

Exotic tree leaf litter accumulation and mass loss dynamics compared with two sympatric native species in south Florida, USA

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Abstract The exotic tree *Melaleuca quinquenervia* (melaleuca) forms dense forests usually characterized by low plant diversities and dense litter biomass accumulations on forest floors of ecologically sensitive ecosystems, including portions of the Florida Everglades. We quantified litter accumulation in mature melaleuca stands and compared decomposition rates of melaleuca leaves with a sympatric native plant, either *Cladium jamaicense* (sawgrass) in sawgrass marshes or *Pinus elliottii* (slash pine) in pine flatwoods habitats that varied in soil types. Total litter accumulation in mature melaleuca forests prior to June 1997 ranged from 12.27 to 25.63 Mg ha⁻¹. Overall, melaleuca leaves decomposed faster in organically rich versus arenaceous soils. Decomposition rates were lower for melaleuca leaves than for sawgrass in both melaleuca-invaded and uninvaded sawgrass marshes. In arenaceous soils of pine flatwoods, melaleuca leaf and pine needle decomposition rates were similar. Complete mineralization of sawgrass leaves occurred after 258 weeks, whereas melaleuca leaves had up to 14% and pine foliage had up to 19% of the original biomass remaining after 322 weeks. Total carbon (C) in intact decomposing leaves varied slightly, but total nitrogen (N) steadily increased for all three species; the greatest being a fourfold in sawgrass. Increases in N concentrations caused decreases in the C/N ratios of all species but remained within an optimal range (20–30) in sawgrass resulting in higher decomposition rates

compared to melaleuca leaves and pine needles (C/N ratio >30). Slower decomposition of melaleuca leaves results in denser litter layers that may negatively affect recruitment of other plant species and impede their establishment in invaded communities.

Keywords C/N ratio · Exotic plants · Invasive trees · *Melaleuca quinquenervia* · Pine needles · Sawgrass leaves

Introduction

The role of litter production, accumulation, and decomposition in nutrient recycling and ecosystem functioning has been reviewed by various authors (Lamb 1985; Xiong and Nilsson 1997; Berg 2000; Ehrenfeld 2003; Zhang et al. 2008). Ehrenfeld (2003) reviewed the influence of exotic plant invasions on soil nutrient cycling and opined that invasive plants may significantly alter carbon, nitrogen, water, and other ecosystem cycles. In particular, Ehrenfeld (2003) mentioned the Australian *Melaleuca quinquenervia* (Cav.) S.T. Blake (hereafter referred to as “melaleuca”) tree as a species that likely modifies overall productivity, decomposition, and water flux within invaded habitats of Florida, USA. Subsequent to its introduction over a century ago, melaleuca has invaded over 200,000 ha of environmentally sensitive wetlands including sawgrass marshes, pine flatwoods, and cypress (*Taxodium* sp.) swamps in southern Florida (Ewel 1986; White 1994). Similar invasions by melaleuca have occurred in natural areas of Puerto Rico and the Bahamian archipelago (Pratt et al. 2008).

The structures of wetlands’ plant and animal communities changed as they were transformed into melaleuca swamp forests (White 1994; O’Hare and Dalrymple 1997). The invasion process and the accompanying loss of

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biodiversity have been reported previously in Lockhart et al. (1999), Myers (1975, 1983, 1984) and Woodall (1981, 1983). During the invasion, for instance, 60–80% of plant species diversity was lost due to displacement by melaleuca trees (Austin 1978). Although ecological impacts are evident, data on the underlying mechanisms attributable to the establishment of near melaleuca monocultures remain unclear (Rayamajhi et al. 2006). White (1994) suggested that melaleuca was capable of altering ecosystem functions partially through deposition of leaf litter and woody debris, which increases soil elevation and modifies hydrological patterns. Additionally, the success of melaleuca may be attributed in part to its inherent ability to produce relatively large amounts of litter biomass, which may decompose at a slower rate than that of native plants. Deposition of litter biomass increased proportionally with tree size (up to 11.28 Mg ha⁻¹ year⁻¹) (Rayamajhi et al. 2006) and the average litter biomass production by mature melaleuca stands in Florida was somewhat higher (8.3 Mg ha⁻¹ year⁻¹, Van et al. 2002) than in its native range (7.6 Mg ha⁻¹ year⁻¹) of Australia (Finlayson et al. 1993; Greenway 1994). The proportion of leaf biomass to all other components in the melaleuca litterfall ranged from 81% in non-flooded to 69% in permanently flooded habitats in Florida (Rayamajhi et al. 2006), which is consistent with data from Australia (Finlayson et al. 1993; Greenway 1994).

Litter accumulation occurs as a result of a disparity between litter production and decomposition rates. While melaleuca trees deposit large quantities of litter on the forest floor annually, the rate of decomposition and mineralization remains undetermined. Generally, slow decomposition rates limit site productivity due to immobilization of nutrients and negatively influence species diversity through physical burial (mulching effect) of propagules as shown in Dames et al. (1998) and Xiong and Nilsson (1997, 1999). Mass loss, the process of decomposition and mineralization of accumulated litter occurs through two steps: (1) an initial stage marked by rapid leaching of nutrients and (2) slow breakdown of lignocellulosic tissue components composed of acid soluble sugars and insoluble carbons by the action of soil microorganisms (Staaf and Berg 1982; Melillo et al. 1989).

The primary objectives of this study were to quantify: (1) leaf litter accumulation, the rate of mass loss, and nutrient dynamics for melaleuca leaves and (2) compare the mass loss attributes with the leaves and needles of two sympatric plant species. Melaleuca occurs on arenaceous as well as in organically rich soils, so rates of leaf mass loss were also compared between organic and arenaceous soil types. The two sympatric species chosen were *Cladium jamaicense* Crantz (sawgrass) and *Pinus elliottii* Engelm. var. *densa* Little & Dorman (slash pine) as they formerly

constituted the dominant plant species in many melaleuca-invaded plant communities.

Materials and methods

Study sites

Sites were located in south Florida, USA. South Florida has a humid, subtropical climate with the lowest average rainfall (ca 3 cm) and temperature (19°C) in January and the highest average rainfall (27 cm) and temperature (28°C) in August–September (Chen and Gerber 1991). Broward (between N26°02'57.3", W080°26'24.2" and N26°03'08.9", W080°26'23.7") and Collier (Picayune State Forest, between N26°05'47.1", W081°39'09.5" and N26°05'49.7", W081°39'08.9") County sites represent two physically separated geographic areas where mass loss studies were conducted. An additional mass loss study site was also established in Collier County. Soils in Broward County sites were dominated by poorly drained organic soil and are generally classified as Histosols (Brown et al. 1991) made up of brown to black peat (Kushlan 1991) containing ca 67% organic matter (Rayamajhi, unpublished data). The Collier County site was comprised mostly of Spodosols dominated by poorly drained arenaceous soils (Brown et al. 1991) with ca 4.1% organic matter in the upper 5-cm layer (Tipping et al. 2009). Within the Broward County site, a short stature *C. jamaicense* marsh (as described by Gunderson 1994) was selected at random which also contained a few individuals of *Myrica*, *Baccharis*, *Eleocharis*, and *Bacopa* (hereafter, referred to as “uninvaded sawgrass marsh”). Melaleuca stands, which had invaded the sawgrass marsh (hereafter referred to as “invaded marsh”), possessed trees of different ages with a few *Myrica*, *Baccharis*, and *Myrsine* individuals in the understory. The study area in Collier County consisted of “pine flatwoods” with a *Pinus elliottii* var. *densa* dominant canopy interspersed with cypress (*Taxodium* sp.) and *Serenoa repens* (Bartr.) Small (saw palmetto) as understory species (hereafter, referred to as “melaleuca-uninvaded flatwoods”). Melaleuca-dominated stands with scattered saw palmettos within the flatwood habitat (hereafter, referred to as “melaleuca-invaded flatwoods”) were randomly selected and used in foliage decomposition studies.

Melaleuca litter accumulation

Accumulated litter biomass was quantified in July 1997 for each melaleuca study site by dividing the trees into three sections (hereafter referred to as “small”, “intermediate”, and “large” tree stands) based upon the prevalent tree size. Stands consisted of predominantly large trees (mean DBH

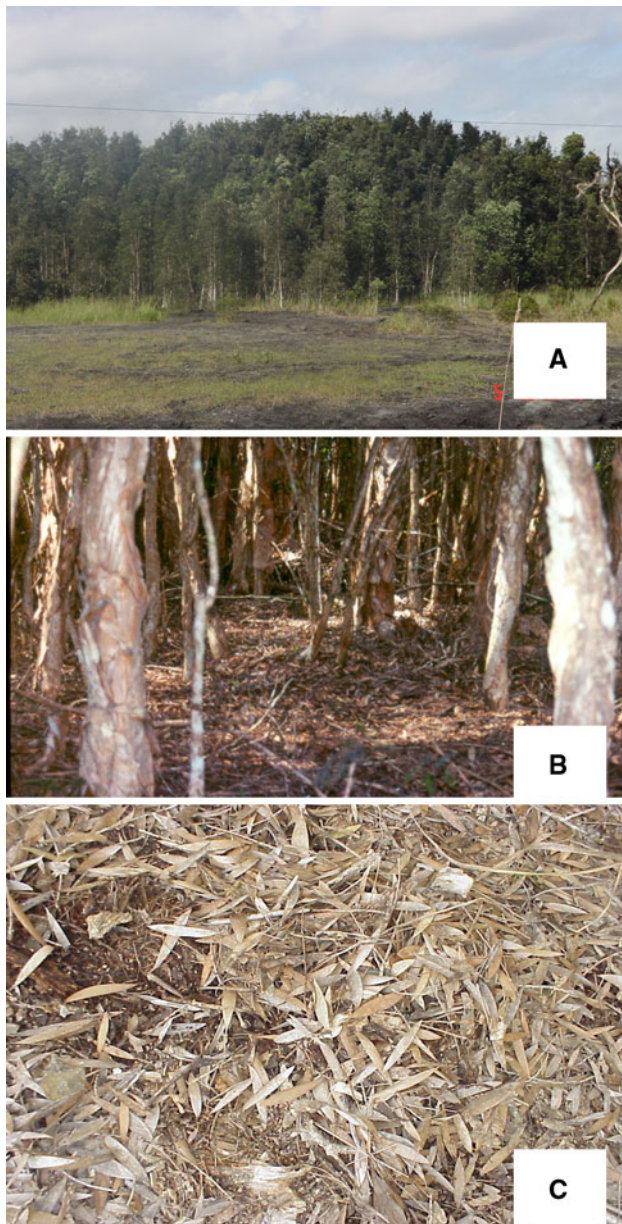


Fig. 1 A typical mature melaleuca stand and a forest floor in south Florida, USA: **a** dome (stretch of melaleuca forest) composed of larger trees at the center and smaller at the invasion front encroaching into a disturbed sawgrass stand; **b** forest floor covered with melaleuca litter biomass accumulated over time; **c** magnified portion of forest floor without understory vegetation, note thick mulch of undecomposed leaf layer (L-fraction) and slightly fragmented litter (F-fraction) layer

9.15 ± 8.84 cm, range 1.0–35.5 cm, and density up to $13,350$ stems ha^{-1}) near the center and gradually tapered toward smaller trees (mean DBH as low as 2.02 ± 1.34 cm, range 1.0–15.1 cm and density up to $69,500$ stems ha^{-1}) at the periphery (see Rayamajhi et al. 2006). Three 0.25-m^2 plots were delineated in each tree-size category by using a corrugated metal frame with a sharp edge.

The metal frame was pressed down into the litter layer, and the biomass (small twigs, leaves, and fruits) was collected within the frame down to the mineralized soil level (Fig. 1). The samples were transported to the laboratory then oven-dried at ca. 70°C to constant weight. The litter biomass from each plot was sorted into an undecomposed L-fraction composed of freshly fallen and unfragmented leaves and twigs ≤ 1.0 cm diameter, and a partially decomposed F-fraction composed of discolored and fragmented litter. The L-fractions were further sorted into melaleuca and other dicotyledonous and monocotyledonous litter fractions.

Leaf and needle mass loss

Sawgrass marshes and pine flat woods communities in Florida are among various habitats that are susceptible to invasion by melaleuca. In addition to soil and vegetation differences described above, sawgrass marshes experience longer hydroperiods when compared to the short hydroperiods of pine flat woods. Within sawgrass marshes, invaded sites may have relatively drier floors due to shorter (non-flooded or seasonally flooded) hydroperiods compared to uninvaded sites where surface soils remain water-saturated year round. An experiment was conducted to quantify mass loss rates of melaleuca leaves at the sawgrass marsh and pine flatwoods sites that were either invaded or devoid of melaleuca. This was done by collecting freshly fallen or senesced melaleuca leaves from the study sites, air-drying them and placing 20 g into each of 144 nylon-mesh pouches (12×12 cm possessing ca 7.1-mm^2 -pore sizes). This reduced to 18.40 ± 0.08 g/pouch final dry weight after oven-drying at 70°C to constant weight. Three randomly selected locations were identified within a melaleuca-invaded and uninvaded area of each community (sawgrass marshes or pine flatwoods). In September 2002, 12 litter pouches were deployed at each of 12 randomly selected locations. In order to quantify the influence of pore size on rates of melaleuca leaf mass loss, an additional 72 nylon-mesh pouches (ca 0.2 mm^2 pore sizes) were each filled with 20 g of air-dried melaleuca leaves. These dried to a final dry weight of 18.40 ± 0.08 g/pouch. They were equally distributed among the three locations within each of the melaleuca-invaded sawgrass marsh and pine flatwoods site described above. Accumulated litter biomass on vegetation floors from ca 1×1 m area of each of the pouch burial locations was removed so that pouches were in direct contact with the mineral soils. Pouches were placed ca. 5–10 cm apart and covered with a nylon net secured with plastic stakes at the four corners. One pouch was removed at 16-wk intervals from each location during 2003–2005 and then once every 52-week until 2008. Naturally accumulated litter was not

removed during periodic harvesting of pouches to minimize disturbance when collecting samples.

A second experiment was designed to quantify mass loss of sawgrass leaves and pine needles within melaleuca-invaded and uninvaded communities as described above. This study was conducted concurrently with the melaleuca study and employed the same methodology except only nylon pouches with 7.1 mm² pores were used. Each of the 72 pouches (12 × 12 cm possessing ca 7.1 mm² pore size) was filled with 20-g air-dried, recently senesced sawgrass leaves that reduced to 19.19 ± 0.04 g/pouch final weight after oven-drying at 70°C to constant dry weight); these pouches were equally distributed among the three melaleuca-invaded and uninvaded sawgrass marsh study locations. Alternatively, each of the 72 pouches was filled with 20-g air-dried, recently senesced slash-pine needles. These reduced to 18.51 ± 0.04 g/pouch final weight after oven-drying at 70°C to constant dry weight; these pouches were equally distributed among the three melaleuca-invaded and uninvaded pine flatwood study locations as described earlier.

For mass loss analyses, a pouch was removed from each of the three melaleuca-invaded and uninvaded sawgrass marsh and pine flatwoods at ca 16-week intervals during 2003–2005 and then once at ca 52-week intervals until 2008. The prolonged interval between harvesting events during the second-half of the study period compared to the first-half was to allow complete exhaustion of the pouched biomass of one of the three test species so as to facilitate comparisons. Litter accumulated on top of pouches during the study period was not removed during harvesting to minimize exposure of the pouches.

Total carbon, nitrogen, and soil characteristics

Total carbon (C) and nitrogen (N) contents were determined for: (1) fully mature melaleuca and sawgrass leaves as well as pine needles freshly collected at the four study sites described above to determine baseline quantity, (2) the decomposing biomass remaining in pouches from each of the 12 sampling periods throughout the study period, and (3) soils samples collected at the end of the study period. Samples 1 and 2 were thoroughly rinsed with tap water to remove mineralized organic materials. Soil samples were collected within 50 cm of each of the 12 pouch locations during the final sampling (December 2008). The surface litter was removed from a 0.25-cm² plot, and the soil was excavated to a depth of 10 cm using a small shovel. Each soil sample was placed in a sealable polythene bag, mixed thoroughly, and transported to the laboratory. Undecomposed roots and other litter were carefully removed, and the remaining soil was refrigerated at 4°C. Foliage, contents of pouches, and a portion of the soil samples were placed in

paper bags and oven-dried at 70°C until they attained a constant dry weight. These samples were ground using a Willey Mill or other grinding devices, passed through 40-mesh screen, and analyzed for percentage C and N using CHN analyzer ((PerkinElmer Series II, CHN/O Analyzer 2400; Norwalk CT 06859). The values obtained for C and N were used to calculate the C/N ratio.

In addition to total C and N, soil samples were tested for pH, moisture content at the time of collection, water-holding capacity, and microbial populations (culturable fungal and bacterial colony forming units, hereafter referred to as “CFUs”). To quantify soil pH, 50 g of each soil sample was suspended in 125 ml of deionized distilled water (DDW), mixed thoroughly by stirring for 10 min, and the pH was measured using a calibrated pH meter (Accumet Basic AB15, Fisher Scientific). Soil moisture content was calculated by comparing recently collected (fresh) soil weights with the dry weights described above. Maximal gravitation water-holding capacity was determined by saturating 200 g of each soil sample (wet weight) with tap water for 24 h and then draining until it ceased to drip for 60 s. Saturated soil samples were then placed in 500-ml glass beakers, dried to constant weight, and subtracted from saturated weights.

Soil microbial populations play an important role in litter decomposition, but identification of each microbial (fungal and bacterial) species was beyond the scope of this study. Therefore, the number of CFUs at each of the 12 mass loss locations was measured by suspending 0.25 g of soil in 9.75 ml of sterile DDW, homogenizing the slurry in a blender for 2 min, and filtering the contents through a 40 × 40-μm-pore nylon cloth. Blenders were thoroughly rinsed with water and 70% EtOH between processing samples. Two hundred and fifty microliters of the homogenized mixture was added to 9.75 ml of the sterile DDW, vortexed thoroughly, and 100 μl was placed at the center of two replicated 8.5-cm-diameter Petri dishes containing full strength potato dextrose agar (PDA). The homogenized soil sample was spread evenly on the plate, incubated at 28°C, and the number of resulting fungal or bacterial colonies was noted every 24 h over a 72-h monitoring period. The total number of CFUs for each sample was used for statistical analysis.

Data analysis

Statistical analyses were performed using the general linear models procedure (PROC GLM) in SAS (1999). We performed analyses of variation (ANOVA) to examine the effects of tree-size classes (independent variables) in the sites on the amount of total litterfall accumulation and its composition (dependent variables) such as melaleuca (stem, leaves, and fruits) versus non-melaleuca (other

dicots and monocots). In order to properly evaluate the mass loss, we calculated the percentages (based on the original dry weight) of mass loss and changes in total C and N, and the C/N ratio of each sample collected was used while performing ANOVA to test the effects of habitat on mass loss and nutrient (C and N) dynamics during the process of mass loss. Percentage data were arcsine transformed for ANOVA and means separations; however, the mean presented is based on the untransformed percentages. The significance of differences in the amount of litter accumulation as well as mass loss and nutritional dynamic mean (\pm SE) habitats or soils types was determined using Waller–Duncan’s multiple range test.

Results

Melaleuca litter accumulation

Melaleuca forest floors, especially within large and intermediate tree-size classes, possessed thick layers of organic materials (Fig. 1). The total amount of accumulated litter biomass increased with the overall tree-size class ($P < 0.0001$); litter accumulation in the large tree-size (25.63 Mg ha^{-1}) class was over two times that of the smaller size (12.27 Mg ha^{-1}) class (Table 1). The accumulated melaleuca litter was proportionally similar between L- and F-fractions within the small tree-size class, but the L-fractions represented the largest amount within the large tree-size class (Table 1). Accumulated non-melaleuca litter biomass was greater among smaller trees at the invasion front compared to that among the larger trees at the center of the melaleuca dome (Table 1). However, the amount of non-melaleuca plant material among all size classes was relatively small compared to melaleuca.

Leaf and needle mass loss

The trend of mass loss of melaleuca leaves in the two habitat/soil types (melaleuca-invaded and uninvaded saw grass marsh and pine flatwoods) is presented in Fig. 2. The loss of melaleuca leaf mass increased over time regardless of soil and vegetation types, although complete (100%) loss was never attained during the 322-week study period. Within this entire period, the main effects of site soil type (i.e., organic and arenaceous soils in marsh and flatwoods respectively), vegetation stand type, sample type (melaleuca leaves, sawgrass leaves, and pine needles), sampling time (temporal), and the interaction term, “soil types*melaleuca-invaded and uninvaded saw grass marsh and pine flatwoods*sample types*sampling time” affected mass loss ($P < 0.00001$). However, litter pouch pore size had no effect ($P = 0.6379$). Because the interaction terms

were significant and we were interested in determining main effects, we further analyzed temporal mass loss data by site, soil, and stand types. When all collection dates within soil types were pooled, the decomposition of melaleuca leaves in arenaceous soils was significantly ($P = 0.0105$) slower ($84.4 \pm 3.8\%$) compared to that in organic soils ($95.0 \pm 1.6\%$). The rate of mass loss for melaleuca leaves varied by dominant vegetation type, i.e., melaleuca-invaded and uninvaded sawgrass marsh and pine flatwoods ($P < 0.0001$). Over the 322-week period, as much as $98.0 \pm 0.7\%$ melaleuca leaf biomass loss occurred in sawgrass marshes invaded by melaleuca when compared to $88.9 \pm 1.0\%$ in melaleuca-uninvaded sawgrass marshes. In pine flatwoods, however, melaleuca litter mass loss was $86.4 \pm 0.0\%$ for uninvaded and $83.8 \pm 5.3\%$ for melaleuca-invaded stands.

Comparative mass loss rates for melaleuca leaves, sawgrass leaves, and pine needles are presented in Figs. 3a–d and 4a–d. The overall effect of species (melaleuca, sawgrass, and pine) on foliage mass loss across habitats was significant ($P = 0.0089$). During the 322-week study period, proportional mass loss was greatest ($100.0 \pm 0.0\%$) for sawgrass leaves compared to that for melaleuca leaves ($91.7 \pm 2.1\%$) and pine needles ($85.3 \pm 2.9\%$); the difference between melaleuca leaves and pine needles was not significant. In melaleuca-invaded sawgrass marsh, the mass losses of melaleuca ($98.0 \pm 0.8\%$) and sawgrass ($100.0 \pm 0.0\%$) after the 322-week period were not significantly different ($P = 0.1133$); however, the difference in mass loss between melaleuca ($88.9 \pm 1.0\%$) and sawgrass ($100 \pm 0.0\%$) in melaleuca-uninvaded sawgrass marsh was significant ($P = 0.0036$). The mass loss of melaleuca ($83.8 \pm 0.0\%$) and pine ($86.7 \pm 0.0\%$) in melaleuca-invaded pine flatwoods, during the 322-week period, was not significantly different ($P = 0.6673$); nor were differences between melaleuca ($86.4 \pm 0.0\%$) and pine ($81.0 \pm 0.0\%$) in uninvaded pine flatwoods (Fig. 4a, b).

The half-life (i.e., 50% mass loss) of melaleuca and sawgrass leaves (as estimated by regression) was ca 91 weeks and 58 weeks in melaleuca-invaded sawgrass marsh (Fig. 3a) and 120 weeks and 70 weeks in uninvaded sawgrass marsh (Fig. 3b). Similarly, half-life of melaleuca leaves and pine needles in melaleuca-invaded pine flatwoods was 106 weeks and 128 weeks (Fig. 4a), respectively, and 127 weeks for foliage of both tree species in uninvaded pine flatwoods (Fig. 4b).

Total nitrogen

Total nitrogen (N) dynamics in the remaining (not mineralized) foliage litter mass is presented in Fig. 5a–d. At the onset, total N concentrations of composite samples of mature foliage were $7.0 \pm 0.0 \text{ mg g}^{-1}$, $7.7 \pm 0.0 \text{ mg g}^{-1}$,

Table 1 Accumulated mean (\pm SE) of litter biomass across non-flooded and seasonally flooded *Melaleuca quinquenervia* invaded sawgrass marshes of south Florida, USA as measured in 1997

Litter components (Mg ha^{-1})	Tree-size plots		
	Small	Intermediate	Large
<i>Melaleuca</i>			
Total litter ^{a,b}	12.27 (± 1.52)b	21.38 (± 1.58)a	25.63 (± 1.46)a
F-fraction ^c	6.22 (± 0.74)b	8.60 (± 0.83)ab	9.71 (± 0.92)a
L-fraction ^c	6.05 (± 1.06)c	12.78 (± 1.11)b	15.92 (± 1.08)a
Stems	1.84 (± 0.84)c	6.08 (± 0.93)b	8.80 (± 0.88)a
Barks	0.072 (± 0.05)c	0.23 (± 0.09)ab	0.45 (± 0.10)a
Leaves	2.90 (± 0.53)b	5.64 (± 0.77)a	5.61 (± 0.42)a
Fruits	0.01 (± 0.00)b	0.11 (± 0.05)ab	0.16 (± 0.03)a
<i>Non-melaleuca (L-fraction)</i>			
Monocotyledons	1.11 (± 0.02)a	0.44 (± 0.11)b	0.01 (± 0.00)c
Dicotyledons	0.12 (± 0.06)b	0.30 (± 0.12)b	0.93 (± 0.31)a

^a Includes partially decomposed (discolored and fragmented) plus undecomposed melaleuca litter comprised of stems (up to 1.0 cm diameter), barks, leaves, and fruits

^b Numbers in the parenthesis represent standard errors of the mean preceding it. Mean within a row represented by the same letter is not significantly different from each other according to Duncan's multiple range test at $P = 0.05$

^c F-fraction = from partially decomposed subsurface layer; L-fraction = from undecomposed surface layer

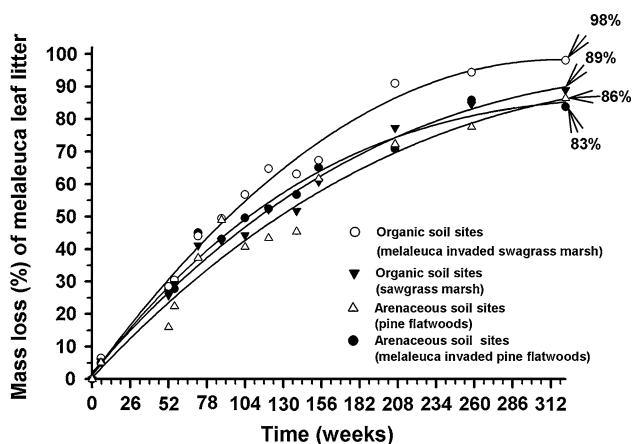


Fig. 2 Melaleuca leaf litter mass loss during 322-week on forest-floor representing two soils (organic and arenaceous) and habitats (sawgrass marshes and pine flatwoods) that included one of the three dominant vegetations (melaleuca, sawgrass, and slash pine) and four sites (melaleuca-invaded sawgrass marsh, melaleuca uninvaded sawgrass marsh, melaleuca-invaded pine flatwoods, and melaleuca uninvaded pine flatwoods) invaded by this invasive tree species. Each data point in the graph is represented by 3 replicated pouches of leaves or needles laid on soil surface of the study sites

and $5.5 \pm 0.0 \text{ mg g}^{-1}$ for melaleuca leaves, pine needles, and sawgrass leaves, respectively (Fig. 5a–d). Sampling times (pouch harvesting time) and sample species (foliage types) and their interaction affected the total nitrogen content of tissues remaining in the pouches ($P < 0.0001$) after the 322-week period. Six weeks after deployment of the litter pouches, the total N concentrations decreased slightly for melaleuca leaves ($6.2 \pm 0.3 \text{ mg g}^{-1}$ and

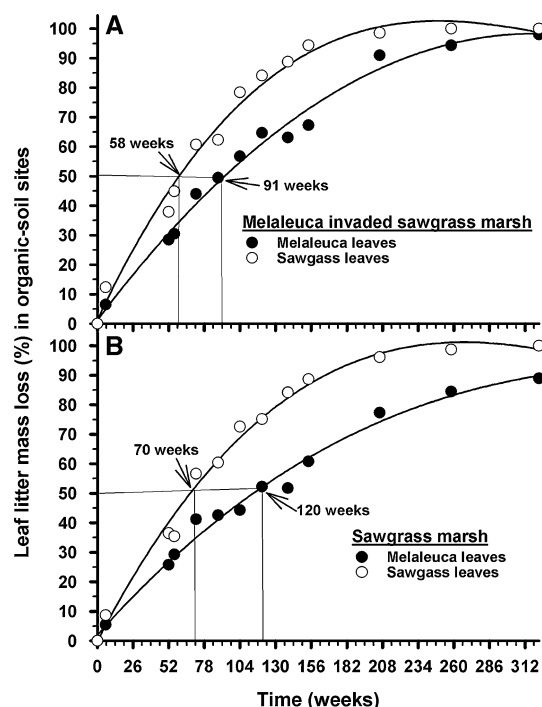


Fig. 3 Comparative foliage litter mass loss trends of melaleuca and sawgrass leaves on the moderately arenaceous organic soils in melaleuca-invaded sawgrass marshes and year round water-saturated soils of melaleuca uninvaded sawgrass marshes. Each data point in the graph is represented by 3 replicated pouches of leaves or needles laid on soil surface of the study sites

$6.5 \pm 0.6 \text{ mg g}^{-1}$ in melaleuca-invaded and uninvaded marshes) and sawgrass leaves ($4.8 \pm 0.0 \text{ mg g}^{-1}$ and $5.1 \pm 0.1 \text{ mg g}^{-1}$ in invaded and uninvaded marshes;

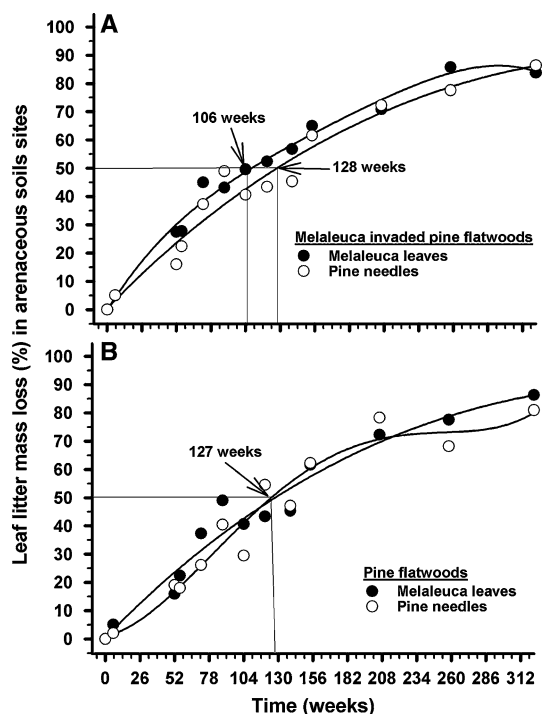


Fig. 4 Comparative leaf litter mass loss trends of melaleuca leaves and pine needles on floors of melaleuca-invaded or uninvaded pine flatwoods grown on edaphic conditions associated with poorly drained lower horizon and predominantly arenaceous surface soils. Each data point in the graph is represented by 3 replicated pouches of leaves or needles laid on soil surface of the study sites

Fig. 5a, b). During the same sampling period, similar reductions in N concentrations were observed for melaleuca leaves in pine flatwoods ($6.8 \pm 0.7 \text{ mg g}^{-1}$ and $5.1 \pm 0.3 \text{ mg g}^{-1}$ in melaleuca-invaded and uninvaded areas). However, the total N in both melaleuca-invaded and uninvaded pine flatwoods decreased precipitously for pine needles to $2.9 \pm 0.2 \text{ mg g}^{-1}$ during the first 6-week sampling period; Fig. 5c, d). During later sampling periods, the total N increased consistently for the remaining of melaleuca, sawgrass, and pine foliage samples (Fig. 5a–d).

Carbon/nitrogen status

Trends in total C concentration and C/N ratio in samples over the study period are presented in Fig. 6a–d. Carbon concentrations in composite samples of recently fallen leaves were 466.0 mg g^{-1} for melaleuca leaves, 448.0 mg g^{-1} for sawgrass leaves, and 511.0 mg g^{-1} for pine needles. In general, total C concentrations in decomposing melaleuca and sawgrass leaf litter fluctuated over time and decreased slightly toward the end of the 322-week study period regardless of soil types and vegetation where the pouches were located. The reduction in C concentration over time was more pronounced for pine needles when compared to that for other species (Fig. 6a–d). Six weeks

after deployment of litter pouches, the C/N ratio for melaleuca leaves increased to 81.7 ± 3.2 , 79.7 ± 5.5 , 100 ± 4.0 , and 75.3 ± 8.1 at the melaleuca-invaded sawgrass marsh, melaleuca-uninvaded sawgrass marsh, melaleuca-invaded pine flatwood, and melaleuca-uninvaded pine flatwood sites, respectively (Fig. 6a–d). Subsequently, the C/N ratio of decomposing melaleuca leaves followed a consistently declining trend during the remaining 304-week study period (Fig. 6a–d). The C/N ratio of decomposing sawgrass leaves increased to 93.0 ± 0.6 and 89.3 ± 0.9 in invaded and uninvaded sawgrass marsh sites, respectively, during the first 6-week sampling period and then decreased to 21.0 ± 2.0 for both marsh locations at the end of the 322-week study period (Fig. 6a, b). Similarly, the C/N ratio of decomposing pine needles increased to 174.4 ± 8.6 and 180.0 ± 19.9 in melaleuca-invaded and uninvaded pine flatwoods at the first 6-week and then steadily decreased to 37.3 ± 2.4 and 36.0 ± 0.0 , respectively at the end of the 322-week study period (Fig. 6a, b).

Edaphic conditions at the sites

Not surprisingly, physical and chemical properties of soil samples varied by site (Table 2). The organic soil of the sawgrass and melaleuca stand was slightly alkaline when compared to the arenaceous soils of the pine flatwoods that were slightly acidic (Table 2). The water-holding capacity of soils was in the following order: uninvaded sawgrass marsh > invaded marsh > invaded pine flatwood > uninvaded pine. Moisture content (%) of the soils collected at the end of 322-week study period in December 2008 showed similar trends. Additionally, organically rich soils in the melaleuca-invaded and uninvaded sawgrass marsh contained significantly higher levels of total C and N compared to those in the pine flatwood sites. However, the overall C/N ratio was greater for pine flatwoods versus sawgrass marsh sites (Table 2).

Soil microbial attributes

Culturable microbes within mass loss samples and soils directly adjacent to the sample locations are presented in Table 3. Overall, the number of CFUs g^{-1} of soil was greater for bacterial versus fungal populations. Similarly, the bacterial populations in adjacent soils were more numerous than that within decomposing melaleuca, sawgrass, or pine pouches across all locations. The number of CFUs g^{-1} was similar for foliage of both species (e.g., melaleuca and sawgrass, and melaleuca and pine) within organically rich or arenaceous soil types (Table 3). When compared between soils, the sawgrass marsh, with soils high in organic matter, supported relatively more bacterial

Fig. 5 Changes in the total nitrogen (N) concentrations (mg g^{-1}) in the decomposing samples of three plant species: **a** melaleuca and sawgrass leaves on floors of mature melaleuca stands; **b** melaleuca and sawgrass leaves on floors of sawgrass stands; **c** melaleuca and pine needles on the floors of mature melaleuca (invaded) stands in pine flatwoods; **d** melaleuca and pine needles on the floors of melaleuca uninvaded mature pine-tree stands. Each data point in the graph is represented by 3 replicated pouches of leaves or needles laid on soil surface of the study sites

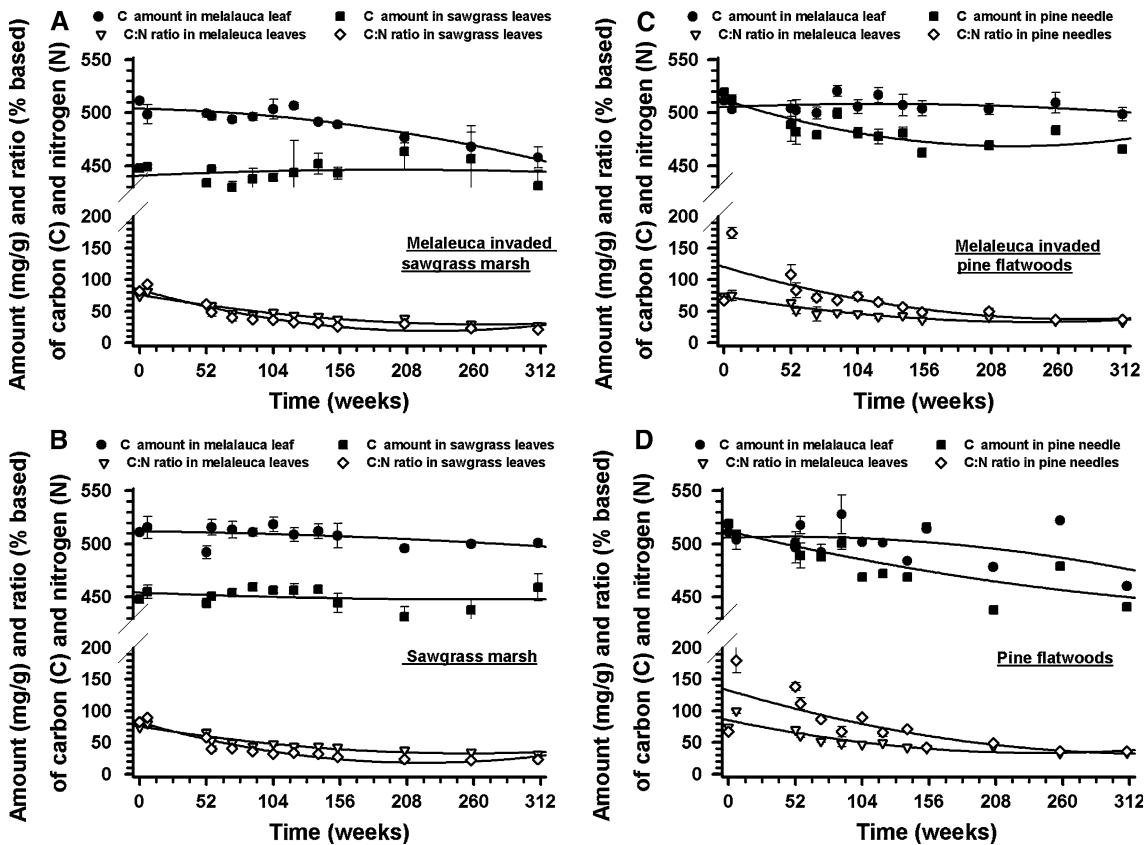
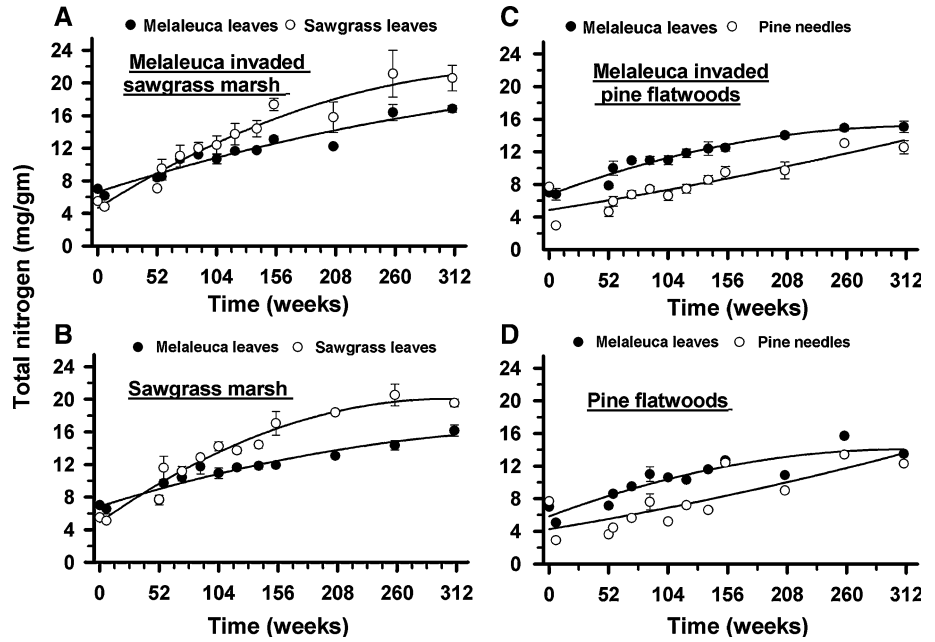


Fig. 6 Changes in the total C concentrations (mg g^{-1}) and C/N ratio in the decomposing samples of three plant species: **a** melaleuca and sawgrass leaves on floors of mature melaleuca (invaded) sawgrass marsh; **b** melaleuca and sawgrass leaves on floors of melaleuca uninvaded sawgrass marsh; **c** melaleuca and pine needles on the floors

of mature melaleuca (invaded) pine flatwoods; **d** melaleuca and pine needles on the floors of melaleuca uninvaded slash-pine stands (pine flatwood). Each data point in the graph is represented by 3 replicated pouches of leaves or needles laid on soil surface of the study sites

Table 2 General properties of composite soil samples in top 10-cm surface horizon near litter pouches deployed spots in litter mass loss study sites

Properties	Sawgrass marsh ^a		Pine flatwoods	
	Mel-invaded ^b	Mel-uninvaded	Mel-invaded	Mel-uninvaded
Soil type	Organic	Organic	Arenaceous	Arenaceous
pH	7.73 (± 0.12)a	7.13 (± 0.13)a	6.03 (± 0.03)b	5.33 (± 0.35)c
Water-holding capacity (%) ^c	512.67 (± 41.37)b	651.93 (± 26.93)a	65.90 (± 13.65)c	46.93 (± 7.04)c
Total carbon (mg/gm)	407.40 (± 9.85)a	420.23 (± 4.70)a	51.30 (± 12.91)b	42.00 (± 9.15)b
Total nitrogen (mg/gm)	27.33 (± 2.46)a	31.70 (± 1.42)a	2.53 (± 0.61)b	2.03 (± 0.33)b
Carbon/nitrogen (C/N ratio)	15.07 (± 1.01)b	13.30 (± 0.46)b	20.03 (± 1.71)a	20.43 (± 1.80)a

^a Numbers in the parenthesis represent standard errors (\pm SE) of the mean preceding it. Mean within a row represented by the same letter is not significantly different from each other according to Duncan's multiple range test at $P = 0.05$

^b "Mel-" = Melaleuca

^c Percentage of water (by weight) held by fully saturated samples in relation to its oven-dried constant weight of the same sample

Table 3 Mean (\pm SE) colony forming units (CFU) of microbial organisms isolated from the last collection of decomposing litters contained in the pouches

Habitat/stands/samples	CFUs (millions gm^{-1} of sample) ^a	
	Bacterial	Fungal
<i>Sawgrass marsh</i>		
Melaleuca invaded		
Melaleuca	39.1 (± 7.9)a	0.4 (± 0.3)a
Sawgrass	40.1 (± 24.7)a	2.8 (± 1.4)a
Melaleuca uninvaded		
Melaleuca	33.2 (± 14.4)a	1.4 (± 0.7)b
Sawgrass	39.7 (± 2.1)a	6.6 (± 0.8)a
<i>Pine flatwoods</i>		
Melaleuca invaded		
Melaleuca	53.9 (± 37.4)a	1.1 (± 0.5)a
Pine	16.9 (± 0.0)a	2.3 (± 0.0)a
Melaleuca uninvaded		
Melaleuca	54.8 (± 22.2)a	1.2 (± 0.5)a
Pine	20.8 (± 0.0)a	1.5 (± 0.0)a

^a Numbers in the parenthesis represent standard errors (STDERR) of the mean preceding it. Two means of a leaf type in two stands presented in a column within a given habitat that are represented by the same letter are not significantly different from each other according to Duncan's multiple range test at $P = 0.05$

and fungal CFUs than did the arenaceous soils of the pine flatwoods (Table 3).

Discussion

Accumulation and mass loss of melaleuca litter

Melaleuca litterfall production in nearly pure monocultures (in Florida) varied among habitats and hydrological conditions of the sites. For example, seasonally flooded habitats

had the most litterfall (compared to non-flooded and permanently flooded), wherein small-, intermediate-, and large-tree stands generated 6.62, 8.82, and 11.28 $\text{Mg ha}^{-1} \text{ year}^{-1}$, respectively (Rayamajhi et al. 2006). The amount of total litter mass that accumulated on the forest floors as determined herein followed trends reported above for litter production. The proportion of partially decomposed litter was also greater in large- versus small tree-size classes, indicating that the rate of melaleuca litter decomposition was slower in stands composed of large when compared to that in small melaleuca trees.

Litter decomposition is a function of various biotic and abiotic factors and the litter quality produced by dominant plant species. The physical and chemical nature of litter, for example, influences rates of litter decomposition under similar abiotic conditions (Berg et al. 1993; Fioretto et al. 1998; Preston et al. 2000; Kang et al. 2009). Abiotic factors likely to affect litter decomposition in wetland environments include availability of oxygen, soil or water pH, temperature, and availability of inorganic nutrients for decomposing organisms (Qualls and Richardson 2000). Generally, water-holding capacity of 20–70% (based on soil particle size) facilitates soil microbial growth, but anaerobic forms of organic matter degradation become more dominant as soil saturation levels increase (King et al. 1998). Herein, the water-holding capacity (weight by weight basis) of soils at the sawgrass marsh site exceeded 600% and at the melaleuca-invaded areas exceeded 500%. Due to long-term accretion of litter, however, melaleuca-invaded sawgrass marshes in our study sites were only occasionally flooded (a few days at a time during heavy rainstorms), while sawgrass stands were constantly saturated throughout the year and were more anaerobic than melaleuca stands. Conversely, arenaceous soils at the pine flatwoods site were relatively moisture deficient (19–21% moisture in December 2008) with up to a 10-fold less

water-holding capacity compared to the organically rich soils at the sawgrass marsh site (47–66% moisture). The pH levels of the organic soils in both melaleuca-uninvaded and invaded sawgrass marshes were more alkaline compared to those arenaceous soils of invaded and uninvaded pine flatwoods. However, these surface soil conditions in organic and arenaceous soils in our study did not affect microbial populations. Nevertheless, combinations of one or more of these attributes may have contributed to the slower rate of melaleuca leaf litter mass loss in acidic arenaceous soils than in organic soils. This is supported by previous reports (Qualls and Richardson 2000) which emphasize slower rates of litter decomposition in acidic soils since pH values below 5 can inhibit decomposition. Additionally, lack of adequate moisture in the arenaceous soils could be another factor contributing to the slower decomposition rate; similar patterns of moisture-dependent reduced decomposition rates have been reported for other plant foliages (Reddy and Patrick 1975; Singh et al. 1999). Within organic soils, melaleuca mass loss was higher in melaleuca-invaded sawgrass marsh than that in uninvaded sawgrass marshes marked by relatively longer hydroperiods. In this case, soil pH was similarly alkaline in both melaleuca and sawgrass stands. Therefore, the reduced rate of melaleuca litter mass loss in sawgrass stands may be attributed to relatively longer anaerobic conditions caused by the constant water-saturation compared to occasional flooding in melaleuca-invaded stands.

During the first third of our 322-week study, the rates of mass loss (50% of total deployed dry weight) of melaleuca leaves exceed that of *Eucalyptus marginata* Donn. ex. Sm. (Myrtaceae) with 44% in 80 weeks (O'Connell 1986) and beech *Fagus sylvatica* L. (Fagaceae) with 35% at 104 weeks (Lorenz et al. 2004). As reported (Staaf and Berg 1982; Lorenz et al. 2004) for other systems, accelerated rates of mass loss during early decomposition phases in melaleuca, sawgrass, and pine foliage in our study may also be attributed to leaching of water soluble phenolics, tannins, sugars, and nitrogenous compounds.

Comparative litter mass loss

Plant foliar litter decomposition and hence mass loss rates differ among functional groups, genera, and species (Dutta and Agrawal 2001; Kang et al. 2009). One would logically assume that the rate of litter mass loss for a given species will be higher in its native habitat due to adaptation to prevailing biological in addition to physical and chemical environments such as temperature, edaphic, and hydrological site conditions (Zhang et al. 2008). In our study, both site and plant-species attributes influenced the rate of mass loss. Overall rates of mass loss to decomposition in our 6-year study revealed the following order: sawgrass

leaves > both melaleuca leaves and pine needles. Based on the regression trends, mass loss of sawgrass leaves in invaded or uninvaded sawgrass marsh occurred faster than the melaleuca leaves in the same sawgrass marsh. Acceleration of mass loss in sawgrass leaves has been reported to occur in early, more nutrient-limited stages of decomposition (Qualls and Richardson 2000). Reeder and Davis (1983) estimated ca 1.1% week⁻¹ (average 1.43/5.0 g in 6-month study period) mass loss for sawgrass leaves in well-aerated nutrient-enriched sawgrass stands in Broward County, Florida. In our study, complete sawgrass mass loss occurred ca 1 year earlier in invaded sawgrass marshes than in uninvaded sawgrass marshes. Though melaleuca mass loss was similar to sawgrass, there to 14% of undecomposed leaf biomass remained after 6 years. This revealed that leaf quality (sawgrass vs. melaleuca) and inherent environmental conditions such as better aeration in surface soils can influence the rate of leaf mass loss. Overall, faster mass loss of sawgrass leaves may partially be attributed to less resistance to microbial colonization of sawgrass leaf tissues (Reeder and Davis 1983). This may relate to lesser anatomical and chemical defense mechanisms compared to melaleuca which is known to contain various terpenoids (Wheeler et al. 2007). Some of these compounds with antimicrobial properties (Boon and Johnstone 1997) may have initially interfered with microbial colonization of melaleuca leaf tissues as reported by Hammer et al. (2006).

C/N status during mass loss

The litter mass loss process involves initial fast rates of mass loss involving the loss of water-soluble simple sugars and nitrogenous compounds that lead to the second step marked by much slower and complex degradation and mineralization processes involving other complex compounds (Berg and Staaf 1980; Melillo et al. 1989). This is corroborated by our findings in which major portion of total N in the pouched materials of all three species was lost within 6 weeks of placement of samples on the ground, being least in sawgrass and highest in pine needles; similar loss of N at the initial phase of decomposition has also been reported in broad-leaved and conifer leaf litter from northwestern Wisconsin (Bockheim et al. 1991). After the 6-week period, the total N concentrations in the remaining fractions of the samples of all three plant species increased steadily (compared to the original concentrations at the time of the placement of samples in the respective study sites) during the study period but at different rates; the least and highest being in pine needles and sawgrass leaves, respectively. These data showed highest levels of immobilization of total N in sawgrass leaves. Up to a fourfold increase in total N concentrations (compared to original

concentrations in respective samples) in the remainder of the samples in organic soils may have occurred from the humic soils. This may occur through passive (to establish equilibrium with the soils in the area) as well as active (through microbial activities) means since the surrounding humic soils had up to 31.7 mg g^{-1} of total N.

Increased N concentrations in decomposing melaleuca leaf and pine needle samples must have occurred against the concentration gradient with the help of colonizing microbes since total N in the arenaceous soils of the site was far less ($2.0\text{--}2.5 \text{ mg g}^{-1}$ in the soils adjacent to samples vs. up to 12.6 mg g^{-1} in pine needle and 15.1 mg g^{-1} in melaleuca leaf samples). Absorption of N by fungi from surrounding soils and subsequent incorporation into decomposing leaf litter has been reported by Berg (1988) and Choonsig (2003). Despite a slight drop in total N at the initial stage of the decomposition process, a substantial increase in its concentration at later phases, e.g., up to threefold (compared to original concentration) over extended period of time due primarily to the migration from surrounding substrates has also been noted in other systems (Staaf and Berg 1982; Twilley et al. 1986; Berg 1988; Melillo et al. 1989; Lorenz et al. 2004; Dubeux et al. 2006).

Leaf litter quality and its rate of decomposition is partly related to C/N (Berg 1988); change in the concentration of one of these two elements in litter will influence their overall ratio. In our study, the amount of total C in the remaining portion of decomposing leaf litters of melaleuca leaves, sawgrass leaves, and pine needles did not fluctuate remarkably, and this occurrence is similar to those reported by Lorenz et al. (2004) in beech, oak, cherry, and pine foliage, and Qualls and Richardson (2000) in sawgrass leaves.

A few studies have shown increased N concentrations in the fresh leaf litter to accelerate the rate of litter decomposition (Tateno et al. 2007); this may be true only during the process of cellulose decomposition, especially if the leaves are N deficient (Berg 1988). Our findings corroborate these reports since the freshly harvested undecomposed sawgrass leaf litter (compared to melaleuca and pine) with the least N concentration had the fastest decomposition rate due to increased N concentration during the later phase of the decomposition process. Additional confounding factors that control leaf litter decomposition rates are also being reported. For example, many studies have shown initial decreases in C/N ratios in decomposing litter due to leaching of soluble forms of N during the first few weeks followed by a steady increase in total N during the remainder of the decomposing process; such decreases in C/N ratio have been linked to the increased N concentrations in the tissues from surrounding environments (Staaf and Berg 1982; Berg 1988; Melillo

et al. 1989; Chabbi and Rumpel 2004; Lorenz et al. 2004; Dubeux et al. 2006). We have recorded similar phenomena in which the C/N ratio increased slightly during the first 6 weeks than steadily decreased in all three types of leaf tissues during the latter period; however, the concentrations differed among species, e.g., lowest (21) in sawgrass, intermediate (average 31) in melaleuca, and highest (average 37) in pine needles at the end of 322-week study period. In general, the C/N ratio of 20–30 is considered favorable for net mineralization of litter biomass (Kavvasias et al. 2001; Dubeux et al. 2006). In general, the C/N ratio of melaleuca leaves was >30 in organic soils until 258-week and >35 in arenaceous soils at the end of 322-week study period. Similarly, slash-pine needles had a C/N ratio >36 even at the end of the 322 weeks. On the contrary, the C/N ratio of sawgrass leaves in organic soils dropped below 30 within 154 weeks. This accelerated reduction in C/N ratio has been implied to result in higher rates of mass loss of sawgrass leaves compared to that of melaleuca leaves and pine needles. The general ranking of litter decomposition rates: sawgrass $>$ melaleuca and pine agrees with the C/N ratio: sawgrass $<$ melaleuca and pine needles. When only melaleuca leaf litters are compared, decomposition was faster in relatively drier organic soils of invaded sawgrass marshes than in uninvaded sawgrass or arenaceous soils in invaded or uninvaded pine flatwoods. These outcomes highlight C/N ratio as an important driving force in litter decomposition. The decreasing trend in C/N ratio in decomposing leaf and needle samples of all three sympatric plant species in our study across four sites may be attributed to the net gain of total N from the surrounding soils through active and/or passive means of immobilization as described in Choonsig (2003) for other plant systems.

As decomposition proceeds, the litters become enriched with N and lignin (Berg and Staaf 1980) as the un-shield cellulose disappears (Berg 2000). Lignin and N concentrations in the remaining litter increase during the later phase of decomposition (Crawford 1981; Zhang et al. 2008). This results in slower litter mineralization since some of the cellulose at the late stage remained shielded by lignin (Berg 2000; Zhang et al. 2008). Lignin being a complex polymer of water-insoluble highly complex C compounds breaks down to smaller molecules by the enzymatic activities of the fungal and bacterial organisms through an oxidation process; the production of this lignolytic enzyme in microbes is repressed by high concentrations of low molecular nitrogenous compounds such as ammonia and nitrates (Crawford 1981; Berg 2000). Therefore, any nitrogen bound to smaller molecules will inhibit the lignolytic activities of the white rot fungus that breaks down and exposes cellulose for further break down into elements. Therefore, combinations of good aeration

and optimum N concentration in the litter fragments will be required for faster mass loss in leaf litter during the later phase. In our study, relatively more anaerobic environments in sawgrass appeared less conducive for melaleuca foliage decomposition for three reasons: (1) increased N concentration, (2) C/N ratio higher than 30 during the later phase, and (3) presumably more lignified tissues compared to sawgrass which is known to have more cellulose (ca 30%) and less lignin (20%) in its tissues (Reeder and Davis 1983). This provided additional assumptions why the rate of decomposition of melaleuca leaves and pine needles is more resistant to decomposition and mass loss compared to sawgrass leaves. Also, in anaerobic environments of sawgrass stands most of the N may have been in the form of ammonia or nitrate both of which are known to repress lignolytic activities of the microbes. Such phenomena may contribute to the slow decomposition and rapid accumulation of melaleuca leaf litter.

High rate of litter decomposition has been implied not only to the efficient mineral recycling in a system but also to the availability of bare soil for plant colonization, especially during the later stages of decomposition that may affect species richness and diversity (Xiong and Nilsson 1997, 1999). The slower decomposition of melaleuca leaves in invaded sawgrass marshes results in thick layers of melaleuca litter which may impede sawgrass seedling recruitment. On the other hand, sawgrass will tend to cede space to melaleuca since its rate of mineralization is ca 50% faster; this makes sawgrass marshes vulnerable to invasion by exotics species like melaleuca. Based on the decomposition rate, pine litter may accrue at a pace similar to melaleuca. However, forest fires are frequent in pine forests and can reduce litter thereby minimizing adverse effects on recruitment of other species (Williams and Wardle 2007); due to seasonal flooding and poorly drained lower horizons of soils the slash-pine dominated forests in our study were vulnerable to invasion by melaleuca.

Conclusion and implication

The amount of melaleuca litter biomass accumulation on forest floor as of 1997 was highest (up to 25.63 Mg ha⁻¹) in largest-tree stands. Comparative litter mass loss due to decomposition processes in melaleuca and sawgrass leaves, and pine needles was faster during the initial one-third to three-fifth duration of the 322-week study period; afterward the rate slowed substantially for the remainder of the study especially for melaleuca leaves and pine needles. Organic soils with higher water-holding capacity and moderate alkalinity with better aeration supported faster mass loss of melaleuca leaf litter compared to the arenaceous soils with moderate acidity and relatively lower water-holding capacity. Complete mass loss of sawgrass leaves occurred

faster than melaleuca leaves or slash-pine needles. Total C concentration in three types of leaf litter remained relatively unaffected, whereas total N decreased slightly during the early stages of the experimental period then steadily doubled in melaleuca and pine and quadrupled in sawgrass. This caused significant declines in C/N ratios in decomposing sawgrass leaves compared to melaleuca leaves and pine needles. Overall sawgrass leaves decomposed more rapidly than melaleuca leaves and pine needles. Sawgrass leaves decomposed at the fastest pace in both sawgrass and melaleuca stands, while melaleuca leaves and pine needles showed similar decomposition rates in arenaceous surface soils with poorly drained lower horizons in pine flatwood areas. Sawgrass leaves with relatively faster mass loss rates are likely to be susceptible to invasion by exotics like melaleuca with slower rates of litter decomposition. On the other hand, pine flatwoods with poorly drained sandy soils are also less resistant to melaleuca invasion especially since frequent forest fires consume pine litter and prepare the seed bed.

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