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Litter Dynamics and Phenology of *Melaleuca quinquenervia* in South Florida

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ABSTRACT

We monitored litterfall biomass at six different sites of melaleuca (*Melaleuca quinquenervia* (Cav.) S.T. Blake) forested wetlands in South Florida from July 1997 to June 1999. Annual litterfall of melaleuca varied between sites from 6.5 to 9.9 t dry wt ha^{-1} yr^{-1} over the two-year period. Litterfall was significantly higher ($P < 0.001$) in seasonally flooded habitats (9.3 t ha^{-1} yr^{-1}) than in non-flooded (7.5 t ha^{-1} yr^{-1}) and permanently flooded habitats (8.0 t ha^{-1} yr^{-1}). Leaf fall was the major component forming 70% of the total litter, woody material 16%, and reproductive material 11%. Phenology of flowering and leaf flush was investigated by examination of the timing and duration of the fall of different plant parts in the litter traps, coupled with monthly field observations during the two-year study. In both years, flowering began in October and November, with peak flower production around December, and was essentially completed by February and March. New shoot growth began in mid winter after peak flowering, and extended into the spring. Very little new growth was observed in melaleuca forests during the summer months, from May to August, in South Florida. In contrast, the fall of leaves and small wood was recorded in every month of the year, but generally increased during the dry season with higher levels observed from February to April. Also, no seasonality was recorded in the fall of seed capsules, which apparently resulted from the continual self-thinning of small branches and twigs inside the forest stand. In planning management for perennial weeds, it is important to determine the period during its annual growth cycle when the plant is most susceptible to control measures. These phenological data suggest that the appropriate time for melaleuca control in South Florida might be during late winter and early spring, when the plant is most active.

Key words: Litterfall; Biomass; Productivity; Biological control; Paperbark tree.

INTRODUCTION

Melaleuca, often referred to as paperbark or broad-leaved paperbark tree, is native to Australia. It is highly invasive in wetland habitats of South Florida where it has infested about 200,000 ha (Bodle et al. 1994). Vast areas of wetlands, including parts of the Florida Everglades, have been converted

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from marshes to closed-canopy melaleuca forests, with major environmental and economic impacts (O'Hare and Dalrymple 1997). As part of a biological control program, the Australian melaleuca snout beetle (*Oxyops vitiosa* Pascoe) and other natural enemies specific to *M. quinquenervia* are being imported into the U.S. (Center et al. 2000). This study was designed to obtain quantitative information on melaleuca productivity in terms of litterfall, and the relative proportions of the litter components, prior to the impact of the released biological control agents.

Litterfall collection is a standard non-destructive technique for assessing productivity, phenology, and turnover of biomass in a forest (Newbould 1967). In general, net productivity of woody trees such as melaleuca, is difficult to measure because a large proportion of the plant material exists in the trees for a long time before entering other parts of the ecosystem. Much of the short-term input from a melaleuca forest to the ecosystem is as the litter falling from the tree canopy to the forest floor, and incorporated into the rest of the system by detritus feeders and decomposer organisms. This compartment of net productivity is relatively easy to measure. In particular, the amount of leaf material falling reflects a forest's productivity. Rainforests, with their dense leaf canopies and high rates of leaf fall, are considered among the most highly productive plant communities (Proctor 1983).

Annual litter production varies primarily with latitude, and ranges from 0.6 t ha^{-1} yr^{-1} in the arctic tundra to 25.4 t ha^{-1} yr^{-1} in a tropical lowland forest of eastern Australia (Lowman 1988). In addition to latitude, the amount of litterfall is affected by precipitation and various attributes of the vegetation (Bray and Gorham 1964). No information is available on litterfall or turnover of melaleuca forests in South Florida. Measurements in its native range in Australia (Finlayson et al. 1993, Greenway 1994) however, have indicated that annual litterfall in melaleuca forests was the highest recorded among other Australian temperate/subtropical forest types, suggesting that these woody wetlands form highly productive ecosystems. This paper presents data on litterfall biomass from six sites representing different hydrological conditions within melaleuca forested wetlands in South Florida. The objectives were to report the first measurements of litter production by melaleuca in South Florida, and secondly to describe important phenological events of flowering and growth of melaleuca through records of the seasonal patterns exhibited by the different components of the litter.

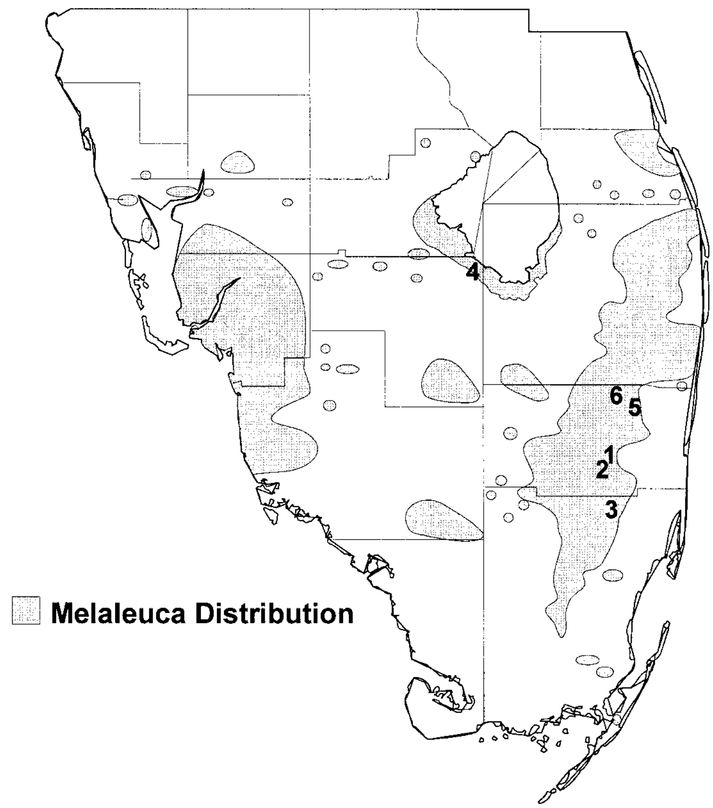

Figure 1. A map of South Florida showing location of the six study sites and their grouping into three different habitats. The Holiday Park sites (1 and 2) were non-flooded, Krome (Site 3) and Clewiston (Site 4) seasonally flooded, and the Conservation Area sites (5 and 6) permanently flooded.

MATERIALS AND METHODS

Six permanent study sites were established throughout the geographic range of melaleuca in the Everglades in South Florida (Figure 1). The sites were selected to encompass different hydrological conditions, as hydro-pattern has been considered as a strong determinant of wetland species and their performance (Mitsch and Gosselink 1986). The sites consist of typical 'glades' characterized by high organic (muck) soils, and were grouped into three habitat categories: seasonally flooded, permanently flooded, and non-flooded (Table 1). There were two sites for each habitat. It should be noted that non-flooded melaleuca forests in the Everglades can still be covered by flood water during periods of heavy rainfall; however, this flooding is usually of short duration and may not happen every year, and thus cannot be considered as seasonal flooding. Therefore, in this study the term 'non-flooded' means 'not flooded seasonally' rather than 'never flooded'.

Mean annual rainfall of the study area was 1420 mm (NOAA).[3] The area received most (75%) rainfall during the months of May through October in the form of convective storms. Mean rainfall during those months was 178 mm per month. Mean monthly temperatures ranged from 19.5C in January to 28.2C in August.

Vegetation at all six selected sites consisted of dense, closed-canopy melaleuca stands similar to those described by O'Hare and Dalrymple (1997) as '75-100% dense, mature melaleuca (DMM)'. The forest under-story was generally sparse, and consisted of shade-adapted shrubs (e.g., *Myrica cerifera* L., *Myrsine guianensis* (Aubl.) Kuntz., *Baccharis* sp.), several ferns (e.g., *Thalypteris* sp., *Osmunda* sp.), sedges (e.g., *Cladium jamaicense* Crantz.), and grasses.

Four 10 by 10 m plots were established in a stratified random design at each of the six study sites. In each plot, all woody individuals >1.3 m tall were identified, counted, and

[3]National Oceanic and Atmospheric Administration (NOAA), 1997-1999, Local Climatological Data Monthly Summary.

TABLE 1. ABOVEGROUND BIOMASS AND OTHER STRUCTURAL CHARACTERISTICS OF MELALEUCA FORESTS AT THE STUDY SITES. HOLIDAY PARK SITES WERE NON-FLOODED, KROME AND CLEWISTON SEASONALLY FLOODED, AND CONSERVATION AREAS PERMANENTLY FLOODED. DATA ARE MEANS ± STANDARD ERROR OF FOUR 100-M² PLOTS FOR EACH SITE, OR EIGHT PLOTS FOR EACH HABITAT. BIOMASS WAS CALCULATED USING REGRESSIONS ON DBH (VAN ET AL. 2000)

Description	DBH Distribution			Density	Biomass
	< 10 cm	10-20 cm	>20 cm		
By Sites:		(Trees 100m^{-2} plot)		(Trees ha^{-1})	(t ha^{-1})
Holiday Park 1	171 ± 49	19 ± 6	3 ± 2	19225 ± 4559	141 ± 27
Holiday Park 2	192 ± 67	19 ± 5	2 ± 1	21375 ± 6349	146 ± 25
Krome	238 ± 43	36 ± 5	9 ± 4	28225 ± 3635	302 ± 53
Clewiston	82 ± 41	21 ± 8	12 ± 6	11450 ± 4394	294 ± 77
Conservation Area 2B1	331 ± 127	25 ± 8	8 ± 4	36275 ± 11658	265 ± 50
Conservation Area 2B2	242 ± 65	34 ± 3	8 ± 3	28400 ± 6120	304 ± 30
By Habitats:					
Non-flooded	181 ± 39	19 ± 4	3 ± 1	20300 ± 3641	144 ± 17
Seasonally flooded	159 ± 40	29 ± 5	10 ± 3	19837 ± 4125	298 ± 44
Permanently flooded	286 ± 68	30 ± 4	8 ± 2	32337 ± 6274	285 ± 27

their stem diameters at breast height (dbh) recorded. Shrubs and herbaceous cover were also enumerated by species for use in vegetation inventory for the plots.

Aboveground biomass and its distribution (wood, leaves, and reproductive parts) were estimated using least-squares regressions on dbh. The regression equations for total biomass (Van et al. 2000) and biomass components (Rayachhetry et al. 2001) were developed previously using nearby melaleuca trees in the same populations. The regressions were applied to all individual trees in the plot, and the resulting tree weights were summed to determine the estimated values for total biomass and biomass of its components for each sample plot where litterfall data were collected.

Eight litterfall collection traps were placed in randomly selected areas at each of the six study sites. The trap consisted of a square wooden frame (0.5 by 0.5 m) with 16-cm high sides, and a bottom made of fiberglass screen (2-mm mesh) to allow for rainwater drainage. The traps were supported on four wooden legs 70 cm high to raise them above the soil surface and to minimize the decomposition of the litter between collections. At the permanently flooded sites, where water levels fluctuated from 0.3 to 1.3 m during the course of the study, the traps were floated 10 cm above water surface using a capped 3.8-liter plastic jug placed under each of the four corners of the trap, and tied to a nearby melaleuca tree.

The 48 traps were emptied in near-monthly intervals for a period of two years, from July 1997 to June 1999. The collected litter was sorted into the following fractions as recommended by Proctor (1983): leaves, twigs (small wood <1 cm in diameter), bark, bracts, flower parts, fruits (capsules), and trash (insect fecal, unidentified plant parts, etc.). Bracts included both floral and foliar bracts but no attempts were made to separate the two types. Flower parts included stamens and prematurely abscised hypanthiums, and non-developed (aborted) capsules. The fractions were dried to constant weight at 60C and weighed to the nearest 0.01 g. Larger branches (>1 cm diameter) which fell on the traps on a few occasions were excluded from the litter sampling. Litter weights were corrected to monthly intervals in cases where the actual collecting departed from schedule. For the calculations involved, it was assumed that daily litterfall rates did not change during collection intervals.

Phenology of melaleuca was determined by examination of the litter components coupled with monthly field observations. For example, different reproductive structures in the litter traps provided empirical data to support visual field observation on the timing and duration of flowering. Floral bracts shed during the early phase of flowering, generally precede or coincide with peak flowering; whereas the presence of flower parts and aborted capsules in the litter indicates a later phase of flower senescence and early fruit development. Similarly, new shoot growth begins with rapid elongation of leaf buds and the shedding of foliar bracts. Therefore, leaf flush, which usually occurs after flowering, is marked by large amounts of foliar bracts in the litter traps. No attempts were made to separate the two types of bracts due to some overlap in morphology, and complete differentiation was not possible. Examination of bract fall is still useful when coupled with visual field observations of flowering or new shoot growth.

Because of the seasonality in many components of litterfall, there was pronounced heterogeneity in the variances for these data which could not be corrected by transformation. However, when the data for all sampling months in each year were combined, they were homoscedastic enough to allow two-way analysis of variance (ANOVA) involving years and sites or habitats. Further, after no significant differences in total litterfall detected between years, data were pooled and tested for habitat effects using one-way ANOVA.

RESULTS

Biomass. Biomass and other structural characteristics of melaleuca forests at the study sites are presented in Table 1. There was more than two-fold variation in aboveground biomass among the six study sites. When sites were grouped according to habitat categories, biomass in non-flooded habitat (144 t dry wt ha^{-1} yr^{-1}) was significantly lower than in seasonally flooded (298 t ha^{-1} yr^{-1}) and permanently flooded (285 t ha^{-1} yr^{-1}) habitats. These biomass differences were due at least partially to different stand ages, as evidenced by the lower numbers of large (dbh >20 cm) and medium trees (dbh 10-20 cm) at the two sites of the non-flooded habitat (Table 1). Plant densities were high at all sites, ranging from 11450 trees ha^{-1} in Clewiston to 36275 trees ha^{-1} in Conservation Area 2B1. These high density values reflect the presence of numerous juvenile trees (dbh <10 cm) in mature melaleuca stands in South Florida (Table 1). These young saplings represented an average of 80% to 89% of total number of trees, but contributed to less than one-third of total biomass. The presence of high percentages of juvenile trees in the sampling plots suggests a high regenerating capacity by melaleuca in South Florida.

Annual Litterfall. Total litterfall of melaleuca averaged 8.3 t dry wt ha^{-1} yr^{-1} (range 6.5 to 9.9 t ha^{-1} yr^{-1}) during the period from July 1997 to June 1999 at the six study sites in South Florida (Table 2). Litterfall was significantly higher ($P < 0.001$) in seasonally flooded (9.3 t ha^{-1} yr^{-1}) than in non-flooded (7.5 t ha^{-1} yr^{-1}) or permanently flooded (8.0 t ha^{-1} yr^{-1}) habitats (Table 2). Leaf litter comprised the largest fraction, ranging from 63 to 79% with an average of 70% for all habitats. Second was the small wood fraction which accounted for 14 to 18% of the total litter. Reproductive material represented an average of 11% of total litterfall, but this fraction was significantly lower ($P < 0.001$) in non-flooded (5%) compared to seasonally flooded (10%) and permanently flooded plots (16%). Of the reproductive material, 77% consisted of mature capsules, the rest being made up of flowers parts and aborted capsules. Bract biomass, including both foliar and floral bracts, averaged 4% of total litterfall.

Table 3 presents the total amounts of leaves and capsules estimated to be in the canopy, compared to portions falling down as parts of litterfall. In non-flooded habitats, annual leaf litter was equivalent to 53% of the foliage indicating a leaf longevity of about two years. Similarly, leaf longevity of three to four years was estimated for melaleuca in seasonally flooded and permanently flooded habitats, respectively. In contrast, similar calculations indicate that capsules may hold on to a tree for as many as 5 to 10 years (Table 3).

Phenology. All sites displayed similar seasonal patterns of litterfall during the two-year study. During both 1997 and 1998, flowering began in October and November, with peak flower production from November to January, and was mostly completed by February and March (Figure 2). Bract peaks generally preceded or coincided with flower peaks, which in turn preceded the peaks of aborted capsules. The bract fall which occurs after flower peaks represents new leaf flush during the active growth phase. This new shoot growth began in mid winter, immediately after peak flowering, and continued into the spring. New shoots were produced from the apical buds of both flowering and non-flowering branches, but not all apical buds were active in the same season. This period of active shoot growth produced large amounts of leaf bracts in the litterfall samples during the winter and spring months. In contrast, bract fall was very limited or completely absent during the summer months from May to August (Figure 2), indicating very little new growth in melaleuca forests during this time of year in South Florida. On the other hand, the fall of leaves and small wood was recorded in every month, but generally increased during the dry and windy season with higher levels observed from February to April (Figure 3). The peak of leaf fall in October 1998 at several study sites was due to wind storm conditions. The fall of mature capsules was also erratic, but followed closely the fall of small wood (Figure 3). Capsules were recorded in every sample, and probably resulted from the continual self thinning of small branches and twigs inside the melaleuca stand.

DISCUSSION

Studies of melaleuca litterfall in its native range in Australia are limited. Greenway (1994) reported annual litterfall values of 7.6 and 8.1 t $ha^{-1}yr^{-1}$ at two sites of a seasonally inundated *M. quinquenervia* forest in subtropical southeastern Queensland. The author reported 1480 trees ha^{-1} with dbh averaging 18.5 cm at the riparian site; and 2170 trees ha^{-1} with average dbh 17.8 cm at the floodplain site. Leaf fall represented the major component (67%) of the litter, twigs 17%, bark 6%, flowers/bracts 6%, and capsules 5%. Finlayson et al. (1993) investigated litterfall from a mixed stand of *M. cajaputi* and *M. viridiflora* in a tropical floodplain in northern Australia. Combined tree density was 294 ha^{-1}, with dbh of 29 cm for *M. viridiflora* and 34 cm for *M. cajaputi*. The authors reported a total litterfall of 7.2 t $ha^{-1}yr^{-1}$, of which leaf material comprised 70%, twigs 15%, bark 4%, bracts 4%, floral parts 17%, and capsules 3%. This study indicate comparable rates of 6.5 to 9.9 t $ha^{-1}yr^{-1}$ litterfall for melaleuca in South Florida, even with very different plant densities. The high plant densities at our study sites could be an artifact of the stand's ages, as 80 to 90% of the trees in our study were young saplings with dbh <10 cm (Table 1). These juvenile trees contribute little to stand biomass and litterfall. When only large trees with dbh >20 cm were counted, plant densities in our sampling plots (200 to 1200 ha^{-1}) were much more comparable to those reported in the two Australian studies.

TABLE 2. LITTER PRODUCTION (T DRY WEIGHT HA^{-1} YR^{-1}) BY MELALEUCA FORESTS IN SOUTH FLORIDA AVERAGED OVER TWO YEARS, FROM JULY 1997 TO JUNE 1999[1].

Habitats	Leaves	Wood	Bracts	Flowers	Capsules	Total
Non-flooded	5.9 b	1.0 b	0.2 b	0.1 c	0.3 c	7.5 b
Seasonally flooded	6.5 a	1.5 a	0.3 a	0.3 a	0.7 b	9.3 a
Permanently flooded	5.1 c	1.4 ab	0.2 b	0.2 b	1.1 a	8.0 b
Average	5.8 (70%)	1.3 (16%)	0.3 (4%)	0.2 (3%)	0.7 (8%)	8.3

[1]Mean values followed by the same letter within each column do not differ significantly at P = 0.05 as determined by the Waller-Duncan Test.

TABLE 3. COMPARISON OF TOTAL AMOUNTS OF LEAVES AND CAPSULES HELP UP IN THE CANOPY[1], AND PORTIONS OF THOSE FALLING DOWN AS PARTS OF LITTERFALL FROM MELALEUCA IN SEASONALLY FLOODED, NON-FLOODED, AND PERMANENTLY FLOODED HABITATS IN SOUTH FLORIDA.[2]

	Leaves		Capsules	
Habitat	Canopy	Litter	Canopy	Litter
	(t ha^{-1})	(t ha^{-1} yr^{-1})	(t ha^{-1})	(t ha^{-1} yr^{-1})
Non-flooded	11.2 b	5.9 b (53%)	2.9 b	0.3 c (10%)
Seasonally flooded	20.2 a	6.5 a (32%)	5.0 a	0.7 b (14%)
Permanently flooded	21.4 a	5.1 c (24%)	5.4 a	1.1 a (21%)

[1]Calculated using regressions on dbh (Rayachhetry et al. 2001).
[2]Mean values followed by the same letter within each column do not differ significantly at P = 0.05 as determined by the Waller-Duncan Test.

Greenway (1994) observed that melaleuca wetlands produced higher levels of litterfall than many other forest types of the same area, e.g., eucalypt forest (Rogers and Westman 1977), rainforest (Webb et al. 1969), and mangrove forest (Davie 1983) communities in subtropical eastern Australia. Similarly, Finlayson et al. (1993) indicate litterfall from a melaleuca forest in tropical northern Australia is either equivalent to or higher than that in many forests elsewhere in Australia, suggesting that the forest is comparatively highly productive. In a more temperate climate, however, a much lower rate of litterfall (4.3 t ha^{-1} yr^{-1}) was measured for *M. cuticularis* in the marshes of the Blackwood River Estuary in southwestern Australia (Congdon 1979). Furthermore, leaf fall represented a smaller proportion (36%) of the total litter, while 58% was twigs and bark, and 5% flowers and fruits.

Comparisons of litterfall from other forest types in Southern Florida were conducted. Total litterfall of 2.2 to 9.4 t ha^{-1} yr^{-1} was reported for cypress forests (Brown 1981), and 8.8 t ha^{-1} yr^{-1} for a mangrove forest (Odum and Heald 1975). Mitsch and Gosselink (1986) calculated productivity of southeastern United States swamp forests and riparian forests between 0.5 to 1.9 g C m^{-2} d^{-1}, and litterfall between 2.5 to 7.5 t ha^{-1} yr^{-1} for swamp forests and 4.0 to 6.0 t ha^{-1} yr^{-1} for riparian forests. The authors also noted that productivity is generally higher in forests which alternate more frequently between wet and dry conditions compared with permanently flooded or rarely flooded wetlands. Greenway (1994) measured *M. quinquenervia* litterfall from two sites with different water availability regime, and reported higher productivity at the seasonally flooded site. Similarly, riverine forests reportedly produce more litter than upland forests of the same location (Conner and Day 1982, Shure and Gottschalk 1985). In this study, melaleuca forests in the Florida Everglades pro-

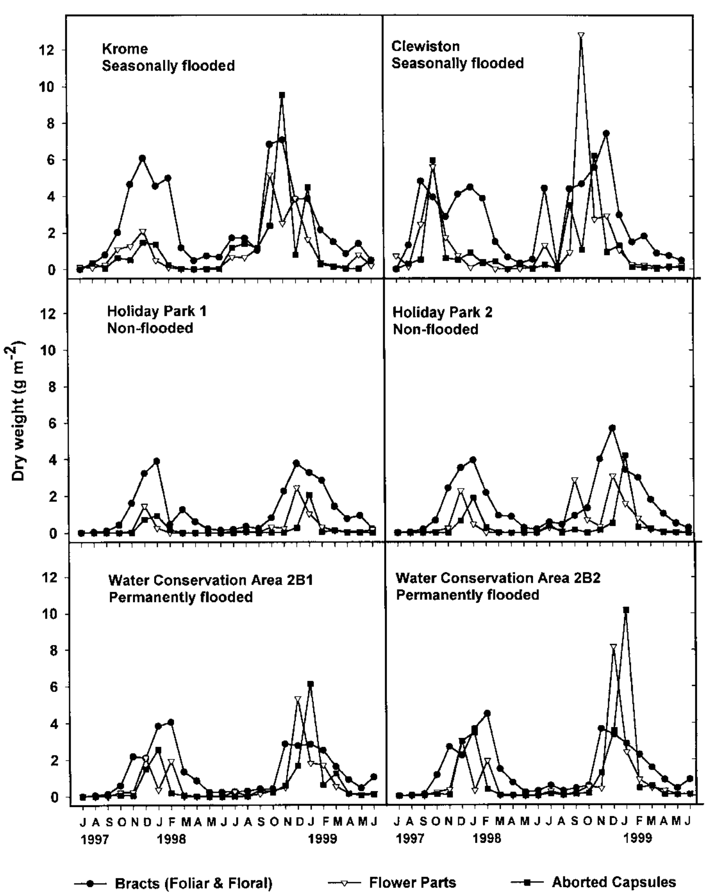

Figure 2. Monthly litterfall of melaleuca at six study sites over two years (July 1997 to June 1999). Data represent the fall of bracts, flower parts, and aborted capsules. Each point represents means of eight litter traps.

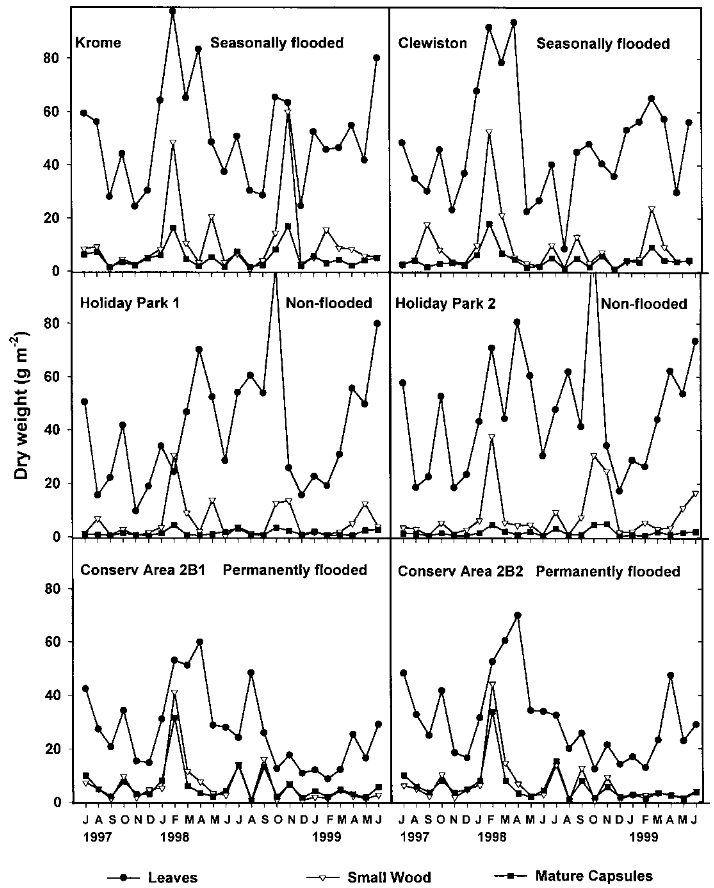

Figure 3. Monthly litterfall of melaleuca at six study sites over two years (July 1997 to June 1999). Data represent the fall of leaves, small wood, and mature capsules. Each point represents means of eight litter traps.

duced significantly more litter at seasonally flooded sites than in non-flooded or permanently flooded sites, although this may be partially due to possible differences in age of the stands. Haase (1999) reported that seasonally flooded evergreen forests in the Pantanal, Brazil produce more litterfall than non-flooded forests in the same study area. The author suggested that, despite seasonal water excess being the prominent feature of the Pantanal, it is water shortage in the dry season that limits forest productivity in the area.

In an analysis of litterfall data from 48 studies in tropical rainforests, Spain (1984) determined that leaf material, on average, comprised 70% of the total dry weight of litterfall. Other studies undertaken in the temperate zone, however, indicated that leaf material did not dominate the weight of litterfall. Congdon (1979) found in a *M. cuticularis* woodland in temperate southwestern Australia that leaves comprised 36%, and twigs and bark 54% of the total weight of litterfall. Similarly, Briggs and Mahler (1983) found leaf material to comprise between 21 to 29% of total litterfall in *Eucalyptus camaldulensis* woodland in southern inland Australia. Twigs made up 19 to 35% and bark 25 to 42% of the total, with the fall of bark positively correlated to wind velocity. Strong seasonal variations in litterfall have been observed in several temperate species (Ashton 1975, Lamb 1985). On the other hand, litterfall in tropical rainforests often does not show the same strong seasonal trend (Bray and Gorham 1964, Spain 1984).

Seasonality of leaf litterfall in a *M. quinquenervia* wetland in Australia has been discussed previously (Greenway 1994). Additional data collection during the period from 1995 to 1999 by the same author (personal communication) together with data from this study indicate that *M. quinquenervia* in South Florida follows similar general patterns of flowering and growth as it does in its native range. In Australia, flowering also occurs from early autumn to late spring. New leaf growth begins mid winter immediately after flowering, and extends into early summer. Additionally, it was observed in Australia that, in seasonally wet years following drought, both flowers and new leaves were produced continuously (Greenway, personal communication). In planning management for perennial weeds, it is important to determine the period during the annual growth cycle of maximum susceptibility to control measures. From these phenological data, we can infer that an appropriate time for melaleuca control in South Florida might be during the spring season, when the plant is most actively growing.

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