Trees (2002) 16:172–180
DOI 10.1007/s00468-001-0156-0

ORIGINAL ARTICLE

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Nutrient dynamics and leaf litter decomposition in a subtropical mangrove forest at Oura Bay, Okinawa, Japan

Received: 10 July 2001 / Accepted: 12 November 2001 / Published online: 11 January 2002
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Abstract Dynamics of nutrients (carbon, nitrogen and phosphorus) in decomposing leaves was studied using litterbags in a subtropical mangrove dominated by *Bruguiera gymnorrhiza* (L.) Lamk and *Kandelia candel* (L.) Druce (Okinawa, Japan). In addition to fresh yellow leaves, degradation of treated leaves (dried at 50°C and 80°C) was also investigated. Comparison was made between species, locations (lower and upper mangroves) and among treatments. Results showed that *K. candel* leaves with higher initial N concentrations (low C:N ratio) decayed faster than *B. gymnorrhiza* leaves; decay constants were 0.062 and 0.022 per day. This finding implies that degradation rate is species specific and depends on the initial chemical composition of leaves, particularly the C:N ratio. Furthermore, *B. gymnorrhiza* leaves, with lower initial N levels, gained more N from external sources (i.e. bacteria) than *K. candel* leaves which exhibit a high initial N content. Leaves in the upper mangroves decayed much more slowly than in lower mangroves; decay constants were 0.019 and 0.022 per day. The overall decay rates of dried leaves were lower than those of fresh leaves, decreasing in the order: fresh leaves 0.022, 50°C 0.019 and 80°C 0.018. The $t_{0.5}$ values were 32, 36 and 38 days respectively. Drying of mangrove leaves prior to incubation in the field significantly altered the pattern of mass loss, nutrient loss and delayed microbial recolonization. A single exponential equation described losses of ash-free dry weight, C, and P for the two species, sites and treatments. Only N in *K. candel* leaves was described by the single exponential equation.

Keywords Mangrove decomposition · Nutrient dynamics · Drying effects · *Bruguiera gymnorrhiza* · *Kandelia candel*

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Introduction

Mangrove litter decomposition and its accompanied release of nutrients is an important aspect of estuarine ecosystem function (Wieder and Lang 1982). The litter, mainly leaves, represents about one-third of production, and up to half this quantity can be exported to adjacent tidal flats and the ocean (Robertson et al. 1992). It is through the degradation processes that nutrients such as carbon, nitrogen, phosphorus and others are released to the estuarine ecosystem and the open ocean. However, the amount of energy and organic matter export to the estuary from mangrove ecosystems depends on the degradation rate of mangrove litter. Mangrove litter degradation also depends on species type, initial chemical contents of degrading leaf detritus and location within a mangrove forest. These factors in turn depend on the degree and frequency of tidal inundation, climate, latitude and the presence or absence of leaf-consuming fauna and macroconsumers (Woodroffe 1982; Robertson 1988; Chale 1993).

Although there have been many studies of mangrove litter decomposition in subtropical regions (e.g. Steinke and Ward 1987; Lu and Lin 1990; Tam et al. 1990; Tam et al. 1998), work on litter decay in subtropical Japan is rare (e.g. Kishimoto et al. 1987; Hardiwinoto et al. 1989). In Oura Bay mangrove forest, dominated by *Bruguiera gymnorrhiza* and *Kandelia candel* (Hardiwinoto et al. 1989), organic matter processed in the mangroves is exported to the intertidal flats in both the rainy and the dry season (Meziane and Tsuchiya 2000). Nevertheless, the rates of degradation of leaf litter, of associated nutrient release, and of supply of organic matter to the estuarine detritus-based food webs are not known. Previously, Hardiwinoto et al. (1989) examined dry mass loss of *B. gymnorrhiza* and *K. candel* leaves and twigs, and found that it was faster in *K. candel*. However, no measurements of nutrients and ash-free dry weights (AFDW) in leaf detritus were made. Therefore this study aimed at investigating changes in nutrient contents (C, N and P) associated with decomposing mangrove leaves of *B.*

gymnorrhiza and *K. candel*, and comparing the natural pattern of decay of yellow senescent mangrove leaves with that obtained when leaves were subjected to artificial drying. In some studies, drying has been used to allow storage of leaves until experiments could be performed. While this may represent the natural situation for most terrestrial litter, most mangrove litter produced falls on wet sediments or in water and remains wet. On this basis then, the use of dried leaves would likely give erroneous results. We tested the hypotheses:

1. That degradation rates of mangrove leaves differ among species, depending on initial leaf chemical composition.
2. That there are spatial variations in degradation rates within mangroves, associated with spatial differences in sediment quality, which in turn are associated with the microflora composition.
3. That drying of mangrove leaves prior to field incubation affects their decay rates and pattern of mass and nutrient loss.

Materials and methods

Study area

The study was carried out at Oura Bay, located in the northern part of Okinawa Island (26°N, 128°E: Fig. 1) in southern Japan. The mangrove forest consists of mixed stands of *B. gymnorrhiza*, *K. candel* and *Rhizophora stylosa*, covering an area of approximately 10 ha at the mouth of the Oura River. *K. candel* is mainly distributed in the low intertidal and along the riverbank while *B. gymnorrhiza* distribution ranges from high to low intertidal. The forest is a natural reserve of significant importance to species of crabs, fish and water birds. Annual mean air temperature is 22.9°C, highest monthly mean occurs in July (28°C) and lowest monthly mean in January (14°C). Annual precipitation averages 218 mm/month, highest in the rainy season (May–July) and lowest in the dry season (October–November). The forest is situated in an enclosed bay and the effects of wave action are relatively small. The sediment surface varies from hard to soft mud, comprised mainly of large pebbles and clay-like particles respectively. Sources of allochthonous inputs, which may be channeled through the river, come from surrounding mountain forests, sugar plantations and human settlements (Fig. 1).

Experimental design

Two sites, in the high intertidal mangroves (ST1) and low intertidal mangroves (ST2) (two locations within a site), were selected (Fig. 1) for investigation. Yellow leaves which had just fallen on sediments, and others which were still attached to branches but were ready to abscise, were picked and rinsed with distilled water in the field in July 2000. In the laboratory, leaves were separated into three categories according to the study hypotheses to be tested. The categories were: fresh leaves (for species and site comparison), leaves dried in oven at 50°C, and at 80°C under air circulation for 2 days (for examination of the effects of drying). Leaves dried in an oven (at 50°C) have been used in previous studies, and leaves dried at 80°C were used to see if the effect increases or decreases with increased drying temperature. All experiments were performed using litterbags (1 mm mesh and 22×18 cm).

To examine whether there are differences in decay rates in *B. gymnorrhiza* and *K. candel*, and whether differences depend on their initial chemical contents, we measured the macronutrient concentrations (C, N and P) in the fresh yellow leaves of both species at the start of the experiment. Then 10 g of fresh leaves (equivalent to 5 g of dried leaves, wet weight to dry weight conversion of complete leaves during the time of investigation was 2) were placed in litterbags and randomly deployed in the low intertidal zone (ST2) sediment floor of the forest. The experiment was performed in the low intertidal zone because both species inhabit this area and no *K. candel* stands are found in the high intertidal of this mangrove forest.

Site variations were investigated using *B. gymnorrhiza* fresh yellow leaves (containing the same C, N and P concentrations) which were placed in litterbags and randomly deployed on the sediments at ST1and ST2. *B. gymnorrhiza* was selected because it is the most dominant mangrove species which extensively covers the whole mangrove forest. Collection and weighing of fresh leaves were performed within 14 h in order to avoid bacterial and fungal colonization.

Effects of drying leaves on the pattern of mass and nutrient loss were examined on *B. gymnorrhiza* leaves (which contained the same initial chemical concentrations) in the low intertidal

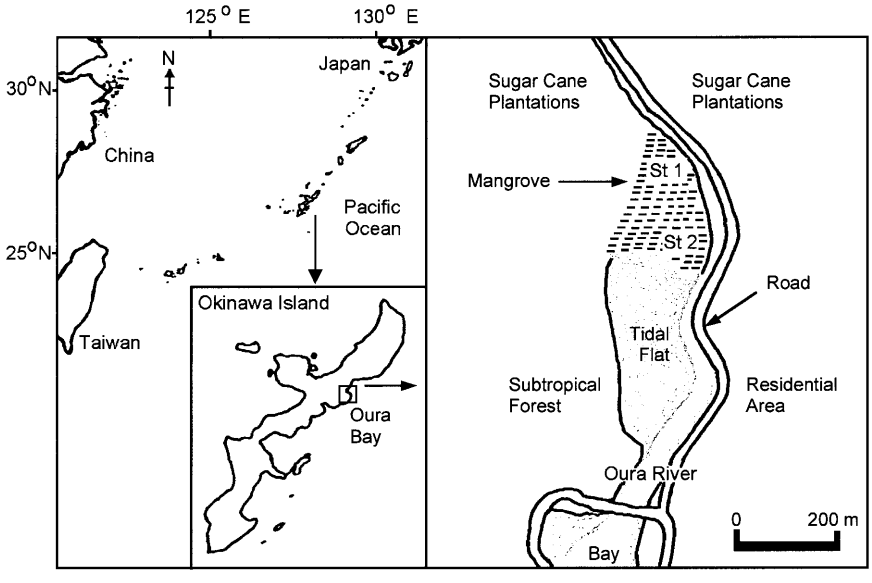


Fig. 1 Location of Okinawa Island and experimental sites at Oura Bay

zone. In addition to fresh leaves (treatment, T1), already dried leaves at the two temperature treatments (T2 and T3, 50°C and 80°C) were used for investigation. Collection, drying and weighing of leaves were performed within 56 h and litterbags were then set out in the field. For all experiments a total of 135 bags were deployed.

Experiments were designed to run for 124 days (4 months) during summer and autumn, from July 6 to November 7 2000. On days 17, 31, 45, 59, 73, 87 and 124, three litterbags for each species, site and treatment were randomly removed (15 bags). On the same day, sediment samples from both stations were taken using a core sampler of 10 cm internal diameter and 20 cm depth. Thereafter cores were extruded and sectioned into 4-cm pieces. Three cores were taken from each sampling location every month during the experiment. In this investigation we will discuss results of the top 4-cm sections, which have direct influence on leaf decay as substrate. The leaf detritus within each retrieved bag was rinsed with fresh water over a 0.5-mm mesh size sieve to remove sediment.

Sample analysis

The remaining leaf material was oven dried for 2 days at 50°C (to constant weights), weighed and then ground to a fine powder with a mortar and pestle. Sediment samples were dried for 2 days at 60°C, cooled and then ground to pass through a 0.250-mm sieve for determination of total C and N contents. Subsamples of the powdered detritus material were used to determine percent AFDW (ignition in a muffle furnace at 550°C for 3 h). Total C and N contents were measured in a Shimadzu high sensitivity CN analyzer model Sumigraph NC-80. Three replicates were measured for each sample. Total P contents were measured spectrophotomically by the ascorbic acid method after digestion in a mixture of concentrated sulfuric acid and nitric acid. Subsamples of fresh yellow leaves (15 leaves) from both species were treated in the same way to obtain percent AFDW, total C, total N and total P concentrations at time 0.

Changes in chemical content during degradation are expressed as concentrations in mg g^{-1} dry weight. The amount (mg) of AFDW, C, N or P remaining at time *t* is expressed as a percentage of the initial value, and was calculated by multiplying the corresponding AFDW value (g) or concentration (mg g^{-1}) with the oven dry weight of litter remaining at time *t*, dividing by the weight of AFDW, C, N or P at time 0, and then multiplying by 100.

Statistical analysis and decay models

A two-way ANOVA test was used to evaluate differences in the mean concentrations (C, N, P and C:N ratios) and in the mean percent weight loss (AFDW, C, N and P) between species, sites and among treatments during the 124 days of the experiment. Fisher's PLSD and Student-Newman-Keuls indicated where there were significant time differences in the means. Raw concentration and percentage data were used in each analysis. The percent weight loss data could not be arcsine *p*-transformed because percentages greater than 100 were common in the data set. All statistical analyses were performed using Stat View 5.

A single negative exponential equation was used to describe the percent of AFDW, C and P remaining in litter from the two species, sites and treatments.

$$W_t = W_{0e}^{-kt} \quad (1)$$

Where W_t and W_0 are weights remaining at time *t* and time 0 respectively, and *k* is a decay constant obtained from the regression models using Kaleidagraph Software. The half-life times, $t_{(0.5)}$ (time taken for loss of half the original AFDW, C or P) were calculated using the formula; $t_{(0.5)}=\ln 2/k$.

Results and discussion

Dynamics of nutrients

The initial nutrient concentration in mangrove leaves is the most important factor that influences associated nutrient change and release to the estuarine environments during leaf decay. This study found significant differences in the changes of C:N ratios and nutrient concentrations between species ($P<0.01$) (Fig. 2). Between sites, N, C:N ratios and P ($P<0.01$) showed clear differences (Fig. 3b–d), but C did not differ significantly ($P=0.2812$) (Fig. 3a). Changes in C concentrations differed significantly among treatments ($P<0.01$), while there were no significant difference in the change of C:N ratios, N and P concentrations amongst treatments ($P=0.1336$, 0.1424 and 0.4778 respectively) (Fig. 6). *K. candel* lost C and P more rapidly through leaching than *B. gymnorrhiza* during the first 17 days of incubation (Figs. 2a, d, 4b, d). C concentrations for both species showed an initial decrease then increased; *K. candel* started increasing after 31 days while *B. gymnorrhiza* started increasing after 59 days of incubation (Fig. 2a). The initial decrease in C indicated dry weight loss per sample, which was caused by rapid release of total non-structural carbohydrates such as sugars, and starches,

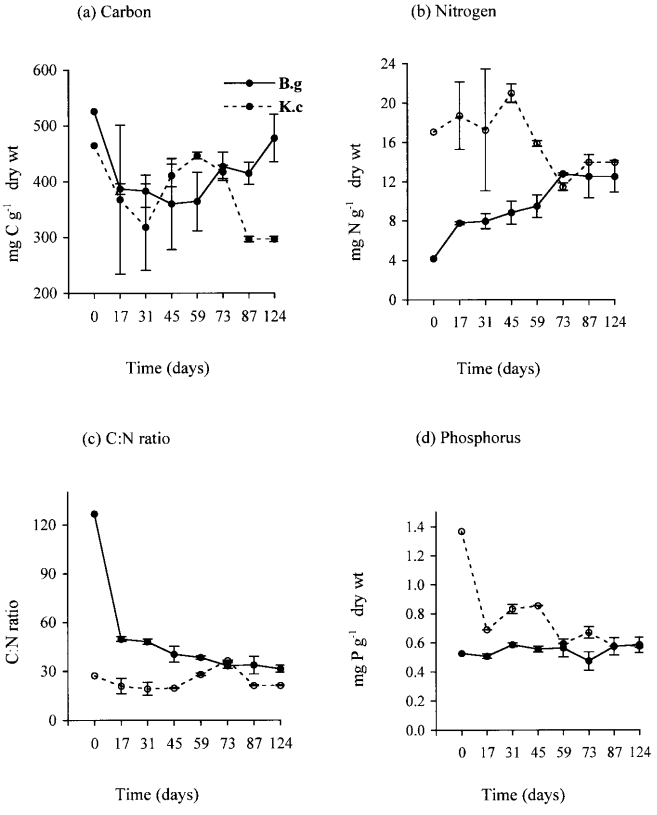


Fig. 2 Changes in concentration of C, N, P and C:N ratio which occurred during the decomposition of leaves of *Bruguieru gymnorrhizu* (*B. g, solid lines*) and *K. candel* (*K. c, dotted lines*). Values are means (± SD)

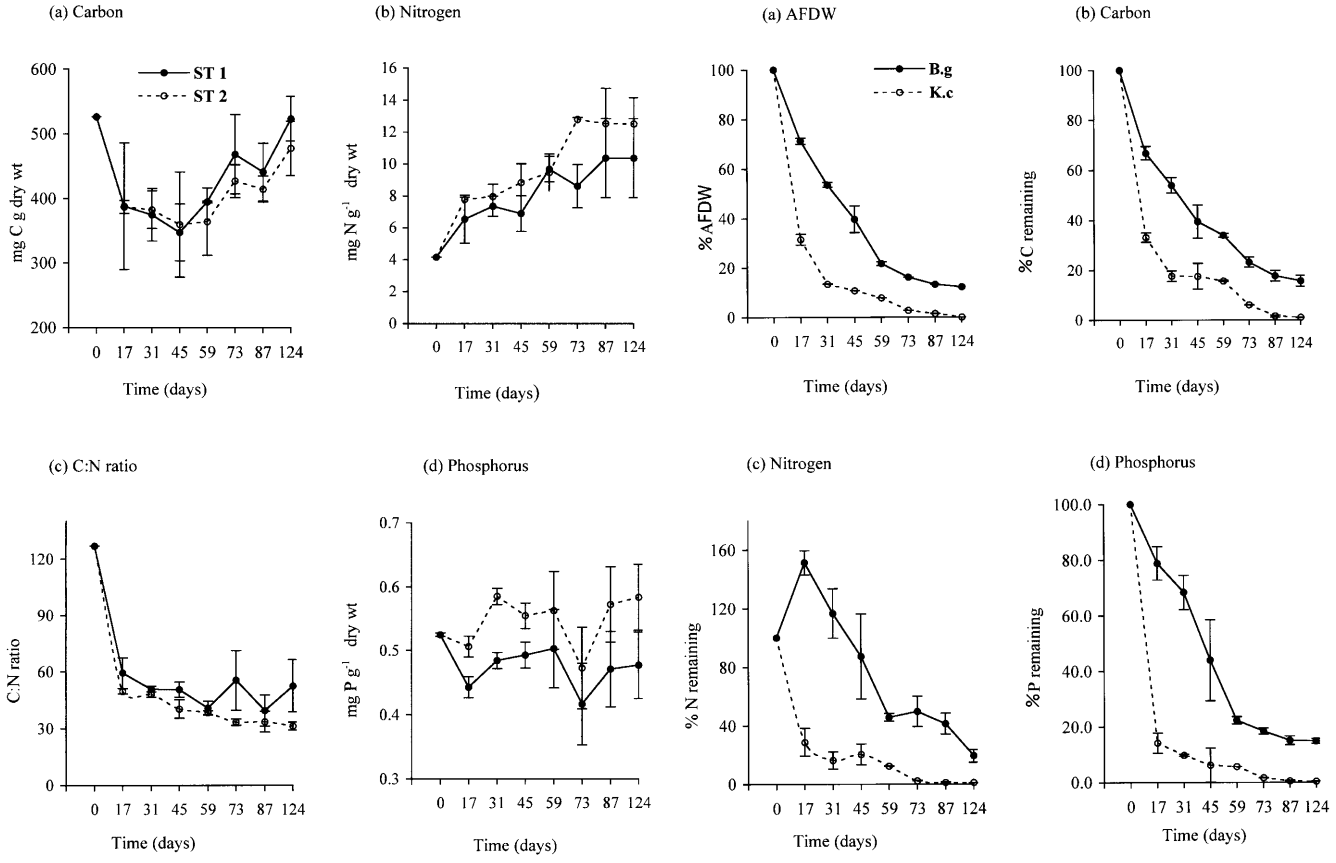


Fig. 3 Changes in concentration of C, N, P and C:N ratio which occurred during the decomposition at ST1 (*solid lines*) and ST2 (*dotted lines*). Values are means (± SD)

Fig. 4 Changes in percentage of original AFDW, C, N and P which occurred during the decomposition of *Bruguieru gymnorrhizu* leaves (*B.g, solid lines*) and *K. candel* leaves (*K.c, dotted lines*). Values are means (± SD)

which can be easily utilized by microbes, but were only present in low concentrations. The increase is due to rising concentrations of structural carbohydrates (such as lignin and hemicelluloses) per dry matter as a result of the loss of other constituents (sugars and starches) in the detritus. The structural carbohydrates often constitute the major portion of the detrital biomass and are usually very resistant to decomposition. Similar trends were found in decaying leaves at ST1 and ST2 and among treatments.

N concentrations were characterized by an increase followed by a decrease in *K. candel* leaves. Many investigators also report increases followed by decreases in N concentrations during incubation (Steinke et al. 1983; Van der Valk and Attiwill 1984; Steinke and Ward 1987; Robertson 1988; Lee 1989; Tam et al. 1990, 1998). Due to low initial C:N ratio (<30) (high N) in *K. candel* leaves, a relatively small amount of N was accumulated by bacteria during the first stages of decay and therefore the C:N ratio either declined or increased slightly throughout the experiment.

The constant increase in N in *B. gymnorrhiza* leaves (Figs. 2b, 3b) was due to immobilization as a result of accumulation of microbial biomass and products of microbial activity, production of mucopolysaccharide exudes by bacteria and their incorporation into humic compounds (Rice 1982; Rice and Hanson 1984). Furthermore the accumulation or constant increase of N in *B. gymnorrhiza* leaf detritus throughout the experiment may have been related to conservation of N by decomposers which resulted in the decrease of the C:N ratio (Mellilo et al. 1984). Alongi et al. (1992) reported that organic materials rich in N (low C:N) favor net mineralization, whereas those poor in N (high C:N) favor net immobilization. The generally high C:N ratio of mangrove tree components, e.g. leaves, indicates that rates of immobilization may be high in mangrove sediments. Evidence that high C:N ratios result in increased immobilization is provided by Alongi et al. (1992), whose study shows clearly that *B. gymnorrhiza* leaves which were poor in N favored immobilization, whereas *K. candel* leaves rich in N favored mineralization. Therefore *K. candel* leaf detritus released N to the surroundings, leading to a faster decrease in N remaining in the litter than in *B. gymnorrhiza* leaf detritus (Fig. 4c).

Few studies have examined changes of P concentration in decomposing mangrove litter (Steinke et al. 1983; Tam et al. 1998). Steinke et al. (1983) showed that P content declined in *B. gymnorrhiza* leaves during the first 4–6 weeks of incubation, but either remained the same or

Table 1 Single exponential model results describing decomposition of *Kandelia candel* (*K. c*) and *Bruguiera gymnorrhiza* (*B. g*) leaves from July to November 2000, at stations ST1 and ST2 and under treatments Tl, T2 and T3; decay constants, k (per day), $t_{0.5}$ (half life time, in days) and R^2 (coefficient of determination) values are indicated. (– data did not fit model)

Remaining%	Parameter	*K.c*	*B.g*	ST1	ST2	Tl	T2	T3
AFDW	k	0.062	0.022	0.019	0.022	0.022	0.019	0.018
	$t_{0.5}$	11.000	32.000	37.000	32.000	32.000	36.000	38.000
	R^2	0.996	0.993	0.988	0.993	0.992	0.987	0.973
C	k	0.052	0.020	0.016	0.020	0.020	0.016	0.015
	$t_{0.5}$	13.000	35.000	42.000	35.000	35.000	42.000	48.000
	R^2	0.981	0.993	0.969	0.993	0.993	0.993	0.926
N	k	0.057	–	–	–	–	–	–
	$t_{0.5}$	12.000	–	–	–	–	–	–
	R^2	0.978	–	–	–	–	–	–
P	k	0.102	0.019	0.018	0.019	0.019	0.013	0.013
	$t_{0.5}$	7.000	36.000	39.000	36.000	36.000	55.000	55.000
	R^2	0.994	0.974	0.960	0.974	0.974	0.961	0.936

gradually increased thereafter, for about 10–24 weeks, suggesting P immobilization. Similar findings were observed in the present study. The rapid initial loss of P in *K. candel* was caused by release of its soluble forms by leaching (Chale 1993; Steinke et al. 1993). After that initial decline, P concentration in leaf detritus increased slightly and then declined. These results were comparable to those obtained in the same species by Tam et al. (1998), suggesting that more P was released to the surroundings by *K. candel* than *B. gymnorrhiza* (Fig. 4d).

Comparison of leaf detritus degradation between species

There were highly significant differences in the mean percentage of the original AFDW, C, N, and P remaining in leaf detritus between species (P<0.0001). During the early phase of the experiment the rate of loss of AFDW, C, N and P was greater from *K. candel* than from *B. gymnorrhiza* (Fig. 4). A single exponential equation described loss of AFDW, C and P in the remaining litter. The percentages of relatively labile material were higher in *K. candel* (80%) than in *B. gymnorrhiza* leaves (<55%). The times taken to lose half the original AFDW, C and P were shorter in *K. candel* than in *B. gymnorrhiza* leaf detritus (Table 1). While the changes in the percentage of the original mass of N remaining in leaves of *K. candel* followed AFDW, C and P trends, the changes in *B. gymnorrhiza* leaves remained over 100% for more than 31 days (Fig. 4c). The degradation pattern of both species progressively followed initial rapid leaching of soluble organics (Rice and Tenore 1981; Benner and Hodson 1985; Camilleri and Ribi 1986; Robertson 1988; Tam et al. 1998) as revealed by rapid loss of litter mass and inorganic material (Steinke et al. 1983, 1993) followed by a period of microbial decomposition due to enzymatic activity of microorganisms such as bacteria and various types of fungi which grew rapidly on leaves (Robertson et al. 1992).

Despite the similarity in litter degradation pattern between the two species, *K. candel* leaves degraded more rapidly than *B. gymnorrhiza* leaves, with a more rapid release of nutrients than those of *B. gymnorrhiza*. Decay constants were 0.062 and 0.022 per day respectively (Table 1). Earlier studies pointed out that the initial chemical status of litter, in particular N, tannin or lignin concentrations, have a controlling influence on decay rates (Hunt 1977; Melillo et al. 1982; Wieder et al. 1983; Twilley et al. 1997), and can vary among plant species substantially (Melillo et al. 1984). Recently, Fenchel et al. (1998) suggested that high initial N concentration or low C:N ratio would result in high microbial assimilation efficiencies and increase in mineralization, but a decrease in immobilization, and hence fast decay rate. The fast decay rate of *K. candel* leaves was therefore attributed to high initial N concentrations (low C:N ratios) that obviously enhanced rapid microbial colonization.

Further evidence suggests that plant material with a low C:N ratio and lignin content will have a relatively lower recalcitrant fraction and thus will decompose faster than plant material with a relatively high initial C:N ratio or lignin content (Wieder and Lang 1982). Our investigation confirmed that differences in the degradation rates between the two species were mainly due to differences in initial N contents and C:N ratios of leaves. Initial C:N ratio can also be a reasonable predictor of the rate of decomposition (Jensen 1929; Witkamp 1966; Melillo et al. 1982).

Decay rates of *K. candel*ia obtained in the present study were comparable to those reported from two other studies performed in summer in the subtropical region of southern China (Lu and Lin 1990; Tam et al. 1998). Only one study reported *B. gymnorrhiza* decay rates during summer in subtropical South Africa (Steinke and Ward 1987), but decay rate values were significantly lower (0.0123 per day) than the values obtained in the present investigation (0.0203 per day) and the mean number of days required for 50% loss in AFDW in this study (32 days) represented approximately half the time taken in South Africa (56 days). Although climatic conditions such as temperature and geographical location affect decay rates (Tam et al. 1998), the differences here might

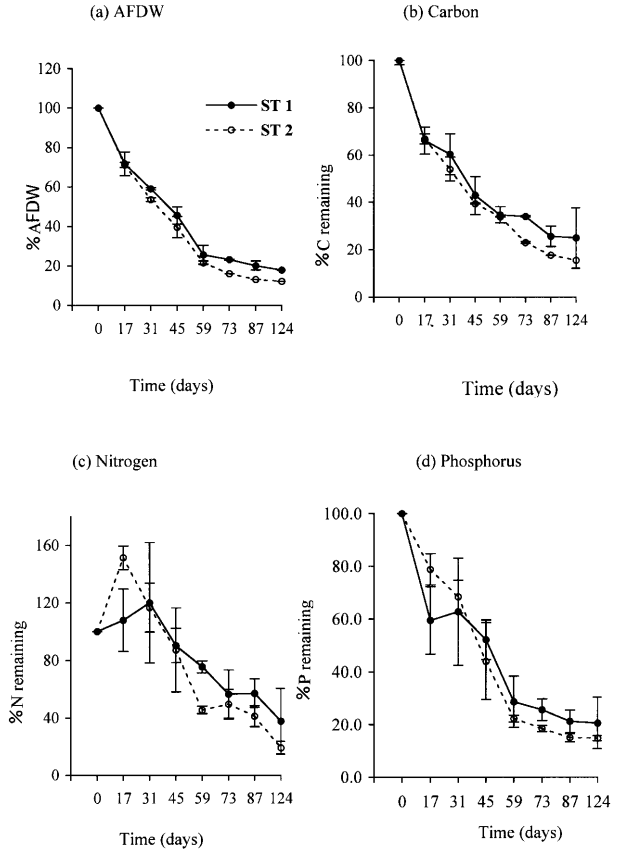


Fig. 5 Changes in percentage of original AFDW, C, N and P which occurred during decomposition at ST1 (*solid lines*) and ST2 (*dotted lines*). Values are means (± SD)

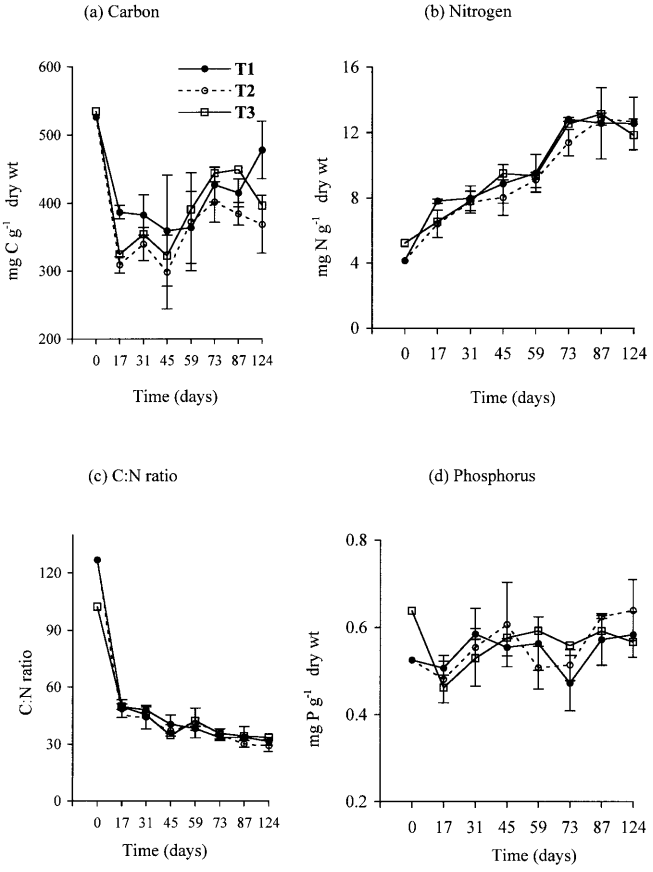


Fig. 6 Changes in concentration of C, N, P and C:N ratio which occurred during the decomposition of Tl, T2andT3; fresh leaves, leaves initially dried at 50°C and 80°C. (T1 *closed circles*, T2 *open circles* and T3 *open squares*). Values are means (± SD)

Table 2 Concentrations of C, N (mg g^{-1} dry weight) and C:N ratio values in the surface sediments (upper 4 cm) of the high intertidal mangroves (*STl*) and low intertidal mangroves (*ST2*) from July to November 2000. Values are means (± SD), *n*=3

Site	Element	Months				
		July	August	September	October	November
ST1	C	27.69±1.22	18.63±0.09	28.12±1.33	27.17±0.90	24.96±1.55
	N	2.02±0.01	1.57±2.02	2.16±0.15	1.92±0.20	1.77±0.06
	C:N	13.69±0.39	11.88±0.25	13.0±0.27	14.21±0.91	14.12±0.36
ST2	C	20.97±1.42	15.80±0.5	22.40±1.99	22.01±4.13	22.64±0.44
	N	1.71±0.04	1.39±0.08	1.97±0.25	2.03±0.41	1.64±0.10
	C:N	12.2±0.53	11.33±0.26	11.38±0.45	10.87±0.24	13.82±0.11

have been due to differences in trophic states or production of the mangrove forests or concentrations of dissolved nutrients in the sediments.

Spatial variation in leaf detritus degradation

There were significant differences in the loss of AFDW and C between sites (P<0.01) (Fig. 5a, b), but no significant difference was found in the loss of N and P between the sites (P=0.4312, and P=0.6884 respectively) (Fig. 5c, d). Leaf detritus in the low intertidal (ST2), decayed faster than that in the high intertidal (ST1) with decay rate values of 0.022 and 0.0186 per day, and half-lives of 32 days and 37 days respectively (Table 1). The percentages of original C, N and P remaining after 124 days of incubation were higher in the high intertidal than in the low intertidal mangroves (Fig. 5). A single exponential model fitted AFDW, C and P remaining in leaf detritus.

Fresh leaf litter and mangrove sediments represent initial and final stages in decomposition (Tam and Wong 1998). The mean surface sediment C:N ratios of the high and low intertidal mangrove were 13 and 11 respectively throughout the experimental period (Table 2, Fig. 6). The C:N ratios of *B. gymnorrhiza* leaf detritus from both sites declined very rapidly during the first 17 days of incuba-

tion as a result of organic C leaching and increasing N concentrations. Concentration of nutrients in the sediments and their C:N ratios can be factors influencing degradation rates of leaf detritus. Leaves incubated in the high intertidal mangroves where the sediment C:N ratios were slightly higher decayed more slowly than leaves incubated in the low intertidal zone, where the sediment C:N ratio is lower. Melillo et al. (1984) found an important interaction between the detritus and substrate of decaying material. The continuous decrease in the C:N ratio reflected the leaf detritus interaction with the mangrove sediments proceeding to an equilibrium level, "the final stage of decomposition process". Leaves in the low intertidal mangroves remained submerged in water for a longer time than leaves in the high intertidal. Furthermore, leaves in the high intertidal may have been subjected to occasional drying during spring tides, thus slowing the leaching and saprophytic decay which are more effective when leaves stay wet (Robertson et al. 1992).

Effects of drying on the pattern of mass nutrient loss

Rogers and Breen (1982) suggested that drying of plant material prior to incubation would increase rates of leaching and affect the position of the decomposition curves on the vertical axis. Our study confirmed this; the dried leaves were significantly different from wet leaves as regards loss of AFDW, C, N and P ($P<0.0001$) (Fig. 7). The pattern of loss of AFDW, C, N and P varied with time, among treatments ($P<0.01$). The overall rate of mass loss from dried leaves was slower than that from fresh yellow leaves, with 6.1%, 9.6% (50°C), 13.02% (80°C) remaining in litterbags after 124 days of incubation in the field. Furthermore, all dried leaves (50°C and 80°C) had higher rates of leaching of C and P than fresh leaves, but still decayed more slowly. Rogers and Breen (1982) suggested that the slower rate of loss from litterbags can be attributed to the different pathways of energy and nutrient transfer, which become operative when plant material is dried, altering the organic matter so that microbes attack it less rapidly. The delay in microflora colonization affected decomposition rates.

Drying of leaves at 80°C elevated their initial C, N and P concentrations, from 525 mg g^{-1}, 4.2 mg g^{-1}, 0.525 mg g^{-1} (of fresh and 50°C dried leaves), to 534.4 mg g^{-1}, 5.2 mg g^{-1} and 0.638 mg g^{-1} dry weight concentrations respectively. The C:N ratio was lowered from 125 to 102.4. The amounts of C, N and P remaining at the end of the experiments were highest for 80°C followed by 50°C and then fresh leaves. Decay rates were described by a single exponential equation for AFDW, C, and P and the decay constants increased and half-life decreased in the order: 80°C, 50°C and fresh leaves (Table 1). Although leaves dried at 80°C had the highest initial nutrient concentrations and the lowest C:N ratios, they decayed most slowly. It is obvious that any kind of drying kills microflora, removes water from plant cell cytoplasm and changes the nutritional and chemical status – important media for microbial growth. In such cases, recolonization by microflora may take significantly longer. Rogers and Breen (1982) suggested that when decomposition is studied using natural plant material the microflora remain alive and relatively undisturbed, and when dried, the microflora would, like the plant cells, be killed by the drying process.

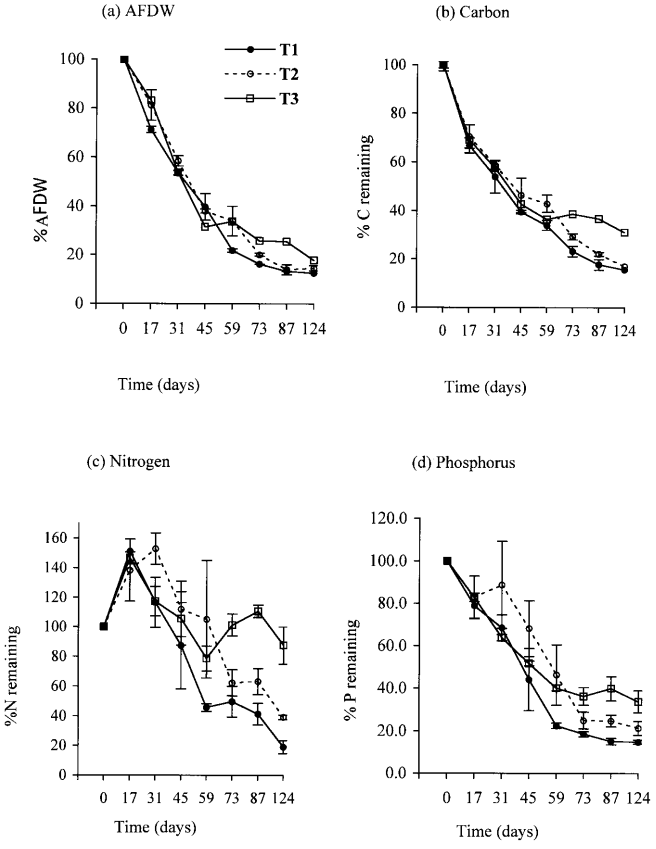


Fig. 7 Change in percentage of original AFDW, C, N and P which occurred during decomposition of Tl, T2 andT3; fresh leaves, leaves initially dried at 50°C and 80°C. (Tl *closed circles*, T2 *open circles* and T3 *open squares*). Values are means (± SD)

Since pre-drying affects the degradation process, previous studies may have underestimated the rates of degradation of mangrove leaves and nutrient transfer within the mangrove ecosystem. In addition, drying leaves does not accelerate the breakdown of the leaf tissues, but increases the rate of leaching during the early stage of decay and then slows the overall decay process due to low microbial abundance.

Nutrient budgets

The estimated budgets (net loss, – or gain, +) of C, N and P during decomposition indicated that *K. candel* leaves (2.302 g, 0.082 g and 0.0068 g of C, N and P respectively) should contribute more to the C, N, and P budgets than *B. gymnorrhiza* leaves (2.094 g, 0.015 g and 0.0022 g) due to their higher initial N concentrations

which enhanced the decay rate. The net budgets of the elements were calculated as follows:

$$W_0 - W_{124} = \text{Netbudget} \quad (2)$$

where W_0 = total weight of C, N or P initially present in the 5 g dry weight (10 g wet weight) of yellow leaves at time 0 and W_{124} = total weight of C, N or P remaining in the leaf detritus after 124 days of incubation. The net budget in C includes the unmeasured losses due to leaching and microbial respiration and gain by DOC from the surroundings. For N net budget includes unmeasured losses due to leaching, mineralization and denitrification and gain by immobilization. For P net budget also included unmeasured losses due to leaching and mineralization and gain by immobilization.

N and P budget contributions to the surroundings were 5 and 3 times higher in *K. candel* than in *B. gymnorrhiza*. However, due to the small amount of leaf litter production by *K. candel* in Oura Bay, its nutrient and organic matter contribution to the mangrove ecosystem and adjacent intertidal flat remains insignificant compared to *B. gymnorrhiza*.

The estimated contribution to the estuarine ecosystem of C, N and P from decaying *B. gymnorrhiza* leaf detritus during summer (July–October) in Oura Bay mangroves was about 22.48 tonnes of C, 161.4 kg of N and 24.7 kg of P per 4 months, assuming that all leaf litter produced from July to October had a similar initial nutrient concentration and decayed at the same rate. Contributions were calculated by:

$$T_{LF} \times C_{NB}/5g \quad (3)$$

where T_{LF}= total leaf litter fall in the 10 ha forest (from July–October 2000) 53,668,900 g (53.67 ton) (Mfilinge and Tsuchiya, unpublished data) and C_{NB}=C net budget. These contribution rates are expected to be the highest in the year because more than 50% of total litter production per year occurs from July to October (with leaf fall accounting for >70% of total litter fall), mainly associated with typhoon winds (Mfilinge and Tsuchiya, unpublished data).

It has been shown that very productive mangroves export more than 500 g C m^{-2} $year^{-1}$ (Twilley et al. 1986). Assuming that all leaf litter was available for export, the present study estimated 224.8 g C m^{-2} in 4 months and was calculated as follows:

$$gCm^{-2} = T_{LF} \times C_{NB} \times 10^{-5} m^{-2}/5g \quad (4)$$

Although other sources of C in the mangroves were not measured, C contribution to export may hardly exceed 500 g C $m^{-2}year^{-1}$ in Oura Bay mangrove forest. A study by Twilley (1985) indicated that other sources of C, such as DOC and POC, represent only a small fraction of total C flux, e.g. a basin in southern Florida had 36.7 g C m^{-2} $year^{-1}$. When compared to the tropical mangroves, subtropical mangroves are less productive, because of decreased growth rate associated with decrease in average and minimum temperatures of both air and soil (Clough 1992). Most of them contribute less organic matter to estuarine ecosystems. The processed litter mass contributes to the detrital pool of the water body (as dissolved or POM) and may be important to linked trophic levels and in cycling of nutrients (Wetzel 1995), while the residual leaf detritus becomes deposited in the bottom sediments, storing the rest of the original nutrient content enriched in immobilization products in the bottom deposits. The requirement of N and P per year for growth of this mangrove forest is not yet known, since these elements are efficiently conserved within mangroves (Alongi et al. 1992, 2000); it is likely that very active recycling of N and P must take place within the mangroves.

In order to construct a total nutrient budget of this mangrove forest three potential sources of POM and P were identified: river, rainfall and tidal flushing. A study by Dittmar (2001) indicated that mangroves play a more important role than rivers in marine C budgets. Output sources from the mangrove forest include tidal flushing and sedimentation within the mangrove forest. N can possibly enter the mangroves through the fixation of atmospheric N by cyanobacteria growing on sediments and on timber lying on the forest floor, by tidal flushing and rainfall runoffs and ground water outflow from the mountain barrier bordering the forest.

In conclusion, the data presented here support the hypothesis that degradation rates of mangrove leaves differ among species, and depend on the initial leaf chemical composition, especially N concentration and the C:N ratio.

Site differences in degradation rates were also significant; these are caused not only by the sediment quality, e.g. C:N ratio, but also by the duration of exposure at low tide.

Drying mangrove leaves prior to field incubation seriously affected the decay rates and pattern of mass and nutrient loss. Dried leaves decayed more slowly and lost mass and nutrients more slowly; using dried leaves thus grossly underestimates the actual decay rates.

Acknowledgements We thank Z. Bachok and L. Alhamd for assistance in the field and valuable suggestions on statistics, M. Black for the editing and corrections, T. Meziane and S. Mohamed for useful comments on an earlier version of this manuscript, Satomi Kamimura and Yu Tamura for technical assistance and all the students in the ecology laboratory for encouragement and help in the field. Many thanks to Dr. Marilyn Ball and two other anonymous reviewers for their helpful comments. The Japanese Monbusho Scholarship Grant to P.L.M. supported this study.

References

Alongi DM, Boto KG, Robertson AI (1992) Nitrogen and phosphorus cycles. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. (Coastal and estuarine series 41) American Geophysical Union, Washington, pp 251–292

Alongi DM, Tirendi F, Trott LA, Xuan TT (2000) Benthic decomposition rates and pathways in plantations of the mangrove *Rhizophora apiculata* in the Mekong delta, Vietnam. Mar Ecol Prog Ser 194:87–101

Benner R, Hodson RE (1985) Microbial degradation of the leachable and lignocellulosic components of laves and wood from

Rhizophora mangle in a tropical mangrove swamp. Mar Ecol Prog Ser 23:221–230
Camilleri JC, Ribi G (1986) Leaching of dissolved organic carbon (DOC) from dead leaves, formation of flakes of DOC, and feeding on flakes by crustaceans in mangroves. Mar Biol 91: 337–334
Chale FMM (1993) Degradation of mangrove leaf litter under aerobic conditions. Hydrobiology 257:177–183
Clough BF (1992) Primary production and growth of mangrove Forests. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. (Coastal and estuarine series 41) American Geophysical Union, Washington, pp 225–249
Dittmar T, Lara RJ, Kattner G (2001) River or mangrove? Tracing major organic matter sources in tropical Brazilian coastal waters. Mar Chem 73:253–271
Fenchel T, King GM, Blackburn TH, (1998) Bacterial biogeochemistry. Academic Press, San Diego
Hardiwinoto S, Nakasuga T, Igarashi T (1989) Litter production and decomposition of mangrove forest at Ohura Bay, Okinawa. Res Bull Coll Exp For 46:577–594
Hunt HW (1977) A simulation model for decomposition in grasslands. Ecology 58:469–484
Jensen HL (1929) On the influence of carbon: nitrogen ratios of organic matter on the mineralization of nitrogen. J Agric Sci 19:71–82
KishimotoT, Miyajima H, Nakasuga T, Baba S (1987) Zonation of mangrove forest. Litter fall and its seasonal change (in Japanese). Trans Jpn For Soc 98:301–302
Lee SY (1989) Litter production and turn over of the mangrove *Kandelia candel* (L.) Druce in a Hong Kong tidal shrimp pond. Estuar Coast Shelf Sci 29:75–87
Lu CY, Lin P (1990) Studies of litter fall and decomposition of *Bruguiera sexatangula* (Lour.) Poir community on Hainan Island. Chin Bull Mar Sci 47:139–148
Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626
Melillo JM Naiman RJ, Aber JD, Linkins AE (1984) Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. Bull Mar Sci 35:341–356
Meziane T, Tsuchiya M (2000) Fatty acid as tracers of organic matter in the sediment and food web of a mangrove/intertidal flat ecosystem, Okinawa, Japan. Mar Ecol Prog Ser 200:49–57
Rice DL (1982) The detritus nitrogen problem: new observations and perspectives from organic geochemistry. Mar Ecol Prog Ser 9:153–162
Rice DL, Hanson RB (1984) A kinetic model for detritus nitrogen: role of the associated bacteria in nitrogen accumulation. Bull Mar Sci 35:326–340
Rice DL, Tenore KR (1981) Dynamics of carbon and nitrogen during the decomposition of detritus derived from estuarine macrophytes. Estuar Coast Shelf Sci 13:681–690
Robertson AI (1988) Decomposition of mangrove leaf litter in tropical Australia. J Exp Mar Biol Ecol 166:235–247
Robertson AI, Alongi DM, Boto KG (1992) Food chains and carbon fluxes. In: Robertson AI, Alongi DM (eds) Tropical mangrove ecosystems. (Coastal and estuarine series 41) American Geophysical Union, Washington, pp 293–326
Rogers KH, Breen CM (1982) Decomposition of *Potamogeton crispus* L.; the effects of drying on the pattern of mass and nutrient loss. Aquat Bot 12:1–12
Steinke TD, Ward CJ (1987) Degradation of mangrove leaf litter in the St. Lucia Estuary as influenced by season and exposure. S Afr J Bot 53:323–328
Steinke TD, Naidoo G, Charles LM (1983) Degradation of mangrove leaf and stem tissues in situ in Mgeni estuary, South Africa. In: Teas HJ (ed) Biology and ecology of mangroves. Junk, The Hague, pp 141–149
Steinke TD, Holland AJ, Singh Y (1993) Leaching losses during decomposition of mangrove leaf litter. S Afr Tydskr Plant 59: 21–25
Tam NFY, Wong YS (1998) Variations of soil nutrient and organic matter content in a subtropical mangrove ecosystem. Water Air Soil Pollut 103:245–261
Tam NFY, Vrijmoed L, Wong YS (1990) Nutrient dynamics associated with leaf decomposition in a small mangrove community in Hong Kong. Bull Mar Sci 47:68–78
Tam NFY, Wong YS, Lan CY, Wang LN (1998) Litter production and decomposition in a subtropical mangrove swamp receiving wastewater. J Exp Mar Biol Ecol 226:1–18
Twilley RR (1985) The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. Estuar Coast Shelf Sci 20:543–557
Twilley RR, Lugo AE, Patterson-Zucca C (1986) Litter production and turnover in basin mangrove forests in southwest Florida. Ecology 67:670–683
Twilley RR, Pozo M, Garcia VH (1997) Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. Oecologia 111:109–122
Van der Valk AG, Attiwill PM (1984) Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. Aquat Bot 18:205–221
Wetzel RG (1995) Death, detritus and energy flow in aquatic ecosystems. Freshw Biol 33:83–89
Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642
Wieder RK, Carrel JE, Rapp JK, Kucera CL (1983) Decomposition of tall fescue (*Festuca elatior* var. *arundinacea*) and cellulose litter on surface mines and tall grass prairie in central Missouri, USA. J Appl Ecol 20:303–321
Witkamp M (1966) Decomposition of leaf litter in relation to environment, microflora and microbial respiration. Ecology 47:194–201
Woodroffe CD (1982) Litter production and decomposition in the New Zealand mangrove *Avicennia marina* var. *resinifera*. N Z J Mar Freshw Res 16:179–188