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Dry weight estimation of the aboveground components of *Melaleuca quinquenervia* trees in southern Florida

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Abstract

Allometric equations were derived and dry weight distribution was determined for aboveground components (total wood, trunk, branch, leaf, seed capsule, seed) of *Melaleuca quinquenervia* trees in south Florida. Aboveground tree components of 42, 46, and 50 trees, harvested from dry, seasonally flooded, and permanently flooded habitats, respectively, were separated, sorted, sub-sampled, dried to constant weight at 70°C, and weighed. The effects of diameter at breast height (dbh) on dry weight of the aboveground components were significant. Predictive allometric equations were derived for each component using dbh and/or $dbh^2 \times tht$ (total tree height) as predictors. Based on R^2 values the accuracy of the equations for biomass prediction are ranked as, total wood>trunk>branch>leaf>seed capsule>seed. Diameter at breast height alone was a good predictor of dry weight of the aboveground components of trees. When dbh was combined with total tree height, R^2 improved somewhat for all components except for seed capsules and seeds. Proportions of the dry weight of total wood and branch increased, but trunk and leaf decreased as dbh increased. Wood constituted the greatest proportion (83–96%) across the dbh range (0.1–38.6 cm) in all three habitats. Leaves and seed capsules represented a greater proportion of dry weight in permanently flooded habitats (leaves, 10–13%; seed capsules, 3–4%) than in both dry and seasonally flooded habitats (leaves, 4–12%, seed capsules, up to 2%). Overall leaf proportion decreased as dbh increased.

Keywords: Biocontrol; Biomass equations; Everglades; Habitats; Exotic tree

1. Introduction

Melaleuca quinquenervia (Cav.) S.T. Blake (melaleuca) is an invasive tree of Australian origin that has caused adverse economic and environmental impacts in southern Florida (Diamond et al., 1991; O'Hare and Dalrymple, 1997). Melaleuca's biological (Hofstetter, 1991) and silvicultural attributes (Meskimen, 1962) combined with the ambient biophysical conditions prevalent in southern Florida (Myers, 1984), have negative environmental, vegetational, and public health impacts (Di Stefano and Fisher, 1983; Myers, 1984; O'Hare and Dalrymple, 1997). Many agencies are attempting to restore and maintain the ecosystems of southern Florida (Bodle et al., 1994) which requires removal of invasive species. Melaleuca management

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necessitates an integrated control strategy that deploys multiple biological control agents to supplement other environmentally acceptable control methods (Woodall, 1981; Bodle et al., 1994; Turner et al., 1998).

The impact of biological control agents on large, perennial trees is difficult to assess. Any such assessment requires nondestructive methods that measure aboveground components of trees (trunks, branches, leaves, seed capsules, seeds) based on some easily measured morphological parameter. Despite *M. quinquenervia*'s distribution in many parts of the world (Holliday, 1989), a limited number of biomass related studies are reported in the published literature. Conde et al. (1981) developed regression equations for bole, branch, and foliage using trees with smaller dbh (0.2–14 cm) and height (0.7–8.6 m). These equations may have limited use in predicting aboveground biomass of trees in mature stands with larger diameter and height. Additionally, regression equations for predicting quantity of seed capsule and seed biomass are not available. Melaleuca trees in Florida invade dry (no standing water), seasonally flooded (standing water present for weeks to months), and permanently flooded (standing water year round) habitats. Reproductive (seed) characteristics differ among these habitats (Rayachhetry et al., 1998), so allometric distribution of biomass might also differ.

Nondestructive estimation of aboveground biomass components along with litterfall data both before and after deployment of biological control agents, could enable assessment of the effects of these agents on melaleuca. Similar approaches were advocated for evaluating biological control of the invasive shrub, *Mimosa pigra* L. (giant sensitive plant) in Australia (Lonsdale, 1988, 1992; Farrell et al., 1992).

Dependable allometric predictive equations based on easily measurable tree dimensions can estimate these components (Jokela et al., 1986) and have been widely reported (Nemeth, 1973; Jokela et al., 1986; Yamakura et al., 1986; Bartelink, 1996, 1997; Clough et al., 1997; Ter-Mikaelian and Korzukhin, 1997). This study provides (1) dry weight predictive equations for aboveground components of trees (trunks, branches, leaves, seed capsules, and seeds) based on tree diameter at breast height and total tree height and (2) baseline parameters that could be useful in assessing the impact of biocontrol agents on *M. quinquenervia* in southern Florida.

2. Materials and methods

2.1. Description of study areas

In general, Florida experiences humid subtropical climate (Chen and Gerber, 1991). The melaleuca stands used in this study are located in and around the fresh water marshes of the Everglades (Kushlan, 1991) in southern Florida. Soil types in the study areas are dominated by poorly drained organic soils classified as Histosols (Brown et al., 1991). The average monthly temperature and rainfall in the study area ranges from ca. 19°C (January) to 28°C (August and September) and ca. 3 cm (January) to 27 cm (September), respectively (Chen and Gerber, 1991). A gross classification of study sites according to hydrological characteristics and geographic coordinates are provided in Table 1. Study areas contained few plant species other than melaleuca.

Two naturally regenerated, uneven-aged melaleuca stands were selected to represent each of dry, seasonally flooded, and permanently flooded habitats of southern Florida. A 100 m^2 plot was delineated within each stand for sampling purposes. Edge effects were avoided and the diameter range of the trees typical to the site was represented by placing plots near the center of the stand and extending them outwards while avoiding trees along the stand margin. All melaleuca trees $\geq$1.3 m height within each plot were counted, and their diameters at breast height (dbh) were recorded.

2.2. Tree sampling

The numbers and attributes of trees sampled at each site are presented in Table 1. Sample trees were selected to represent the diameter range within each delineated plot and were felled at ground level. Tree height (tht), dbh, and the length and base-diameter of the live crown were measured on each felled tree. The main trunk and branch components were then separated. The trunk was cut into short, manageable segments, weighed fresh, and one segment with associated bark was placed in a paper bag then dried to determine fresh to dry weight ratio. Total branch weight (including branches, twigs, and leaves) was recorded for smaller saplings. A 5 kg random subsample was weighed from larger trees. The branch

Table 1
Site characteristics, locations, and the dimensions of *M. quinquenervia* trees used for the study of their aboveground components in southern Florida

Hydrological characteristics	Sites	Coordinates	Stand density[a]	Trees sampled	dbh[b] (cm) range	Height (m) range
Dry	Tree Top Park	N26°05′ W80°19′	23.8	19	0.1–31.1	1.3–21.0
	Holiday Park	N26°03′ W80°26′	15.8	23	1.3–29.7	3.0–19.3
Seasonally flooded	Thompson Park	N25°55′ W80°27′	28.8	24	0.8–31.2	2.9–13.4
	Clewiston area	N26°47′ W80°57′	10.6	22	0.9–34.3	2.8–25.4
Permanently flooded	Water Conservation area 2B1	N26°13′ W80°24′	132.2	27	0.8–24.6	2.7–9.6
	Water Conservation area 2B2	N26°09′ W80°21′	8.0	23	0.5–38.6	1.6–11.8

[a] Thousand/ha.
[b] dbh=diameter at breast height.

sample or sub-sample was then further separated into bare branch, foliage and seed capsule components, and weighed fresh while at the site. These samples plus the trunk-sample segments were oven-dried at 70°C to a constant dry weight and the fresh to oven-dry weight conversion factor was calculated for each tree. The dry weight of major tree-components (trunk, branch, leaf, and seed capsule/seed) was determined for each sample tree by using the conversion factor.

2.3. Data analyses

Statistical analyses were performed using SAS (1988). Analyses of variance (ANOVA) were performed using nested designs where two sites for each of the three habitats were considered nested within their respective habitat.

The ANOVA and the prediction equations for the aboveground components of trees were developed using the ln-transformed dry weight (kg) of the components of individual trees and their corresponding ln-transformed dbh and height. The relationship between diameter and height with each of the major aboveground components were determined using a linear regression procedures.

Dry weight percentages of the major aboveground components (total wood, trunk, branch, leaf, seed capsule, and seed) were calculated for each tree. As the percentages were continuous (i.e., not binomial or discrete), the data expressed as percentages were analyzed without arc-sine transformation. The data were then analyzed to detect significant differences ($P = 0.05$) in dry matter (weight) among three habitats and diameter ranges within habitat. Linear trends of the dry weight distribution among aboveground components were analyzed for diameter ranges within each habitat.

3. Results

3.1. Allometric relationship

The overall dbh and height relationship was linear as described by the following equation (Eq. (1)) with double logarithmic transformation (ln):

$$\ln(\mathrm{tht}) = 0.4484 + 0.0527\ln(\mathrm{bdh}) \quad (R^2 = 0.79) \tag{1}$$

where tht is the total tree height (m) and dbh is the diameter (cm) at breast height. Diameter at breast height explained about 80% of the variability in tree height. The remaining variability may be attributed to inherent tree, stand (densities and age class distribution), and/or site characteristics (soil and hydrological parameters).

The results of the ANOVA of the effects of habitat on the aboveground components of trees (total wood, trunk, branch, leaf, seed capsule, and seed) are presented on Table 2. In general, the effect of habitat on estimation of the dry weight of all except the branch component was insignificant ($P = 0.05$).

The coefficient of determination (R^2) of the relationship of single and/or combined independent variables (dbh, tht, live crown height, density) on the dry

Table 2
Analyses of variance for the effects of habitat at breast height (dbh) on the allometric relationship of the dry weight (kg) of the aboveground components of *M. quinquenervia* trees in southern Florida

Source	Tree components	d.f.	*F*	PR>*F*
Habitat	Total wood	2	4.4	0.0978
	Trunk	2	4.7	0.0903
	Branch	2	7.3	0.0461
	Leaf	2	0.3	0.7582
	Seed capsule	2	3.1	0.1515
	Seed	2	3.9	0.1141

weight of the major tree components are presented in Table 3. Over 90% variability in the total wood, trunk, branch, and leaf dry weight is explained by ln(dbh). The ln–ln relationships of dbh with the dry weight of the aboveground components are presented in Fig. 1a–f. In general, the natural logarithm of the aboveground components showed a linear relationship with the natural logarithm of the dbh. The following equation describes the general relationship between dry weight of aboveground components of trees and dbh:

$$\ln(y) = y_0 + a\ln(\text{bdh}) \qquad (2)$$

where, y = dry weight of a given component, y_0 = intercept, a = slope, and dbh = tree diameter at breast height. Anti-ln(y)×CF (correction factor) will give the predicted value (kg dry weight) of the component, where, CF is the anti-ln((s.e.e.)^2/2 or the residual mean square error/2) as shown in Sprugel (1983).

The values for the y_0, a, R^2, and standard error estimates (s.e.e.) for each tree component are summarized in Table 4. More than 90% of the dry weight variability in the total wood, trunk, branch, and leaf dry weight is explained by dbh. Similarly, more than 70% of the variability in the seed capsule and seed component was explained by dbh alone.

The following equation describes the general relationship between dry weight of aboveground tree components and dbh^2×tht:

$$\ln(y) = y_0 + a\ln(\text{bdh}^2 \times \text{tht}) \qquad (3)$$

where, y = dry weight of a given component, y_0 = intercept, a = slope, dbh = diameter at breast height and tht = total tree height.

More than 90% of the dry weight variability in the total wood, trunk, branch, and leaf components is explained by the dbh^2×tht (Table 4). However, only 70 and 66% of the variability in the dry weight of seed capsule and seed, respectively, was accounted for by the dbh^2×tht. Generally, the dry weight of all major components increased with increasing dbh.

3.2. Biomass distribution

Habitat did not influence (P = 0.05) the proportion of dry weight as total wood, trunk, and foliage but did

Table 3
Coefficients of determination (R^2) for two-sided ln-transformed equations of independent and dependent (dry weight of tree components) variables of *M. quinquenervia* in southern Florida

Predictors[a]	Aboveground components					
	Total wood	Trunk	Branch	Leaf	Seed capsule	Seed
ln(dbh)	0.96	0.95	0.92	0.90	0.73	0.70
ln(tht)	0.90	0.91	0.81	0.76	0.48	0.44
ln(dbh×tht)	0.98	0.99	0.93	0.89	0.67	0.63
ln(dbh^2×tht)	0.98	0.98	0.93	0.90	0.70	0.66
ln(lcrht)	0.78	0.78	0.73	0.79	0.55	0.51
ln(lcrv)	0.81	0.81	0.77	0.79	0.56	0.53
ln(den)	0.09	0.09	0.07	0.12	0.24	0.22
ln(dbh^2×den)	0.70	0.70	0.70	0.63	0.38	0.37
ln(dbh×tht×den)	0.67	0.67	0.65	0.56	0.28	0.26
ln(dbh×lcrv)	0.91	0.91	0.87	0.88	0.64	0.61
ln(dbh×tht×lcrv)	0.93	0.93	0.88	0.88	0.63	0.59
ln(dbh×tht×lcrv×den)	0.90	0.90	0.86	0.82	0.55	0.52

[a] dbh=diameter at breast height; tht=total tree height; lcrht=live crown height; lcrv=live crown volume; den=tree density.

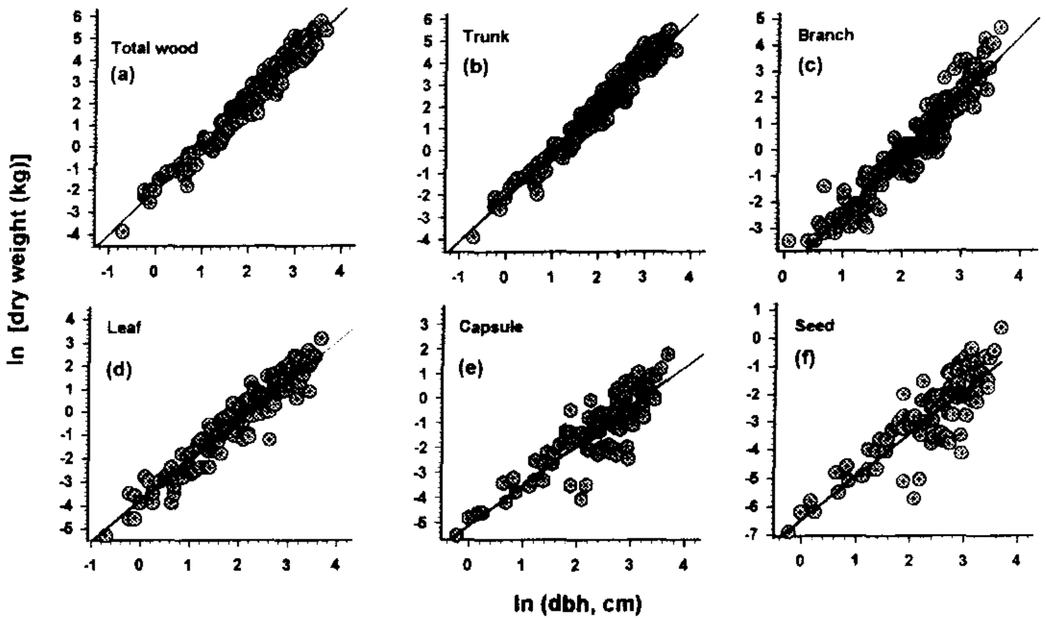

Fig. 1. (a–f) The ln–ln relationship of diameter at breast height (dbh) with the dry weight of the aboveground components of *M. quinquenervia* trees in southern Florida. The solid lines represent the regression functions.

affect branch, seed capsule, and seed components (Table 5). The proportion of the dry weight of the aboveground components of trees by habitat is presented in Table 6. Overall, 62% of the sampled trees (85/138) bore seed capsules. A partitioning of seed capsule-bearing trees by habitat showed 55% (22/42), 46% (21/46), and 84% (42/50) of the trees to be seed capsule-bearing in the dry, seasonally flooded, and permanently flooded habitats, respectively.

For 'all trees' (seed capsule-bearing plus non-bearing), the difference in the proportions of the dry weight of total wood, trunk, branch, and leaf across habitats

Table 4
Equations for predicting dry weight (kg) of the aboveground components of *M. quinquenervia* in southern Florida[a]

Components	n	y_0	a	R^2	s.e.e.
ln(dbh)					
Total wood	138	−2.0163	2.0409	0.96	0.4651
Trunk	138	−2.0889	2.0135	0.95	0.4701
Branch	138	−4.7717	2.2725	0.92	0.6569
Leaf	138	−3.7867	1.7193	0.90	0.5893
Seed capsule	85	−5.1166	1.6034	0.73	0.9008
Seed	85	−6.4857	1.5408	0.70	0.9358
ln(dbh^2×height)					
Total wood	138	−2.8850	0.8134	0.98	0.3118
Trunk	138	−2.9522	0.8035	0.98	0.3052
Branch	138	−5.6634	0.8934	0.93	0.6229
Leaf	138	−4.4692	0.6769	0.91	0.5855
Seed capsule	85	−5.5147	0.6017	0.70	0.9526
Seed	85	−6.8486	0.5753	0.66	0.9918

[a] n=number of sample trees, y_0=intercept, a=slope, dbh=diameter at breast height, R^2=coefficient of determination, and s.e.e.=standard error of the estimate.

Table 5
Analyses of variance showing the effects of habitat on the percentage of dry weight in the aboveground components of *M. quinquenervia* trees in southern Florida

Source	Tree components	d.f.	*F*	PR>*F*
Habitat	Total wood	2	2.8	0.1710
	Trunk	2	3.5	0.1338
	Branch	2	8.9	0.0339
	Leaf	2	1.1	0.4106
	Seed capsule	2	148.5	0.0002
	Seed	2	248.1	0.0001

was not significant (P=0.05) (Table 5). However, the trees in permanently flooded habitats bore significantly greater proportions of seed capsule (3.2%) and seed (0.8%) compared to dry (seed capsule, 0.4%; seed, 0.1%) and seasonally flooded (seed capsule, 0.7%; seed, 0.1%) habitats (Table 6). A similar trend was also observed within the 'seed capsule bearing trees' across three habitats.

Within a given habitat, the percentages of total wood, trunk, branch, and leaf dry weight in corresponding dbh classes in 'all trees' and 'seed capsule-bearing trees' were slightly different (Table 6). The overall proportion of foliage was lower in 'seed capsule-bearing trees' than in 'all trees'.

Trends in total wood, trunk, branch, leaf, seed capsule, and seed proportions among 'seed capsule-bearing trees' are presented by habitat (Fig. 2a–f). The distribution of the dry weight of total wood, trunk, branch, leaf, seed capsule, and seed followed the same trends in both dry and seasonally flooded habitats (Fig. 2a–d). In these habitats, the dry weight proportion of total wood and branch increased but trunk, seed capsule, and seed decreased with increasing tree dbh. In permanently flooded habitats, the dry weight proportion of total wood, leaf, seed capsule, and seed increased but branch decreased with increasing dbh (Fig. 2e and f). In this habitat the proportion of seed capsule and seed increased with increasing dbh decreased with increasing dbh among 'seed capsule-bearing trees'.

The average proportion of foliage among smaller trees (dbh<10 cm) was up to 12% in permanently

Table 6
Distribution of dry weight (%) in the aboveground components of *M. quinquenervia* trees in southern Florida

Components	Habitats		
	Dry	Seasonally flooded	Permanently flooded
All trees	(n=42)	(n=46)	(n=50)
Total wood	91.7 (0.9) a[a]	92.6 (0.4) a	83.7 (0.9) a
Trunk	80.1 (1.2) a	83.0 (0.8) a	74.0 (1.3) a
Branch	11.6 (1.1) a	9.5 (0.7) a	9.8 (0.9) a
Leaf	8.1 (0.9) a	7.5 (0.7) a	12.3 (0.7) a
Seed capsule	0.4 (0.1) b	0.7 (0.2) b	3.2 (0.3) a
Seed	0.1 (0.0) b	0.1 (0.0) b	0.8 (0.1) a
Seed capsule-bearing trees	(n=22)	(n=21)	(n=42)
Total wood	93.4 (0.8) a	92.7 (0.7) a	83.9 (1.0) a
Trunk	79.6 (1.6) a	82.5 (1.1) a	73.5 (1.5) a
Branch	13.8 (1.5) a	10.2 (1.0) a	10.4 (1.0) a
Leaf	5.9 (0.6) a	5.6 (0.5) a	12.0 (0.7) a
Seed capsule	0.7 (0.2) b	1.5 (0.2) b	3.8 (0.2) a
Seed	0.1 (0.1) b	0.3 (0.0) b	0.9 (0.1) a

[a] Means (standard errors) among dry, seasonally flooded, and permanently flooded habitats within a row with the same letters are not significantly different from each other at P=0.05, according to Waller–Duncan's multiple range test.

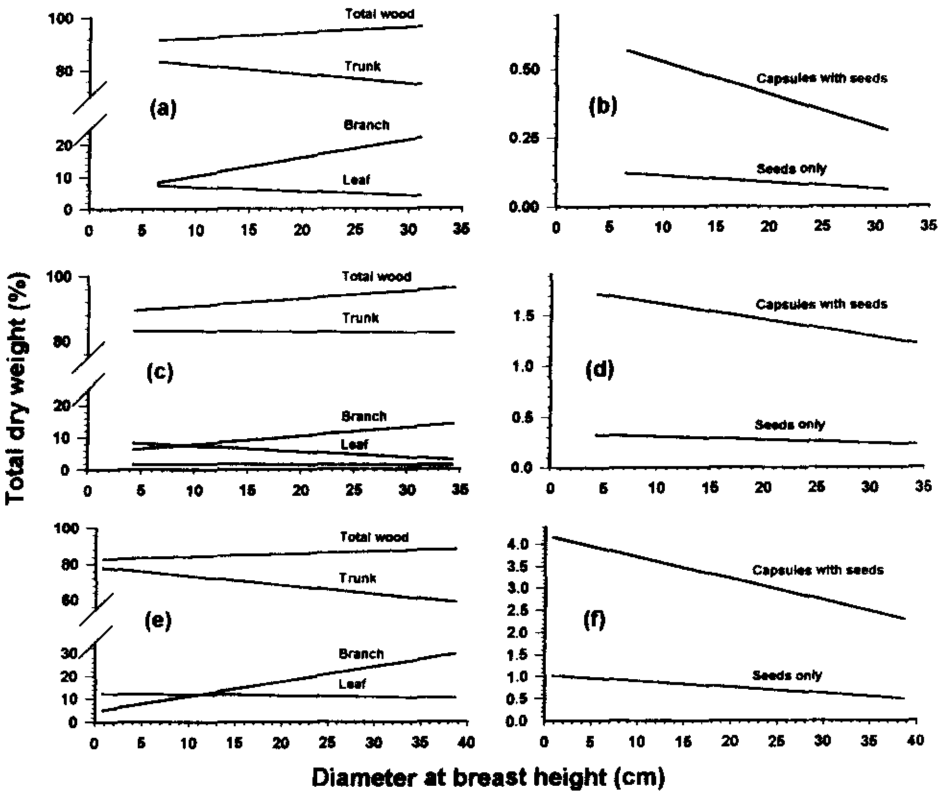

Fig. 2. Dry weight proportions of the aboveground components of seed-capsule bearing *M. quinquenervia* trees, presented by habitats ((a and b) dry; (c and d) seasonally flooded; (e and f) permanently flooded) in southern Florida. N=21, 22, and 42 for dry, seasonally flooded, and permanently flooded habitats, respectively.

flooded and 9% in dry and seasonally flooded habitats (Fig. 2a, c and e). Among larger trees (dbh>30 cm) trees, the proportion decreased to less than 5% in dry and seasonally flooded habitats, but remained greater than 10% in permanently flooded habitats. Smallest dbh of the trees that bore seed capsules varied in three habitats (Fig. 2b, d, and f). Trees with the smallest dbh that bore seed capsules were 6, 4, and 1 cm, in dry, seasonally flooded, and permanently flooded habitats, respectively.

4. Discussion

4.1. Allometric relationship

The amount of the dry weight for aboveground components of standing trees can be estimated non-destructively using appropriate equations for each component or proportional relationships with total biomass previously developed or determined through destructive sampling. Such equations and the proportional relationships are based on easily measured parameters such as tree diameter and/or height. Total tree height and diameter are the most widely used parameters in predicting stem volume, and often are also used singly or in combination to predict tree dry weight (Bunce, 1968). In this study we analyzed the effects of habitat, tree density, diameter at breast height, total tree height, live crown height, and live crown volume (Table 3). The effects of habitat on the aboveground components (total wood, trunk, branch, leaf, seed capsule, and seed) were not significant (Table 2) indicating that a simple general equation developed for each component can be used to predict dry weight of the given component among three habitat types. As single variables, diameter at breast height, total tree height, live crown volume, live crown height, and tree density ranked best to worst in terms of their ability to account for variance in dry weight of the aboveground tree components (Table 2). Diameter at breast height showed higher (above 90% for total, trunk, branch, leaf; and above 70% for seed capsule and seed) correlations (PR>F=0.0001) with aboveground components. Similar types of relationships have also been reported for other species (Nemeth, 1973; Bartelink, 1996; Clough et al., 1997).

In our study, dbh alone was the overall best predictor of total wood, trunk, branch, leaf, seed capsule, and seed dry weight (Tables 3 and 4; Fig. 1a–f) which is in accordance with other species (Jokela et al., 1986). When height was combined with dbh^2 it added very little to the model. The R^2 increased only slightly and the s.e.e. for total wood, trunk, and branch only decreased slightly. However, both R^2 and s.e.e. for both seed capsule and seed components decreased when height was combined with dbh^2 (Table 4).

The relationship between dbh and trunk dry weight is reported to be stand independent for beech (*Fagus sylvatica*) and Douglas fir (*Pseudotsuga menziesii*) since both are cumulative parameters (Bartelink, 1996). In our study both dbh and dbh$^2\times$tht based equations (Table 4) explained over 90% of the variance for total wood, trunk, branches, and leaves of melaleuca in all three habitats. Similar accuracy of predictive equations has been reported for comparable aboveground components in other tree species (Clough et al., 1997). In our study, the equations for the seed capsule and seed components had the largest unexplained variations and standard errors of the estimates.

The addition of the height variable to the model may reduce its practical usefulness since it is difficult and time consuming to measure. Diameter measurement can be accomplished easily and a large number of trees may therefore be sampled to account for possible heterogeneity among forest stands (Bunce, 1968). For this reason, use of tree girth/diameter has been recommended for dry weight distribution in other tree species (Bunce, 1968; Jokela et al., 1986). Therefore, allometric equations based on dbh alone are recommended for predicting the dry weight of the aboveground components of melaleuca trees in south Florida. Equations presented in Table 4 permit estimation of dry weight of the components in both seed capsule bearing as well as non-bearing trees. Total aboveground tree dry weight, if desired, may be estimated by adding the dry weight of components (total wood+leaf+seed capsules).

Other researchers (Sprugel, 1983; Jokela et al., 1986; Yamakura et al., 1986; Bartelink, 1996, 1997; Clough et al., 1997; Ter-Mikaelian and Korzukhin, 1997) have noted that an inherent bias occurs when a linear regression is applied to the ln-transformed data and the predicted values are converted to arithmetic units. Therefore, the predicted dry weight of components for a given dbh or height will not sum up exactly to the predicted total tree dry weight (Jokela et al., 1986). The non-additivity of the components has been attributed to the discrepancies in fitted models for components and total tree dry weight, logarithmic transformation of dependent variables, and missing values in some of the components (Kozak, 1972). Sprugel (1983) suggested the integration of a correction factor to the equation to remove the systematic bias introduced by the use of linear regression to ln-transformed data. Standard error estimates (s.e.e.) as presented in Table 4 and explained in Eqs. (2) and (3) in the results section should be used while estimating the aboveground components of melaleuca in southern Florida.

4.2. Biomass distribution

In general, the major portion of a tree is composed of wood (Yamakura et al., 1986), which in turn, is constituted mainly of the trunk. In our study, the proportional representation of total wood dry weight increased, trunk dry weight decreased, and branch dry weight increased with increasing tree dbh (Fig. 2). In addition to the height, diameter of a tree may be considered to be an indicator of its dominance in a stand, and dominant trees usually occupy larger canopy space due to increased branching (Bartelink, 1997). This is consistent with our results that show an increased proportion of branch dry weight with increasing dbh. On the other hand, the proportion of leaf decreased with increased branching, which is in accordance with other reports on hardwood and coniferous species (Bartelink, 1996, 1997). Leaves on dominant trees are positioned near the end of the branches in order to optimize radiation interception

(Kellomaki et al., 1981). So, more branches are needed to optimize leaf biomass for photosynthate production (Bartelink, 1996).

The seed capsule proportion decreased with increased dbh. Melaleuca capsules are usually borne in series of clusters on the twigs. These are retained several years until the vascular connection between seed capsules and the twig is disrupted (Rayachhetry et al., 1998). As a result, numerous seed capsules are lost as the trees grow. This is reflected as a decrease in capsule proportions with increasing trunk diameter.

Melaleuca trees in permanently flooded sites bore relatively greater proportions of seed capsules compared to dry or seasonally flooded habitats (Table 6). Trees growing in moist environments tended to retain leaves longer than those growing in drier environments. Similarly, the capsules open when the moisture supply is disrupted and are then detached from the twig. Thus, conditions for retaining leaves and seed capsules are more favorable in permanently flooded habitats than in drier habitats.

A general trend of increasing total wood proportion with increasing dbh was observed for melaleuca trees in all three habitats. A similar trend of increased woody materials with increasing tree age has been reported for other tree species (Nemeth, 1973; Clough et al., 1997). Leaf dry weight distribution in dry and seasonally flooded habitats decreased with increasing dbh while it was fairly equally distributed among all dbh classes in permanently flooded habitats. Trees as small as 1 cm dbh bore seed capsules in permanently flooded habitats, whereas, the trees that bore seed capsules in dry and seasonally flooded habitats were at least 4 cm dbh. This suggests that the trees with a given dbh in permanently flooded habitats are either older than those with the same dbh in dry and seasonally flooded habitats, or that trees in the permanently flooded sites are precocious relative to those in dry or seasonally flooded habitats.

This study presents generalized allometric equations to predict the dry weight of aboveground components of melaleuca trees. These equations will be useful in predicting stand productivity over time. In combination with litterfall studies, this will provide a tool for evaluating performance of introduced biocontrol agents. Similarly, if total tree dry weight and/or dbh is known, the dry weight in aboveground components can be estimated by using proportion data provided in Table 6.

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References

Bartelink, H.H., 1996. Allometric relationships on biomass and needle area of Douglas-fir. For. Ecol. Manage. 86, 193–203.

Bartelink, H.H., 1997. Allometric relationships for biomass and leaf area of beach (*Fagus sylvatica* L). Ann. Sci. For. 54, 39–50.

Bodle, M.J., Ferriter, A.P., Thayer, D.D., 1994. The biology, distribution, and ecological consequences of *Melaleuca quinquenervia* in the Everglades. In: Davis, S.M., Ogden, J.C. (Eds.), The Everglades, the Ecosystem and its Restoration. St. Lucie Press, Delray Beach, FL, pp. 341–355.

Brown, R.B., Stone, E.L., Carlisle, V.W., 1991. Soils. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, FL, pp. 35–69.

Bunce, R.G.H., 1968. Biomass and production of trees in a mixed deciduous woodlands. I. Girth and height as parameters for the estimation of tree dry weight. J. Ecol. 56, 759–775.

Chen, E., Gerber, J.F., 1991. Climate. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, FL, pp. 11–34.

Clough, B.F., Dixon, P., Dalhaus, O., 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. Aust. J. Bot. 45, 1023–1031.

Conde, L.F., Rockwood, D.L., Fisher, R.F., 1981. Growth studies on melaleuca. In: Geiger, R.K. (Ed.), Proceedings of Melaleuca Symposium, FDACS Division of Forestry, Tallahassee, FL, pp. 23–28.

Diamond, C., Davis, D., Schmitz, D.C., 1991., The addition of *Melaleuca quinquenervia* to the Florida prohibited aquatic plant list. In: Center, T.D., Doren, R.F., Hofestetter, R.H., Myers, R.L., Whiteaker, L.D. (Eds.), Proceedings of the Symposium on Exotic Pest Plants, 2–4 November 1988. U.S. Dept. Inter., National Park Service, Washington, DC, pp. 87–110.

Di Stefano, J.F., Fisher, R.F., 1983. Invasion potential of *Melaleuca quinquenervia* in southern Florida. U.S.A. For. Ecol. Manage. 7, 133–141.

Farrell, G.S., Wilson, C.Z., Napompeth, B., 1992. Monitoring the biological control of *Mimosa pigra*. In: Harley, K.L.S. (Ed.), A

Guide to the Management of *Mimosa pigra*. CSIRO, Canberra, pp. 63–84.

Hofstetter, R.H., 1991. The current status of *Melaleuca quinquenervia* in South Florida. In: Center, T.D., Doren, R.F., Hofestetter, R.H., Myers, R.L., Whiteaker, L.D. (Eds.), Proceedings of the Symposium on Exotic Pest Plants, 2–4 November 1988. U.S. Dept. Inter., National Park Service, Washington, DC, pp. 159–176.

Holliday, I., 1989. A Field Guide to Melaleucas. Hamlyn Publishing Group, Sydney, Australia, 254pp.

Jokela, E.J., Vangurp, K.P., Briggs, R.D., White, E.H., 1986. Biomass estimation equations for Norway spruce in New York. Can. J. For. Res. 16, 413–415.

Kellomaki, S., Hari, P., Kanninen, M., Honen, P., 1981. Ecophysiological studies in young Scots pine stands: II. Distribution of needle biomass and its application in approximating light conditions inside the canopy. Silva. Fenn. 14, 243–257.

Kozak, A., 1972. Methods for ensuring additivity of biomass components by regression analysis. For. Chron. 46, 402–404.

Kushlan, J.A., 1991. Swamps. In: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, FL, pp. 324–363.

Lonsdale, W.M., 1988. Litter fall in an Australian population of *Mimos pigra*, an invasive tropical shrub. J. Tropical Ecol. 4, 381–392.

Lonsdale, W.M., 1992. The biology of *Mimosa pigra*. In: Harley, K.L.S. (Ed.), A Guide to the Management of *Mimosa pigra*. CSIRO, Canberra, pp. 8–32.

Meskimen, G.F., 1962. A silvical study of the melaleuca tree in South Florida. M.S. Thesis. School of Forest Resources and Conservation, University of Florida, Gainesville, FL, 177 pp.

Myers, R.L., 1984. Ecological compression *Taxodium distichum* var. *nutans* by *Melaleuca quinquenervia* in South Florida. In: Ewel, C., Odum, H.T. (Eds.), Cypress Swamps. University Press of Florida, Gainesville, FL, pp. 358–364.

Nemeth, J.C., 1973. Dry matter production in young loblolly (*Pinus taeda* L.) and slash pine (*Pinus elliotii* Engelm.) plantations. Ecol. Monogr. 43, 21–41.

O'Hare, N.K., Dalrymple, G.H., 1997. Wildlife in southern Everglades wetlands invaded by melaleuca (*Melaleuca quinquenervia*). Bull. Florida Mus. Nat. Hist. 41, 1–68.

Rayachhetry, M.B., Van, T.K., Center, T.D., 1998. Regeneration potential of the canopy-held seeds of *Melaleuca quinquenervia* in south Florida. Int. J. Plant Sci. 159, 648–654.

SAS Institute Inc., 1988. SAS/STAT Procedures Guide, Release 6.03. Cary, NC, 441pp.

Sprugel, D.G., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64, 209–210.

Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manage. 97, 1–24.

Turner, C.E., Center, T.D., Burrows, D.W., Buckingham, G.R., 1998. Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, USA. Wetlands Ecol. Manage. 5, 165–178.

Woodall, S.L., 1981. Integrated methods for melaleuca control. In: Geiger, R.K. (Ed.), Proceedings of Melaleuca Symposium, FDACS Division of Forestry, Tallahassee, FL, pp. 135–140.

Yamakura, T., Hagihara, A., Sukardjo, S., Ogawa, H., 1986. Aboveground biomass of tropical rain forest stands in Indonesian Borneo. Vegetatio 68, 71–82.