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RESEARCH ARTICLE

Inter-specific and geographical variations in the fatty acid composition of mangrove leaves: implications for using fatty acids as a taxonomic tool and tracers of organic matter

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Abstract Fatty acid compositions of the leaves of six species of mangroves were studied to ascertain their use as biomarkers for determining the fate of mangrove organic matter in the habitat and as taxonomic tool. Mangrove leaves were collected from three locations in the western Pacific Ocean: Moreton Bay (MB) (Australia), Hong Kong (China) and Okinawa (Japan). In MB, samples were collected from two sites separated by 15 km: Logan River Estuary (LRE) and Jabiru Island. In addition, along the LRE, leaves were collected from five stations at ~2–3 km apart. Results show that the analysis of the entire fatty acid profiles of the mangrove leaves is a promising taxonomic tool as the profiles of most species were sufficiently different to be separated in an non-metric multidimensional scaling plot. In addition, geographically separated populations of the same species could also be identified by their fatty acid profiles. In most cases, two non-ubiquitous groups of fatty acids dominated in the mangrove leaves: the polyunsaturated 18:2ω6 and 18:3ω3 and the long chain fatty acids (≥24:0). With respect to the relative contributions of these fatty acids, three groups of species were identified, in which one or both groups of fatty acids may potentially be used as markers of the mangrove organic matter in the estuarine environment.

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Introduction

Mangroves dominate in the shorelines and the estuaries of tropical and sub-tropical areas. In term of species number, the diversity of these trees is relatively low (~70 species, Duke et al. 2002; Ellison 2002). However, a large numbers of studies are showing a high genetic diversity within and among populations of a large number of mangrove species (Duke et al. 1998, 2002; Melville et al. 2004; Tan et al. 2005), which have led to contrasting conclusions in term of evolution and distribution of these plants (Dodd et al. 1998; Duke et al. 2002). This diversity may be due in part to inadequate species identification of mangroves (Dodd et al. 1998), but it nevertheless reflects a high degree of adaptability to the coarse conditions that characterize their environments (Hogarth 1999). This adaptability can, for

instance, lead to a greater inter-specific similarity of biochemical compounds (epicuticular waxes and triterpenoids) than that of geographically isolated populations of the same species (Dodd et al. 1998).

In many habitats, mangroves are the basis for a complex food web and sustain a high diversity of organisms from microfungi (Schmit and Shearer 2004) to brachyuran crabs (Lee 1997) and fishes (Sheaves and Molony 2000). Chemical tracers such as stable isotopes and fatty acids are increasingly used for investigating the dietary source of organisms (Meziane and Tsuchiya 2000; Dalsgaard et al. 2003; Howell et al. 2003). Some tracers are further employed as a means for differentiating taxa and even species of plants and animal (Graeve et al. 2002; Meziane et al. 2006). However, an inherent assumption of this application is that populations of the same species demonstrate smaller degrees of variation compared to inter-specific differences in chemical signature. Likewise, the use of species or group-specific stable isotope signatures in tracing trophic relationships is based on the premises that within-species or within-group variation in signatures is small compared to between-group differences and that consumers either do not alter the signature or do this only in a predictable way. While chemical tracers such as stable isotopes and fatty acids are commonly used for trophodynamic analysis, few attempts have been made to evaluate this assumption underlying the techniques. It has been demonstrated that mangroves growing under different nutrient regimes have significantly different $\delta^{13}C$ and $\delta^{15}N$ signatures (e.g., Smallwood et al. 2003). Additional factors like geographic location may also influence the universality of chemical tracer signatures, thus compromising their usefulness as indicators of trophic relationship.

The use of the fatty acid biomarker technique to determine the fate of the sources of organic matter (from green plants and microbial producers) relies on the ability to find the compounds that exclusively characterize these sources. Mangrove leaves do not have known unique fatty acids but rather those that are common to most vascular plants, although they do not necessarily occur in the same proportions from one species to another (Wannigama et al. 1981; Meziane and Tsuchiya 2000; Mfilinge et al. 2003, 2005). The fatty acids used as vascular plant markers in coastal environment are mainly certain polyunsaturated fatty acids, especially 18:2ω6 and 18:3ω3 (Napolitano et al. 1997; Meziane et al. 2006) and the long chain fatty acids (LCFAs ≥ 24:0) (Meziane and Tsuchiya 2000; Dalsgaard et al. 2003). Nevertheless, the polyunsaturated fatty acids, 18:2ω6 and 18:3ω3, in contrary to LCFAs, are also common in other organisms than vascular plants, such as fungi and macroalgae (Chen et al. 2001; Graeve et al. 2002). Therefore, in studies concerned with the export of the mangrove leaf organic matter to the sediment through litter production and with the role of the mangrove as a primary food source for animals, preliminary checking must be done to ensure (1) the importance of these plants in the environment and (2) the composition of fatty acids in their tissues. Finally, another aspect to consider is the behavior of these fatty acids while they are in the decomposing litter, during sediment diagenesis process, and when ingested by benthic consumers.

In this study, we investigated variations in fatty acid profiles of common mangrove species at different spatial scales in the west Pacific region, with the aim of determining if differences occur in the fatty acid profiles of mangrove leaves and examining the prospect of using individual or groups of fatty acids as taxonomic and trophic markers.

Materials and methods

Sampling strategy and study locations

Leaf samples of six species of mangroves were collected from three locations in the west Pacific Ocean in spring (Fig. 1), namely, Hong Kong (HK, China), Okinawa Archipelago (OKI, Japan) and Moreton Bay (MB, Australia). In HK, leaves of *Kandelia obovata*, *Aegiceras corniculatum* and *Avicennia marina* were picked randomly from tree branches (three trees for each species) at the Mai Po Nature Reserve on the northwest of HK (24°30′N; 114°01′E, Fig. 1). In OKI, leaves of *K. obovata*, *Rhizophora stylosa* and *Bruguiera gymnorrhiza* were collected randomly from tree branches at Oura Bay (north of OKI Island, 26°N, 128°E, Fig. 1). Leaves of three *Avicennia marina* trees were taken from Ishigaki Island situated 400 km south of OKI mainland (24°N, 124°E, Fig. 1). Two sites in MB were sampled (27°45′S, 153°25′E, Fig. 1), separated by a distance of ~15 km. These sites, Jabiru Island (JI) and Logan River Estuary (LRE), form part of southern MB, an enclosed water body with direct communication with the Coral Sea at only a few locations. Five sampling stations (stn 1 to stn 5) were selected in the LRE estuary, separated by ~2–3 km and situated along a salinity gradient. During low tide, the salinity of the most 'upstream' station varied from 27 to 31‰ in summer and from 31 to 34‰ in autumn (Meziane et al. 2006). Mangrove forests are well developed in the estuary and are dominated by *Avicennia marina*. Other species include *Aegiceras corniculatum*,

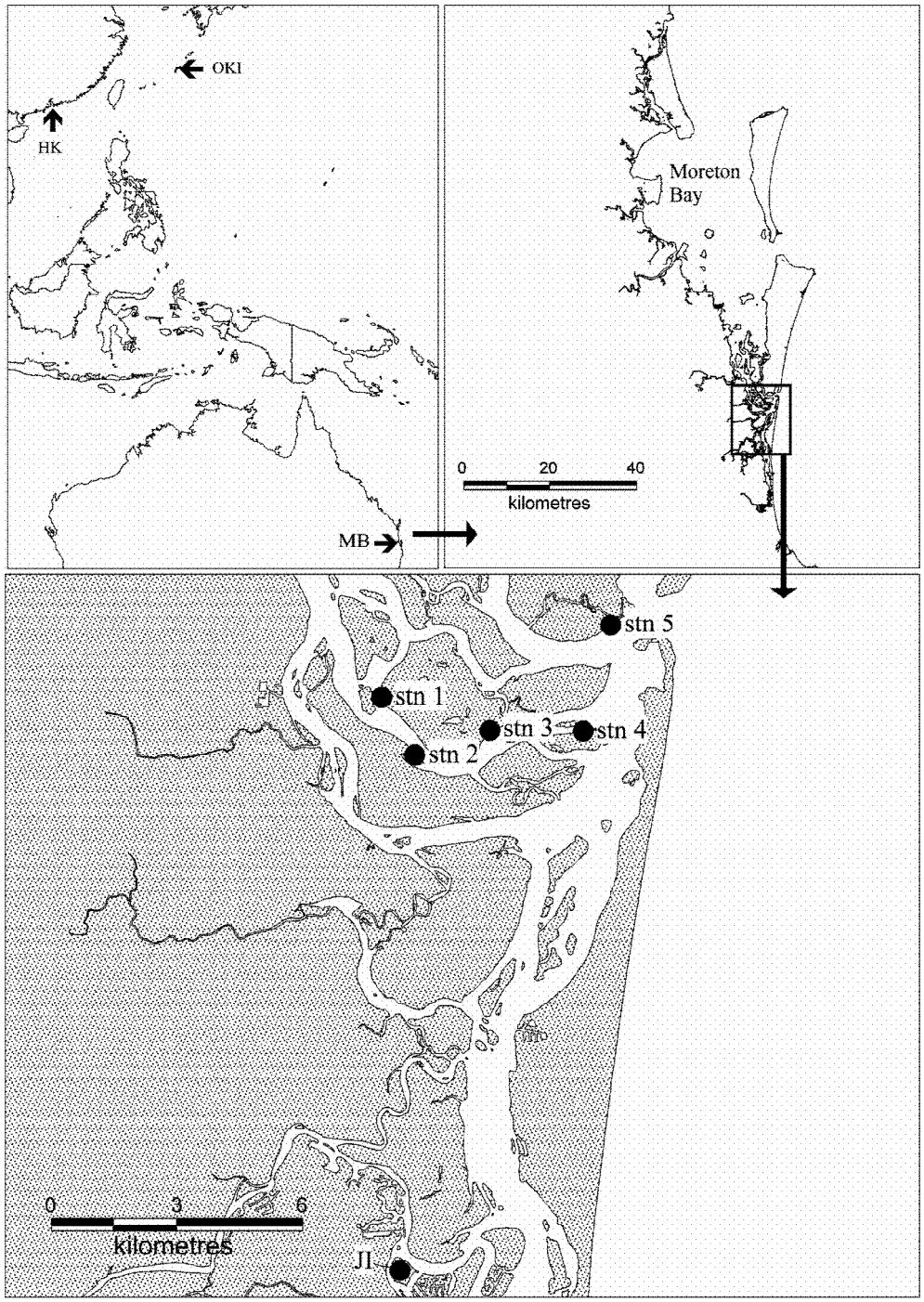


Fig. 1 Maps of sampling locations: Moreton Bay (*MB*, Australia), Hong Kong (*HK*, China) and Okinawa (*OKI*, Japan); sites: Jabiru Island (*JI*) and Logan River Estuary (*LRE*) and stations (*stn 1* to *stn 5* in LRE)

B. gymnorrhiza, *R. stylosa* and *Ceriops australis*. At each station, leaves of these five mangrove species were collected randomly from three trees (three leaves per tree).

All leaves were kept on ice, transported to the laboratory and stored at −20°C until lipid analysis, which occurred within a week after collection.

Fatty acid analysis

All samples were processed using the same method. Mangrove leaves from the same tree were cut into small pieces and pooled together. Sub-samples of 2 g (wet weight) of the cut pieces were then used for lipid analyses. Samples were processed following a slightly

modified version of Bligh and Dyer (1959). Lipids were extracted by homogenization for 2 min followed by ultrasonication for 20 min with a mixture of distilled water:methanol:chloroform (1:2:1, v:v:v). The addition of a distilled water:chloroform mixture (1:1, v:v) formed an aqueous-organic two-layer system enhanced by centrifugation (2,000 rpm). The lower chloroform phase, comprising the lipids, was retained and the concentrated by rotary evaporation. The lipid extracts were fully dried under nitrogen and then saponified under reflux (2 h, 100°C) with a solution of 2 mol NaOH/methanol (1:2, v:v). Saponification and methylation were done according to Meziane and Tsuchiya (2002) in order to obtain total fatty acids. Fatty acid methyl esters (FAMEs) were purified by high-performance thin-layer chromatography technique using plates coated with silica gel (Meziane and Tsuchiya 2002). The solvents used for developing was a mixture of hexane/diethyl ether/acetic acid (8:2:0.1, v:v:v). Duplicate plates were run for the samples, with one plate developed for identification of the fatty acid bands, and the other for further analysis by gas chromatography (GC). Bands containing FAMEs were scraped off the plates and were dissolved in a mixture of chloroform/methanol (2:1, v:v) at 40°C for 60 min. FAMEs were then isolated in the same solution until GC analysis.

The FAMEs were separated and quantified by GC (Varian 2000) equipped with a flame ionization detector. Separation was performed with a Supelco OMEGAWAX capillary column (30 m × 0.32 mm internal diameter, 0.25 μm film thickness) with hydrogen as carrier gas. After injection at 60°C, the oven temperature was raised to 150°C at a rate of 40°C min^{-1}, then to 240°C at 3°C min^{-1}, and finally held constant for 30 min. Flame ionization was held at 240°C. Most FAMEs peaks were identified by comparing their retention times with those of authentic standards (Supelco Inc., Bellefonte, PA, USA). For some samples, peaks of FAs were confirmed with GC-mass spectrometry. The analytical precision for samples was generally <5% for FAMEs components.

Fatty acids are designated as X:$Y\omega Z$, where X is the number of carbon atoms, Y is the number of double bonds and Z is the position of the ultimate double bond from the terminal methyl group.

Data analysis

The PRIMER software was used for multivariate analysis (Clarke and Warwick 2001). The data matrices (composition of fatty acids of leaf samples) were used to create triangular similarity matrices, based on Bray–Curtis similarity coefficient, followed by non-metric multidimensional scaling (n-MDS). Only identified fatty acids were used in these analyses and no transformation was performed on the data. Using the same triangular matrices, cluster analyses were also performed. Differences in fatty acid compositions between locations/sites were tested using a one-way analysis of similarity (ANOSIM). The test statistic was computed after 5,000 permutations. Similarity percentage (SIMPER), a module of PRIMER, was used to determine which fatty acids drive the observed differences in fatty acids composition between two sets of data.

The comparison between LRE stations for each mangrove species was limited by the ANOSIM test not being powerful enough to point out potential differences between groups formed by only three replicates. A one-way ANOSIM test to compare these two groups, will allow only ten distinct permutations and a significance level better than 10% could never be attained (Clarke and Warwick 2001). To tackle this statistical limitation and in order to examine the possible differences in fatty acid compositions of mangrove species along the salinity gradient, we pooled the data of stn1 and stn2, and of stn4 and stn5, which represent the upper and the lower end of the gradient, respectively. By pooling and thereby obtaining more than three replicates, we were able to use a one-way ANOSIM test at the 5% significance level.

Differences in the median percentage of individual fatty acids of a group of fatty acids between samples were performed using the ANOVA test with α set at 0.05.

Results

Inter-location comparisons of the same mangrove species

Twenty-two fatty acids represent >95% of total fatty acids identified in nearly all the leaf samples (Tables 1, 2, 3, 4, 5, 6, 7, 8). In most cases, the fatty acids 16:0, 18:1ω9, 18:2ω6 and 18:3ω3 contributed up to 76–89% of the total fatty acid content. Except for *Aegiceras corniculatum* and *Avicennia marina*, classification and ordination analysis separated most mangrove leaves into groups corresponding to their geographically distinct locations of sampling (Fig. 2).

Avicennia marina (HK–MB–OKI)

Fatty acid profiles of *Avicennia marina* exhibit an average dissimilarity (AD) of about 30% (SIMPER analysis) between samples from HK and MB, 26% between

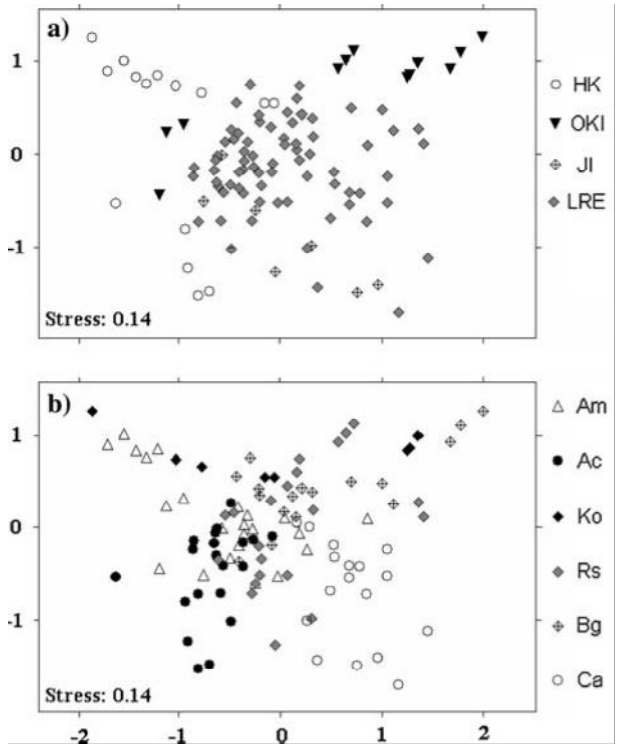


Fig. 2 n-MDS ordination of Bray–Curtis similarities for each mangrove leaf replicate. **a** The n-MDS with superimposed symbols for the locations and sites: Jabiru Island (*JI*), Logan River Estuary (*LRE*), Hong Kong (*HK*) and Okinawa (*OKI*) and **b** the same n-MDS but with *superimposed symbols* for mangrove species: *Avicennia marina* (Am),*Aegiceras corniculatum* (Ac), *Kandelia obovata* (Ko), *Rhizophora stylosa* (Rs), *Bruguiera gymnorrhiza* (Bg), *Ceriops australis* (Ca)

HK and OKI, and 23% between MB and OKI. The main observed difference within *Avicennia marina* is the relatively higher contribution of 18:3ω3 in HK and OKI than in MB (stn 1) to (stn 4) (Tables 1, 2, 3, 4, 5, 6, 7, 8).

Rhizophora stylosa (OKI–MB)

Similarity percentage analysis returns an AD of fatty acids profiles of *R. stylosa* between OKI and MB of 28%. This dissimilarity is due to higher contributions of 16:0, 16:1 and 16:2ω6 and lower contributions of 18:0 and 18:1ω9 in MB leaves than in OKI (Tables 1, 3, 6). The n-MDS plot shows a separation between the two sites, although the FAs profiles of leaves from OKI are clustered with the dispatched profiles of the LRE samples (Fig. 2).

Kandelia obovata (HK–OKI)

Fatty acid profiles of the *K. obovata* leaves exhibit a dissimilarity of 35% between samples collected from

Table 1 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of three mangrove species collected from Hong Kong ($n = 3$)

	Am-HK	Ac-HK	Ko-HK
12:0	0.25 ± 0.2	1.81 ± 0.4	0.80 ± 0.2
14:0	3.59 ± 1.9	1.66 ± 0.5	3.99 ± 1.1
14:1	0.00 ± 0.0	0.75 ± 0.1	0.68 ± 0.1
15:0	0.10 ± 0.1	0.13 ± 0.0	0.18 ± 0.1
16:0	12.02 ± 1.3	13.21 ± 2.9	20.22 ± 4.8
16:1	0.85 ± 0.1	0.74 ± 0.2	0.76 ± 0.2
17:0	0.78 ± 0.3	0.98 ± 0.2	1.16 ± 0.4
17:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
18:0	3.84 ± 0.5	2.37 ± 0.4	3.27 ± 0.8
18:1ω9	8.03 ± 0.3	19.77 ± 1.7	9.12 ± 2.3
18:2ω6	13.63 ± 1.0	26.95 ± 1.9	17.34 ± 4.8
18:3ω3	47.96 ± 7.0	24.39 ± 6.7	39.61 ± 15.7
20:0	0.00 ± 0.0	0.51 ± 0.1	0.48 ± 0.1
20:2	0.00 ± 0.0	0.00 ± 0.0	0.16 ± 0.0
20:4	0.00 ± 0.0	1.88 ± 0.4	0.00 ± 0.0
21:0	0.50 ± 0.1	0.21 ± 0.1	0.00 ± 0.0
22:0	1.20 ± 0.3	0.77 ± 0.1	0.42 ± 0.1
22:2	0.00 ± 0.0	0.43 ± 0.2	0.00 ± 0.0
24:0	6.87 ± 3.2	0.81 ± 0.5	0.30 ± 0.1
26:0	0.00 ± 0.0	1.15 ± 0.2	0.00 ± 0.0
28:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
30:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

Am *Avicennia marina*, Ac *Aegiceras corniculatum*, Ko *Kandelia obovata*

Table 2 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of four mangrove species collected from Okinawa ($n = 3$)

	Ko-OKI	Rs-OKI	Bg-OKI	Am-OKI
12:0	0.56 ± 0.4	0.34 ± 0.2	1.00 ± 0.8	0.0 ± 0.0
14:0	3.48 ± 1.0	2.23 ± 0.6	4.09 ± 0.7	0.4 ± 0.2
14:1	0.65 ± 0.1	1.46 ± 1.2	0.45 ± 0.4	0.2 ± 0.1
15:0	0.24 ± 0.2	0.06 ± 0.1	0.05 ± 0.1	0.0 ± 0.0
16:0	38.05 ± 0.4	32.21 ± 1.9	39.88 ± 2.8	20.2 ± 2.0
16:1	8.40 ± 0.6	12.07 ± 0.2	11.57 ± 1.8	0.9 ± 0.1
17:0	1.99 ± 0.1	1.60 ± 0.2	1.84 ± 0.2	0.4 ± 0.1
17:1	0.15 ± 0.1	0.15 ± 0.1	0.00 ± 0.0	0.1 ± 0.0
18:0	5.20 ± 0.3	3.44 ± 0.6	8.33 ± 0.6	2.1 ± 0.4
18:1ω9	9.13 ± 0.4	7.75 ± 0.5	9.17 ± 0.8	19.8 ± 7.3
18:2ω6	11.12 ± 0.1	14.65 ± 0.7	6.99 ± 0.7	7.2 ± 0.1
18:3ω3	13.01 ± 1.1	20.39 ± 0.4	10.15 ± 1.1	42.2 ± 5.2
20:0	0.38 ± 0.0	0.29 ± 0.0	0.57 ± 0.0	1.7 ± 0.1
20:2	0.00 ± 0.0	0.15 ± 0.3	0.21 ± 0.4	0.0 ± 0.0
20:4	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.0 ± 0.0
21:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.4 ± 0.0
22:0	0.56 ± 0.0	0.35 ± 0.2	0.46 ± 0.1	0.8 ± 0.0
22:2	0.33 ± 0.3	0.19 ± 0.2	0.18 ± 0.2	0.0 ± 0.0
24:0	0.95 ± 0.2	1.00 ± 1.0	0.86 ± 0.0	0.5 ± 0.0
26:0	0.51 ± 0.5	0.31 ± 0.0	0.40 ± 0.3	0.2 ± 0.0
28:0	0.43 ± 0.4	0.20 ± 0.2	0.98 ± 0.1	0.6 ± 0.1
30:0	1.68 ± 0.2	0.19 ± 0.2	0.79 ± 0.8	0.8 ± 0.2

Ko *Kandelia obovata*, Rs *Rhizophora stylosa*, Bg *Bruguiera gymnorrhiza*, Am *Avicennia marina*

HK and those from OKI. In HK, 18:3ω3 and 18:2ω6 accounted in much higher amount than in the OKI samples (Tables 1, 2). On the contrary, the percentages

Table 3 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of five mangrove species collected from Jabiru Island ($n = 3$)

	Ca-JI	Rs-JI	Am-JI
12:0	0.73 ± 0.7	0.71 ± 0.4	1.04 ± 0.7
14:0	2.20 ± 1.5	1.42 ± 0.6	0.91 ± 0.3
14:1	0.00 ± 0.0	0.08 ± 0.1	0.11 ± 0.2
15:0	0.00 ± 0.0	0.09 ± 0.2	0.00 ± 0.0
16:0	20.55 ± 4.1	19.59 ± 1.1	19.21 ± 2.0
16:1	1.55 ± 0.8	1.49 ± 0.2	1.13 ± 0.8
17:0	2.73 ± 1.5	0.89 ± 0.4	0.39 ± 0.2
17:1	0.52 ± 0.9	0.18 ± 0.3	0.00 ± 0.0
18:0	6.18 ± 1.5	4.92 ± 1.8	3.27 ± 0.6
18:1ω9	14.36 ± 0.8	24.63 ± 2.5	21.01 ± 5.1
18:2ω6	8.62 ± 1.0	9.21 ± 1.9	13.31 ± 2.7
18:3ω3	14.16 ± 1.0	21.96 ± 4.0	29.77 ± 3.1
20:0	2.93 ± 1.8	2.49 ± 2.2	0.62 ± 0.5
20:2	0.74 ± 0.6	0.00 ± 0.0	0.00 ± 0.0
20:4	0.59 ± 0.6	0.00 ± 0.0	0.00 ± 0.0
21:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
22:0	1.63 ± 1.3	4.16 ± 2.6	0.48 ± 0.8
22:2	1.23 ± 1.3	0.20 ± 0.4	0.00 ± 0.0
24:0	7.64 ± 2.4	5.33 ± 1.8	6.43 ± 2.1
26:0	3.57 ± 2.5	1.18 ± 0.4	0.53 ± 0.9
28:0	5.98 ± 2.3	0.00 ± 0.0	0.00 ± 0.0
30:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

Ca *Ceriops australis*, Rs *Rhizophora stylosa*, Ac *Aegiceras corniculatum*

of 16:0 and 16:1ω7 in the leaves from OKI are higher than those from HK (Tables 1, 2). The FA profiles of *K. obovata* from these two sites can therefore be separated in the n-MDS plot despite some other similar features (Fig. 2).

Bruguiera gymnorrhiza (OKI–MB)

Average dissimilarity of fatty acids profiles of *B. gymnorrhiza* between OKI and MB is 31%. This dissimilarity is mostly due to the higher contributions of 16:0, 18:0 and 16:1 and lower contributions of 18:3ω3, 16:2ω6 and 18:1ω9 in the leaves collected in MB than those collected in OKI. The n-MDS analysis shows a clear separation between the samples from the two sites (Fig. 2).

Aegiceras corniculatum (HK–MB)

Average dissimilarity of fatty acids profiles of *Aegiceras corniculatum* between HK and MB is 24%. This value is much smaller than those obtained with for other species (see above). Nevertheless, this level of dissimilarity is high enough to allow a separation between the two groups of *Aegiceras corniculatum* leaves (no over-lap) in the n-MDS analysis (Fig. 2). However, the HK samples have much in common with those of MB and can be clustered in the same region of the n-MDS plot (Fig. 2b), away from the main HK cluster formed with *Avicennia marina* and *K. obovata*. The dominant fatty acids that characterize samples of *Aegiceras corniculatum* in HK and in MB are mainly 16:2ω6 (higher in HK than in MB) and 18:3ω3, 16:0 and 20:0 (higher in MB than in HK) (Tables 1, 4, 5, 6, 7, 8).

Inter-site comparisons of same mangrove species in MB

The n-MDS analysis clearly demonstrates a grouping of FAs profiles from MB according to the species, irrespective of the sampling sites (LRE and JI, Fig. 2). In particular, *Aegiceras corniculatum*, *C. australis* and *B. gymnorrhiza* occupy the lower left, lower right and upper parts, respectively, in the MDS plot (Fig. 2). An inter-site comparison within MB (JI–LRE) returns ADs between 18% (*Avicennia marina*) and 22% (*R. stylosa*). There is no significant difference between FAs profiles from JI and LRE for *C. australis* and *Avicennia marina* (ANOSIM, $P > 0.5$) but surprisingly, a significant difference for *R. stylosa* ($R = 0.564$, $P = 0.01$) occurred.

Inter-station comparisons of same mangrove species in MB

There is no significant difference in fatty acid compositions of *Avicennia marina* leaves between the lower and the upper estuary stations ($R = 0.536$, $P > 0.1$). The one-way ANOSIM tests show no significant differences in the composition of fatty acid of *R. stylosa* leaves between LS and US ($R = -0.054$, $P > 0.5$). A significant difference exists in the fatty acid compositions of *C. australis* leaves between the US and LS samples ($R = 0.25$, $P<0.022$). The one-way ANOSIM tests show no significant differences in the composition of fatty acid of *Aegiceras corniculatum* leaves between LS and RS ($R = -0.085$, $P > 0.5$). There is a significant difference in fatty acid compositions of *B. gymnorrhiza* leaves between the lower and the upper estuary stations (one-way ANOSIM, $R = 0.263$, $P<0.02$).

Discussion

Fatty acid profiles reflect geographical and local differences

In this study, the entire FAs profiles were used as a fingerprint of the leaves from different mangrove species. This approach, as revealed by the n-MDS plots,

Table 4 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of *Avicennia marina* (Am) collected from five stations (stn 1 to stn 5) along the Logan River Estuary, Queensland, Australia ($n = 3$ except Am-stn 1)

	Am-stn 1 ($n = 1$)	Am-stn 2	Am-stn 3	Am-stn 4	Am-stn 5
12:0	0.52	0.36 ± 0.6	0.15 ± 0.2	0.05 ± 0.1	0.00 ± 0.0
14:0	0.89	1.14 ± 0.8	0.82 ± 0.4	0.66 ± 0.4	0.45 ± 0.2
14:1	0.00	0.00 ± 0.0	0.53 ± 0.9	0.00 ± 0.0	0.00 ± 0.0
15:0	0.00	0.17 ± 0.3	0.61 ± 0.7	0.00 ± 0.0	0.00 ± 0.0
16:0	39.25	24.78 ± 3.3	23.48 ± 0.7	22.87 ± 1.2	20.48 ± 1.2
16:1	1.19	1.76 ± 0.4	5.07 ± 3.6	2.35 ± 1.4	3.60 ± 0.4
17:0	0.50	0.88 ± 0.01	1.06 ± 1.3	0.40 ± 0.4	0.09 ± 0.2
17:1	0.00	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
18:0	2.17	3.98 ± 1.3	4.27 ± 0.4	4.50 ± 0.4	3.99 ± 1.0
18:1ω9	18.76	15.60 ± 3.6	12.40 ± 2.2	12.63 ± 1.2	15.88 ± 2.1
18:2ω6	10.80	12.62 ± 3.6	16.16 ± 2.9	15.86 ± 1.8	17.28 ± 2.9
18:3ω3	17.47	26.74 ± 2.5	25.94 ± 4.7	31.57 ± 2.0	28.93 ± 1.0
20:0	0.99	2.35 ± 0.8	2.08 ± 0.1	2.19 ± 0.3	2.27 ± 0.7
20:2	0.00	0.45 ± 0.8	0.00 ± 0.0	0.00 ± 0.0	0.22 ± 0.4
20:4	0.00	0.42 ± 0.7	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
21:0	0.00	0.46 ± 0.8	0.00 ± 0.0	0.07 ± 0.1	0.00 ± 0.0
22:0	0.61	3.25 ± 1.3	0.45 ± 0.5	0.75 ± 0.3	0.47 ± 0.3
22:2	0.00	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
24:0	2.08	1.78 ± 0.8	2.46 ± 1.3	4.78 ± 5.1	1.90 ± 0.8
26:0	2.18	0.25 ± 0.4	3.53 ± 1.2	0.66 ± 0.4	1.67 ± 0.8
28:0	0.00	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
30:0	0.00	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

Table 5 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of *Bruguiera gymnorrhiza* (Bg) collected from five stations (stn 1 to stn 5) along the Logan River Estuary, Queensland, Australia ($n = 3$)

	Bg-stn 1	Bg-stn 2	Bg-stn 3	Bg-stn 4	Bg-stn 5
12:0	1.09 ± 0.4	0.55 ± 0.5	0.46 ± 0.2	0.75 ± 0.8	0.77 ± 1.1
14:0	2.73 ± 0.7	2.46 ± 0.3	1.90 ± 0.1	2.76 ± 1.2	2.20 ± 1.3
14:1	0.13 ± 0.2	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
15:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.66 ± 0.5
16:0	35.04 ± 3.8	32.10 ± 3.1	30.51 ± 5.8	28.85 ± 3.0	22.02 ± 3.2
16:1	1.75 ± 0.3	0.82 ± 0.6	1.00 ± 0.4	1.63 ± 1.0	1.45 ± 0.7
17:0	1.14 ± 0.3	0.56 ± 0.4	1.35 ± 0.2	0.91 ± 0.2	0.98 ± 0.6
17:1	0.00 ± 0.0	0.28 ± 0.5	0.55 ± 0.2	0.00 ± 0.0	0.00 ± 0.0
18:0	5.89 ± 0.7	3.57 ± 0.1	5.78 ± 1.7	5.89 ± 2.5	3.80 ± 0.3
18:1ω9	10.56 ± 1.3	10.54 ± 0.3	12.34 ± 3.3	8.96 ± 1.6	13.29 ± 4.1
18:2ω6	9.97 ± 1.0	11.45 ± 0.2	11.10 ± 1.7	13.38 ± 0.9	12.10 ± 2.0
18:3ω3	22.22 ± 7.6	27.82 ± 0.6	26.30 ± 9.6	31.22 ± 5.9	32.09 ± 6.2
20:0	1.54 ± 1.2	1.97 ± 0.7	1.04 ± 0.8	1.49 ± 1.4	2.89 ± 1.4
20:2	0.00 ± 0.0	0.00 ± 0.0	0.07 ± 0.1	0.00 ± 0.0	0.00 ± 0.0
20:4	0.21 ± 0.4	0.00 ± 0.0	0.26 ± 0.4	0.00 ± 0.0	0.00 ± 0.0
21:0	0.24 ± 0.4	0.00 ± 0.0	0.00 ± 0.0	0.19 ± 0.3	0.00 ± 0.0
22:0	1.19 ± 1.3	1.31 ± 1.4	0.11 ± 0.2	0.75 ± 0.5	1.07 ± 1.9
22:2	0.55 ± 0.2	0.00 ± 0.0	0.05 ± 0.1	0.00 ± 0.0	0.00 ± 0.0
24:0	2.93 ± 1.3	5.26 ± 0.1	1.45 ± 1.8	2.10 ± 0.6	3.13 ± 1.4
26:0	1.10 ± 0.9	1.20 ± 0.5	1.28 ± 1.1	0.35 ± 0.5	1.18 ± 1.0
28:0	0.53 ± 0.1	0.00 ± 0.0	0.38 ± 0.3	0.00 ± 0.0	0.00 ± 0.0
30:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

shows that FAs profile analysis is a promising taxonomic tool that enables the characterization of mangrove populations according to specific identity and, intra-specifically, their geographical location. In microalgae, it has been argued that the fatty acid profile is a result of both genotypic and phenotypic influences (Dalsgaard et al. 2003). Intra-specific variations in FA profiles have also been recorded in animal populations exposed to different environmental conditions, e.g., the mussel *Mytilus galloprovincialis* (Freites et al. 2002) and fish species (Budge et al. 2002). The present study also suggests that while broad patterns of similarity exist amongst different mangrove species (i.e., the prevalence of 18:2ω6 and 18:3ω3) there are still substantial differences in the FA profile to differentiate species, and in some species, to differentiate between populations on different spatial scales (1,000's km among MB, HK, OKI; 15 km: LRE, JI; ~2–3 km,

Table 6 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of *Rhizophora stylosa* (Rs) collected from five stations (stn 1 to stn 5) along the Logan River Estuary, Queensland, Australia ($n = 3$)

	Rs-stn 1	Rs-stn 2	Rs-stn 3	Rs-stn 4	Rs-stn 5
12:0	0.30 ± 0.2	0.94 ± 0.3	0.53 ± 0.4	0.61 ± 0.2	0.00 ± 0.0
14:0	1.18 ± 0.4	2.44 ± 0.9	1.82 ± 0.9	2.37 ± 1.3	1.30 ± 0.8
14:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
15:0	0.31 ± 0.3	0.24 ± 0.4	0.00 ± 0.0	0.01 ± 0.0	0.00 ± 0.0
16:0	23.25 ± 0.8	36.62 ± 7.2	23.36 ± 5.9	37.82 ± 4.9	20.62 ± 1.8
16:1	1.13 ± 0.2	0.65 ± 0.6	1.13 ± 0.6	1.07 ± 0.3	3.08 ± 1.7
17:0	0.46 ± 0.3	0.68 ± 0.8	0.39 ± 0.4	0.23 ± 0.2	0.19 ± 0.3
17:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
18:0	2.64 ± 0.6	4.02 ± 1.6	3.80 ± 2.2	5.84 ± 1.0	3.27 ± 1.1
18:1ω9	17.41 ± 3.9	14.08 ± 2.9	17.81 ± 3.1	12.76 ± 3.3	16.27 ± 1.7
18:2ω6	12.06 ± 0.8	8.14 ± 2.5	11.98 ± 3.7	10.95 ± 4.2	8.06 ± 0.6
18:3ω3	30.68 ± 4.6	24.06 ± 6.2	33.73 ± 2.7	24.58 ± 8.2	27.85 ± 2.0
20:0	0.98 ± 0.6	1.06 ± 0.1	0.67 ± 0.5	0.14 ± 0.2	2.06 ± 0.5
20:2	0.09 ± 0.2	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	1.32 ± 1.3
20:4	0.56 ± 0.8	0.44 ± 0.8	0.26 ± 0.4	0.00 ± 0.0	0.34 ± 0.6
21:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
22:0	1.90 ± 1.6	1.70 ± 1.8	0.05 ± 0.1	1.28 ± 1.5	3.19 ± 0.7
22:2	0.00 ± 0.0	0.84 ± 0.7	0.00 ± 0.0	0.00 ± 0.0	0.23 ± 0.04
24:0	1.54 ± 0.2	0.71 ± 0.3	1.42 ± 0.6	1.05 ± 0.8	4.40 ± 1.0
26:0	0.97 ± 0.7	0.34 ± 0.3	1.08 ± 0.9	0.00 ± 0.0	1.72 ±.0.8
28:0	0.60 ± 0.4	0.00 ± 0.0	0.84 ± 1.3	0.00 ± 0.0	1.02 ± 0.9
30:0	0.69 ± 0.3	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	1.23 ± 1.1

Table 7 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of *Ceriops australis* (Ca) collected from five stations (stn 1 to stn 5) along the Logan River Estuary, Queensland, Australia ($n = 3$)

	Ca-stn 1	Ca-stn 2	Ca-stn 3	Ca-stn 4	Ca-stn 5
12:0	0.82 ± 0.4	0.37 ± 0.3	0.58 ± 0.7	0.36 ± 0.2	0.98 ± 0.6
14:0	1.93 ± 1.2	2.11 ± 0.2	2.01 ± 1.6	2.10 ± 0.3	2.46 ± 1.1
14:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
15:0	0.83 ± 0.7	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.47 ± 0.4
16:0	18.45 ± 2.5	26.63 ± 1.7	25.49 ± 1.5	27.26 ± 0.5	25.64 ± 4.8
16:1	1.00 ± 1.0	1.18 ± 0.2	1.07 ± 0.3	1.09 ± 0.3	0.88 ± 0.4
17:0	2.13 ± 1.6	1.19 ± 0.3	1.15 ± 0.4	1.19 ± 0.0	0.74 ± 0.2
17:1	0.16 ± 0.3	0.25 ± 0.4	0.13 ± 0.2	0.15 ± 0.3	0.00 ± 0.0
18:0	5.56 ± 0.9	3.70 ± 0.4	5.21 ± 2.2	6.00 ± 0.7	3.25 ± 1.8
18:1ω9	14.58 ± 3.8	11.75 ± 1.9	11.51 ± 3.2	23.10 ± 2.7	18.54 ± 3.4
18:2ω6	8.86 ± 2.0	10.78 ± 0.9	11.44 ± 1.6	10.13 ± 0.3	10.54 ± 4.5
18:3ω3	13.57 ± 2.3	23.45 ± 1.1	15.93 ± 2.0	16.47 ± 1.4	21.49 ± 2.7
20:0	3.55 ± 2.9	1.72 ± 0.7	0.87 ± 0.2	0.88 ± 0.3	2.69 ± 3.2
20:2	0.71 ± 1.2	0.25 ± 0.2	0.00 ± 0.0	0.00 ± 0.0	0.28 ± 0.5
20:4	0.00 ± 0.0	0.00 ± 0.0	0.22 ± 0.4	0.00 ± 0.0	0.00 ± 0.0
21:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
22:0	2.93 ± 0.6	1.37 ± 1.0	0.68 ± 0.3	0.65 ± 0.3	0.85 ± 1.1
22:2	0.56 ± 0.4	1.19 ± 0.3	0.78 ± 0.7	0.19 ± 0.2	0.22 ± 0.4
24:0	6.28 ± 3.3	3.47 ± 0.9	4.98 ± 1.7	2.76 ± 0.7	2.48 ± 1.7
26:0	3.29 ± 1.7	3.39 ± 0.7	4.67 ± 1.6	4.46 ± 0.9	2.45 ± 1.9
28:0	6.80 ± 1.5	5.60 ± 4.0	5.46 ± 2.3	2.62 ± 1.4	2.21 ± 2.6
30:0	5.64 ± 5.1	0.32 ± 0.6	1.78 ± 2.0	0.00 ± 0.0	0.29 ± 0.5

stations located in different positions at LRE). Studies like this one may therefore provide further evidence concerning mangrove adaptation and dispersal (Kathiresan and Bingham 2001), which is still not fully understood and for which theories remain unsettled (Duke et al. 2002).

In HK, the genetic diversity of *K. obovata* collected from several stations is strong enough to reveal two, spatially distinct, sub-populations (Sun et al. 1998). It is therefore not surprising that FAs profiles of *K. obovata* leaves collected in this study from two distant locations (HK–OKI) can easily be distinguished in the n-MDS plot. It has been demonstrated that genetic differences of populations from the same species can induce biochemical differentiation in the tissues (see Kathiresan and Bingham 2001, and references therein).

Despite a widespread geographic distribution, *Aegiceras corniculatum* has been reported to have a remarkably low genetic diversity (Ge and Sun 1999). This may explain the high similarity of the FAs profiles of the

Table 8 Fatty acid compositions (% of total identified FAs ± S.D.) of the leaves of *Aegiceras corniculatum* (Ac) collected from five stations (stn 1 to stn 5) along the Logan River Estuary, Queensland, Australia ($n = 3$)

	Ac-stn 1	Ac-stn 2	Ac-stn 3	Ac-stn 4	Ac-stn 5
12:0	0.00 ± 0.0	1.50 ± 0.4	0.26 ± 0.2	0.50 ± 0.2	0.75 ± 0.3
14:0	0.79 ± 0.5	2.38 ± 0.7	1.02 ± 0.3	1.68 ± 0.6	1.58 ± 0.5
14:1	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
15:0	0.09 ± 0.2	0.96 ± 0.5	0.44 ± 0.4	0.62 ± 0.4	0.81 ± 0.3
16:0	18.10 ± 2.2	21.88 ± 3.5	19.20 ± 2.1	21.54 ± 2.4	16.63 ± 1.2
16:1	1.45 ± 0.3	2.11 ± 0.4	1.84 ± 0.4	0.58 ± 0.4	2.79 ± 1.5
17:0	0.59 ± 0.1	1.07 ± 0.1	0.70 ± 0.2	1.03 ± 0.1	1.80 ± 1.9
17:1	0.00 ± 0.0	0.33 ± 0.3	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
18:0	2.47 ± 0.6	3.08 ± 0.6	2.62 ± 0.2	2.42 ± 0.2	3.20 ± 0.7
18:1ω9	15.50 ± 4.7	16.90 ± 1.5	16.19 ± 1.0	18.22 ± 4.6	20.19 ± 4.0
18:2ω6	12.69 ± 0.5	13.91 ± 1.7	13.45 ± 2.3	14.59 ± 1.8	13.17 ± 1.9
18:3ω3	31.74 ± 2.7	28.92 ± 4.1	31.49 ± 3.7	34.33 ± 3.3	27.01 ± 2.6
20:0	7.08 ± 1.4	2.46 ± 0.2	4.25 ± 0.2	2.09 ± 0.4	6.75 ± 2.0
20:2	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
20:4	0.00 ± 0.0	0.25 ± 0.4	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
21:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
22:0	6.61 ± 1.7	1.63 ± 0.4	3.11 ± 1.7	1.27 ± 0.2	3.01 ± 1.6
22:2	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.42 ± 0.7
24:0	2.01 ± 1.0	0.31 ± 0.5	1.80 ± 1.4	0.85 ± 0.4	1.33 ± 0.3
26:0	0.25 ± 0.2	0.00 ± 0.0	0.47 ± 0.8	0.00 ± 0.0	0.00 ± 0.0
28:0	0.33 ± 0.6	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0
30:0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0	0.00 ± 0.0

leaves of *Aegiceras corniculatum* between HK and MB as shown by the homogeneous group formed by different geographical populations of this species in the MDS plot.

Ceriops australis is the only species in this study that was collected in a single site (LRE) and it cannot therefore be compared to individuals from other sites or locations. However, FAs profile differences between sites and location can be expected, as in one of its sibling species *Ceriops decandra*, a high genetic differentiation was found among populations collected from two distant locations (Malay Peninsula and North Australia, Tan et al. 2005).

The FAs profiles of the three populations of *Avicennia marina* are dissimilar enough to be clearly separated in the n-MDS plot. This can be explained by the fact that geographically separated populations of *Avicennia marina*, the most widely distributed mangrove in the Indo-West Pacific region, exhibit a high genetic diversity (Duke et al. 1998). At a smaller scale, a downstream genetic diversity gradient of *Avicennia marina* along a polluted river has been reported (Melville et al. 2004). In LRE, there was no significant difference in FA profiles of *Avicennia marina* leaves between lower and upper stream stations. The absence of this gradient along the LRE was also observed in the case of *Aegiceras corniculatum* and *R. stylosa*. The absence of a gradient was expected for *Aegiceras corniculatum*, the most homogenous species of this study in term of FAs profiles whereas in the case of *R. stylosa*, one can expect a gradient, similar to those observed for the other members of the Rhizophoraceae present in LRE (*B. gymnorrhiza* and *C. australis*).

Nonetheless, it is unlikely that distinct profiles of FAs could be attributed solely to an expression of genetic differences, knowing that local climatic and physical conditions may modify the composition of fatty acids (Hogarth 1999; Kunst and Samuels 2003). For instance, the LCFAs are usually cuticular wax materials that are important in conferring resistance to water shortage or herbivory attack in mangroves. These protections are expected to vary according to local growing conditions as well as other chemical and structural adaptations acting in concert. Indeed, it has been suggested that differences in hydrocarbon chain length and lipid diversity observed between South American and African mangroves populations including *Avicennia* and *Rhizophora* species, are influenced by climatic diversity (Dodd et al. 1998). Now, some fatty acids are precursor to hydrocarbon synthesis (Kunst and Samuels 2003) and both compounds, as membrane constituents, are strongly affected by the physiological condition of the plants.

Fatty acids as tracers of mangrove-derived organic matter

Leaf litter is the most important source of mangrove organic matter in tropical estuaries. In MB, Mackey and Smail (1995) have shown that for *Avicennia marina*, the most abundant mangrove species, leaf material is the main contributor to decomposing litter in most of the year, including during our sampled period (spring). A similar dominant contribution of leaf material to the litter of mangroves has also been

reported for OKI (Mfilinge et al. 2002) and HK (Lee 1989). In HK, Lee (1989) reported that leaves of *K. obovata* (previously *Kandelia candel*) contributed 54% of the total litter biomass. In fact, this dominance by leaf material in mangrove litter generally applies to the Indo-Pacific region (Robertson et al. 1992).

Xu et al. (1997) reported that unsaturated FAs contributed 20–30% to the total fatty acids content of most propagules in ten species of Chinese mangroves. The percentage of LCFAs was, however, significantly higher than those reported for leaf materials analyzed in the present study. In all species common to both studies except *Aegiceras corniculatum*, Xu et al. (1997) reported that the contributions of LCFAs in the propagule FAs were between 16% (*Avicennia marina*) to 32% (*R. stylosa*), compared to generally <10% of the present study. Conversely, the concentrations of 18:2ω6 + 18:3ω3 are relatively low in the propagules, ranging from 1.3% (*Aegiceras corniculatum*) to 18.4% (*B. gymnorrhiza*) (Xu et al. 1997) in comparison with this leaves of this present study (>20%). Similar reports on the lipid profile of other mangrove litter components are rare, but it seems that mangrove leaf litter is the largest contributor of mangrove-derived unsaturated fatty acids to estuarine food chains.

From all the fatty acid profiles obtained in this present study, one can cluster the mangrove species into three groups with respect to the relative contributions of the polyunsaturated 18:2ω6 and 18:3ω3 and the LCFAs, which are used as markers of terrestrial inputs in coastal environment (Napolitano et al. 1997; Budge and Parrish 1998; Dalsgaard et al. 2003; Meziane et al. 2006).

The first group comprises *K. obovata* collected from HK and OKI and *R. stylosa* collected from OKI and MB. In *K. obovata* leaves, the polyunsaturated 18:2ω6 and 18:3ω3 were present in both locations with a total contribution varying from ~21% (OKI) to up to 70% (HK), whereas LCFAs were only minor components in HK (<0.5% of total fatty acids) compared to OKI (>3.5% on average). A similar trend can be observed for *R. stylosa*. In OKI, LCFAs, are present in low amounts (<2% in average), whereas in some MB stations these markers exhibited a contribution >6% of the total fatty acids.

The second group comprises only *Aegiceras corniculatum* collected from HK and MB. These two distant populations of *Aegiceras corniculatum* exhibit a high similarity of FAs profiles of their leaves with their LCFAs contributing always <2% of total fatty acids. In contrary, the contribution of 18:2ω6 + 18:3ω3 constitutes in most cases >50% of the total identified fatty acids of both populations of *Aegiceras corniculatum*.

The third group is made up of *Avicennia marina* collected in MB, HK and OKI, *B. gymnorrhiza* collected in OKI and MB and the population of *C. australis* collected in MB. Contributions of both groups of markers, 18:2ω6 + 18:3ω3 and LCFAs, to the total fatty acids leaves are relatively high.

Hence, with respect to these three groups of species and assuming the prevalence of mangrove as source of organic matter, it is clear that the polyunsaturated 18:2ω6 and 18:3ω3, because of their prevalence in the FA composition of the mangrove leaves, can always be used as tracers of mangrove-derived organic matter, independent of the geographical location. On the other hand, LCFAs may not be useful as biomarkers of mangroves if their presence is not beforehand found or only little in the leaves of the study location (i.e., *Aegiceras corniculatum* and *K. obovata* in HK).

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