

Naturalization and Biomass Allocation of the Invasive Tree *Melaleuca quinquenervia* in Wetlands of the Bahamas

PAUL D. PRATT¹, M. B. RAYAMAJHI¹, C. S. SILVERS¹ AND A. P. FERRITER²

ABSTRACT

The myrtaceous tree *Melaleuca quinquenervia* (Cav.) Blake occurs naturally along Australia's eastern coast and has been internationally disseminated for ornamental and agroforestry purposes. We describe the naturalization of *M. quinquenervia* in the Bahamas and compare stand characteristics to other populations in the exotic tree's native and adventive ranges. Naturalized *M. quinquenervia* stands were assessed at single locations on Grand Bahama, New Providence and Andros Island. We conclude that *M. quinquenervia* is at an incip-

ient stage of invasion at these locations, based on the small spatial distribution of stands and the relatively smaller size class distributions at each site. Densities of the *M. quinquenervia* stands varied dramatically among sites, ranging from 11,800 to 105,800 trees per ha and fell within the range of stands observed in other adventive ranges, including Florida (USA) where the tree is among the most insidious invaders of natural areas. *M. quinquenervia* trees in the Bahamas have greater biomass dedicated to reproductive structures than other adventive ranges. The number of capsular fruit produced per cm of infructescence is similar among adventive ranges but markedly greater in comparison to its native range of Australia. As a result of invasion, native plant diversity was negatively correlated with increases in *M. quinquenervia* densities. Consistent with many plant invasions, the most probable seed sources for these naturalized populations are

¹USDA-ARS, Invasive Plant Research Laboratory, 3225 College Ave., Ft. Lauderdale, FL 33314; e-mail: pratt@saa.ars.usda.gov.

²Boise State University, 1910 University Drive, Boise, ID 83725. Received for publication November 6, 2006 and in revised form December 11, 2006.

nearby ornamental plantings. We predict that timely implementation of appropriate control tactics at this early stage of invasion with adequate follow-up efforts and continued vigilance will greatly enhance the probability of averting a large scale *M. quinquenervia* invasion in the Bahamas.

Key words: Caribbean, exotic plant, invasive weed, paperbark tree, punk tree.

INTRODUCTION

Invasion of natural populations and communities by exotic species is a severe threat to ecosystem integrity (OTA 1993, Wilcove et al. 1998, Myers and Bazely 2003). Invasive alien plants, for instance, threaten native ecosystems by altering hydrological and disturbance regimes, nutrient cycling, energy budgets, and species diversity (Vitousek et al. 1997, Mack 2000). While spread of exotic plants is a global phenomenon, a growing body of literature suggests that oceanic islands are particularly vulnerable to invasions and the resulting ecological impacts (D'Antonio and Dudley 1994, Simberloff 1995, Lonsdale 1999, Denslow 2003, Myers and Bazely 2003, Fornwall and Loope 2004). The susceptibility of islands to invasive plants is particularly concerning when one considers that many of these systems harbor unique floral and faunal assemblages.

The Caribbean islands are recognized as an important center of biodiversity, with approximately 7000 species of endemic plants and 779 endemic vertebrates (Myers et al. 2000, Brooks et al. 2002). Consistent with other island biota, these endemics face habitat loss due to development as well as displacement by introduced species. Forty-two native Bahamian species, for instance, are listed as Threatened according to the International Union for the Conservation of Nature (IUCN) Red List criteria (Baillie et al. 2004). In response to the realized as well as potential impacts of exotic species invasions on the biodiversity of the Bahamas, a pilot project was funded in 2003 by the United States Geological Survey and Inter-American Biodiversity Information Network to disseminate invasive species information regionally. This effort resulted in the development of a National Invasive Species Strategy (NISS) for the Bahamas (Best Commission 2003), which advocates a sequenced approach to invasive species control: prevention, early detection and response, eradication when possible, and control. The NISS also identified priority species for eradication or control, which included the Australian tree *Melaleuca quinquenervia* (Cav.) S.T. Blake.

M. quinquenervia has been internationally disseminated over the course of the last century for ornamental, revegetation, and agroforestry purposes (Turner et al. 1998, Dray 2003, Serbersoff-King 2003). It was introduced into California, Texas, and Louisiana, but has not been reported as an invasive pest in these areas of the United States. In contrast, *M. quinquenervia* was widely planted in Florida and in Puerto Rico (Dray 2003, Pratt et al. 2005b), where the tree has naturalized and proven to be a superior competitor to most, if not all, native vegetation in forested and sawgrass dominated wetlands (Turner et al. 1998, Pratt et al. 2005b). After its introduction in Florida, *M. quinquenervia* spread at an estimated rate of 2850 ha/yr (Laroche and Ferriter 1992) and now dominates ca. 200,000 ha of Everglades ecosystems, with

dense stands of up to 132,000 saplings and trees/ha (Turner et al. 1998, Rayachhetry et al. 2001). These *M. quinquenervia* wetland forests typically form dense monocultures characterized by continuous upper canopies with sparse understories (Rayamajhi et al. 2002a).

While the invasion and negative ecological impacts of *M. quinquenervia* are well documented in Florida and to a lesser degree in Puerto Rico (Serbersoff-King 2003, Pratt et al. 2005b), knowledge concerning the naturalization and performance of the tree in the Bahamian archipelago remains limited (Kairo and Ali 2003). When considering the tree's performance in other environmentally similar habitats, we hypothesized that *M. quinquenervia* is also invasive in the wetlands of the Bahamas. To address this hypothesis, recent aerial and ground vegetation surveys quantified the geographic distribution of several exotic plant species, including *M. quinquenervia*, on Grand Bahama, New Providence, Andros, and the Berry Islands (Ferriter et al. 2006). Occurrence, however, is not sufficient evidence to conclude that *M. quinquenervia* is invasive in the Bahamas. To acquire more convincing evidence of invasion, we questioned 1) if *M. quinquenervia* has developed spatially dominant stands in the Bahamas, 2) if increased stand density is negatively correlated with plant species diversity, and 3) if similar patterns of resource allocation and reproduction exist between populations in the Bahamas and other adventive ranges.

MATERIALS AND METHODS

Study System—The Bahamas are a chain of 700 (25 permanently inhabited) islands and keys located between 21-27° north latitude and 72-80° west longitude. The archipelago extends 970 km on a northwest to southeast axis and totals an estimated land area of 8662 km². Geologically, the islands are composed of aeolian limestone and exhibit minor changes in elevation, with the highest point reaching ca. 60 m. Terrestrial plant communities on larger islands commonly shift from a central ridge to scrub woodland, and finally to a pioneer-dune or mangrove intertidal zone. Despite the geographical proximity of the northern Bahamas with Florida, flora and faunal assemblages most closely parallel those of the West Indies rather than North America (Campbell 1978).

In general, the Bahamas experience distinct wet and dry seasons with warm temperatures year round. The average low temperature in January is 18.3°C, the average high 25.0°C, and average precipitation 3.6 cm. In August, the average low temperature is 24.4°C, the average high is 31.7°C, and average precipitation is 13.5 cm. The mean annual rainfall is 121.6 cm, with 63.5 percent falling in June through October, based on 35 year normals for the period of 1930 to 1965 (Muller 1982).

Study Species—In its native range, *M. quinquenervia* occurs along Australia's northeastern coast from Sydney in New South Wales to the tip of Cape York Peninsula in northern Queensland, in New Guinea, and in New Caledonia (Boland et al. 1987). It is the southern-most representative of the *M. leucadendra* complex which is comprised of 15 closely related species with a center of diversity in tropical Queensland (Craven 1999). It occurs in coastal wetlands, typically in freshwater "paperbark swamps" which often occupy sandy

soils behind heath-dominated headlands as well as along streams and in brackish water behind mangrove swamps. Most melaleuca habitats are threatened by development in Australia, being located in highly desirable coastal areas of low topography, high rainfall, and mild climate (Boland et al. 1987, Turner et al. 1998).

Multiple introductions of *M. quinquenervia* seeds were made on both the eastern and western coasts of South Florida, resulting in highest concentrations of the weed along the coastal areas south of the northern rim of Lake Okeechobee. In Florida, synchronized flowering events occur during winter (dry season) although some *M. quinquenervia* trees reproduce at unpredictable intervals (Meskimen 1962). Inflorescences are indeterminate, 2 to 5 cm long, and arranged in bottlebrush-like spikes (Holliday 1989). Persistent capsular fruits arise from flowers and are arranged in a series of clusters, which may remain attached to the trunks, branches, or twigs for several years (Meskimen 1962). For the purposes of this study, the most distally located capsule clusters are referred to as first clusters, with subsequent proximal clusters described as second, third, etc. A flower spike in its adventive range can produce 30 to 70 sessile capsules and up to seven consecutive capsule clusters (which may or may not be separated by series of leaves) have been recorded from *M. quinquenervia* branches (Rayachhetry et al. 1998). These serotinous capsules release seeds when vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (Woodall 1982). Capsules contain 200 to 350 seeds each (Meskimen 1962), yet only 9 percent of these seeds are viable (Rayachhetry et al. 1998). A mature tree (38 cm diameter at breast height and 12 m tall) has a canopy that may hold up to 1.4 kg of seeds (about 56 million seeds, Rayamajhi et al. 2002b). Because of the massive seed release from mother trees, dense, even-aged, monospecific *M. quinquenervia* stands are common (Hofstetter 1991, Van et al. 2000).

Experimental Design—Naturalized populations of *M. quinquenervia* in the Bahamas were first surveyed from systematic reconnaissance flights or ground assessments in 2004 by a team that included Bahamian, U.S. and non-governmental agencies (Ferriter et al. 2006). These efforts resulted in the enumeration of multiple populations of the tree on three islands: Grand Bahama, New Providence and Andros (Figure 1). Tree occurrences were categorized as individual trees (outliers), low density stands (less than 75% stocked) or dense stands (greater than 75% stocked). We selected one dense stand from each of the three islands to carry out a more detailed characterization of the naturalization of *M. quinquenervia* in the Bahamas.

We quantified the density and size-class distribution for each selected *M. quinquenervia* population by establishing randomly located plots within each study population during December 2005. The number and dimensions of study plots varied according to stand size, demographics, and spatial limitations. At the Rocky Creek site (N 26.65899, W - 78.00917) on Grand Bahama, three stratified 9 m² study plots were delineated along each of three transects (n = 9 plots) that originated near the center of the stand (largest trees) and extended to the stand edge (Van et al. 2002, Pratt et al. 2004, Pratt et al. 2005b). Three 9 m² plots were randomly de-

linedated within the relatively smaller stand near the Nassau airport (N 25.05827, W -77.45352) on New Providence. Due to the range in size classes and related labor, a single 50 m² plot was delineated at the Andros Town site (N 24.71348, W - 77.79996) on Andros Island to quantify parameters from predominately larger trees while three additional 1 m² sub plots were arranged near the main plot to assess seedling recruitment. The stem diameter at the soil line, the diameter at breast height (DBH, = 1.3 m), and the presence of capsule clusters for each individual was recorded. Basal area was calculated for each plot by summing all *M. quinquenervia* stem diameters measured at the soil line. All other vegetation occurring in the sample plots was tallied by species and percent coverage was recorded for both arboreal canopy and understory strata. Plant species diversity within each of the nine plots at the Rocky Creek site was estimated using the Shannon-Weiner diversity index (H'). According to Magurran (1988), the index is calculated as:

$$H' = \sum p_i \ln p_i,$$

where the quantity p_i is the proportion of individuals found in the i th species. In addition, Simpson's index (D), which is weighted towards the most abundant species, was estimated as:

$$1/D = \sum \frac{n_i(n_i - 1)}{N(N - 1)},$$

where n_i is the number of individuals of the i th species and N is the total number of individuals in the study plot (Magurran 1988). Comparisons of indices among plot locations were analyzed with ANOVA and means were compared with a Tukeys HSD test. Inferences from these analyses are based on the assumption that all study plots at the Rocky Creek site were equally vulnerable to invasion. This assumption was not considered valid at other study sites due to a patchwork of human disturbance and natural barriers so assessments were restricted to the Rocky Creek population.

Plant biomass allocation was quantified at each stand by cutting trees at the soil level, measuring tree height, live crown height, and separating the main trunk and branch components: branches, twigs, leaves, and capsule clusters. From 20 to 35 trees were harvested at each site. Trees were randomly selected for biomass sampling from within all diameter classes with a goal of representing the whole range of stem diameters present within the stands. Each component for all trees was weighed in the field to obtain fresh weights (FW). Final dry weights (DW) were calculated from DW to FW ratios developed by Van et al. (2000) and Rayachhetry et al. (2001) for Florida populations of the tree. We tested the assumption that DW:FW ratios were similar between Florida and Bahamian populations by drying small quantities of the leaf and trunk biomass fractions of six randomly selected trees. The DW:FW ratios for the Bahamian populations were compared to Florida ratios reported in the literature (Van et al. 2000, Rayachhetry et al. 2001).

Dry weights for partitioned components of each tree, as well as the corresponding explanatory variables, were log transformed (double-sided natural logarithm) to account for

non-constant variance, thereby converting the exponential model to a linear relationship (Baskerville 1972, Sprugel 1983, SPSS 1999). Other researchers have noted (Sprugel 1983, Yamakura et al. 1986, Rayachhetry et al. 2001) 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. Sprugel (1983) suggested the integration of a correction factor to the biomass equation as a means of removing the systematic bias introduced through transformation. Therefore, the back-transformed (anti-ln(y)) data were multiplied by the correction factor anti-ln(standard error)²/2 to adjust for inherent biases of the transformation as shown in Sprugel (1983).

Previous assessments of biomass allocation were based on trees measuring ≥ 1.3 m in height (see Van et al. 2000, Rayachhetry et al. 2001). However, this approach neglects smaller individuals from analyses and complicates comparisons among populations dominated by individuals of this transitional life stage. Herein, we quantified DBH and diameter at tree base (= soil line; DAB), the latter providing a more universal independent variable for biomass predictions. In addition, we evaluated a "combined" independent variable that is based on DBH but incorporates DAB when trees are < 1.3 m. Linear regression and coefficients of determination (R^2) were used to compare the predictability of independent variables. Differences in plant partitioned biomass among sites were compared with ANCOVA, with tree diameter as the covariate (SAS Institute 1999). International comparisons of biomass allocation were based on pooled data from four sites in Florida (Holiday Park, Thompson Park, Lake Okeechobee, Tree Tops Park) and multiple sites from eastern Queensland and New South Wales Australia, as reported by Rayachhetry et al. (2001, 2002). These data were compared to Bahamian populations with ANCOVA. Natural log transformed DBH was used as the independent variable for Florida data, as DAB was not noted during original data collection (Rayachhetry et al. 2001). Due to the rank, columnar growth of *Melaleuca*, however, differences between DAB and DBH decrease as tree size increases. For the Florida population, with an average diameter at breast height of 12.2 cm (SE 9.6), we assumed DAB and DBH were synonymous, as indicated by Van et al. (2002) and Pratt et al. (2005b).

Reproductive characteristics of naturalized *M. quinquenervia* trees were investigated at each site. Between 30 and 74 capsule clusters were randomly harvested at each site and the capsule cluster length as well as the number of capsules per cluster was recorded. We compared seed quality between capsule cluster positions by randomly removing a single capsule from four replicate clusters located in the first through fifth positions, respectively. A single hardened and seemingly mature capsule was collected per tree. Harvested capsules were placed into individual vials, transported to the laboratory and began to release seeds three days after collection. Seed parameters were assessed by evenly spreading the seeds from each capsule into individual petri dishes (5-cm diam; Microfiltrations Systems, Dublin, Calif.) containing a sterile filter paper as described by Rayamajhi et al. (2002b). Filter papers were soaked with 1.5-2 mL of 1 percent 2,3,5-triphenol tetrazolium chloride (TTC; Sigma Chemical Co., St. Louis), leaving a film of liquid on the surface. The dishes were closed and sealed

with Parafilm®, wrapped in aluminum foil and placed in a dark cabinet drawer for 20 d at ambient conditions (21-28°C). Filled (embryonic) *M. quinquenervia* seeds appear dark (non-transparent) when viewed with back lighting. However, seeds with living, respiring embryos stained red after soaking in TTC and were considered viable while non-viable seeds remained white to light pink (Grabe 1970, Rayachhetry et al. 1998). Seeds were considered germinable if they possessed an emerging radicle. Capsule cluster and seed characteristics from Bahamian populations were compared to those from adventive and native ranges as reported by Pratt et al. (2005b). Comparisons of measured parameters among sites were analyzed with ANOVA and means were compared with a Tukey HSD test.

RESULTS

Early citations of *M. quinquenervia* in the Bahamas date back to the late seventies and early eighties, when Campbell (1978) and Correll and Correll (1982) reported that the distribution of the Australian tree was limited to the northern islands, including Exuma north to Grand Bahama. Campbell (1978) subsequently described *M. quinquenervia* as the "most insidious of the exotic Bahamian plants" and reported its establishment in "several swampy areas of New Providence." These statements suggest that the exotic tree was introduced to New Providence well before 1978 and original introductions probably coincided with other Caribbean importations of the plant decades prior to the earliest published reports (Britton and Wilson 1926, Little and Wadsworth 1964, Pratt et al. 2005b). Further investigations of records at the Nassau Botanical Gardens and various herbaria (BNH, INB, JBSD, UPRRP, NY) did not elucidate additional records documenting the occurrence of *M. quinquenervia* in the Bahamas.

Naturalized *M. quinquenervia* populations were studied in detail at a single location on each of Grand Bahama, New Providence and Andros Island (Figure 1). The Grand Bahama site was located near the Rocky Creek settlement, where *M. quinquenervia* has invaded the swashland between the beach dunes and the higher elevation pine flatwoods. Long hydroperiods and outcrops of weathered oolitic limestone characterize the site. The stand follows the shoreline east to west and is concentrated over a 4 ha area with isolated individual trees dispersed in the vicinity. The stand is characterized by a dominance of trees in an early reproductive stage at a density of 9.25 trees/m² (SD = 3.52) and an average DBH of 1.55 cm (SD = 0.61; DBH range = 15.6 to 0.1 cm). Capsule clusters were present on 39.5 percent of the trees, with 90 percent of individuals < 5 cm at DBH. Although they did not fall within our sampling plots, large trees measuring > 45 cm DBH were located near the beach.

Species diversity was negatively correlated with increases in *M. quinquenervia* densities (Table 1). Study plots on the edge of the invasion front contained the greatest number of species and those near the stand's center had the lowest, with central plots intermediate (Table 1). In plots with few to no *M. quinquenervia*, the understory vegetation was dominated by *Cladium jamaicense* Crantz (25.63%), *Serenoa repens* (Bartr.) Small (20.70%), *Conocarpus erectus* L. (18.23%) and *Chrysobalanus icaco* L. (14.47%), with the remaining species covering < 5 percent of the plots. Central plots, where vegetation tran-

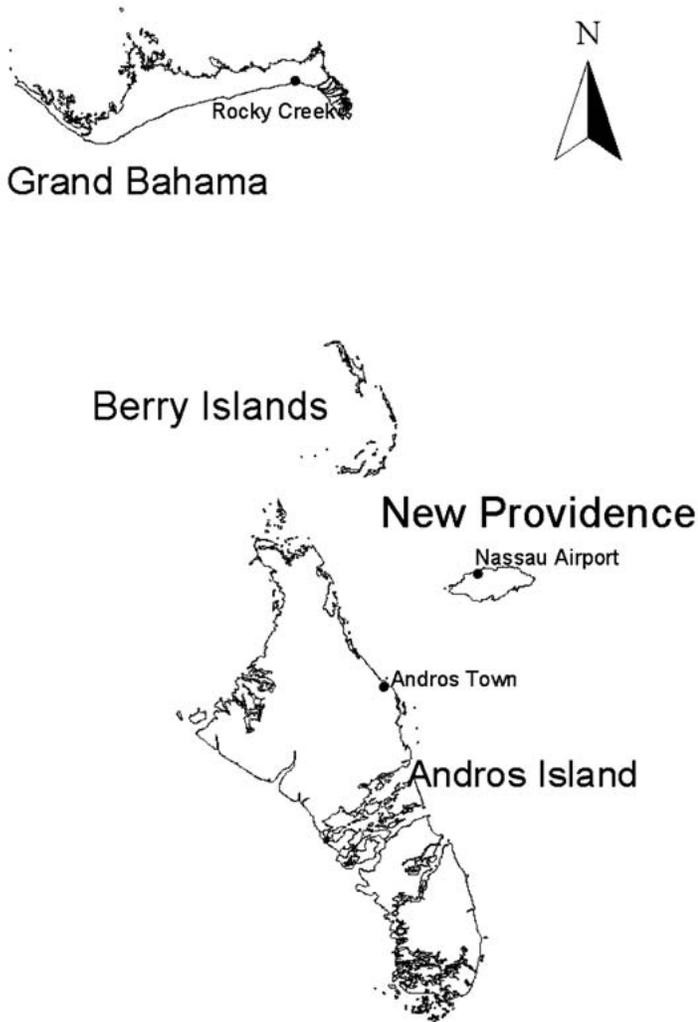


Figure 1. *Melaleuca quinquenervia* study sites in the northern Bahamas.

sitioned between undisturbed native vegetation and heavily invaded areas, were again dominated by *C. jamaicensis* (47.13%) and *C. erectus* (16.67%), but no other species covered >5 percent of the area except for *M. quinquenervia* (23.33%). Near the stand's center, *M. quinquenervia* occupied 60.0 percent of the plots and *C. jamaicensis* covered 30.33 percent with the remaining species representing <2 percent coverage each. A regression of species diversity and a measure of tree's abundance, the basal area, indicate that an increase in *Melaleuca* basal area of 50 cm resulted in a decrease in 2.15 species per plot ($= 9 \text{ m}^2$; $F_1 = 11.01$, $P = 0.0128$, $R^2 = 0.61$).

The second *M. quinquenervia* study site was located near the Nassau airport on New Providence. At this location, the *M. quinquenervia* population has invaded 1.3 ha of the *S. repens* dominated pine flatwoods. Widely dispersed reproductively mature trees and a predominance of smaller diameter saplings and early reproductives characterize the stand. Tree density was 10.56 stems/ m^2 ($SD = 4.62$) and an average DBH of 0.91 cm ($SD = 0.15$; range = 10.73 to 0.08), with 25.3 percent of the trees possessing seed capsules. While the arboreal stratum was dominated by *M. quinquenervia* (41%), other tree species also occurred within the stand, including the

exotic *Casuarina equisetifolia* L. (1%) and the native *Pinus caribaea* (2.66%). The dominant understory species was also *Melaleuca* (55.67%), followed by *S. repens* (18.33%), *C. jamaicensis* (12.66%) and *Myrica cerifera* L. (10%); the remaining species covering <5 percent of the stratum.

The third *M. quinquenervia* study site was located near the Andros Town airport on Andros Island. The area was originally slated for development in the 1960s but efforts were abandoned after initial clearing of roads and partial dredging of canals that feed into Fresh Creek. Oolitic limestone outcrops, shallow sandy soils, and a short hydroperiod characterize the site. The invasive tree is distributed over 16 ha at a total tree density of 1.18 stems/ m^2 ($SD = 0.56$; Table 1), with 64 percent bearing capsule clusters. A subset of this area dominated by seedlings, however, support densities of 725 ($SD = 306$) individuals/ m^2 and a mean diameter at soil level of 2.06 mm ($SD = 0.51$). Consistent with the previous locations, *M. quinquenervia* was the dominant arboreal species, covering 44 percent of the canopy stratum and 35 percent of the understory. Other shrub or tree species observed within the stand included *P. caribaea* and *Metopium toxiferum* (L.) Krug and Urban, each representing <5 percent of the arboreal coverage. In plots dominated by seedlings, *M. quinquenervia* (46%) constituted the largest proportion of the understory vegetation, with other taxa representing minor components of this stratum, particularly grasses (10.5%) of several genera and *Waltheria indica* (L.) (2.75%).

Comparisons between DW:FW ratios for Florida versus Bahamian *M. quinquenervia* populations indicated no difference for leaf ($df_{1,11}$, $F = 2.77$, $P = 0.1302$) and trunk fractions ($df_{1,11}$, $F = 0.02$, $P = 0.8997$). Dry weights, therefore, were calculated by multiplying fresh weights by their corresponding DW:FW ratios derived from Florida data. The coefficients of determination for the regression of independent variables on dry weight of plant partitioned biomass are presented in Table 2. DAB explained >90 percent of the variability for tree height and total biomass, where as DBH alone and the combination of DBH and DAB were less predictive.

Plant partitioned biomass was similar among Bahamian populations, except for leaves and seed capsules (Table 3). Foliar biomass for the Rocky Creek population on Grand Bahama was lower than the remaining sites tested and no differences were detected among the other Bahamian populations. Seed capsule biomass was greatest for the Andros Town population; no differences were observed between the Rocky Creek and Nassau trees. However, the actual number of capsules per tree was not influenced by site (Table 3). Florida trees were taller, which may account for differences in biomass fractions (Table 4). In contrast to this trend, however, greater reproductive biomass occurred on Bahamian *Melaleuca* trees as compared to those on the mainland (Table 3). The overall relationship between DAB and total above ground dry biomass for the combined Bahamian population is best described by:

$$\ln(\text{total biomass}) = 2.3879(\ln(\text{DAB})) - 1.1283 \quad (R^2 = 0.96).$$

The number of capsules within a cluster was greater in the tree's adventive range, with the exception of the Rocky Creek population (Table 4). Among the invasive populations, capsules per cluster were similar for trees of the Bahamas and

TABLE 1. INVASION OF *M. QUINQUENERVIA* REDUCES PLANT DIVERSITY IN SWATHLANDS NEAR ROCKY CREEK, GRAND BAHAMA. LOCATION REFERS TO THE POINT ALONG THE RANDOMLY PLACED TRANSECT, FROM NEAR THE STAND CENTER TO THE ADVANCING EDGE OF THE POPULATION. VALUES REPRESENT AVERAGES (STANDARD ERRORS). DIFFERENT LETTERS INDICATE SIGNIFICANT DIFFERENCES BETWEEN TREATMENT MEANS ($P < 0.05$; TUKEY'S HSD).

Location	<i>Melaleuca</i> density ^a	Species richness	Species diversity	Dominance
Invasion front	2.67 (2.67)	13.67 (2.33) a	1.93 (0.20) a	4.89 (1.24)
Mid section	64.33 (24.17)	9.67(1.20) ab	1.39 (0.09) ab	2.83 (0.15)
Stand center	74.67 (18.81)	4.00 (0.58) b	0.88 (0.13) b	2.11 (0.28)
<i>p</i> -value	0.0566	0.0129	0.0061	0.0863

^aIndividuals per plot (=9 m²).

numerically, if not statistically, larger in Puerto Rico and Florida (Table 4). The length of the capsule clusters, in contrast, was similar for all populations (Table 4). However, *M. quinquenervia* trees in adventive ranges possessed infructescences with higher capsule densities (number/cm) than those sampled in the tree's native range. The average number of seeds per capsule did not differ when comparing native versus adventive ranges (Table 4). Comparisons within Bahamian populations indicated seed number per capsule was ~15 percent greater for Andros Town populations than trees growing at the other two sites ($df_{2,58}$, $F = 5.74$, $P = 0.0053$), although the biological relevance of this difference is questionable. Position of the capsule along the branch axis (indicating relative differences in age) did not influence seed quantities when compared between ranges (seed per capsule*location: $df_{12,535}$, $F = 1.41$, $P = 0.1562$), or when pooling data across all ranges ($df_{4,535}$, $F = 0.04$, $P = 0.9969$). Seed quality varied by site (Table 4). The percentage of seeds containing embryos was greatest for trees growing at the Rocky Creek sites, lowest for the Australian population and intermediate for the other locations. Seed viability and germination, in contrast, were higher for seeds derived from the Florida population as compared to all other sites (Table 4).

DISCUSSION

A growing body of literature suggests that the probability of establishment and spread of an exotic plant is related, in part, to its performance in other climatically similar ranges (Reichard and Hamilton 1997, Kolar and Lodge 2001, NAS 2002, Daehler et al. 2003). *Melaleuca quinquenervia* has proven to be one of the most pernicious invasive plants in South Florida (Bodle et al. 1994, Turner et al. 1998, Rayamajhi et al. 2002a),

with cumulative control costs reaching in excess of 30 million \$US and estimates of losses to the local economy as a result of this invasion ranging as high as 168.6 million \$US per year (Diamond et al. 1991). When considering its invasion of the nearby mainland (<150 km) and the ecological similarities between the Bahamas and Florida, it is not surprising that *M. quinquenervia* has also naturalized in wetlands of the archipelago. The magnitude of invasion, however, appears to be limited geographically and suggests that *M. quinquenervia* is at an early stage of invasion in the northern Bahamas. Evidence to support this inference includes the small spatial extent of stands relative to the suitable habitat in their immediate vicinity. At the Rocky Creek site, for instance, hydric soils dominated by *C. jamaicense* and *C. erectus* extends in all directions of the existing *Melaleuca* stand, all of which is predicted to be susceptible to invasion. We hypothesize that expansion rates from these and other incipient *M. quinquenervia* populations will accelerate over time if not controlled (Ferriter et al. 2006). Experience suggests that timely implementation of appropriate control tactics at this early stage of invasion with adequate follow-up efforts and continued vigilance will greatly enhance the probability of averting a large scale *M. quinquenervia* invasion in the Bahamas.

The rapid spread and subsequent ecological impacts of *M. quinquenervia* in Florida are often attributed to the tree's formidable reproductive potential (Rayamajhi et al. 2002a). When comparing resource allocation between adventive ranges, however, trees in the Bahamas have greater biomass dedicated to reproductive structures than those in Florida (Table 3, Figure 2). These data also indicate that trees in the Bahamas begin reproducing at a smaller, and presumably younger, stage (Figure 2). This conclusion may be biased by the lack of data for Florida trees <1.3 m tall, although it is un-

TABLE 2. COEFFICIENTS OF DETERMINATION (R^2) FOR TWO-SIDED LN-TRANSFORMED EQUATIONS OF INDEPENDENT VARIABLE AND BIOMASS ALLOCATION OF *M. QUINQUENERVIA* GROWING IN THE BAHAMAS AND FLORIDA, USA. N/A INDICATES THAT SIMILAR DATA WERE NOT COLLECTED FOR THE FLORIDA POPULATIONS.

Predictor	Biomass								No. of capsule clusters
	Height	Crown height	Total	Trunk	Branches	Twigs	Leaves	Capsules and seed	
Bahamas									
ln(dbh)	0.72	0.43	0.78	0.80	0.53	0.74	0.64	0.46	0.41
ln(dab)	0.93	0.82	0.96	0.98	0.58	0.93	0.94	0.65	0.55
ln(combined)	0.77	0.64	0.82	0.84	0.58	0.79	0.78	0.62	0.54
Florida									
ln(dbh)	0.87	N/A	0.97	0.97	0.81	0.83	0.85	0.52	N/A

TABLE 3. BIOMASS ALLOCATION OF DRY WEIGHT COMPARISONS FOR ABOVE GROUND COMPONENTS OF *MELALEUCA QUINQUENERVIA* OCCURRING ON THREE ISLANDS IN THE BAHAMAS AND MAINLAND FLORIDA. VALUES REPRESENT LOG TRANSFORMED LEAST SQUARE MEANS (STANDARD ERRORS) FROM ANALYSIS OF COVARIANCE, WHERE TREE DIAMETER AT BASE IS THE COVARIATE. DIFFERENT LETTERS FOLLOWING VALUES WITHIN ROW INDICATE SIGNIFICANT DIFFERENCES ($P < 0.05$; LSD). N/A INDICATES THAT SIMILAR DATA WERE NOT COLLECTED FOR FLORIDA POPULATIONS.

Parameter	The Bahamas				p-value
	Rocky Creek	Nassau Airport	Andros Town	Florida	
Height	2.50 (0.02) a	2.46 (0.02) a	2.43 (0.02) ab	2.87 (0.01) c	<0.0001
Crown height	1.85 (0.05) a	1.87 (0.04) a	2.09 (0.03) b	N/A	0.0014
Total biomass	2.98 (0.05) a	2.91 (0.05) a	3.00 (0.04) a	3.71 (0.03) b	<0.0001
Trunk	2.79 (0.04) a	2.73 (0.04) a	2.77 (0.04) a	3.61 (0.10) b	<0.0001
Branches	1.31 (0.19) a	1.34 (0.20) ab	1.28 (0.17) a	1.76 (0.10) b	0.0021
Twigs	1.82 (0.07) a	1.81 (0.07) a	1.90 (0.06) a	2.40 (0.01) b	<0.0001
Leaves	1.98 (0.06) a	2.18 (0.06) b	2.27 (0.06) b	2.57 (0.03) c	0.0003
Capsules + seeds (g)	1.20 (0.21) a	1.23 (0.21) a	1.78 (0.18) b	0.70 (0.11) c	0.0349
No. of capsule clusters	1.03 (0.20)	0.87 (0.17)	1.23 (0.14)	N/A	0.0781

likely as only a small proportion (0.09) of the trees <1.3 m possessed capsule clusters in the Bahamas. These results lend additional support to the hypothesis that *M. quinquenervia* is well poised for a large scale invasion of the Bahamas. Our findings also support previous reports that capsule cluster length, in contrast, is similar between adventive and native ranges studied herein (Table 4). We conclude that resource allocation, as indicated by infructescence length, is similar among native and adventive ranges but the realization of this allocation (seed production) is greatly reduced in Australia.

Commonly cited examples of invasive plants altering species diversity are typically blanket invaders that form large monospecific stands (Mack 2000, Myers and Bazely 2003). The ecological impacts of these invaders are visually dramatic but difficult to quantify as pre-invasion data and disturbance histories are rare. *M. quinquenervia* forms dense monospecific stands and is considered by the Florida Exotic Pest Plant Council as a Category I species, a designation for weeds that are “displacing native plants or otherwise disrupting the natural community” (Langeland and Burks 1998). However, evidence from the scientific literature documenting species displacement by *M. quinquenervia* is limited (Mazzotti et al. 1981, O’Hare and Dalrymple 1997). Herein we document a negative correlation between the diversity and richness of native Bahamian wetland plant species and increasing *M. quinquenervia* density (Table 1). Based on the assumption that all study plots at the Rocky Creek site were

equally vulnerable to invasion, these data also indicate that *M. quinquenervia* is competitively superior to the native flora encountered thus far.

Frequency and intensity of disturbance influences recruitment and spread of *M. quinquenervia* (Rayamajhi et al. 2002a). Signs of fire, including scorched bark of large trees, were observed at each site. As a fire-adapted species with multilayered insulating bark, mature *M. quinquenervia* trees rarely suffer mortality from such disturbances. Fires of sufficient intensity, however, induce a massive seed rain from the canopy-held capsule clusters, resulting in high levels of recruitment under suitable hydrological conditions. Seedling densities at the Andros Town site, for instance, are comparable to the highest population densities of the invasive tree in Florida (Franks et al. 2006). The presence of numerous juvenile trees (DBH ≤ 5 cm) occurring on the invasion front of the Bahamian populations studied herein underscores the high regenerative capacity and invasion potential of *M. quinquenervia* under these periodic disturbance regimes.

The use of a single, easily obtained plant parameter for the prediction of plant biomass or size has broad application in various disciplines of plant biology (Niklas 2004). The extrapolation of these biometric relationships to exotic plant management is also applicable, although it has received less attention in the scientific literature. After comparing various explanatory variables, Rayamajhi et al. (2002a) determined DBH was an effective predictor for biomass allocation and

TABLE 4. SEED CHARACTERISTICS OF *MELALEUCA QUINQUENERVIA* IN ITS NATIVE AND ADVENTIVE RANGES. VALUES REPRESENT AVERAGES (STANDARD ERRORS). DIFFERENT LETTERS INDICATE SIGNIFICANT DIFFERENCES BETWEEN TREATMENT MEANS ($P < 0.05$; TUKEYS HSD).

	Australia ^a	Florida ^a	San Juan Bay Estuary ^a	Rocky Creek	Nassau Airport	Andros Town	F	P
No. capsules/cluster	18.0 (0.9) a	49.0 (2.5) d	44.3 (2.9) cd	27.8 (2.2) ab	36.6 (1.9) bc	30.7 (1.9) b	2.85	0.0235
Cluster length (cm)	5.7 (1.6)	6.0 (1.3)	5.4 (2.6)	4.1 (0.19)	4.4 (0.17)	4.7 (0.13)	1.75	0.1375
Capsules/cm	3.0 (0.1) a	8.0 (0.3) bc	8.2 (0.3) bc	6.8 (0.48) bc	8.3 (0.32) c	6.5 (0.37) b	5.61	0.0002
No. seed/capsule	267.2 (11.8)	275.9 (6.3)	262.3 (12.9)	249.0 (13.4)	233.3 (12.0)	284.8 (2.9)	2.87	0.0574
% embryonic seed	8.2 (0.6) b	14.3 (1.9) ab	8.2 (0.8) ab	15.5 (3.4) a	14.7 (3.3) ab	14.6 (2.7) ab	12.45	<0.001
% viable seed	3.5 (0.4) a	10.5 (1.6) b	4.2 (0.5) a	2.3 (0.6) a	1.0 (0.3) a	2.8 (0.9) a	38.58	<0.001
% germinable seed	2.7 (0.3) a	9.9 (1.5) b	1.3 (0.3) a	1.0 (0.3) a	0.2 (0.1) a	0.4 (0.2) a	33.77	<0.001

^aAs reported by Rayamajhi et al. (2002) and Pratt et al. (2005b).

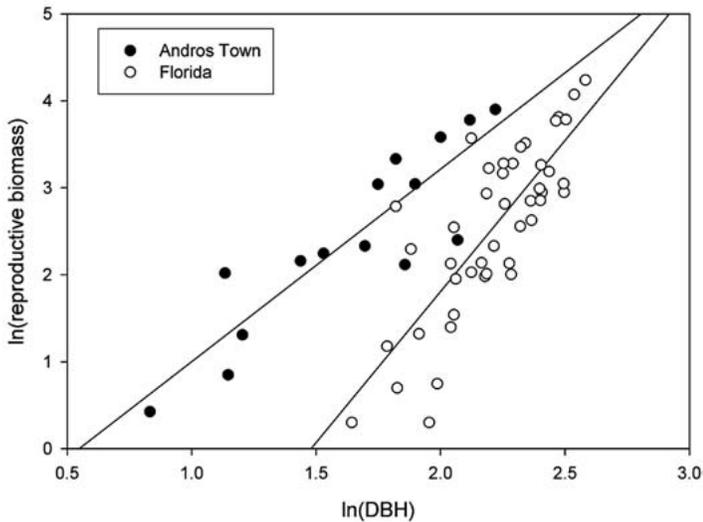


Figure 2. Log-log relationship between reproductive biomass (capsules and seeds) and diameter at breast height (=1.3 m) for *Melaleuca quinquenervia* populations near Andros Town (Andros Island) and Florida.

height of *M. quinquenervia* in Florida. DBH has subsequently been used to forecast *Melaleuca* removal costs, carrying capacity for herbivores, and assessment of the tree's natural enemies (Pratt et al. 2004, Laroche and McKim 2004, Pratt et al. 2005a). For the data presented herein however, DAB was a better predictor of *Melaleuca* biomass fractions in the Bahamas. In addition to greater accuracy in the Bahamas, DAB also offers the advantage of including all individuals regardless of stature. However, DAB may not be as easily quantified as DBH due to possible difficulties in accessing the tree's base in situations of heavy understory vegetation or standing water.

ACKNOWLEDGMENTS

Comments by F. Allen Dray, Deah Lieurance, and two anonymous reviewers were helpful in preparing this manuscript. We are indebted to Carrol Forester, Melanie Williams, Christopher Hinsey, and Ken Massie for their logistical assistance in the Bahamas. This research was supported, in part, by the USDA TAME *Melaleuca* Program (<http://tame.ifas.ufl.edu/>). Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

LITERATURE CITED

Baillie, J. E. M., C. Hilton-Taylor and S. N. Stuart. 2004. IUCN Red List of Threatened Species. A Global Species Assessment. IUCN, Gland, Switzerland and Cambridge, UK.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. Forestry* 2:49-53.

BEST Commission. 2003. The National Invasive Species Strategy for The Bahamas. BEST, Nassau, The Bahamas.

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

Boland, D. J., M. I. H. Brooker, G. M. Chippendale, N. Hall, B. P. M. Hyland, R. D. Johnston, D. A. Kleinig and J. D. Turner. 1987. *Forest Trees of Australia*. Nelson Wadsworth, Melbourne, Australia.

Britton N. L. and P. Wilson. 1926. *Botany of Porto Rico and the Virgin Islands*. Scientific Survey of Porto Rico and the Virgin Islands. New York Academy of Sciences, New York.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin and C. Hilton-Taylor. 2002. *Habitat Loss and Extinction in the Hotspots of Biodiversity*. *Cons. Biol.* 16:909.

Campbell, D. G. 1978. *The Ephemeral Islands: A Natural History of the Bahamas*. Macmillan Education Ltd., London.

Correll, D. S. and H. B. Correll. 1982. *Flora of the Bahama Archipelago*. J. Cramer, Vaduz, Liechtenstein.

Craven, L. A. 1999. Behind the names: The botany of tea tree, cajuput and niaouli, pp. 11-28. In: I. Southwell and R. Lowe (eds.). *Tea Tree: the genus Melaleuca*. Hardwood Academic, Amsterdam.

Daehler, C. C., J. S. Denslow, S. Ansari and H.-C. Kuo. 2003. A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Cons. Biology* 18:360-368.

D'Antonio, C. M. and T. Dudley. 1994. Biological invasions as agents of change on islands versus mainlands, pp. 103-121. In: P. Vitousek, L. Loope and H. Adersen (eds.). *Islands: Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin.

Denslow, J. S. 2003. Weeds in paradise: Thoughts on the invasibility of tropical islands. *Ann. Mis. Bot. Garden* 90:119-127.

Diamond, C., D. Davis and D. C. Schmitz. 1991. Economic impact statement: The addition of *Melaleuca quinquenervia* to the Florida prohibited aquatic plant list. In: T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers and L. D. Whiteaker (eds.). *Proceedings of the Symposia of Exotic Pest Plants*, pp. 87-110. National Park Service, Denver, CO.

Dray, F. A., Jr. 2003. *Ecological Genetics of Melaleuca quinquenervia* (Myrtaceae): Population Variation in Florida and Its Influence on Performance of the Biological Control Agent *Oxyops vitiosa* (Coleoptera: Curculionidae). Ph.D. diss., Florida International University, Miami.

Ferriter, A. P., T. Pernus, K. Langeland, P. D. Pratt, M. Bodde and C. Silvers. 2006. An assessment and recommendations for control of *Melaleuca quinquenervia*, *Schinus terebinthifolius* and *Casuarina* spp. in the western Bahamas. *Bahamas J. Sci.* (in press).

Fornwall, M. and L. Loope. 2004. Toward a comprehensive information system to assist invasive species management in Hawaii and Pacific Islands. *Weed Sci.* 52:854-856.

Franks, S. J., A. M. Kral and P. D. Pratt. 2006. Herbivory by introduced insects reduces growth and survival of *Melaleuca quinquenervia* seedlings. *Environ. Ent.* 35(2):366-372.

Grabe, D. F. 1970. Tetrazolium testing handbook for agricultural seeds. Contribution No. 29 to the Handbook on Seed Testing, Tetrazolium Testing Committee of the Association of Official Seed Analysts, Lincoln, NE.

Hofstetter, R. L. 1991. The current status of *Melaleuca quinquenervia* in southern Florida. In: T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers and L. D. Whiteaker (eds.). *Proceedings of the Symposium on Exotic Pest Plants*, pp. 159-176. U.S. Department of Interior, National Park Service, Miami.

Holliday, I. 1989. *A Field Guide to Melaleucas*. Hamlyn, Port Melbourne, Australia.

Kairo, M. and B. Ali. 2003. *Invasive Species Threats in the Caribbean Region Report to the Nature Conservancy*, CAB International, Trinidad and Tobago.

Kolar, C. S. and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends Eco. Evol.* 16:199-204.

Langeland, K. A. and K. C. Burks. 1998. *Identification and Biology of Non-Native Plants in Florida's Natural Areas*. University of Florida, Gainesville.

Laroche, F. B. and A. P. Ferriter. 1992. The rate of expansion of melaleuca in South Florida. *J. Aquat. Plant Manage.* 30:62-65.

Laroche, F. B. and J. McKim. 2004. Cost comparison of *Melaleuca* treatment methods. *Wildland Weeds* 7:12-15.

Little, E. L. and F. H. Wadsworth. 1964. *Common trees of Puerto Rico and the Virgin Islands*. USDA Forest Service, Washington, D.C.

Lonsdale, W. M. 1999. Global patterns of plant invasion and the concept of invasibility. *Ecology* 80:1552-1536.

Mack, R. N. 2000. Assessing the extent, status, and dynamism of plant invasions: current and emerging approaches. In: H. A. Mooney and R. J. Hobbs (eds.). *Invasive Species in a Changing World*, pp.141-168. Island Press, Washington, D.C.

- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton Univ. Press, Princeton, NJ.
- Mazzotti, F. J., W. Ostrenko and A. T. Smith. 1981. Effects of the exotic plants *Melaleuca quinquenervia* and *Casuarina equisetifolia* on small mammal populations in the eastern Florida Everglades. Fla. Sci. 44:65-71.
- Meskimen, G. F. 1962. A silvical study of the melaleuca tree in south Florida. M.S. thesis. University of Florida, Gainesville.
- Muller, M. J. 1982. Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science. Dr. W. Junk Publishers, The Hague.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Da Fonseca and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853-858.
- Myers, J. H. and D. R. Bazely. 2003. Ecology and Control of Introduced Plants. Cambridge University Press, Cambridge, England.
- NAS. 2002. Predicting Invasions of Nonindigenous Plants and Plant Pests. <http://books.nap.edu/books/0309082641/html/index.html>.
- Niklas, K. J. 2004. Plant allometry: is there a grand unifying theory? Biol. Rev. 79:871-889.
- O'Hare, N. K. and G. H. Dalrymple. 1997. Wildlife in southern everglades wetlands invaded by melaleuca (*Melaleuca quinquenervia*). Bull. Fla. Museum Nat. Hist. 41 (1):1-68.
- OTA. 1993. Harmful non-indigenous species in the United States. OTA-F-565, US Government Printing Office, Washington, D.C.
- Pratt, P. D., M. B. Rayamajhi, T. K. Van and T. D. Center. 2004. Modeling the influence of resource availability on population densities of *Oxyops vitiosa* (Coleoptera: Curculionidae), a biological control agent of the invasive tree *Melaleuca quinquenervia*. Biocontrol Sci. Tech. 14:51-61.
- Pratt, P. D., M. B. Rayamajhi, T. K. Van, T. D. Center and P. W. Tipping. 2005a. Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quinquenervia*. Ecol. Ent. 30:316-326.
- Pratt, P. D., V. Quevedo, L. Bernier, J. Sustache and T. D. Center. 2005b. Invasions of Puerto Rican wetlands by the Australian tree *Melaleuca quinquenervia*. Car. J. Sci. 41:42-54.
- Rayachhetry, M. B., T. K. Van and T. D. Center. 1998. Regeneration potential of the canopy-held seeds of *Melaleuca quinquenervia* in south Florida. Int. J. Plant Sci. 159:648-654.
- Rayachhetry, M. B., T. K. Van, T. D. Center and F. Laroche. 2001. Dry weight estimation of the aboveground components of *Melaleuca quinquenervia* trees in southern Florida. For. Eco. Manage. 142:281-290.
- Rayamajhi, M. B., M. F. Purcell, T. K. Van, T. D. Center, P. D. Pratt and G. R. Buckingham. 2002a. 8. Australian Paperbark Tree (*Melaleuca*). In R. G. Van Driesche, B. Blossey, M. S. Hoddle, S. Lyon and R. Reardon (eds.). Biological control of invasive plants in the Eastern United States, pp. 117-130. Forest Health Technology Enterprise Team, Morgantown, WV.
- Rayamajhi, M. B., T. K. Van, T. D. Center, J. A. Goolsby, P. D. Pratt and A. Racelis. 2002b. Biological attributes of the canopy-held melaleuca seeds in Australia and Florida, US. J. Aquatic Plant Manage. 40:87-91.
- Reichard, S. H. and L. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Cons. Bio. 11:193-203.
- SAS Institute. 1999. The SAS System for Windows, Version 8. SAS Institute Inc., Cary, NC.
- Serbesoff-King, K. 2003. *Melaleuca* in Florida: A literature review on the taxonomy, distribution, biology, ecology, economic importance and control measures. J. Aquatic Plant Manage. 41:98-112.
- Simberloff, D. 1995. Why do introduced species appear to devastate island more than mainland areas? Pac. Sci. 49:87-97.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. Ecology. 64:209-210.
- SPSS 1999. SPSS Base 10.0 Application Guide Computer Program, Version 10.0. SPSS, Chicago.
- Turner, C. E., T. D. Center, D. W. Burrows and G. R. Buckingham. 1998. Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, U.S.A. Wetl. Ecol. Manage. 5:65-178.
- Van, T. K., M. B. Rayachhetry and T. D. Center. 2000. Estimating above-ground biomass of *Melaleuca quinquenervia* in Florida, USA. J. Aquatic Plant Manage. 38:62-67.
- Van, T. K., M. B. Rayachhetry, T. D. Center and P. D. Pratt. 2002. Litter dynamics and phenology of *Melaleuca quinquenervia* in South Florida. J. Aquatic Plant Manage. 40:22-27.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zeal. J. Ecol. 21:1-16.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607-615.
- Woodall, S. L. 1982. Seed dispersal in *Melaleuca quinquenervia*. Fla. Sci. 45:81-93.
- Yamakura, T., A. Hagibara, S. Sukardjo and H. Ogawa. 1986. Above-ground biomass of tropical rain forest stands in Indonesian Borneo. Vegetatio. 68:71-82.