor to estimate the litter production and litter accumulation in PC-1. Five baskets
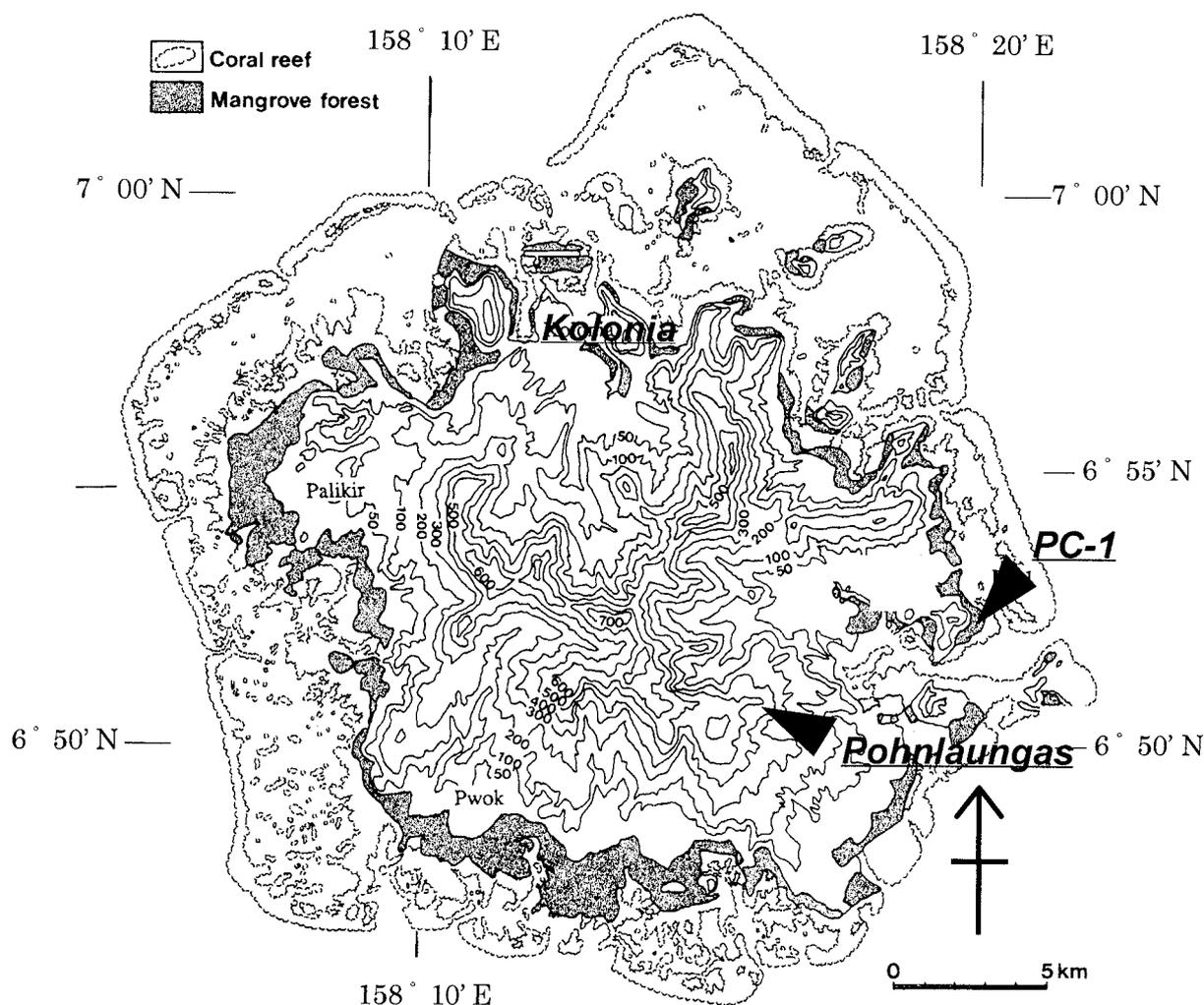
Fig. 1. Map showing the Pohnpei Island topography, distribution of mangrove forests, and location of research plots.

(0.47 m × 0.35 m) were arranged as litter traps in the respective subplots in PC-1 on the prop roots of *R. apiculata* at a height of about 1 m from the ground; they were not immersed. Litterfall samples were collected monthly from mid-September 2002 to mid-September 2003 and weighed fresh. They were subsequently taken back to the laboratory and dried in an oven at 75 °C for 48 h. The samples were then sorted into leaves, branches, bark, flowers, and seeds, and the material in each of these categories was then weighed.

The leaf and branch litter on the forest floor in each subplot in PC-1 was sampled from 0.5 m × 0.5 m in 13rd September 2002, taken back to the laboratory, dried in an oven at 75 °C for 48 h, then weighed to estimate the amount of litter deposited on the forest floor. Hexplicate sampling of each subplot was then carried out.

The annual litterfall rates and the amounts of litter deposited on the forest floor were analyzed using Student's *t*-test for independent samples to compare differences between the subplots. Significance was accepted at $P < 0.05$.

Leaf decomposition rate on forest floor

Decomposition experiments with the mangrove leaves were carried out using the litterbag method (Crossley & Hoglund, 1962) to determine the litter decomposition rate due to biological and chemical denaturation and fragmentation. We used intact *Rhizophora stylosa* fresh leaves rather than the dominant *Rhizophora apiculata* leaves for following reasons. *R. stylosa* and *R. apiculata* hybridize each other in nature and are quite closely related although they were distinct species (Duke *et al.*, 2002). Substantially, the *R. stylosa* tree is small and grows along the seacoast, so it was relatively easy for us to obtain a large sample of leaves. Intact mangrove leaves were sampled from live *R. stylosa* trees at the

seacoast near PC-1 in September 2002, and used for the leaf decomposition experiment. About 15 grams of fresh leaves were put into 1-mm mesh nylon bags (20 cm × 25 cm). Samples of fresh leaves were taken back to the laboratory, dried in an oven at 75 °C for 48 h to calculate the dry weight, and analyzed for their carbon and nitrogen concentrations. In September 2002, 80 litterbags in all were set on the forest floor at each subplot. All of the litterbags were tied to one another with wire. One end of the wire was attached to the prop root of the nearest tree to prevent the tide from washing away the bags. The bags were collected five times: in October, November, and December 2002, and in March and August 2003. On each sampling occasion except for the final one, six litterbags were collected from each placement in both subplots. In all, 16 litterbags were collected from each placement in each subplot on the final sampling occasion, because most of the leaves had decomposed and disappeared. The remnants were put in nylon bags and taken to the laboratory.

Another decomposition experiment with mahogany leaves was also conducted using the litterbag method in a mahogany plantation forest near PC-1 in Pohnlaungas (Fig. 1) to compare the leaf decomposition between mangrove and tropical terrestrial ecosystems. Fresh mahogany (*Swietenia mahogani*) leaves were sampled from live mahogany trees at the plantation in September 2002. In all, 58 litterbags were set on the forest floor. The litterbags were collected five times, at the same time as the mangrove leaves. At each sampling except for the final one, 10 litterbags were collected from the forest floor. On the final sampling, 18 litterbags were collected from the forest floor. They were treated according to the same methods as the mangrove leaves to estimate the decomposition rates.

The weight loss process of litter was approximated by the following equation (Olson, 1963):

$$Wt = W_0 \times \exp(-k \times t),$$

where W_0 is the initial dry weight of leaves, Wt is the weight at time t, and k (in year) is the decomposition constant.

Tidal litter transportation

Tidal current is an important factor in the dynamics of litter, because the tide washes over the mangrove forest floor every day. We examined the distance the litter was carried by the tide to evaluate the influence of the high-tide level on litter transportation. Tidal litter transportation was examined between 14 and 15 September 2004 during the spring tide. The highest tide level during our examination was 0.7 m above mean sea level and the tidal range was 1.3 m. Twenty-five leaves marked with numbered tags were placed on the forest floor at each of four points, 30, 130, 230, and 330 m from the coastline in and around PC-1. The ground levels at these points were –0.3, 0.1, 0.2, and 0.3 m above mean sea level, and the highest tide levels at these points were 1.0, 0.5, 0.3, and 0.2 m above mean sea level, respectively, between 14 and 15 September 2004. The ground levels at these points were calculated using relative height from sea level at the time of the survey and predicted tide data (Japan Coast Guard, 2003) at the nearest point, Madolenihmw, on Pohnpei Island. The highest tide levels at these points were also calculated using the ground level data and decrement value of the tide level (Fujimoto *et al*., 1995). During the examination, high tide occurred twice. We looked for the marked leaves in the forest and the tidal flat in front of the forest, and measured the movement from the initial positions.

RESULTS

Litterfall rate and amount of litter deposited on the forest floor

Figure 2 shows the seasonal fluctuations in the litterfall rate from October 2002 to September 2003 in PC-1 on the seaward and landward sides. The annual litter production was 15.0 ± 1.4 (mean ± standard deviation) Mg ha^{-1} year^{-1} on the landward side and 15.3 ± 2.9 Mg ha^{-1} year^{-1} on the seaward side; the subplots did not differ significantly (P > 0.05). The monthly fluctuations of the litterfall rate ranged from 0.7 Mg ha^{-1} month^{-1} to 2.4 Mg ha^{-1} month^{-1} in both subplots. The seasonal fluctuation was not clear, though the rate seemed to be higher during the rainy period (from April to July) than in the other months of the year. The subplots did not differ from each other in their monthly mean litterfall rates. The litterfall was composed of leaves (55%), reproductive organs such as flowers and seeds (34%), and bark and small branches (11%) in both plots (Table 1). Leaves and reproductive organs fell throughout the year, although the amount of fallen reproductive organs was slightly lower in February and March. Small amounts of bark and small branches fell throughout the year.

Most of the mangrove forest floor was denuded by the daily tidal wash, and was sometimes covered mosaically with fallen yellowish and green mangrove leaves. Mangrove seeds were also distributed on the

forest floor. It was easy to distinguish the litter on the forest floor from mangrove mud. The main component of the deposited litter was fallen leaves. The mean amounts of litter deposited on the forest floor were low on both the seaward and landward sides, but were significantly lower on the seaward side (0.51 ± 0.25 Mg ha^{-1}) than the landward one (0.76 ± 0.14 Mg ha^{-1}; P<0.05) (Table 1).

Leaf decomposition on forest floor
Figure 3 shows the time courses of the mass of mangrove and mahogany leaves remaining for one year on the forest floor. The mangrove leaf masses decreased quite rapidly on both sides of the island in the early stage, and thereafter decreased gradually. The mangrove leaves lost more than 60% of their initial weight during the first month and 80% within three months after settlement on the forest floor in both subplots. The decomposition rate was markedly higher on the seaward side than on the landward side. In contrast, the decomposition rate of the mahogany leaves in the terrestrial zone was markedly lower than that of the mangrove leaves in the mangrove forest, particularly in the first half year. The decomposition processes of the leaves in the forests were approximated as an exponential curve; the decomposition constants (k) and coefficients of determination (R^2) were 18.2 year^{-1} and 0.72 on the seaward side, 7.0 year^{-1} and 0.60 on the landward side, and 0.3 year^{-1} and 0.77 on the mahogany plantation (Table 1). The decomposition constants were much higher in the mangrove forest than in the mahogany forest.

Tidal litter transportation
Figure 4 shows the relationships between the tidal litter transportation and the highest tide levels. The tidal litter transportation into the seaward side was described as a positive value, while that into the landward side was negative. No marked leaves that had settled at the nearest

point to the coastline (highest tide level = 1.0 m above mean sea level) were found at daybreak, as the tide may have moved most leaves from the forest to the sea. At a point 330 m from the coastline (highest tide level = 0.2 m above mean sea level), the mean tidal litter transportation was close to zero. As the highest tide level decreased, the average distance of tidal litter transportation decreased. When the highest tide level was under 0.5 m (130 m from the coastline), some of the marked leaves were found to have been transported to either the landward or seaward side. This shows that the litter did not stay in its initial position continuously except for non-immersion points and that the litter remaining was influenced by the tide on the tidal immersion points.

It was observed that most of the mangrove leaves that was not moved by the tide were bitten by crabs during the night and were taken away by the crabs to their nesting cavities, especially on the landward (Personal observation). Appetites of small crabs are very sharp.

DISCUSSION
Litter production
The annual litter production in the mangrove forest was 15 Mg ha^{-1} year^{-1}, with no significant difference between the seaward and landward sides (Table 1). In both subplots, more than half of the annual litterfall was composed of leaves throughout the year. A certain quantity of leaves and reproductive organs always ripened and fell throughout the year. Cox & Allen (1999), Twilley *et al.* (1986), and Hardiwinoto *et al.* (1989) reported that litterfall showed distinct seasonal patterns, but in the present study the fluctuation was not distinct. Pohnpei Island has a higher temperature, higher humidity, and milder changes than Hawaii or Southeast Florida (Cox & Allen, 1999; Twilley *et al.*, 1986; Hardiwinoto *et al.*,

Table 1. Annual litterfall rates (L), the amounts of deposited organic matter in the forest floor (M), and decomposition constants (k) in mangrove leaves and mahogany leaves.

placement	Litterfall (L) (Mg ha^{-1} yr^{-1})				M (Mg ha^{-1})	L/M[a] (yr^{-1})	k[b] (yr^{-1})	R^2[c]
	leaves	reproductive organs	others	total				
Mangrove								
Seaward	8.4	5.2	1.7	15.3	0.51	30.0	18.2	0.72
Interior	8.3	5.1	1.7	15.0	0.76	19.7	7.0	0.60
Mahogany	--	--	--	--	--	--	0.3	0.77

[a]Ratio of litterfall to the forest floor mass, as calculated from the measurement data obtained in this study.
[b]Decomposition constant, as calculated using an exponential equation (Fig. 3).
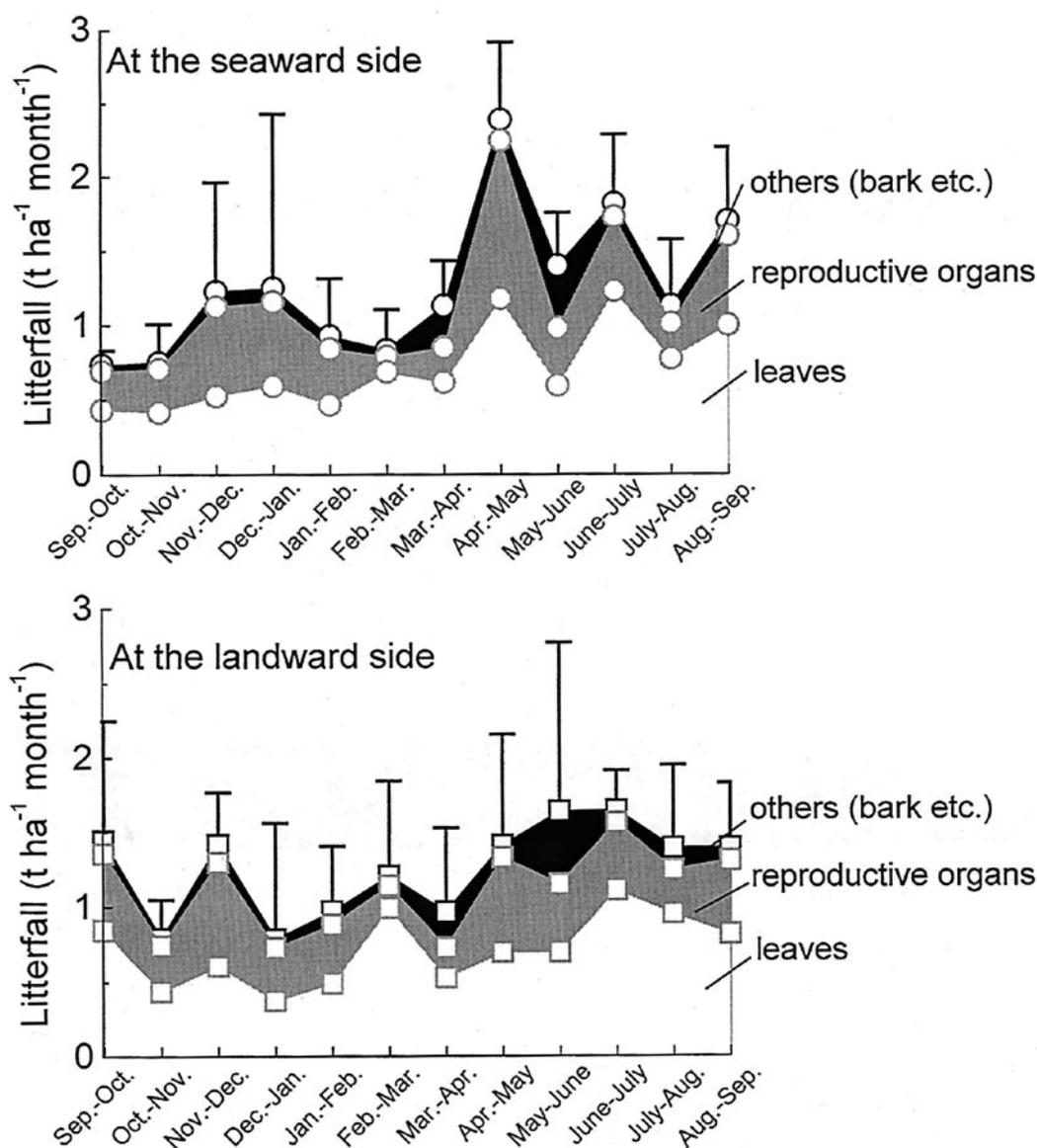[c]Coefficient of determination.

Fig. 2. Seasonal fluctuations of litterfall rate in coral-reef-type *Rhizophora apiculrata* dominant forest in PC-1. Error bars indicate standard deviation of total monthly litterfall rate. Annual litterfall rate was 15.3 ± 2.9 Mg ha⁻¹ yr⁻¹ at the seaward side and 15.0 ± 1.4 Mg ha⁻¹ yr⁻¹ at the landward side.

1989). The annual litterfall rate obtained in this study was higher than the $7.7 - 10.7$ Mg ha^{-1} year^{-1} litter production of Okinawa, Japan (Hardiwinoto *et al.*, 1989), the $3.5 - 8.7$ Mg ha^{-1} year^{-1} found in South Florida (Twilley *et al.*, 1986), and the 7.5–8.8 Mg ha^{-1} year^{-1} on Iriomote Island, Japan (Kishimoto *et al.*, 1987). It was lower than the 25 Mg ha^{-1} year^{-1} recorded for Hawaii (Cox & Allen, 1999). The annual litter production at this site was higher than that found in previous reports, except for the data for Hawaii. However, the forest biomass is markedly larger in our study site than in other mangrove forests (Twilley *et al.*, 1986; Kishimoto *et al.*, 1987; Cox & Allen, 1999). We cannot compare our data with those of previous

reports directly and indiscriminately, because our site is at lower latitude than the sites reported on previously, and because the dominant species and forest succession at our site differed from those at the previous sites. We concluded that the mangrove forest at our site might be a precious environment, having both a larger biomass and higher litter production than other mangrove forests.

Litter accumulation and disappearance on mangrove forest floor
The amounts of litter deposited on the forest floor were markedly low: 0.51 Mg ha^{-1} on the landward side and 0.76 Mg ha^{-1} on the seaward side (Table 1). This result

shows that the litter deposited on the forest floor has an extremely low capacity as a carbon sink in comparison with the mangrove substratum: 750 Mg ha^{-1} carbon accumulation up to 1.1 m depth (Fujimoto *et al.*, 1999). One reason for this was obtained by the results of the litterbag experiment. Those results showed that the mangrove leaves rapidly lost mass during the early decomposition stage: more than 80% was lost in the first three months (Fig. 3). The decomposition constant (*k*) of the mangrove leaves was extremely high in the mangrove forest compared with that of mahogany leaves in the mahogany forest (Table 1). This agreed with the results of previous studies in Southern Thailand (Angsupanich and Aksornkoae, 1994) and in Okinawa, Japan (Angsupanich *et al.*, 1989; Hardiwinoto *et al.*, 1989). This rapid rate on the mangrove forest floor might partially prevent deposited litter from contributing to carbon accumulation in mangrove substrata. The biological and chemical denaturation of organic materials was generally induced in the liquid phase, because substrate-enzymatic reactions

occur in that phase fundamentally. Therefore, this rapid decomposition in the mangrove forest, in comparison with a tropical terrestrial forest, might be attributable to the acceleration of leaf leaching and autolysis under the constant wet conditions of immersion in brine. Of course, it might also be attributable to high microbial activity under warm and high-humidity conditions (Angsupanich & Aksornkoae, 1994). Furthermore, litter decomposers such as small crabs were quite active at the landward side; most of the marked mangrove leaves in this investigation were bitten by crabs during the night and were taken away by the crabs to their nesting cavities, especially on the landward side (Personal observation). The litter decomposers might play important roles similar to those of termites in tropical terrestrial ecosystems, but we did not examine the role of litter decomposers in this study.

The amount of litter deposited on the forest floor on the seaward side was 0.51 Mg ha^{-1}: it was two thirds on the landward side (0.76 Mg ha^{-1}) (Table 1, P<0.05).
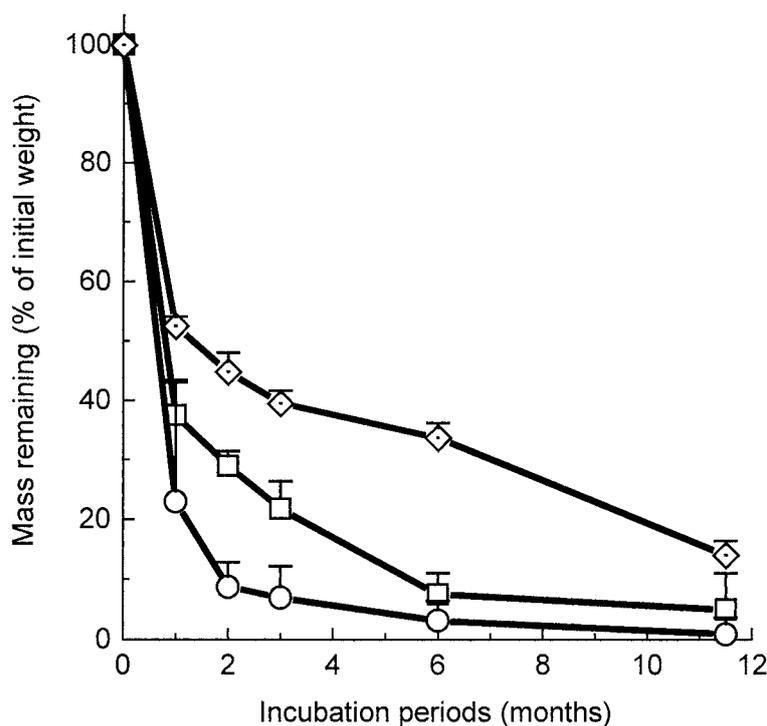

Fig. 3. Time courses of the remaining mass of mangrove leaves in coral-reef-type mangrove forest and mahogany leaves in mahogany forest during an incubation period of one year on each forest floor. Error bars indicate standard deviations.

in Mangrove forest
—□— Landward side   —○— Seaward side
in Mahogany forest
—◇—

This result seems not to explain the difference in decomposition rates between the two sides (Fig. 3 and Table 1) because the decomposition constant of mangrove leaves on the seaward side was 2.6 times higher than that on the landward side (Table 1). It was necessary to examine how tidal immersion transported litter. We investigated the transportation distance during the spring tide. When the highest tide level increased, the distance of tidal litter transportation increased (Fig. 4). Especially, as the highest tide level was over 0.5 m above mean sea level, more than half of the leaves had been transported more than 10 m by daybreak to the seaward side. This result implied that litter at the seaward side disappeared mainly by the tide dependently of microbial denaturation, and showed the potential for the rapid export of litter to the ocean. On the other hand, on the landward side more than half of the leaves had been transported only one meter by daybreak and stayed on the forest floor near their initial position. Therefore, at the landward side litter disappearance was slightly influenced by tidal transportation. Litter deposited on the forest floor was moved from the landward side to the seaward side, supplied to the forest floor at the seaward side as the deposited litter, and decomposed by the forest floor organisms. These processes might lessen the difference between the two sides of the island in the amount of litter remaining on the forest floor. Furthermore, the keen appetites of small crab at the landward side might also influence the litter disappearance. For above-mentioned reasons, deposited litter at the seaward side might remain on the mangrove forest floor more than it was expected from leaf decomposition rate.

In terrestrial ecosystems, the ratio (L/M) of litterfall (L) to the amount of litter deposited on the forest floor (M)
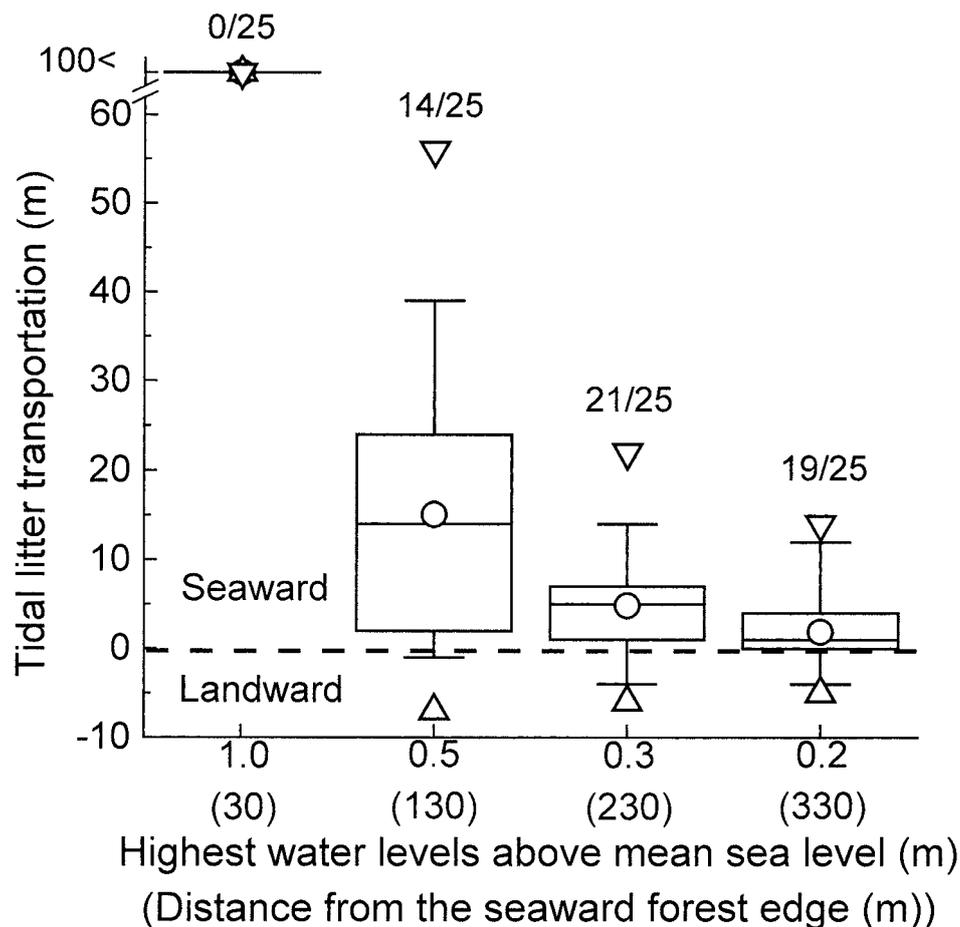

Fig. 4. Relationships between tidal litter transportation and highest tide level above mean sea level between 14 and 15 September 2004. Triangles indicate the maximum and minimum values. Circles indicate the average values. The upper and lower bars indicate values of 5% and 95%. The upper and lower sides of the box indicate values of 25% and 75%. The line in the box indicates the median value. Different fractions within a figure indicate the discovery rates of 25 marked leaves.

is generally considered comparable to the decomposition constant (k), which was determined theoretically from litter decomposition studies in a steady-state forest (Takeda, 1995; Chapin *et al.*, 2002; Berg & McClaugherty, 2003). We calculated the L/M in the mangrove forest and compared it with the decomposition constant (k) (Table 1) assuming that this study site is a steady-state forest. The L/M was considerably higher than the k value. In a terrestrial forest, there was not much erosion of the forest floor by overland flow and wind erosion, except on steep slopes and at windy sites. In contrast, the tide washed away the mangrove forest floor daily (Fig. 4). This result also suggests that microbial activity, leaf autolysis, and tidal litter transportation into the sea accelerate litter mass loss under the high humidity, high salinity, and frequent immersion conditions typically found in mangrove forests. The results of this study imply that leaf mass losses aside from the decomposition process considerably influence marine ecosystems because of the export of organic matter into the sea.

CONCLUSION

This study shows that the litter deposited on a mangrove forest floor did not directly contribute much to carbon accumulation in the mangrove forest relative to the mangrove substratum, although this forest had relatively high litter production. The primary reason for this was the extremely rapid litter decomposition through denaturation and fragmentation processes on the forest floor. Tidal transportation of litter was also a factor in litter disappearance, especially near the seacoast.

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