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Fatty acids in decomposing mangrove leaves: microbial activity, decay and nutritional quality

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ABSTRACT: Changes in lipid content and fatty acid (FA) composition in decomposing mangrove leaves of *Bruguiera gymnorrhiza* (L.) Lamk and *Kandelia candel* (L.) were investigated in a subtropical mangrove forest on Okinawa Island, Japan (26.5°N, 128°E) by field experiments for 18 wk (July to November 2000), using yellow senescent leaves, and compared with FAs in the green leaves and mangrove sediments. We tested the hypothesis that changes in FA composition during decomposition can indicate the state of leaf decay and periods of high and low microbial activity, and that bacteria may rapidly degrade polyunsaturated fatty acids (PUFAs). During decay, FA composition in the yellow leaves changed in 2 wk from predominantly saturated FAs to monounsaturated FAs, and to the more branched FAs typical of bacteria, and lipid and N increased due to microbial colonization. However, the microbial decomposition of leaves did not alter the concentrations of long-chain fatty acids (LCFAs), suggesting that these vascular plant-markers remain unchanged in mangrove detritus and surface sediments for more than 4 mo. Furthermore, bacteria did not degrade PUFAs as we had hypothesized, indicating that during decomposition of mangrove leaves, bacteria tend to conserve PUFAs (as they do nitrogen), thus enriching the detritus with nutrients. Comparison of ω3 and ω6 PUFAs between the 2 species showed that nutritional quality varies greatly with the state of the leaf material, increasing through time in *B. gymnorrhiza* and decreasing through time in *K. candel.*

KEY WORDS: Fatty acid · Mangrove decomposition · Biomarkers · Microbial activity · Nutritional quality · Detritus nitrogen · *Bruguiera gymnorrhiza* · *Kandelia candel*

INTRODUCTION

Mangroves are potential sources of organic matter and nutrients to the estuarine ecosystem (Robertson et al. 1992). Litter, mainly leaves, is exported from mangrove ecosystems by tidal waters either fresh, or in various states of decomposition, in the form of large and fine pieces of leaf detritus which enrich the intertidal sediments with nutrients (Bano et al. 1997, Wafar et al. 1997). Recent studies have used fatty acid markers to trace the origin and flow of organic matter from mangroves through marine food webs (Meziane & Tsuchiya 2000, Meziane & Tsuchiya 2002). For example, fatty acids (FAs) with more than 24 carbon atoms are synthesized only by vascular plants (Volkman et al. 1980), and consequently can be used as markers of material of vascular plant origin in sediments and animal tissues (LeBlanc et al. 1989, Meziane & Tsuchiya 2002, Meziane et al. 2002). The branched-chain fatty acids (BrFAs) 15:0 and 17:0, iso and anteiso, and the monounsaturated fatty acid (MUFA) 18:1ω7, are generally considered to be predominantly synthesized by bacterial communities (Jeffries 1972, Volkman et al. 1980) and, consequently, are useful as bacterial biomarkers and indicators of bacterial biomass (Parkes 1987).

Microbial transformation of plant-produced FAs is an important process that has yet to be investigated in detail

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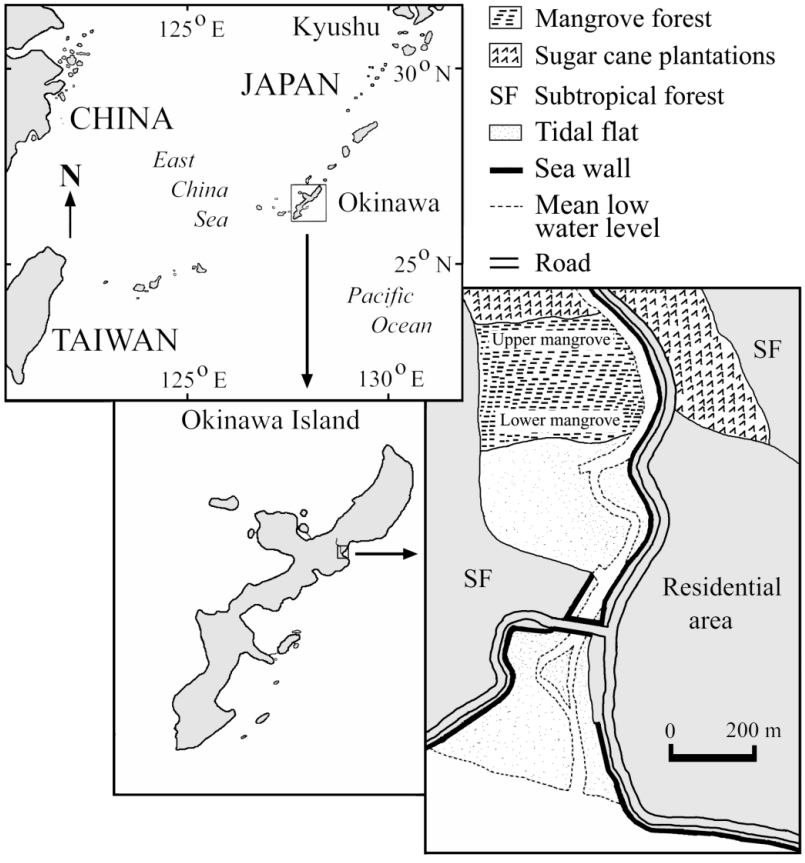

Fig. 1. Location of Okinawa Island and Oura Bay mangrove forest indication river bank and upper and lower mangrove forest where mesh bags were randomly deployed and leaf samples and sediments collected

in mangrove ecosystems. Understanding such transformations is essential, in order to identify the source of organic inputs such as lipids into marine sediments, and to understand the transfer of energy from mangroves through estuarine ecosystems. During decomposition of marsh grass, FA composition changes from predominantly unsaturated, straight-chain compounds, to branched, saturated compounds typical of bacteria (Johnson & Calder 1973, Schultz & Quinn 1973). If a similar process is evident in mangrove ecosystems, the FA composition in senescent mangrove leaves should be rapidly altered during decomposition. Furthermore, if the decomposition process is predictable, composition changes through time could be used to determine the degradation state or age of decaying leaves. For example, Carrie et al. (1998) suggested that high levels of PUFAs in sediment indicate fresh detritus, because bacteria rapidly degrade PUFAs.

The aim of this study was to examine changes in FA composition in mangrove leaves during microbial decomposition in the field and to relate these to the state of decay, microbial activity and nutritional quality of detritus. We compared FA composition in the senescent (yellow and brown leaves) and decaying leaves with FA in mangrove sediments (which represent the final state of leaf decomposition) and fresh leaves (mature green leaves). Since detritus source and original content of N in the fresh leaves affect microbial decay (Robertson 1988, Mfilinge et al. 2002), and may also affect the lipid content and FA composition, senescent yellow leaves from 2 species of mangroves (*Bruguiera gymnorrhiza* and *Kandelia candel*) that differ significantly in their N concentrations were used.

MATERIALS AND METHODS

Study area. The leaf-degradation experiment was carried out in a subtropical mangrove forest in the northern part of Okinawa Island in southern Japan (26.5°N, 128°E) (Fig. 1). The mangrove forest is situated in an enclosed bay at the mouth of Oura River. It consists of mixed stands of *Bruguiera gymnorrhiza*, *Kandelia candel* and *Rhizophora stylosa* that cover an area of about 10 ha. *B. gymnorrhiza* dominate in the forest. More detailed information on the study site has been given in a previous study (Mfilinge et al. 2002).

Experimental design. The experiment was conducted during the warm season between July and November 2000. Freshly fallen, yellow leaves of *Bruguiera gymnorrhiza* and *Kandelia candel* on sediments at low tide, and those still attached to branches but ready to abscise, were collected randomly and rinsed with distilled water in the field. In the laboratory, ~10 g fresh weight of leaves was placed in prepared mesh bags made of nylon (1 mm mesh, 22 × 18 cm) (Mfilinge et al. 2002). A subsample of 20 yellow leaves was processed and analyzed immediately for lipids, carbon and nitrogen to determine the lipid and fatty acid compositions and nutrient contents in leaves, at Time 0. A total of 60 mesh bags containing fresh yellow *B. gymnorrhiza* and *K. candel* leaves were randomly deployed on the mangrove sediments. The experiment ran for 18 wk. We removed 3 mesh bags for each mangrove species at random after 5 d (0.7 wk), when the leaves of both species had turned brown. Also 3 mesh bags for each mangrove species, chosen at random, were removed every 2 wk starting at Time 0, except for Weeks 14 and 16, during which weight loss was slow-

est. The mesh bags were washed with freshwater to remove attached sediments and adhering particles. A subsample of leaf tissue was removed and immediately stored at –20°C for lipid analysis. In addition to the yellow leaves, 20 mature green leaves for each species were picked at random from trees and mangrove sediments collected randomly from 3 locations (along the riverbank, the lower mangroves and the upper mangroves) by scraping the top 5 to 10 mm of sediment.

Lipid and fatty acid analysis. Fresh samples of green and yellow leaves and leaf detritus were chopped into small pieces and milled in a miller. Subsamples of 4 and 2 g of the milled fresh leave and leaf detritus respectively, and 2 g of fresh mangrove sediments were used for analysis. We measured 2 replicates for each fresh leaf group and sediments, and for each retrieved mesh bag. Lipids were extracted following a slightly modified version of the method of Bligh & Dyer (1959), as detailed by Meziane & Tsuchiya (2000). Each sample was extracted twice. The extracted lipids were filtered through GF/C filter paper to remove any fine sediments or particulate matter, concentrated by rotary evaporation, and stored in pre-weighed 4 ml vials (Wilson et al. 2001). To estimate the total lipid content, chloroform was evaporated completely under a stream of nitrogen, then on a hot plate set at 50°C. The remaining lipid was weighed on an electronic balance (ER-182A). Total lipid content was calculated from an average of 6 vials and expressed as mg g^{-1} dry weight. The preparation of methyl ester fatty acids (FAMEs) and analysis was carried out according to Meziane et al. (2002).

As there are no reliable conversion factors from bacterial fatty acids (BFAs) and fungal fatty acids (FFAs) to actual bacterial and fungal biomass (Haack et al. 1994, Frostegard & Baath 1996), percent contributions of the biomarkers were used as indicators of microbial biomass to assess their contribution to detritus N. The C and N contents were measured in a Shimadzu high-sensitivity CN analyzer, Model Sumigraph NC-80; 3 replicates of powdered leaf material for each retrieved mesh bag and for the mangrove sediment were measured.

Statistical analysis. We used a 2-way ANOVA with species (2 levels) and time (11 levels) as fixed factors to compare changes in lipid and fatty acid concentrations. Fatty acid classes were compared using MANOVA. Any significant species and time effect was further examined using Fisher's protected least significance difference (PLSD) test. The factor 'time' in the statistical analysis represents ageing of the leaf through a green mature state, senescence and microbial decomposition and its fate in the mangrove sediments. Arcsine p-transformed data were used in all statistical analysis, except for the lipid-content data. All statistical analyses were performed using StatView 5 software with 95% confidence intervals.

RESULTS AND DISCUSSION

Lipid content and fatty acid composition

There was a significant interaction between species and time in the mean total lipid content ($F = 51.96$, df = 10, $p < 0.0001$). The highest lipid concentration, which was also significantly higher than in the senescent leaves of both species (Fisher's PLSD, $p < 0.0001$), was found in the second week of incubation in the field (Fig. 2). This corresponded with elevated concentrations of BFAs (markers of bacteria) and the FFAs 18:1ω9 and 18:2ω6 (markers of fungi) (Chen et al. 2001). It is known that bacteria contain large amounts of BrFAs (Jeffries 1972, Volkman et al. 1980). The increase in branched components in the detritus is indicative of a significant bacterial population (Fig. 3a). This suggests that microbial colonization and growth on the litter made a significant contribution to the increase in total lipid content. Mangrove sediments, which represent the end of the degradation process, contained significantly lower lipid concentration than the leaf detritus at the end of the experiment (Week 18) (Fisher's PLSD, $p < 0.0001$), probably due to low microbial abundance.

Overall 57 FAs were identified. The fatty acid composition in *Bruguiera gymnorrhiza* and *Kandelia candel* leaves changed from predominantly saturated straight chains to the monounsaturated FAs and more branched saturated FAs, as the leaf detritus aged. This is indicated by the decline in percent concentration of SAFAs and increase in BrFAs and MUFAs (Fig. 3a,b,d). There was a significant interaction between species

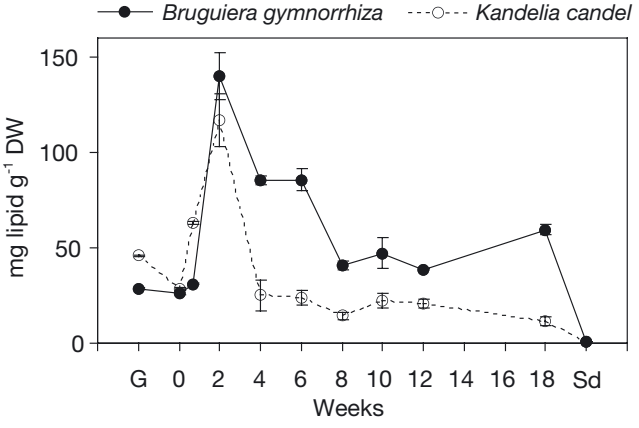

Fig. 2. *Bruguiera gymnorrhiza* and *Kandelia candel*. Changes in total lipid content during leaf decomposition compared with lipid content in green leaves (G) and mangrove surface-sediments (Sd). Values are means ± SD (n = 3)

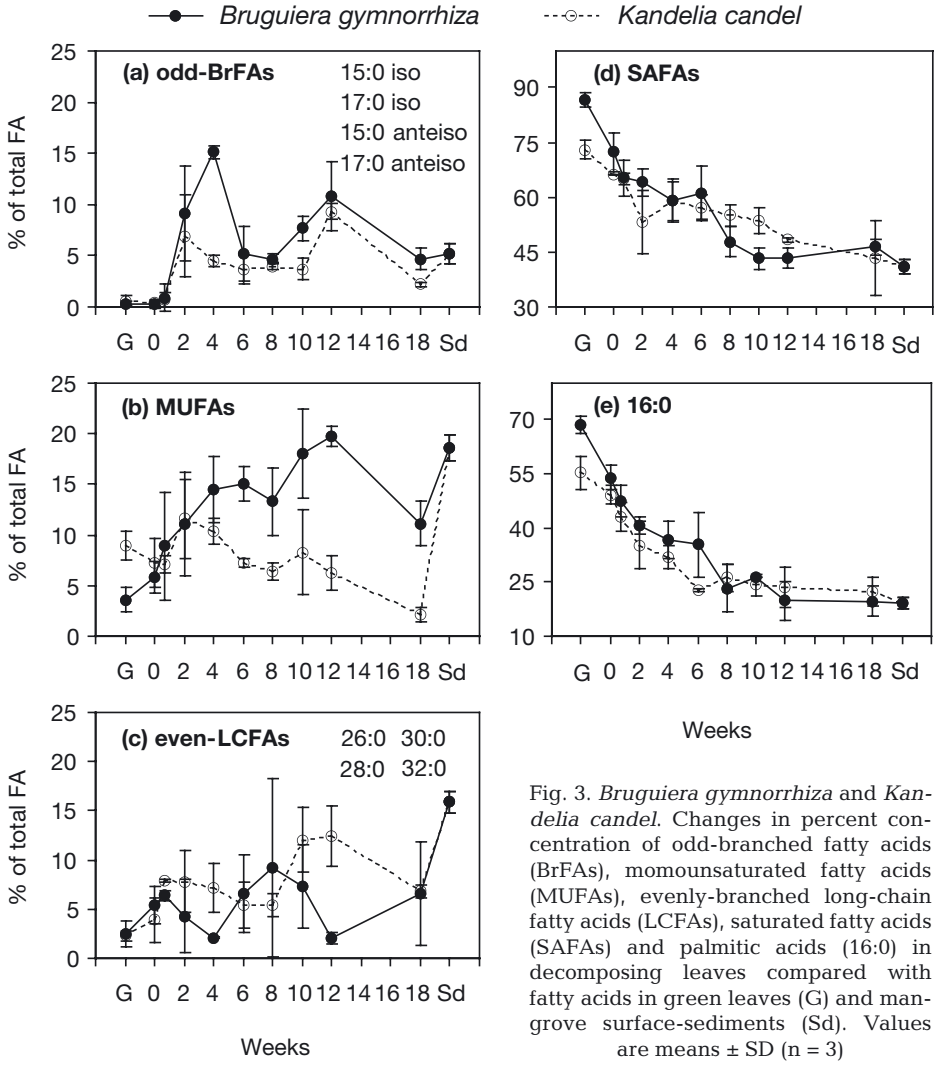

Fig. 3. *Bruguiera gymnorrhiza* and *Kandelia candel*. Changes in percent concentration of odd-branched fatty acids (BrFAs), momounsaturated fatty acids (MUFAs), evenly-branched long-chain fatty acids (LCFAs), saturated fatty acids (SAFAs) and palmitic acids (16:0) in decomposing leaves compared with fatty acids in green leaves (G) and mangrove surface-sediments (Sd). Values are means ± SD (n = 3)

and time in the mean percent concentration of the fatty acid classes (BrFAs, SAFAs, MUFAs, PUFAs and LCFAs) (Pillai's trace, $F = 4.37$, $p < 0.0001$), indicating that the mean concentration of all FA classes and FA compounds differed through time. Earlier studies have indicated that bacterial production contributes to increases in BrFAs and MUFAs (Gillan & Hogg 1984, White et al. 1984). Therefore, increases in the composition and percent concentration of BrFAs, MUFAs, and the total FA concentration during leaf decay, are most probably related to increases in bacterial colonization and growth on the leaves. However, the lipid content and the percent concentration of BrFAs and MUFAs varied through time between the 2 species because of differences in detritus quality.

There was no significant difference between the mean percentages of LCFAs in Weeks 18 and 0 (Fisher's PLSD, $p > 0.05$), indicating that microbial degradation did not affect LCFAs in the detritus and that the LCFAs may remain in detritus for a long time. Previous studies have shown that LCFAs are associated with the waxy leaf-coating of higher plants (Scribe et al. 1991, Colombo et al. 1996). Since waxes decompose very slowly in nature, LCFAs in the detritus may remain in sediments for several years, as indicated by their significantly higher levels in the mangrove surface sediments than in the leaf detritus (Fisher's PLSD, $p < 0.0001$) (Fig. 3c). This has important implications for the study of seasonal variations in the flux of organic matter from mangroves when LCFAs are used as biomarkers.

Fatty acid composition indicative of state of degradability

SAFAs were the most abundant fatty acids in fresh and decaying leaves of both species and in mangrove

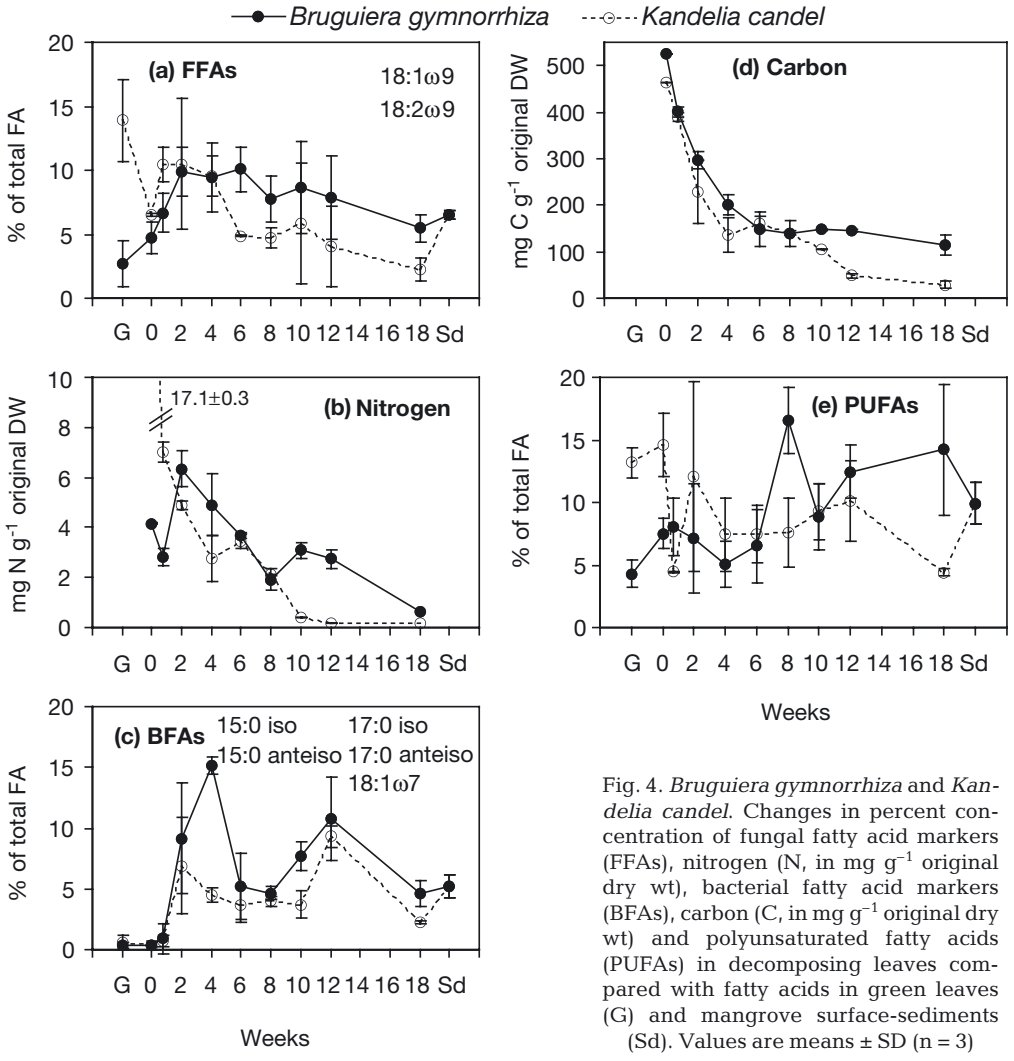

Fig. 4. *Bruguiera gymnorrhiza* and *Kandelia candel*. Changes in percent concentration of fungal fatty acid markers (FFAs), nitrogen (N, in mg g^{-1} original dry wt), bacterial fatty acid markers (BFAs), carbon (C, in mg g^{-1} original dry wt) and polyunsaturated fatty acids (PUFAs) in decomposing leaves compared with fatty acids in green leaves (G) and mangrove surface-sediments (Sd). Values are means ± SD (n = 3)

sediments. The highest concentrations of SAFAs were found in the green leaves, and the lowest in the decomposing leaves (F = 9.26, df = 10, $p < 0.0001$). After 18 wk, concentrations were not significantly different from those in the mangrove sediments (Fisher's PLSD, $p > 0.05$) (Fig. 3d). Mangrove leaves contain higher ratios of SAFAs to PUFAs in their green leaves and detritus (P. Mfilinge & M. Tsuchiya unpubl. data). Unlike SAFAs, PUFAs can be quickly degraded by bacteria (Carrie et al. 1998), and therefore have been used as markers of comparatively undegraded organic phytodetrital material (Carrie et al. 1998, Fileman et al. 1998) because these plants contain large proportions of PUFAs (18:2ω6, 18:3ω3, 18:3ω6, 18:4ω3, 20:5ω3, 22:6ω3) in their fresh state (Johns et al. 1979, Napolitano et al. 1997, Pond et al. 1998, Meziane & Tsuchiya 2000). The reason for the declining trend in percent concentration of SAFAs during the present study was not determined, and there was no evidence to suggest that bacterial activity could be important in producing such changes: 2 possible reasons were increase in other FAs during decomposition, or the loss of non-structural carbohydrates and lignocelluloses.

Palmitic acid (16:0) was the most common compound (68.4 and 54.8%) in the green leaves of *Bruguiera gymnorrhiza* and *Kandelia candel* respectively. Its concentration indicated a remarkable decline during leaf senescence and decomposition. After 18 wk, values in the detritus were close to those in the mangrove sediment, i.e. 19.2 ± 1.7% (Fig. 3e). Previously, Findlay et al. (1986) measured the FA composition in the senescent leaves and black leaves of *Rhizophora mangle*, and found that the amount of 16:0 in the senescent leaves was significantly higher than in the black leaves. Although the exact age of the black leaves were unknown, this suggests a relationship between decay and the amount of 16:0 in mangrove detritus.

A significant correlation was found between 16:0 and the amount of C remaining in the detritus of

Bruguiera gymnorrhiza ($R^2 = 0.84$, $p < 0.01$) and *Kandelia candel* ($R^2 = 0.91$, $p < 0.001$). This positive correlation indicates that the declining trend in 16:0 during decomposition is related to the loss of C. Since mangrove leaves show common decomposition pathways (Alongi et al. 1992), the amount of 16:0 in mangrove leaves may be an indicator of their degradation state. In Week 18, the amount of 16:0 in the leaf detritus did not vary significantly from that in the mangrove sediments, suggesting that the leaf detritus were in the late stages of degradation.

Role of microbes and microbial activity

There was a significant interaction between species and time in the mean percent concentration of FFAs ($F = 5.53$, df = 10, $p < 0.0001$) and BFAs (BrFAs + 18:1ω7) ($F = 8.52$, df = 10, $p < 0.0001$), indicating that colonization of fungi and bacteria differed with leaf age between the 2 species (Fig. 4a,c). Tenore et al. (1982) suggested that detritus rich in N (low C:N ratio), and low in tannin (Ulken 1984) support greater fungal growth than those poor in N. Therefore the *Kandelia candel* leaves (which are richer in N than *Bruguiera gymnorrhiza* leaves) were colonized faster by fungi. However, as decay progressed, fungal biomass of *K. candel* declined, probably due to rapid loss of N (Fig. 4b).

The role of thraustochytrid fungi in mangrove-leaf decomposition and the sequence of fungal populations during different decay stages have been emphasized by Fell & Master (1973, 1975, 1980). Fell & Master (1980) concluded that fungi were required for N immobilization, and that in the presence of fungi the amount of organic C leaching from the leaves increases. The rapid increase in fungal markers between Weeks 0 and 2 indicates a rapid increase in fungal biomass and fungal activity. Since microbial biomass correlates well with microbial activity (Findlay et al. 1986), there was a rapid loss of C in leaves of both species between 0 and 2 wk, and a rapid increase in N in *Bruguiera gymnorrhiza* leaves and loss of N in *Kandelia candel* leaves (Fig. 4b,d).

Previous studies have indicated that organic materials rich in N (low C:N) favor net mineralization while those poor in N (high C:N) favor net immobilization (Alongi et al. 1992). In addition, Fenchel et al. (1998) suggested that high initial N (low C:N) results in high microbial assimilation efficiencies and an increase in mineralization, but a decrease in immobilization, and hence a fast decay rate. Therefore, the rapid loss of N from *Kandelia candel* (apart from some loss caused by leaching) was due to mineralization, and the accumulation of N in *Bruguiera gymnorrhiza* was probably due to immobilization. These results suggest that fungi play a central role early in decay, in particular in C loss (Fell & Master 1980), in loss of leaf biomass and cellulosic materials (Bremer 1995), and in enriching the detritus with N (Fell & Master 1980).

However, it remains questionable which organisms play the most important role in N immobilization. Previously, Fell & Master (1980) demonstrated that fungi were more important than bacteria in N immobilization. A study on the decomposition of marine macrophytes suggested that an increase in total detrital N occurs through the production of mucopolysaccharide exudates by bacteria (Hobbie & Lee 1980), and that such exudates may be incorporated in humic macromolecules in the detritus (Rice & Hanson 1984). Recently, Nieminen & Setala (2001) indicated that organic C increases in the presence of bacteria because bacteria are more efficient at decomposing organic C than fungi. In Week 18, the concentration of FFAs in *Bruguiera gymnorrhiza* was not significantly different from FFAs in the mangrove sediments. However, mangrove sediments contained a significantly higher percent of FFAs than *Kandelia candel* detritus (Fisher's PLSD, $p < 0.01$), indicating that fungi enrich the mangrove sediments with nutrients from the decomposing leaves.

We identified 2 peaks of BFA markers, suggesting that bacterial decomposition occurred in 3 phases: an initial and rapid growth of bacteria (Weeks 0 to 4), corresponding to a rapid increase in lipid and N; a second phase in which bacterial growth ceased (from Week 6 to 8) following the disappearance of most of the degradable fractions (this phase corresponded with a decline in lipid and N); and a third phase (Weeks 10 to 12) associated with a significant increase in bacterial growth as the humification process began (Hedges 1988, Kristensen 1994) (Fig. 4c). Similar patterns have been described by Kristensen (1994) for decomposing macroalgae, seagrasses and leaves from trees.

The bacterial dynamics of the Okinawan system during summer are similar to those in a Queensland mangrove forest (Australia), where bacterial biomass in decaying mangrove leaves of *Rhizophora stylosa* and *Ceriops tagal* was estimated by microscopic count (Robertson 1988). Peaks in bacteria abundance appeared between 0 and 80 d and between 80 and 160 d of incubation in the field, a similar time frame to the Weeks 2 to 4 and Weeks 10 to 12 in this study. This may indicate that there is a similarity in the sequence of bacterial populations during different stages of decay, and that bacterial biomass is not constant during the decomposition process.

Change in BFAs in relation to PUFAs

The species-time interaction in the statistical analysis indicates that the change in composition of PUFAs

through time differed between species (F = 6.08, df = 10, p < 0.0001). PUFAs were more abundant in the green and yellow leaves of *Kandelia candel* (mainly 18:2ω6 and 18:3ω3) than in the decomposing leaves (Weeks 0.7 to 18). Although concentrations decreased gradually with increasing detritus age in *K. candel*, there was no significant decrease in PUFAs related to the highest detection of BFAs markers in the detritus in Weeks 2 and 12 (Fisher's PLSD, p > 0.05) (Fig. 4c,e). In *Bruguiera gymnorrhiza*, the concentration of PUFAs increased with increasing detritus age. However, in contrast to our hypothesis that the concentration of PUFAs in both species would decline rapidly due to bacterial processing (Prahl et al. 1984, Harvey et al. 1987, Carrie et al. 1998), there was a significant decline in PUFAs corresponding with elevated BFAs only in Week 4 (Fisher's PLSD, p < 0.01).

The increase in PUFAs in *Bruguiera gymnorrhiza* detritus and the absence of any significant decline in PUFAs in *Kandelia candel* corresponding with the highest abundance of BFAs markers (Week 2) indicates that processing of PUFAs by bacteria in mangrove detritus is a slow process, as bacteria tend to enrich the detritus with PUFAs rather than utilize them. Nonetheless, PUFA degradation by bacteria is rapid in green macroalgae (Carrie et al. 1998) due to high proportions of the acids and nutrients in their fresh tissues. Therefore, we rejected the hypothesis that PUFAs in mangrove detritus may be degraded rapidly by bacteria. The low concentration of nutrients in the leaves probably discouraged bacterial growth. In Week 18, the percent concentration of BFAs in *B. gymnorrhiza* was not significantly different from that in the mangrove sediments (Fisher's PLSD, p > 0.05), indicating low bacterial activity towards the end of the decay process (Fig. 4c).

Nutritional quality of detritus

ω3 and ω6 PUFAs are biosynthesized by vascular plants and are essential dietary factors for all animals (Sargent et al. 1990). Comparison of these dietary factors in the 2 species indicated that in *Kandelia candel*, fresh leaves and the 2 wk-old detritus are nutritionally of higher quality than the aged detritus, due to a high N content (low C:N ratio) that also supports greater fungal growth (Tenore et al. 1982, Chen et al. 2001) than in fresh leaves of *Bruguiera gymnorrhiza* (Fig. 5a). However, in *B. gymnorrhiza*, nutritional value increased with increasing detritus age as result of enrichment with the ω3 and ω6 PUFAs. A major source of these FAs, in particular 20:5ω3, 22:6ω3 and 22:5ω6, is thraustochytrid fungi (Findlay et al. 1986, Bowles et al. 1999).

Findlay et al. (1986) suggested that an increase in the long-chain PUFAs in decayed mangrove leaves plays a significant role in nutrient enrichment of the mangrove

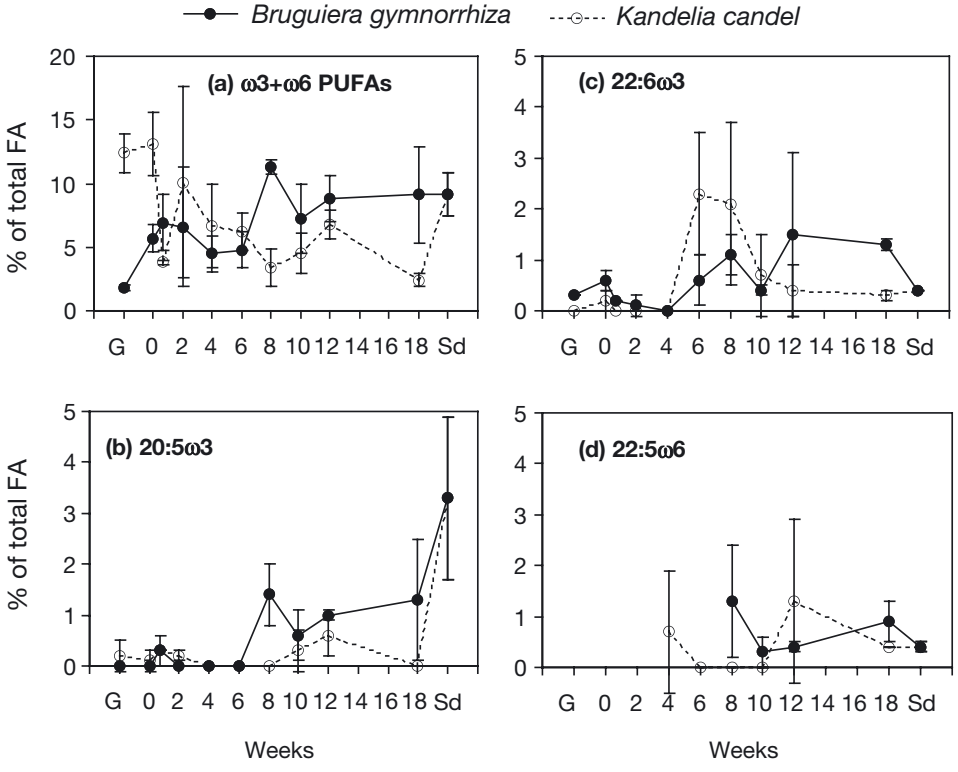

Fig. 5. *Bruguiera gymnorrhiza* and *Kandelia candel*. Changes in percent concentration of ω3 + ω6 PUFAs and long-chain PUFAs (20:5ω3, 22:6ω3 and 22:5ω6) in decomposing leaves compared with fatty acids in green leaves (G) and man-grove surface-sediments (Sd). Values are means ± SD (n = 3)

detritus. These FAs were detected in lower amounts (<3%) after 1 and 2 mo incubation than those reported for pure isolates by Bowles et al. (1999) (Fig. 5b,c,d). Although concentrations in nature are usually lower than in laboratory cultures, the main reason for the low amounts is that thraustochytrids from subtropical mangroves produce a low concentration of long-chain PUFAs but a high lipid biomass (Bowles et al. 1999). The detection of 20:5ω3 (a microalgae marker) in the fresh leaves of *Kandelia candel* may also be attributed to colonization of epiphytic diatoms and protozoans, since these organisms colonize fresh plant materials rich in N (Tenore et al. 1982). These differences in nutritional qualities between species and state of degradation influence feeding preferences by macrozoobenthos, in particular crabs.

Short-term experiments on feeding, indicated that green leaves of *Kandelia candel* were consumed faster than yellow and brown leaves of *Bruguiera gymnorrhiza*; however, there was no significant difference in the consumption rate between the green and yellow leaves of *K. candel*, suggesting a preference for leaf species with high nutritional quality (P. Mfilinge & M. Tsuchiya unpubl. data). Mangrove sediments had similar nutritional qualities to those of aged *B. gymnorrhiza* detritus, suggesting that sediments in this mangrove forest may equally fulfill the nutritional requirements of leaf-eating macrozoobenthos.

In conclusion, microbial activity in decaying leaves appears to cause major changes in the composition and concentration of plant-produced fatty acids and lipids. Major changes included an increase in BrFAs and MUFAs, and a decrease in SAFAs. The changes were rapid early in the decay process and varied between the mangrove species. This study suggests that the percent of SAFAs in the total FA, together with the palmitic fatty acid 16:0, may indicate the state of decay of the mangrove leaves and may have potential for the characterization of mangrove detritus. The BFAs and FFAs were suitable indicators of microbial activity in the detritus, supporting the hypothesis that changes in fatty acid composition during leaf decomposition may provide indications of the state of decay and microbial activity.

However, there was no evidence to suggest that bacteria quickly degrade PUFAs, because PUFAs increased over time, particularly in *Bruguiera gymnorrhiza*. This short-term field-decomposition experiment had no effect on LCFA concentrations, suggesting that LCFAs remain in nature for at least 4 mo, a period longer than predicted. Increases in PUFAs in *B. gymnorrhiza* and decreases in PUFAs in *Kandelia candel* leaf detritus had important implications for determining their utilization by mangrove macrozoobenthos.

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