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Temporal and structural effects of stands on litter production in *Melaleuca quinquenervia* dominated wetlands of south Florida

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Abstract

Melaleuca quinquenervia dominates large areas of the Florida Everglades in the southeastern USA where it has transformed sedge-dominated marshes into melaleuca forests. Despite its prevalence, very little is known about the ecology and stand dynamics of this invasive tree. We delineated large-, intermediate-, and small-tree stands in non-flooded, seasonally flooded and permanently flooded areas of Florida in 1997, measured their biological attributes, and then quantified litterfall components for 3–4 year periods. Melaleuca wood components and mature seed-capsules comprised the largest and the smallest portions of aboveground biomass, respectively, while leaves, fine stems, mature fruits, bud scales, floral structures, and residues represented decreasingly smaller fractions of the litter during the succeeding year. Dry weight proportion of leaves in litter was greatest (80.9%) in non-flooded and least (69.1%) in permanently flooded habitats. It was also greatest in small (85.6%) and least in large (64.7%) tree stands. Reproductive structures and mature-fruit fractions in litter were highest in large-tree stands whereas the bud-scale fraction showed no relationship to tree size. Seasonally flooded habitats had the most litterfall, wherein small-, intermediate-, and large-tree stands generated 0.662, 0.882, and 1.128 kg m^{-2} yr^{-1}, respectively. Dry weight of stems, leaves, bud–scales, floral structures, and mature fruit fractions in litter increased as the predominant size of the trees in the stand increased. Total annual litter production was highest during 1999–2000. Leaf fall occurred year-round with maximal amount during April, July, and October. Highest amounts of bud scales and floral structures fell during October–January, which corresponded with flushes of vegetative growth and major flowering events. Overall, melaleuca alone accounted for nearly 99% of the total litterfall dry weight in all habitats and months sampled. The amount of non-melaleuca litter was greater in small-tree stands than in intermediate- or large-tree stands. Litterfall data of this nature will be helpful in detecting changes occurring in melaleuca canopies in response to biological control impact and in prescribing site-specific management strategies.

Introduction

Melaleuca quinquenervia (Cav.) Blake (henceforth referred to as ‘melaleuca’) was introduced into south Florida, USA, during the late 1800s to early 1900s (Gifford 1937; Meskimen 1962). It then rapidly invaded wetlands and other native plant communities (Hofstetter 1991; Bodle et al. 1994).

Melaleuca stands often appear as 'domes' with larger founder trees near the center, tapering progressively towards smaller trees at the periphery. Saplings and seedlings in the interior of these stands experience intense intraspecific competition, as compared to the stand periphery where they compete with native vegetation as they invade surrounding areas. Tree densities vary from 132,000 stems ha^{-1} for saplings to under 5000 stems ha^{-1} for mature trees (Hofstetter 1991; Rayachhetry et al. 2001). Immature melaleuca stands form thickets of seedlings or saplings, whereas advanced stages consist of monocultures of up to 25-m tall dominant and co-dominant trees that produce continuous upper canopies with understories comprised almost entirely of smaller, suppressed trees.

The structure and dynamics of melaleuca-invaded systems change over time (O'Hare and Dalrymple 1997) as marshes become transformed into melaleuca-swamp forests (White 1994). The mechanisms of melaleuca invasion and the associated loss of biodiversity in invaded sites have been discussed in various reports (Woodall 1981, 1983; Myers, 1975, 1983, 1984; Lockhart et al. 1999). However, the aspects of melaleuca invasion, related to alteration of topography by soil accretion resulting from the accumulation of litter (White 1994), the build-up of root mass, and interception as well as retention of detritus inside stands and at invasion fronts are poorly understood.

The need to manage melaleuca invasions in order to reduce deleterious impacts to south Florida wetlands was recognized decades ago and the search and deployment of biological agents was proposed as a part of integrated approach (Bodle et al. 1994). Biological control agents influence overall tree health by removing or damaging root, stem, leaf, and reproductive tissues. Repeated foliage removal by biological control agents will force trees to divert stored energy towards production of new foliage and maintenance of life-sustaining activities. This will deplete stored energy and result in decreased flower or fruit production over time, thus predisposing melaleuca trees to native microbes and arthropods that otherwise would not be as effective. This logic led to the screening and release of two biological control agents, a weevil (Center et al. 2000) and a psyllid (Wineriter et al. 2003). However, many variables such as stand structures (related to tree sizes and densities) and hydrologic conditions of sites may alter the performance of these and other biological control agents, and such alterations may be reflected in the quantity (absolute amount) and quality (proportions in relation to total amount) of litter components (leaves, stems, buds, flowers, fruit capsules and seeds). Therefore, litterfall data collected and analyzed prior to the realized impact of biological control agents could provide an indirect but non-destructive mean of gauging biological control successes. In this regard, Lonsdale (1988) has demonstrated the utility of litterfall measurements before and after the deployment of biological control agents to assess their impacts on *Mimosa pigra* L. populations in Australia.

Despite its occurrence in many parts of the world (Holliday 1989), only limited short-term litterfall data (Finlayson et al. 1993; Greenway 1994; Van et al. 2002) are available for melaleuca, and these data do not address variations in litter production among differently structured stands within various hydrologic regimes. Therefore, we elaborated upon Lonsdale's (1988) approach by including hydrological and tree size categories in our litterfall studies to account for variations due to stand structure within and among habitats. Herein, we compared rates of litter throughfall and proportions of litterfall components among portions of tree-size stands delineated according to the predominant size of the trees in three hydrologically distinct melaleuca habitats. This is part of a larger, ongoing study focused on understanding the ecology and dynamics of *Melaleuca*-dominated wetlands in south Florida.

Materials and methods

Physical characteristics of study site

Description of soil types and hydrological characteristics of the research sites presented herein are in accordance with the descriptions of Brown et al. (1991) and Kushlan (1991) for other systems in south Florida. Sites designated as 'non-flooded' may be inundated intermittently for a few hours to several days during or following periods of heavy rain but are not continuously flooded nor flooded every year (hence not seasonally flooded). Sites designated as 'seasonally flooded' remain inundated for variable periods every year, and 'permanently flooded' sites remain flooded year-round. Soils in all study areas are dominated by poorly drained organic 'muck', and are generally classified as Histosols (Brown et al. 1991)

South Florida experiences a humid subtropical climate with the average monthly temperatures ranging from ca. 19 °C in January to 28 °C in August–September, and rainfall averages range from about 3 cm in January to 27 cm in September (Chen and Gerber 1991). Melaleuca stands occur in and around fresh water marshes often associated with the Florida Everglades (Kushlan 1991). Surface water depths fluctuate in accordance with this wet-dry seasonality (Kushlan 1991).

Plot establishment

Based on empirical observations of several sites throughout melaleuca distribution range, two melaleuca forests (composed of uneven-sized trees) were selected from each of three hydrological regimes (hereafter referred to as "habitats"): non-flooded, seasonally flooded, and permanently flooded habitats in southeastern Florida. These forests form characteristic 'domes' with predominantly large trees near the center and gradually tapering towards smaller trees and saplings near the edges. One dome (hereafter referred as a "site") in each of the two forests was divided into three sections (hereafter referred to as "small", "intermediate", and "large" tree stands) based upon the prevalent tree size. Two permanent plots (10 m × 10 m for the large and intermediate, and 5 m × 5 m for small tree stands) were established in each section of the two sites within each of the three habitats (2 plots × 2 sites × 3 habitats = 12 plots).

All woody species and prominent monocotyledonous species within each plot were recorded to determine plant biodiversity at the onset of the study. Stem density, tree diameters, soil types, and general hydrological attributes of delineated plots were also determined at the onset of the study. All melaleuca and non-melaleuca plants $\leq$1.3 m high were considered capable of contributing to litterfall in our experiments. These were counted and their diameters at breast height (dbh) were measured. Average stem density, dbh, and basal area coverage were calculated for each plot in each of the two sites within non-flooded, seasonally flooded, and permanently flooded habitats.

Total aboveground biomass of melaleuca and its allocation into wood, leaves, and reproductive fractions for trees $\leq$1-cm dbh (1.3 m above tree base) in permanent plots were estimated in June 1997 using allometric equations previously generated from same or nearby stands (Rayachhetry et al. 2001). Dry weights of individual trees were summed to estimate live aboveground biomass within each plot.

Litterfall and tree phenology

Two litterfall collection traps were randomly placed in each plot, so each habitat contained 24 traps (2 plots × 3 tree size categories × 2 sites × 2 traps per plot). These consisted of square wooden frames (0.5 × 0.5 m) with 16-cm high sides, and copper wire screened bottoms (2-mm mesh) to provide drainage. The traps were raised 70-cm above the forest floor in non-flooded and seasonally flooded sites on wooden legs mounted at each corner to minimize litter decomposition between collections. Water levels in permanently flooded sites fluctuated from 0.3 to 1.3 m. The traps were therefore modified to float at least 10 cm above the water surface by mounting a capped 3.8-liter plastic jar under each of the four corners of the supporting frame and tying them loosely to a nearby tree to secure them in place. The traps in all plots were emptied at monthly intervals from July 1997 to June 2001 in non-flooded and seasonally flooded sites. Collections terminated after 3 years (June 2000) in permanently flooded habitats as a fire swept through the plots destroying trees and litter traps.

Litterfall samples were oven-dried at ca. 70 °C to constant weight and separated into melaleuca and non-melaleuca fractions. The melaleuca fraction was further sorted into leaves, fine woody materials ($\leq$1-cm diameter twigs and bark fragments), bracts of floral and vegetative buds, flower parts, immature and mature fruits, and residues (insect frass, minute plant fragments, and dirt particles). Non-discernable bracts (floral and vegetative) were included in the bud scale fraction.

Stamens and prematurely abscised hypanthia (henceforth referred to as "immature seed-capsules" or "immature fruits") were sorted separately but together comprised the floral fraction. Reproductive buds, identifiable stamens and carpels, and immature fruits were considered floral structures. The majority of the mature seed capsules (henceforth referred to as "mature fruit") had shed their seeds. All fractions were weighed to the nearest 0.001 g. Large branches (>1 cm diameter) that occasionally fell on the traps were excluded. Melaleuca growth and flowering phenology was ascertained from examination of litter components coupled with visual monthly field observations.

Data analysis

Aboveground biomass and litterfall data were analyzed using SAS (SAS 1999) and visualized graphically using (SigmaPlot 2001). Effects of habitats, months, and tree-size categories on litterfall components were analyzed using repeated measures analysis of variance (ANOVA). The Huynn-Feldt adjustment was used when the covariance data matrix did not meet the assumption of sphericity (von Ende 1993). Means and standard errors of dbh and basal area coverage were determined. Means separations were accomplished using Waller–Duncan Multiple Range test procedure.

Results

Stand attributes

The biophysical characteristics of the stands in the study areas are presented in Table 1. Small-tree stands were consistently more dense than the intermediate- and large-tree stands in both non-flooded and seasonally flooded habitats. Densities in intermediate-, and large-tree categories were similar between non-flooded and seasonally flooded habitats, but were greater in permanently flooded habitats. Among intermediate-tree stands, the highest tree densities were observed within permanently flooded habitats. Tree diameters of corresponding stands in non-flooded and permanently flooded habitats were similar, whereas they were larger among corresponding stands in seasonally flooded habitats. Average dbh and basal area coverage increased with the increasing tree-size in the stands.

In general, melaleuca trees dominated study sites, but a few other species (*Baccharis*, *Blechnum*, *Cephalanthus*, *Cladium*, *Ficus*, *Ilex*, *Myrica*, *Myrsine*, *Osmunda*, *Persea*, *Psilotum*, *Schinus*, *Thelypteris*, and some grass species) occurred in small numbers in tree gaps and newly invaded areas. The sedge *Cladium jamaicense* Crantz and *Myrica* sp. occurred in relatively large numbers in small-tree plots near ecotonal invasion fronts. These accounted for the majority of non-melaleuca litterfall fractions.

Table 1. Physical and biological characteristic of three tree-size categories of *M. quinquenervia* stands in three habitats as determined in 1997 and used for litterfall studies during 1997–2001 in Florida.

Habitat[a]	Soil type	Tree-stand structure	Stems/ha[b]	dbh (cm)			BA[c]
				Mean	Range	Standard error	
Non-flooded	Muck (compact)	Small	45866	2.37	1.0–15.1	1.34	26.74
		Intermediate	26875	3.64	1.0–15.5	2.65	42.81
		Large	12750	6.87	1.0–35.5	5.69	79.59
Seasonally Flooded	Muck (compact)	Small	69500	2.02	1.0–7.2	1.34	31.98
		Intermediate	25700	4.94	1.0–24.5	4.35	87.62
		Large	13350	9.15	1.0–32.0	8.84	169.61
Permanently flooded	Muck (loose)	Small	37200	2.59	1.0- 8.6	1.31	24.55
		Intermediate	46450	3.47	1.0–29.0	3.21	101.48
		Large	18200	7.37	1.0–35.4	6.87	144.74

[a] Based on hydroperiod: non-flooded = flooded for hours to few days after heavy rain; seasonally flooded = flooded for few to several months each year; permanently flooded = year round wet, variable water depth, up to 1.3 m.

[b] ≤1-cm diameter at breast height (dbh).

[c] Basal Area (m^2)/ha at breast height.

Proportion of aboveground biomass falling as litter during the succeeding year

The dry weight of live aboveground biomass components as estimated during early 1997, and the amounts and proportions of the estimated biomass that fell as litter during the succeeding year (1997–1998) was related to tree size (Table 2). Total aboveground biomass increased as tree sizes increased and woody materials, leaves, and fruits comprised the first, second, and third largest fractions, respectively. While woody tissues (trunks, branches, and twigs) comprised the bulk of aboveground biomass, fine stems (<1-cm diameter) represented only a small fraction of the litterfall. Leaf biomass was estimated at 7–13 mt ha^{-1}, 8–25 mt ha^{-1}, and 6–23 mt ha^{-1} in small- to large-tree stands in non-flooded, seasonally flooded, and permanently flooded habitats, respectively. Of the total canopy-held leaf biomass, 61–44%, 64–30%, and 34–27% fell as litter during the year in small- to large-tree stands in non-flooded, seasonally flooded, and permanently flooded habitats, respectively. Proportions of aboveground wood biomass falling as litter during one year in both non-flooded and permanently flooded habitats increased with increasing tree size. Proportions of canopy-held fruits in non-flooded habitats followed the trend similar to that of the fine stems. On the other hand, proportions of twig as well as mature fruit fall in seasonally flooded habitats, and mature fruit fall in permanently flooded habitat did not reflect the trend observed in non-flooded habitats. Proportions of canopy-held fruits falling in ensuing year as litter increased with tree size, being highest (27–37% in small- to large-tree categories) in permanently flooded habitats.

Variations in proportion of tree components in accumulated litter

The proportional representation of the major litterfall components was not consistent among tree-size stand, as shown by a significant ($p = 0.0274$) habitat × tree-size category interaction (Table 3). In general, the proportions of fine stems, floral structures, and immature and mature fruits in all habitats increased ($p \leq 0.0006$) with the average tree diameters in the stand. The leaf fraction consistently comprised the major portion of the total litterfall. In general, the leaf-litter proportion decreased in small- to large-tree stands from 85.6 to 76.8% and 80.3 to 68.1% in non-flooded and seasonally flooded habitats, respectively. On the other hand, the proportion of fine melaleuca stems in litter increased with tree-size categories in all three habitats. The proportions of floral structures, and immature and mature fruits in non-

Table 2. Amount of aboveground live biomass (mt ha^{-1}) of *M. quinquenervia* trees as estimated in June 1997 and the litterfall components during the ensuing 1-year period (July 1997 to June 1998) in south Florida.

Habitat/ stand-structure	Total biomass		Woody biomass		Leaf biomass		Fruit biomass	
	Above-ground mt ha^{-1}	Litterfall mt ha^{-1} (%)	Above-ground mt ha^{-1}	Litterfall[a] mt ha^{-1} (%)	On canopy mt ha^{-1}	Litterfall mt ha^{-1} (%)	On canopy mt ha^{-1}	Litterfall mt ha^{-1} (%)
Non-flooded								
Small	61.60	4.22 (6.86)*	53.24	0.24 (0.45)	6.48	3.96 (61.11)	1.88	0.02 (1.28)
Intermediate	98.52	5.36 (5.44)	87.40	0.60 (0.69)	8.75	4.68 (53.49)	2.37	0.08 (3.44)
Large	183.91	7.49 (4.07)	167.41	1.32 (0.79)	13.20	5.76 (43.64)	3.30	0.41 (12.36)
Seasonally flooded								
Small	73.79	5.91 (8.01)	63.73	0.60 (0.94)	7.78	5.00 (64.32)	2.28	0.31 (13.58)
Intermediate	202.23	7.68 (3.80)	182.64	1.08 (0.59)	15.59	6.12 (39.26)	4.00	0.48 (12.00)
Large	394.23	10.74 (2.72)	363.44	2.16 (0.59)	24.89	7.44 (29.89)	5.90	1.14 (19.32)
Permanently flooded								
Small	56.52	2.62 (4.63)	48.87	0.12 (0.25)	5.93	2.04 (34.40)	1.72	0.46 (26.51)
Intermediate	233.74	6.10 (2.61)	208.86	0.70 (0.33)	19.66	4.80 (24.42)	5.22	0.60 (11.49)
Large	335.48	10.20 (3.04)	307.20	2.28 (0.74)	22.74	6.12 (26.91)	5.54	1.80 (32.49)

[a] $\leq$1-cm diameter twigs represent woody materials in litterfall.

*Numbers in parentheses represent the percentage of aboveground tree component that fell as litter throughfall during the ensuing year.

Table 3. Proportions (% dry weight of total litterfall) of the components of *Melaleuca quinquenervia* litterfall in stands of three tree-size stands within three habitats during July 1997 to June 2001 in Florida.

Habitat/tree-stand structure	Stems	Leaves	Floral structures	Bud scales	Fruits		Residue
					Immature	Mature	
Non-flooded (N^A = 384)							
Small[B]	7.31 b	85.61 a	1.29 b	4.37 a	0.44 b	1.07 c	0.31 ab
Intermediate	11.14 a	80.22 b	1.62 b	4.16 a	0.61 b	2.42 b	0.44 a
Large	12.52 a	76.75 c	2.59 a	3.53 a	1.06 a	4.37 a	0.24 b
Average	10.32	80.85	1.83	4.02	0.70	2.62	0.33
Seasonally flooded (N = 384)							
Small	7.56 c	80.27 a	2.90 b	4.04 a	1.24 b	4.81 c	0.40 a
Intermediate	11.42 b	77.32 b	2.13 c	2.97 b	0.74 c	5.95 b	0.20 a
Large	16.61 a	68.06 c	3.70 a	3.71 a	1.68 a	7.53 a	0.39 a
Average	11.84	75.22	2.91	3.57	1.22	6.10	0.33
Permanently flooded (N = 144 *to* 288)							
Small	3.95 c	68.23 b	4.26 a	4.93 a	2.23 a	18.49 a	0.26 ab
Intermediate	9.31 b	74.33 a	2.90 a	3.06 b	1.54 a	10.11 c	0.35 a
Large	16.84 a	64.70 c	3.09 a	2.49 b	1.18 a	12.70 b	0.17 b
Average	10.03	69.10	3.42	3.50	1.65	13.77	0.26

[A] 'N' represents the number of litter traps sampled in each tree-size plots over 3 to 4-year study period. Note that rows will not add up to >100% as the weight of "Immature fruits" within rows have been added to both 'Floral structures (reproductive buds + stamens + immature fruits)' structures" and 'Fruits' fractions.

[B] Mean values followed by the same letter(s) in the same row are not significantly different according to Waller-Duncan's *K*-ratio *t*-test at p = 0.05.

flooded habitats were in the declining sequence of large > intermediate > small tree-size stands, but the other two habitats showed no consistent trends in this respect.

In order to detect habitat level litterfall trends, the corresponding proportion of litterfall components in small-, intermediate-, and large-tree categories within habitats were pooled and averaged (Table 3). Among habitats, the proportional representation of fine stems was highest (11.8%) in seasonally flooded and least in permanently flooded habitats (10.0%). However, the leaf fractions were highest in non-flooded (80.9%) and least in permanently flooded habitats (69.1%). The largest and smallest proportions of floral structures (3.4% and 1.83%), immature fruits (1.7% and 0.7%), and mature fruits (13.8% and 2.6%) fell in permanently flooded and non-flooded habitats, respectively. The bud-scale and residue proportions were similar among habitats.

Variations in amount of annual litterfall

The means for each annual litterfall component in small-, intermediate-, and large-tree stand categories were assessed by habitats (Table 4). Combined total dry weights for melaleuca and non-melaleuca fractions were greatest in large- and least in small-tree categories. Melaleuca comprised over 99% of the total litterfall in all habitats and months sampled. Dry weights of fine stems, leaves, floral structures, immature fruits, and mature seed capsules declined from large- to intermediate- to small-tree categories in all three habitats. Dry weight of non-melaleuca litter was highest in small-tree stand categories in seasonally (0.018 kg m^{-2} yr^{-1}) and permanently (0.075 kg m^{-2} yr^{-1}) wet habitats and in intermediate-tree categories (0.014 kg m^{-2} yr^{-1}) in non-flooded habitats. Non-melaleuca litterfall in small-tree stands consisted mainly of *C. jamaicense* and *Myrica* sp. leaves while in large-tree stands, it was mainly foliage of various fern species, *Schinus terebinthifolius* Raddi, and *Cephalanthus occidentalis* L, and "needles" (modified stems) of *Casuarina* sp.

Melaleuca litter components were analyzed by habitat and year averaged across tree-size stands (Table 5). Dry weight of yearly litterfall components varied within habitats. The coefficient of variation in the annual amount of total (annual)

Table 4. Mean litterfall components (kg m^{-2} yr^{-1}) among melaleuca tree-size categories in Florida during July 1997 to June 2001.

Habitat/tree-stand structure	Total melaleuca	Melaleuca litterfall components							Non-melaleuca
		Stems	Leaves	Floral structures	Bud scales	Immature capsules	Mature capsules	Frass & residue	
Non-flooded (N[A] = 96)									
Small	0.510 c[B]	0.048 c	0.440 c	0.005 b	0.013 b	0.002 b	0.005 c	0.001 b	0.003 b
Intermediate	0.620 b	0.086 b	0.499 b	0.006 b	0.014 b	0.002 b	0.013 b	0.002 a	0.014 a
Large	0.878 a	0.164 a	0.640 a	0.014 a	0.019 a	0.006 a	0.040 a	0.002 a	0.002 b
Seasonally flooded (N[A] = 96)									
Small	0.662 c	0.069 c	0.516 c	0.017 b	0.021 b	0.008 b	0.034 c	0.006 a	0.018 a
Intermediate	0.882 b	0.154 b	0.636 b	0.017 b	0.021 b	0.007 b	0.052 b	0.003 a	0.001 b
Large	1.128 a	0.270 a	0.693 a	0.035 a	0.032 a	0.018 a	0.092 a	0.005 a	0.001 b
Permanently flooded (N[A] = 48–96)									
Small	0.248 c	0.011 c	0.178 c	0.008 c	0.007 c	0.005 b	0.043 b	0.001 b	0.075 a
Intermediate	0.548 b	0.067 b	0.402 b	0.014 b	0.013 b	0.008 b	0.051 b	0.002 a	0.007 b
Large	0.886 a	0.184 a	0.510 a	0.024 a	0.019 a	0.147 a	0.147 a	0.002 a	0.001 b

[A] 'N' represents the number of litter traps sampled in each tree-size plots over 3 to 4-year study period.

[B] Mean values followed by the same letter(s) in the same column representing three stand-structures within a given habitat are not significantly different according to Waller-Duncan's *K*-ratio *t*-test at $p = 0.05$.

melaleuca litterfall within non-flooded, seasonally flooded, and permanently flooded habitats during 4-yr period was 13, 21, and 14%, respectively. Total melaleuca litterfall for all tree stands in both non-flooded and seasonally flooded habitats was highest during 1999–2000 while it was highest

Table 5. Overall amounts (kg m^{-2} yr^{-1}) of litterfall in melaleuca stand by habitat and year pooled across tree-size categories.

Habitat/duration (12-month period)	Total melaleuca	Melaleuca litterfall components[A]							Non-melaleuca
		Stems	Leaves	Floral structures	Bud scale	Immature capsules	Mature capsules	Frass & residue	
Non-flooded									
1997–1998	0.5924 b[B]	0.0734 b	0.4835 b	0.0190 b	0.0012 b	0.0024 bc	0.0153 b	0.0011 c	0.0076 a
1998–1999	0.7249 a	0.0866 b	0.5856 a	0.0319 a	0.0017 a	0.0043 ab	0.0205 ab	0.0001 d	0.0058 a
1999–2000	0.7620 a	0.1442 a	0.5654 a	0.0256 a	0.0011 b	0.0056 a	0.0233 a	0.0034 a	0.0050 a
2000–2001	0.5978 b	0.0931 b	0.4690 b	0.0164 b	0.0010 b	0.0017 c	0.0175 ab	0.0017 b	0.0054 a
Seasonally flooded									
1997–1998	0.8491 b	0.1282 b	0.6192 b	0.0442 c	0.0022 b	0.0072 c	0.0571 b	0.0008 b	0.0150 a
1998–1999	0.7968 b	0.1099 b	0.5604 c	0.0719 a	0.0028 a	0.0178 a	0.0545 b	0.0002 b	0.0047 b
1999–2000	1.1620 a	0.3039 a	0.7200 a	0.0412 b	0.0015 c	0.0126 b	0.0868 a	0.0092 a	0.0058 b
2000–2001	0.7537 b	0.1152 b	0.5598 c	0.0029 c	0.0016 c	0.0058 c	0.0390 c	0.0068 ab	0.0044 b
Permanently flooded (N[A] = 240–288)									
1997–1998	0.6558 a	0.1028 a	0.4355 a	0.0280 b	0.0014 a	0.0058 b	0.0895 ab	0.0178 c	0.078 b
1998–1999	0.5950 a	0.0871 ab	0.3700 b	0.0461 a	0.0014 a	0.0166 a	0.0917 a	0.0281 b	0.0281 bc
1999–2000	0.4976 b	0.0716 b	0.3446 b	0.0120 c	0.0006 b	0.0077 b	0.0596 b	0.0394 a	0.0394 a
2000–2001	–	–	–	–	–	–	–	–	–

[A] Each data point represents a mean of 288 (8 traps × 3 tree-size categories × 12 month) replicated litter traps/year for non-flooded and seasonally flooded habitats; but components represent means of 240 (48, 96, and 96 replicated traps represented large-, intermediate- and small-tree categories, respectively) replicated litter traps/year in permanently flooded habitat. Note that tree plots in permanently flooded habitat were destroyed by wildfire during the spring of 2001 and hence data collection in this habitat was stopped after April 2001 and only 3-year data are reported.

[B] Mean values of litter fraction (during 3-to-4-yr period) followed by same letter(s) in a column within a given habitat are not significantly different according to Waller-Duncan's *K*-ratio *t*-test at $p = 0.05$.

during 1997–1999 in permanently flooded habitat. Dry weight of fine stem, leaf, and mature fruit components tracked total litterfall. Dry weight of floral structures, bud scales, and immature fruits in the litter were highest during 1998–1999 in all three habitats. Mature-capsule litter was higher during 1997–1998 in all three habitats, but additional peaks occurred during 1999–2000 in non-flooded and seasonally flooded habitats. Large trees in permanently flooded habitats were toppled by strong winds during September–November 1998, so the overall litterfall in these stands gradually diminished during the ensuing months. In addition, a crown fire swept through both permanently flooded areas during the spring of 2000 and inflicted severe damage to the trees, so litterfall collections were discontinued in these sites.

Variations in amount of monthly litterfall components

The dry weights of each litterfall component were summarized by month (average of corresponding months) over the study period (Figure 1). Overall melaleuca litterfall peaked during April, July, and October while non-melaleuca and residue fractions showed little monthly variation. Dry weights of melaleuca leaves and mature seed-capsules in the litter tracked total litterfall trends, but stem fall

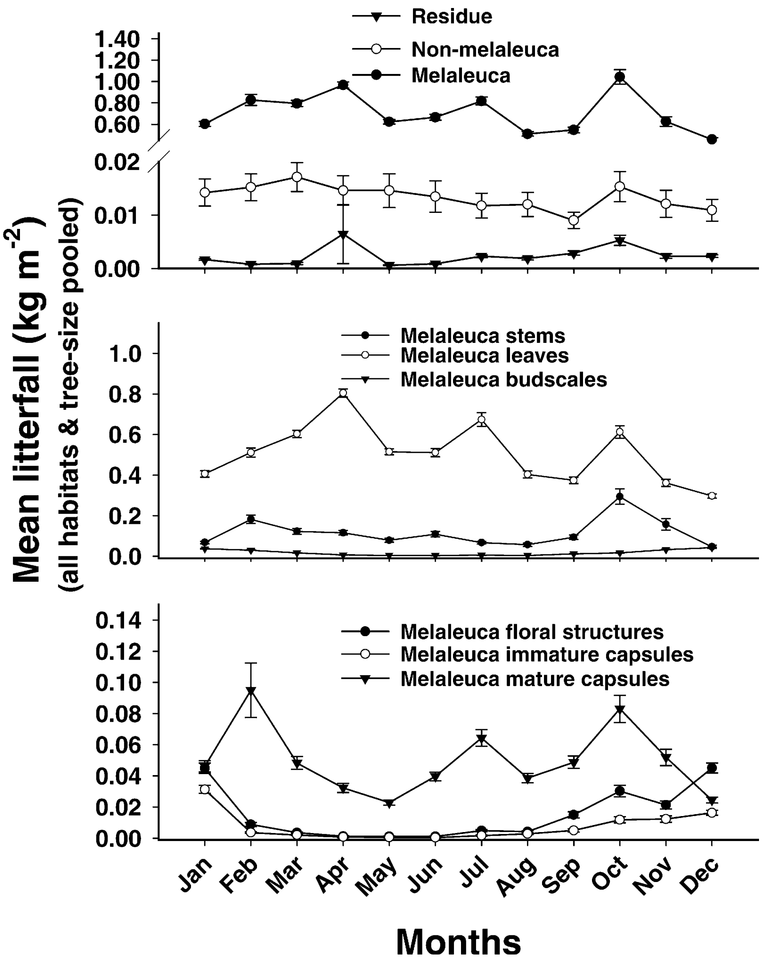

Figure 1. Overall monthly means and error bars (± 1 standard error of the mean) of litterfall components computed. Each data point on graph for each litterfall component represents the mean of 272 [(24 traps/mo × 2 habitats, i.e., non-flooded and seasonally flooded × 4 corresponding months in 4 years) + (20 traps/mo × 1 habitat, i.e., permanently flooded × 4 corresponding months in 3 years)] replicated litter traps.

was greatest during February and October. In contrast, bud-scales, floral structures, and immature capsule-fall peaked during October to January.

Variations in the quantities of litterfall components were significant ($p < 0.0001$) for both years and tree-size categories. Therefore, the litterfall components within corresponding tree-size categories among habitats were pooled, averaged, and graphed to detect monthly trends for the whole study period (Figure 2). Dry weights of all litterfall components were consistently greatest in large-tree stands and least in small-tree stands. Total melaleuca litterfall in all tree-size stand categories peaked during October–November and February–April of each year, though some secondary peaks arose during June 1999 and 2001, and August 2000. The residue fraction tracked total melaleuca

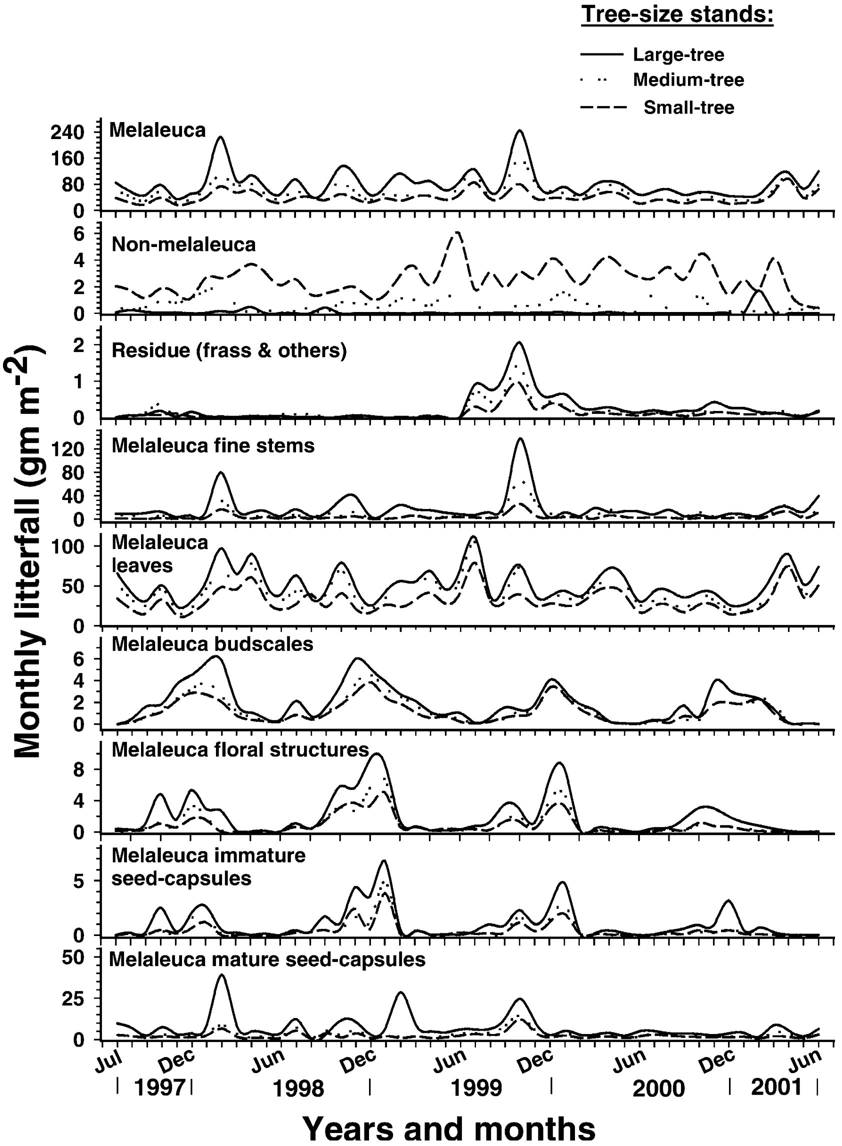

Figure 2. Monthly litterfall rates of total melaleuca, non-melaleuca, and major melaleuca components, calculated by pooling dry weight data of corresponding tree-size stand categories from all three habitats to detect monthly litterfall trends over a 3–4-year study period. Monthly data points in graph are means of 32 litter traps for small- and intermediate-, and 24 litter traps for large-tree stand category.

litterfall until after June 1999 when it sharply increased.

Throughfall of melaleuca stem, leaf, and bud-scale components (Figure 2) likewise increased as tree size increased. Fine stem fall occurred throughout year with pronounced peaks during February and November 1998 and February and October 1999. Leaf fall occurred during all months, but prominent peaks occurred in April, July, and October of every year during 1997–2001 with an additional prominent peak during February 1998. Bud-scales (floral and vegetative) exhibited a major peak each year between October and January.

Dry weight of floral structures and immature fruits in litter peaked annually during September to January (Figure 2). Each major peak split, with sub-peaks in September–October and in December–January. The immature fruit fraction tracked the trend for floral structures. Several major peaks representing throughfall of large quantities of mature seed capsules were also apparent. Of these, the peaks in February 1998 and February and October 1999 were greatest. The dry weight of mature fruits in the litter decreased markedly after 1999.

Discussion

Stand structure and litterfall

Comparisons of aboveground biomass allocation and litterfall rates for components of invasive trees are uncommon in the literature. The aboveground melaleuca biomass of fine wood, leaves, and fruits increased in all habitats as the predominant tree size increased. On the other hand, the proportional representation of these components in the litter did not reflect their allocation as standing biomass. Tree density (stems ha^{-1}) varied inversely while basal area coverage varied directly with tree stature. Increased basal area coverage was associated with increased live biomass, which in turn, was associated with increased litterfall. Linear relationships between standing live biomass and total litterfall have also been reported for other tropical forest ecosystems (Brown and Lugo 1982), where basal area coverage in forests stands showed positive correlation with the amount of litterfall (Turnbull and Madden 1983).

Aboveground biomass & litterfall in succeeding year

The proportion of each aboveground biomass component that was shed as litter revealed additional trends. Dry weight of fine twig in the litter varied inversely with tree density but directly with dbh and aboveground biomass. This suggests that branchiness increases on larger trees or, perhaps, that twig fall from mature stands increases due to natural pruning of lower branches and mortality of suppressed trees.

The proportion of canopy-held leaf biomass that fell as litter within a given habitat varied inversely with tree stature. Stands of small trees tended to produce proportionately more leaf litter than the large-tree stands. In addition, trees of comparable sizes growing in non-flooded and seasonally flooded habitats generated proportionately more leaf litterfall than those in the permanently flooded habitats. Complete leaf turnover in melaleuca stands has previously been estimated to occur over periods of 2, 3, and 4 years in non-flooded, seasonally flooded, and permanently flooded habitats, respectively (Van et al. 2002). Based on the total leaf amount in canopies and the proportions falling as litter during the ensuing year, we detected leaf longevity differences among tree-size categories among habitats. The leaf turnover rates were 1.6 years in small- and 2.3 years in large-tree stands in non-flooded habitats, 1.6 years in small- and 3.3 years in large- tree stands in seasonally flooded habitats, and 2.9 years in small- and 3.7 years in large-tree stands in permanently flooded habitats. This high rate of leaf turnover among juvenile trees in all habitats is attributable to their fast growth rates and greater competition for light, which likely would induce rapid leaf abscission from lower portions of tree canopies owing to shading effects.

The estimated annual fruit turnover rate (based on the canopy-held amount) was least (7%) in non-flooded and greatest (23%) in permanently flooded habitats. This could possibly be due either to low rates of fruit production or longer persistence of fruits on tree canopies in non-flooded habitats.

Habitat, tree-size, and annual litterfall

Limited published data demonstrate temporal or spatial variations in melaleuca litterfall, either in its native or adventive ranges. Greenway (1994) noted slight differences in litterfall composition between riparian and floodplain sites of *M. quinquenervia* in Queensland, Australia (Table 6). Finlayson et al. (1993) measured litterfall in mixed stands of *M. cajuputi* Powell (mean dbh, 31.0 cm) and *M. viridiflora* Sol. Ex Gaertner (mean dbh, 29.0 cm) on a tropical floodplain in northern Australia. Their results were similar to Greenway's (1994), but with a higher proportion of floral structures. Van et al. (2002) reported remarkably high melaleuca stem densities in mature stands in Florida compared to matured stands in Australia. On the other hand, a majority of melaleuca trees in Australia were bigger (ca. 18 to 34 cm dbh) compared to Florida, where the dbh of 80 to 89% of the trees was below 10-cm. However, overall litter production appeared to be nominally influenced by higher densities of smaller diameter trees as shown in Table 6. Overall, annual total litterfall was higher in the USA (8.3 t ha^{-1} yr^{-1}) compared to Australia (7.6 t ha^{-1} yr^{-1}). Additionally, the proportion of fine stem and overall floral structures in the litterfall was higher in the USA than in Australia.

In this study, total litterfall (melaleuca and non-melaleuca) among trees of similar stature compared within habitats was highest (0.688, 0.890, and 1.146 kg m^{-2} yr^{-1} in small-, intermediate-, and large-tree stands, respectively) in seasonally flooded, and least (0.248, 0.548, and 0.886 kg m^{-2} yr^{-1}, in small-, intermediate-, and large-tree stands, respectively) in non-flooded habitat. Higher litterfall amounts in seasonally flooded habitats may relate to greater overall basal area of melaleuca trees reflecting the greater tree dimensions (Table 1), coupled with higher amount of leaf production during wet periods and rapid shedding of older leaves during dry periods. Haase (1999) studied litterfall in two Brazilian forest habitats with similar stem densities and basal areas and reported significantly higher amounts of litterfall in seasonally flooded (0.753 to 1.027 kg m^{-2} yr^{-1}) compared to non-flooded (0.486 to 0.771 kg m^{-2} yr^{-1}) habitats. Similar studies conducted in bottomland forests along the Ohio River in the USA (Mitsch et al. 1991) also reported a higher productivity in wetlands with pulsing hydroperiods (similar to seasonally flooded systems) than in stagnant (similar to permanently flooded habitats in our study) conditions.

Litterfall rates in non-melaleuca forests (mangrove and other freshwater systems) in Florida range from 0.510 to 1.170 kg m^{-2} yr^{-1} (Brown and Lugo 1982), which is less than or comparable to the litterfall in our large tree stands (1.129 kg m^{-2} yr^{-1}) in seasonally flooded habitats. Greenway (1994) on the other hand, reported

Table 6. Comparison of litterfall data for melaleuca forests in Australia and the USA as reported in the literature.

Component	Australia				USA			
	SE Queensland[a]		Northern[b] flood plain	Overall	Florida[c]			
	Riparian	Flood plain			Non-flooded	Seasonally flooded	Permanently flooded	Overall
Density (number ha^{-1})	1480	2170	294	1315	20300	19937	32337	24115
Mean dbh (cm)	18.5	17.8	29 & 34		Mature stands with 80–89% trees of < 10 cm dbh			
Total litterfall (t ha^{-1} yr^{-1})	7.6	8.1	7.2	7.6	7.5	9.3	8.0	8.3
Of the total litterfall								
Leaves (%)	67		70	–	–	–	–	70
Twigs and bark (%)	23		19	–	–	–	–	16
Floral parts (%)	6		6	–	–	–	–	15
Mature seed-capsules	5		3	–	–	–	–	In floral parts[d]
Miscellaneous parts (%)	Not known		3	–	–	–	–	Not known

[a] Greenway (1994), seasonally flooded *M. quinquenervia* forests in subtropical, native range.

[b] Finlayson et al. (1993), mixed *M. viridiflora* (average dbh 34 cm)-*M. cajeputi* (average dbh 29 cm) forest in tropical floodplain, native range *M. viridiflora* (average dbh 34 cm).

[c] Van et al. (2002), *M. quinquenervia* forests, adventive range.

[d] In Florida, mature seed-capsules (fruits) are included in floral parts.

0.760 and 0.810 kg m^{-2} yr^{-1} of total melaleuca and non-melaleuca litter for mature *M. quinquenervia* forests in riparian and flood plain sites, respectively in Queensland, Australia. This suggests that mature melaleuca dominated tree stands in Australia are less productive than in Florida. Furthermore, the higher amounts of non-melaleuca litter reflect greater biodiversity or higher frequency of non-melaleuca plants in melaleuca forest communities of Australia than in the forest communities in Florida.

The fall of fine stems, leaves, floral structures, bud–scales, immature and mature fruits, and residual fractions were consistently higher in large- than in intermediate- and small-tree stands in all habitat types; this relates to larger live crown volumes in large-tree stands yielding more total litterfall than the smaller crown volumes of intermediate or small trees. Production of larger amounts of 'necromass' by large compared to small-trees has also been reported in *Pseudotsuga menziensii* (Mirb.) Franco stands (Maguire 1994).

Litterfall components in a forest stand may be an indicator of plant diversity. Analyses showed a greater (0.075 kg m^{-2} yr^{-1}) amount of non-melaleuca fraction in permanently flooded habitats compared to those in seasonally flooded (0.018 kg m^{-2} yr^{-1}) and non-flooded (0.003 kg m^{-2} yr^{-1}) habitats. Throughout habitats, small-tree stands produced more non-melaleuca litter than did large- and intermediate-tree stands. The reduction in non-melaleuca litter fractions among mature tree stands may be due to increased melaleuca-canopy coverage. Melaleuca canopy coverage beyond 75% of the surface area of stand reduces light penetration and primary productivity of understory vegetation (O'Hare and Dalrymple 1997). Therefore, the decrease in non-melaleuca fraction with increasing maturity of melaleuca stands is indicative of the gradual loss of biodiversity during the invasion process and the reflection of the level of invasion and the displacement of native plants.

Lonsdale (1988) studied litterfall of an invasive woody plant *Mimosa pigra* in northern Australia over a period of 27 months and found no difference between years in terms of total litterfall. In our study, the most total and fine stem fall occurred during 1999–2000 in both non-flooded and seasonally flooded habitats. The lowest annual litterfall was recorded during 1997–1998 and year-to-year variation within habitat was as much as 35%. These results parallel the findings of others (Hegarty 1991;Whigham et al. 1991; Spain 1984) who reported that drought, rainfall, and strong wind generated notable increases in the amount and proportions of litterfall components in various broadleaf forests (Lugo et al. 1978; Lowman 1988).

Notably, the quantity of annual leaf fall did not show remarkable variation from year to year. However, the fall of the quantities of floral structures was less during 1997–1998 and 2000–2001 and more during 1998–1999 and 1999–2000. The quantities of the floral structures, such as hypanthia and stamens indicate the degree of flowering intensities in melaleuca stands (Van et al. 2000). In addition, the prolific production of floral structures during 2 years followed by lesser amounts in subsequent years suggests that flowering events may be cyclical.

Tree-size stands and monthly litterfall

Overall, melaleuca litterfall peaked during October–November and February–April each year during the four-year study period. As expected, both melaleuca and residual litterfall was highest in large- and least in small-tree stands, whereas the reverse was true for non-melaleuca litterfall. Non-melaleuca species occurred as understory in the marginal areas of stands.

Melaleuca stem fall occurred all year-round but the major peaks were during February and November of 1998 and October 1999, all with a prolonged low rainfall followed by a combination of heavy rainfall and storm during these 3 months. Leaf fall occurred year-round but was most pronounced after prior periods of low rainfall, e.g., drought conditions during March to May 1999 (data not presented) led to maximal leaf fall during June-July (Figures 1, 2). Similar fine stem and leaf fall trends have also been observed in other forest systems (Spain 1984; Twilley et al. 1986; Hegarty 1991; Whigham et al. 1991; Finlayson et al. 1993).

In general, floral structures in the litter traps provide empirical data that support visual observations on the timing and duration of flowering (Van et al. 2002). Amount of bud-scales during the early phase of flowering within a year generally preceded or coincided with peak flowering and/or vegetative bud extensions (Figure 2). Similarly, new shoot growth began with rapid elongation of vegetative buds and shedding of bract-scales. Therefore, their abundance in the litter traps appears to signal a vegetative flush, which usually occurs after flowering. Corollas, stamens and pistils, and immature fruits in the litter indicate post-anthesis and the onset of fruit development. Major peaks of melaleuca floral structures and immature fruits generally occurred during October to January with the highest peak each year during December (Figure 2). Therefore, the flowering intensity in the canopy along with other unknown variables may be dictating the intensity of immature fruit fall. On the other hand, mature seed-capsules exhibited several peaks, which were most prominent during February, July, and October which generally coincided with either drought or storm.

In summary, litterfall in melaleuca dominated systems in south Florida is affected by the hydrologic environment and seasonality (months). Stands growing in seasonally flooded areas produce more litter than those in dry or permanently flooded areas. Melaleuca litter fractions were greater in large-tree stands, while non-melaleuca fractions were greater in intermediate- and small-tree stands. The quantity (dry weight) and quality (proportion of the total litterfall) of the components depended on the prevalent size of trees in the stand. Fruit and leaf fall ratio when compared to the total amount present on the canopy was higher in large- and small-tree stands, respectively. Absolute amount of leaf and fruit litter increased with the melaleuca tree stature in the stand; on the other hand, the rate of decomposition of melaleuca litter is slower than that of native plants (Van and Rayamajhi, unpublished data). Such slow decomposition may result in accumulation of thick layers of duff on forest floors. These changes may limit recruitment of native flora and make restoration and management of melaleuca-infested sites more challenging.

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