

Melaleuca quinquenervia dominated forests in Florida: analyses of natural-enemy impacts on stand dynamics

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Abstract *Melaleuca quinquenervia* (melaleuca) is a native of Australia but has become an invasive plant in Florida, USA. We conducted a long-term demographic study of melaleuca in three sections (central, transitional, and peripheral) of monoculture stands located in Florida, and quantified absolute density, diameter at breast height and basal area of trees by section at three sites. Additionally, we monitored the impacts of natural enemy (insects and fungi) on melaleuca populations which became apparent after 2001. Both absolute density and basal area, from before (1997–2001) and after noticeable natural-enemy impact (2002–2005), were compared. Prior to the natural-enemy impact, absolute density of melaleuca trees declined primarily due to self-thinning and associated losses of small trees, but diameter at breast height increased, as did the basal area. Later during the period when natural enemies prevailed, absolute density declined at a significantly greater rate across all sections but was highest at the periphery. The decrease in mean

absolute density and basal area/ha of melaleuca during the natural-enemy impacted period coincided with the increased incidence of the populations of plant-feeding insects and fungi. The mean diameter at breast height continued to increase in all sections of the stands throughout the study period. An increasing trend in basal area prior to natural-enemy impact was reversed after increase in natural-enemy abundance and noticeable impact in all three sections of the stands. These findings lend support to a growing body of literature that implicates natural enemies as increasingly important density-independent regulators of *M. quinquenervia* populations.

Keywords Basal area · Biological control · *Boreioglycaspis melaleucae* · Density · Diameter at breast height · *Oxyops vitiosa* · *Paratachardina lobata* · *Puccinia psidii*

Introduction

Herbivores and pathogens, as integral components in natural systems, can play a role in determining which plant species successfully naturalize or spread subsequent to introduction (Kosola et al. 2001; Crawley 1989). Only a few papers report dynamics of plant invasions as influenced by plant-feeding insects or plant pathogens, with the majority coming from the

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biological control literature (Morris 1999; Paynter 2005). Such information could help in the formulation of strategies for restoration of habitats degraded by invading plants.

Tree densities in both managed and natural stands tend to decrease in a density-dependent manner due to competition for resources such as space, light source, and nutrients which leads to self-thinning (Davies 2001; Zhang et al. 2005). Often, stand characteristics, such as stand basal area and biomass, increases (Binkley et al. 2004) despite decreases in stand density caused by the mortality of suppressed trees. In general, these trends in the stand attributes are negatively affected if and when natural enemies colonize the system (Straw et al. 2005). Herein, we present a study that reports the effects of a mixture of natural enemies (including two recently introduced biological control insects) on an exotic invasive plant. Australian native *Melaleuca quinquenervia* (Cav.) S.T. Blake (hereafter “melaleuca”) trees, considered to be one of the most aggressive invaders of south Florida environments (Hofstetter 1991; Bodle et al. 1994), is ideal for studying natural-enemy impact on the performance of an invasive plant.

Melaleuca trees are erect, exceeding 20 m in height (Hofstetter 1991) with multi-layered, thick white or grayish papery bark that insulates the trunk and branches (Holliday 1989; Bodle et al. 1994). Inflorescences are indeterminate, 2–5 cm long, and arranged in bottlebrush-like spikes (Holliday 1989). Persistent capsular fruits develop 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). These capsules release copious quantities of seeds when their 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; Hofstetter 1991). Because of the massive seed release from reproductively active trees, extremely dense melaleuca forests are common (Hofstetter 1991; Van et al. 2000). Standing biomass of 129–263 metric tons/ha has been reported for melaleuca stands in the United States and Australia (Van et al. 2000).

Melaleuca has aggressively invaded many south Florida ecosystems, including portions of

Florida Everglades systems (Hofstetter 1991; Bodle et al. 1994). In doing so, it has displaced native vegetation, degraded wildlife habitat, created fire hazards, and caused human health problems (Morton 1969; Diamond et al. 1991). The extent of melaleuca infestations in southern Florida has been estimated at 0.20–0.61 million ha, an area encompassing 7–20% of the total region, and many remaining natural areas within this region are considered vulnerable to continued invasion (Bodle et al. 1994). According to a 1997 estimation, melaleuca still occurs in ca 0.17 million ha of southern Florida (Bodle and Van 1999) despite chemical and mechanical control efforts (Laroche 1999). Agencies charged with the responsibilities of managing natural areas have shown interest in long-term environment-friendly methods to restore and maintain the ecosystems of southern Florida (Bodle et al. 1994; Molnar et al. 1991). Therefore, an integrated control strategy that deploys multiple biological control agents to supplement chemical and mechanical methods has been advocated for melaleuca control in Florida (Bodle et al. 1994; Turner et al. 1998).

Biological control of melaleuca was implemented beginning in 1997 with the release of *Oxyops vitiosa* Pascoe, a specialist weevil whose larvae and adults feed on foliage and bud tissues (Center et al. 2000). Impacts caused by this weevil to melaleuca populations began to appear in research plots during 2001. A second biological control agent, the melaleuca psyllid [*Boreioglycaspis melaleucae* (Moore), attacking foliage and inflorescence], was released during spring 2002 (Center et al. in press). In addition, infestations of the lobate lac scale [*Paratachardina lobata lobata* (Chamberlin) attacking green bark and foliage tissues] now impact melaleuca. This scale insect, which is a true generalist known to infest numerous plant species in several phylogenetically unrelated plant families, became very prevalent in the south Florida landscape during the spring of 2002 (Pemberton 2003). An unidentified sooty mold (indiscriminately covering foliage and green stems) is also associated with heavy infestations of this scale. In addition, the rust fungus *Puccinia psidii* Pascoe (attacking succulent stems and foliage), which is specific to plants in the family

Myrtaceae (Laundon and Waterson 1965; Marlatt and Kimbrough 1979), was recently discovered heavily infecting the young foliage of melaleuca trees (Rayachhetry et al. 1997). Attributes such as growth, reproductive performance, survival, and rate of invasion of new areas determine melaleuca's invasiveness while stand density and basal area determine its dominance at a given location. Based on the ability of the current natural enemies of melaleuca to inflict leaf-damage, defoliation, twig dieback, smaller tree mortality (Rayachhetry et al. 2001; Pratt et al. 2003, 2004a, b, 2005; Franks et al. 2006; Morath et al. 2006) and the general patterns of self-thinning of trees of different stature, we hypothesize that natural-enemy impacts in melaleuca dominated stands will result in (1) a decreasing overall density in peripheral plots that have an abundance of smaller trees, (2) an increasing mean diameter throughout the stand due to mortality of smaller trees, and (3) a decreasing overall basal area increment in stands with predominantly larger trees but none or a slight change in this attribute where stands are composed of predominantly smaller trees.

Methods

Study areas

South Florida is characterized by a humid subtropical climate with an average monthly temperatures ranging from about 19°C in January to 28°C in August–September, and an average rainfall range of about 3 cm in January to 27 cm in September (Chen and Gerber 1991). Melaleuca stands occur in and around fresh water marshes as well as in relatively drier areas such as sandy ridges, oftentimes associated with the Florida Everglades. Surface water depths in these areas fluctuate in accordance with the wet–dry seasonality (Kushlan 1991), thus producing hydroperiods of varying lengths.

Three permanent study sites were established in melaleuca-infested portions of southeastern Florida, USA, to generate baseline data on melaleuca density, basal area, litter production, and plant species composition for use in future

evaluations of the impact of introduced natural enemies on these attributes. These three sites represented typical melaleuca habitats (nonflooded and seasonally-flooded) in south Florida. Sites designated as “nonflooded” became inundated intermittently for a few hours to several days during or following periods of heavy rain but were not continuously flooded nor flooded every year (hence not seasonally flooded). Soils in all study areas were dominated by poorly drained organic muck soils generally classified as histosols (Brown et al. 1991). Understory vegetation in research stands at the onset of this study in 1997 was absent or, if present, was sparsely confined to a few plants that occur sporadically under canopy gaps and at the invasion fronts of developing melaleuca stands.

Plot establishment and data collection

The research stands were typical melaleuca domes or “heads” with large, older trees near the center then grading into progressively smaller trees and saplings towards the edges (the invasion front). For study purposes, we divided these melaleuca domes into three sections, based upon their prevalent position: “Central” located towards the middle of the dome and consisting of the oldest trees mixed with a few scattered suppressed trees and seedlings; “Transitional” comprised mainly of the trees of intermediate stature with a few saplings and seedlings; and “Peripheral” located at the edges of the domes and comprised mainly of saplings and seedlings. Two 10 m × 10 m plots in each of the central and transitional sections and three 5 m × 5 m plots (to account for the greater variability among smaller trees unlike in the central and transitional sections where tree distributions were relatively homogenous) in peripheral sections of each site were delineated. Thus, seven plots were established at each of the three sites for a total of 21 plots used for density, diameter, and basal area assessments.

All melaleuca trees within plots were counted regardless of size to determine absolute density in each plot. Diameter was recorded at height of 1.3 m, which hereafter will be referred to as the diameter at breast height (DBH). These DBH

values were used to estimate the basal area in each plot. Tree counts and DBH measurements were initiated during March/April of 1997, then repeated once in 2000, and thereafter every year until 2005.

The 8-year study was divided into two periods: the pre-natural-enemy impact period (hereafter abbreviated as PNEI), which included the initial 4-year period (1997–2001) when herbivores and pathogens were absent or, if present, at very low densities. The second is referred to as the natural-enemy impact period (hereafter abbreviated as NEI), which included the later 4-year period marked by extensive insect herbivory and rust-fungus damage.

Impact of herbivores and pathogens

Weevil and rust in litter traps: The tall heights of the mature melaleuca trees complicated visual observations and collection of data on herbivore and pathogen populations and required us to indirectly quantify densities and impacts of natural enemies. Two litterfall traps were randomly placed in the understory of each permanent plot, for a total of 12 traps (2 plots \times 3 stand positions \times 2 traps per plot) at each site (Rayamajhi et al. 2006). Unlike in stand density and basal area studies where three peripheral plots were used as described earlier in “Plot establishment and data collection”, only two peripheral plots per site were used in this study. Fully grown weevil larvae drop to the forest floor where they pupate in the soil and litter. We intercepted these and other life stages (larval exuviae, dead or living larvae, and dead adults) in the litterfall traps to estimate the relative insect abundance. The number of weevils captured in these traps by no means represented the actual number of larvae that may have fallen into the traps because some may have escaped before they could be collected, but the data nonetheless represented a relative measure of overall trends in abundance during the evaluation period.

The traps were emptied each month after tallying the weevil counts and the plant litter was placed in zip-lock bags before being transported to the laboratory. Litter samples were oven-dried at ca. 70°C to constant weight and

weighed to the nearest 0.001 g. The foliage fraction was separated from the other litter components and then further sorted into non-damaged, weevil damaged, and rust damaged sub-fractions. Average weights per leaf were determined for intact healthy leaves (0.123 ± 0.009 g/leaf, $N = 120$), partially eaten insect-damaged leaves (0.0359 ± 0.005 g/leaf, $N = 120$), and rust-diseased leaves (0.0813 ± 0.02 g/leaf, $N = 120$) using a portion of these sub-fractions. The total leaf weight for each fraction in each trap was then converted using that fraction’s average leaf weight multiplied by the number of undamaged, weevil damaged, or pathogen damaged leaves per trap per month. Damaged-leaf data were gathered beginning in January 1999 (when damaged leaves were first observed in traps) and continuing through October 2005. Weevil data were gathered beginning in January 2000 (when first weevil larvae were observed in traps) and continuing through October 2005. Tallies of weevil life stages (dead or alive) were then converted to total numbers per ha per month within each year based on the capture-area of the traps (0.25 m²).

Visual estimation of damage to trees by all agents: Damage caused by the psyllids and the lobate lac scales are difficult to discern from leaf litter because they leave no telltale signs of damage on fallen leaves. Rain washes off the diagnostic waxy flocculence produced by the psyllids (Pratt et al. 2004b). Similarly, lobate lac scales attack green portions of branches which remain attached to the trees for a considerable time. Combinations of the weevils, rust, lobate lac scale, psyllids, and sooty mold caused defoliation, twig die-back and mortality of seedlings and saplings in the field conditions (Rayachhetry et al. 2001; Franks et al. 2006; Morath et al. 2006; Rayamajhi et al. unpublished data). We felled 28 (≥ 1.3 m tall) randomly selected (random among several same-diameter trees) melaleuca trees during 2003 at two sites adjacent to the permanent plots in transitional positions within the melaleuca domes. These selected trees represented the diameter range in the melaleuca dome. Damage caused by weevils, rust, lobate lac scale, psyllids, and sooty mold on these sample trees was visually estimated. Felled trees were divided into three DBH classes: I = 1.0–10.0 cm,

II = ≥ 10.1 –20.0 cm and III = ≥ 20.1 cm at breast height (1.3 m from the tree-base). Total leaf damage (insect and pathogen) was rated as: 0 = no damage or defoliation by rust or weevil; 1 = $\leq 1\%$ of foliage; 2 = 1.1–25% damaged or defoliated; 3 = 25.1–75% damaged or defoliated; 4 = 75.1–100% damaged or defoliated; 5 = Dead.

Weevil feeding incidence (percentage of leaves bearing signs of herbivory by weevil larvae and adults), lobate lac scale incidence (percentage of live bark harboring lac scale colonies on twigs and branches and/or percentage of infested leaves), psyllid incidence (percentage of branch tips and leaves with psyllid flocculence and nymphs), rust pustule incidence (percentage of branch tips bearing rust pustules), and sooty mold mycelial felt coverage (percentage of total foliage and stem surfaces with dark-colored mycelial felt coverage) on each of the felled trees in three DBH classes were visually estimated for each tree. These visual estimations of the natural-enemy incidence were assessed independently by four observers and their ratings were averaged.

Data analysis

In this study we were concerned with the effects of natural enemies on overall densities, DBH, and basal area of melaleuca trees in three sections (central, transitional, and peripheral) of melaleuca dominated stands during two periods (PNEI and NEI) and hence we did not focus our analyses on site differences. Data from three sites were pooled by stand positions within melaleuca domes or heads and a multivariate repeated measure ANOVA was performed to test the effects of year and stand positions on absolute density (trees/ha), DBH (cm/tree by plot), and basal area (m²/ha).

Dependent variables absolute density, DBH, and basal area were calculated for each site by year and stand positions. Analysis of covariance (ANCOVA) was used to test differences in the rate of change for response variables between PNEI and NEI periods, with the year within a period as the covariate. The analysis modeled the dependent variables as:

$$Y = \text{period} + \text{year} + \text{period} * \text{year}$$

Where Y = dependent variables (absolute density, DBH or basal area) and *period* = PNEI or NEI. To meet assumptions of normality and homogeneity of variances implicit in the parametric analyses, impact of natural enemies presented herein as percentages were arcsine transformed prior to analysis of variance and mean separation tests (Waller-Duncan's multiple range test; SAS 1999). However, data presented in the figures are based on the nontransformed percentages.

Results

Stand densities

Both time (year) and stand position influenced absolute density and DBH but only stand position affected basal area (Table 1). The absolute density gradually declined during the PNEI period in central (−7.2% per year), transitional (−10.2% per year), and peripheral (−1.4% per year) stand positions. However, this decline intensified during the NEI period (compared to PNEI) in central (−14.8% per year), transitional (−14.8% per year), and peripheral (−16.3% per year) stand positions.

Table 1 Analyses of variance for the effects of year and plot position in the stand on diameter at breast height (DBH), basal area and densities of *Melaleuca quinquenervia* in Florida

Independent variables	d.f.	Absolute density ^a		DBH		Basal area ^b	
		F	P	F	P	F	P
Year	6	11.88	<0.0001	24.99	<0.0001	0.93	0.4768
Stand position	2	114.53	<0.0001	438.44	<0.0001	54.47	<0.0001
Year × stand positions	12	3.07	0.0008	3.49	0.0002	0.14	0.9997

^a Absolute density (stems/ha): includes melaleuca trees of all sizes

^b Basal area (m²/ha): calculations based on melaleuca trees taller than 1.3 m from the base

The periodic annual decrement rate in absolute density during the PNEI period was least in central and highest in peripheral stand positions (Table 2). This trend was intensified in peripheral stand positions during the NEI period when absolute density decreased by 64% in comparison to the PNEI period (Fig. 1, Table 2).

Diameter and basal area

Mean diameter at breast height during the entire study period (1997–2005) increased over time (Fig. 2). The mean stand DBH was 3.6 (± 0.1) cm for peripheral, 5.6 (± 0.2) cm for transitional, and 9.2 (± 0.4) cm for central stand positions at the onset of the PNEI period (1997). Mean DBH increased to 4.4 (± 0.2), 6.7 (± 0.4), and 10.2 (± 0.4) cm for corresponding stand positions late in the PNEI period (2001). At the end of the NEI period (2005), the DBH means were 5.2 (± 0.2), 9.2 (± 0.9), and 14.3 (± 0.8) cm in peripheral, transitional, and central stand sections, respectively. A comparison of the two periods showed different periodic annual rates of DBH increase within central and transitional positions, but it remained virtually unchanged within peripheral positions (Table 2). These increases during the NEI over the PNEI period were 5.0-, 2.5-, and 1.5-fold in

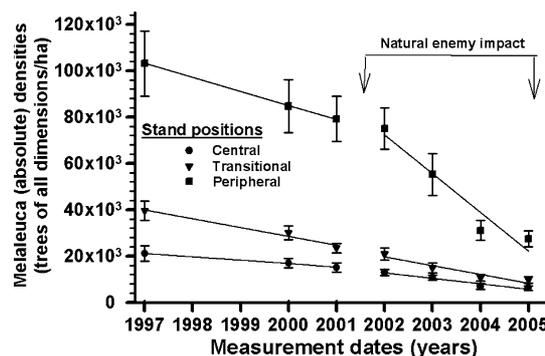


Fig. 1 Absolute density of *Melaleuca quinquenervia* stands during 8-year study period. Measurement periods 1997–2001 and 2002–2005 represent pre-natural-enemy impacted (PNEI) and natural-enemy impacted (NEI) periods, respectively. Symbols with vertical bars (standard error of the mean) and solid lines represent observed and predicted values, respectively

central, transitional, and peripheral stand positions, respectively. The annual DBH increment was consistently greater in the portions of the stands comprised of the larger trees compared to those consisting of predominately smaller trees at the stand periphery.

An overall upward trend in total basal area (m^2/ha) was observed within all stand positions during the PNEI period (Fig. 3). Mean basal area was 22.4 (± 5.0), 59.1 (± 11.0), and 108.8 (± 19.3) m^2/ha for peripheral, transitional, and central

Table 2 The periodic annual increment/decrement as described from the slopes (periodic annual rates) of the lines in the ANCOVA for absolute density that included melaleuca trees of all stature, diameter at breast height,

Stand		PNEI slopes ^a	NEI slopes ^a	F-value ^b	Pr > F ^b
Attributes	Position				
Absolute density (stem/ha/year)	Central	-1486	-2397	4.84	0.1152
	Transitional	-3838	-3773	0.00	0.9688
	Peripheral	-6076	-16724	10.98	0.0453
DBH (cm/tree/year)	Central	0.2577	1.3920	13.41	0.0352
	Transitional	0.2688	0.7550	34.73	0.0098
	Peripheral	0.2000	0.2450	0.45	0.5501
Basal area ($\text{m}^2/\text{ha}/\text{year}$)	Central	6.8938	-6.2070	39.60	0.0081
	Transitional	4.4012	-2.4080	16.42	0.0271
	Peripheral	5.7962	-1.6760	30.62	0.0116

^a Means are based on the predicted value calculated using the model used was of the form: $Y = \text{Period} + \text{Year} + \text{Period} \times \text{Year}$; where, Y = dependent variables ((stem/ha/year), DBH or basal area) and Period = PNEI and NEI. Here, PNEI-slopes = $\text{Year} + \text{Year} \times \text{Period}_{(\text{PNEI})}$ and NEI-slopes = $\text{Year} + \text{Year} \times \text{Period}_{(\text{NEI})}$

^b This test is comparing the differences between PNEI and NEI periods within the same row

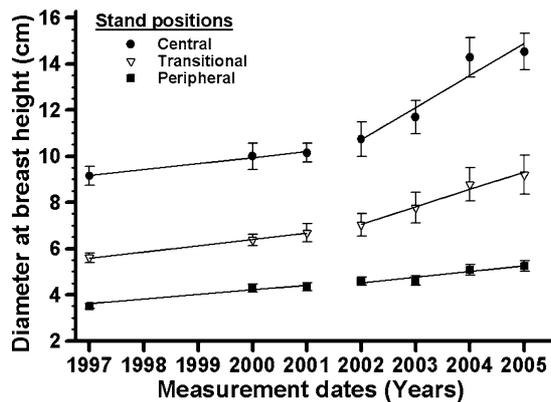


Fig. 2 Mean stand diameter (cm) at breast height (DBH) of *M. quinquenervia* trees during 8-year study periods. Measurement periods 1997–2001 and 2002–2005 represent pre-natural-enemy impacted (PNEI) and natural-enemy impacted (NEI) periods, respectively. Symbols with vertical bars (standard error of the mean) and solid lines represent observed and predicted values, respectively

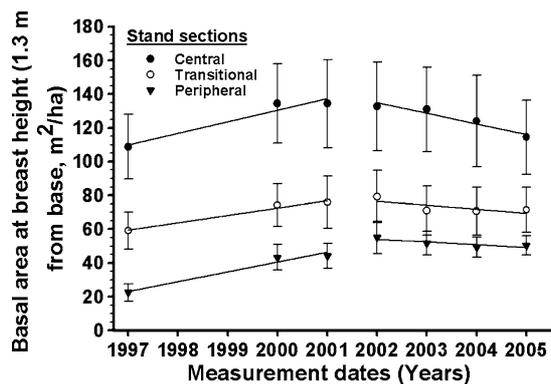


Fig. 3 *Melaleuca quinquenervia*-tree basal area (m^2/ha) calculated based on the stem diameter at breast height (≥ 1.3 m tall). Measurement periods 1997–2001 and 2002–2005 represent pre-natural-enemy impact (PNEI) and natural-enemy impacted (NEI) periods, respectively. Symbols with vertical bars (standard error of the mean) and solid lines represent observed and predicted values, respectively. Trees that were at least breast height (≥ 1.3 m) tall were included in this analysis

stand positions during early (1997) PNEI period. These increased to $44.2 (\pm 7.3)$, $76.0 (\pm 15.5)$, and $134.3 (\pm 26.1)$ m^2/ha at the end of the PNEI period. At the close of the NEI period, the mean basal area was $50.3 (\pm 5.6)$, $71.4 (\pm 13.5)$, and $114.4 (\pm 22.1)$ m^2/ha at peripheral, transitional, and central positions, respectively. The periodic annual increment in basal area during the PNEI

period was least in transitional and highest in the central stand positions (Table 2). The periodic annual change in basal area was negative in all stand positions during the NEI period (Table 2). The basal area decline during the NEI period in central and peripheral positions of the stands indicated increased mortality of larger trees inasmuch as they accounted for the major portion of basal area in the stand. A comparison of the two periods (PNEI vs NEI) showed significantly different periodic annual rates of basal area change within central, transitional, and peripheral positions (Table 2).

Herbivore and rust impact

Numbers of weevils collected in litterfall traps differed among years ($P = 0.0001$). The fewest were collected during 2004 and the most were collected during 2001. The weevil populations in the canopy (as indicated by the number of larvae dropping in the litter traps) appeared to taper towards the end of our study period (Fig. 4).

The proportion of leaves in litterfall traps that exhibited insect damage differed during years ($P = < 0.0001$, Fig. 5A). The least (ca. 5%) and

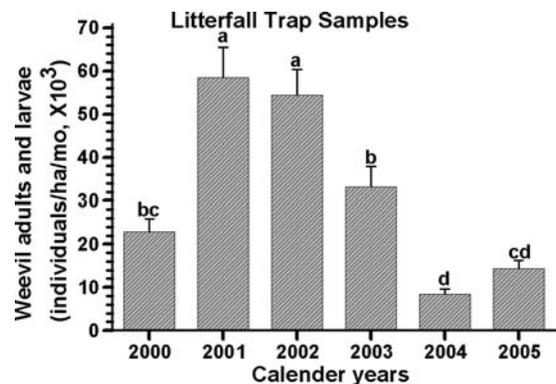


Fig. 4 *Oxyops vitiosa* (weevil) life stages (adults, pupae and larvae) trapped in litter-trap and counted on monthly basis over a 6-year period. Vertical bar (year) represent mean number of weevils (larval exuviae, dead or living larvae, and dead adults), and averaged across 216–432 traps and calculated to reflect the numbers per ha per month basis. Vertical columns (with standard error bars) representing mean weevil life stages among calendar years with the same letters are not significantly different from each other at $P = 0.05$ according to Waller-Duncan's multiple range tests

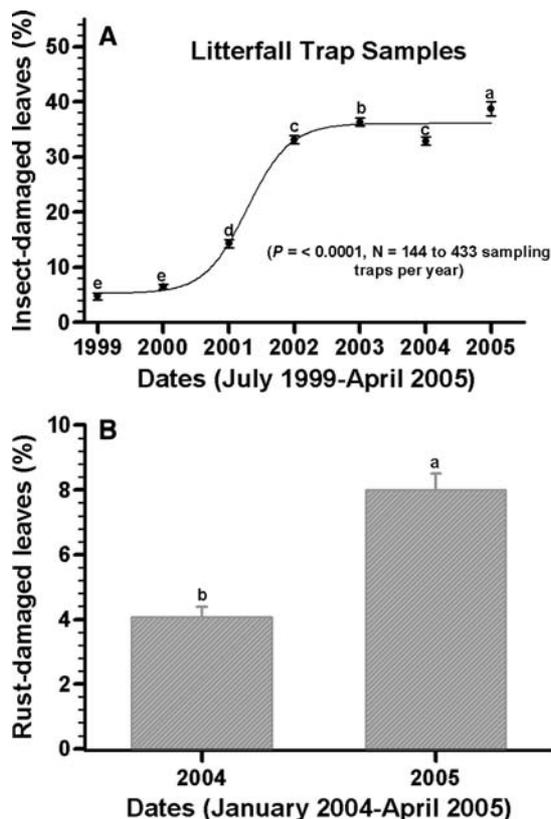


Fig. 5 Proportion of total leaves collected monthly from litter-traps which bore characteristic symptoms caused by *O. vitiosa*, and *P. psidii*. (A) weevil adult and larval feeding damage; data points (with standard error bars) representing percentage of leaves with weevil damage among calendar years with the same letters are not significantly different from each other at $P = 0.05$ according to Waller-Duncan's multiple range tests. (B) Rust damage as determined by the presence or absence of rust pustules on leaves: vertical columns (with standard error bars) representing percentage of leaves with rust damage in two calendar years with different letters are significantly different from each other at $P = 0.05$ according to Waller-Duncan's multiple range tests

the highest (ca. 45%) proportions of weevil damaged leaves in total leaf samples were recovered during 1999 and 2005, respectively. The overall increasing trend leveled off and remained relatively constant after 2002. Although rust was prevalent in the study areas, rust-damaged leaves only became obvious in the litter traps during late 2003 so they were not counted until early 2004 (Fig. 5B). The incidence of rust-diseased leaves increased significantly during 2005 accounting for about 9% of the total number of leaves in the traps.

Overall damage (leaf damage and defoliation) was significantly ($P = 0.0017$) greater on small- and medium-trees (<20-cm DBH) compared to the larger (≥ 30 -cm DBH) trees (Table 3). The proportional incidence of weevil damage ($P = 0.5282$), psyllid colonies ($P = 0.4271$), rust pustules ($P = 0.2056$), lobate lac infestation ($P = 0.1798$), and sooty mold coverage ($P = 0.6224$) on melaleuca leaves and stems was not significantly different among the three DBH-classes (Table 3).

Discussion

Inter- and intraspecific competition among plants along with the natural-enemy impact seemed to influence plant mortality rates in a given population. These sources affecting plant survivorship are often categorized as density-dependent and density-independent mortality factors in natural as well as artificial ecosystems (Harper 1977). The term “density-dependent mortality”, as coined by Smith (1935), has been considered synonymous with “self-thinning” and has been contrasted with “alien thinning” which is equivalent to density-independent mortality (Harper and McNaughton 1962; Yoda et al. 1963) due to causes other than competition among individuals of the same species. Melaleuca stand dynamics (density, DBH, and basal area) presented herein were influenced by density-dependent mortality prior to the introduction and advent of natural enemies. The combined effects of density-dependent and density-independent causes dramatically increased melaleuca tree mortality rates during the later phases of our 8-year study period.

Literature on density-dependent mortality in naturally regenerated forest ecosystem, especially in monocultures, is rare. Swaine et al. (1987) reviewed the dynamics of forest tree recruitment, growth, and mortality in natural tropical forests and reported tree mortality between 1% and 2%. Fu et al. (1996) compared the stand dynamics of naturally regenerated and planted mature mahogany stands and reported that the tree mortality rates under normal weather conditions were relatively higher (4–5% per year) in plantations (which are often monocultures composed of same age plants) as compared to similarly aged naturally

Table 3 Incidence and impacts of natural enemies of *M. quinquenervia* trees (as determined in July 2003) adjacent to the permanent plots used in stand dynamics studies in Broward County, Florida, USA

Variables	DBH-classes		
	I (1.0–10.0 cm) (<i>n</i> = 11 trees)	II (≥10.1–20.0 cm) (<i>n</i> = 11 trees)	III (≥20.1 cm) (<i>n</i> = 6 trees)
Total damage ¹	2.82 (±0.35) a ²	2.00 (±0.23) a	1.00 (±0.00) b
Weevil damage ³	21.82 (±3.82) a	22.73 (±3.33) a	16.67 (±3.33) a
Psyllid colonies ⁴	20.91 (±8.64) a	18.27 (±8.23) a	4.50 (±1.88) a
Rust pustules ⁵	0.00 (±0.00) a	0.18 (±0.12) a	0.00 (±0.00) a
Lac-scale colonies ⁶	24.00 (±8.35) a	11.46 (±4.83) a	5.67 (±3.22) a
Sooty mold coverage ⁷	36.35 (±6.61) a	40.46 (±4.18) a	45.00 (±5.63) a

¹ Total damage incurred due to herbivores and pathogen at the scale of 1 to 5; 1 = up to 1%, 2 = 1.1% to 25%, 3 = 25.1% to 75%, 4 = 75.1% to 100% of the total leaves are damaged or defoliated, and 5 = the plant was completely killed. Numbers in the parenthesis represent standard error of the mean

² Means (stand errors) among DBH classes 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 tests

³ Percentage (mean) of total leaves showing signs of weevil damage

⁴ Percentage (mean) of total branch tips and leaves showing psyllid colonies

⁵ Percentage (mean) of total tips showing signs and symptoms of rust damage

⁶ Percentage (mean) of total branches and twigs (on live bark), and leaves bearing lac-scale colonies

⁷ Percentage (mean) of total live crown covered with mycelial felts of shooty mold

regenerated stands (which tend to be composed of plants of different species) of the same species. Melaleuca stands in our study, especially those in the central positions, were monocultures (often closed canopy and absence of other plant species on the forest floor) and their annual mortality rates were clearly higher (ca. 7–10% per year for absolute density) compared to those reported for the stands of mature mahogany trees. The most likely explanation for the mortality of melaleuca trees during PNEI in our study is self-thinning due to intraspecific competition. Such self-thinning mortalities have also been documented among other annual and perennial plants (Harper and McNaughton 1962). It has been experimentally demonstrated that the individual plant weight decreases with the increase in stand density and results in plants of smaller girth with smaller diameter to height ratio (Yoda et al. 1963).

Overall, tree density changes in the PNEI period (without the impact of natural enemies in melaleuca stands) were influenced by the tree positions within the melaleuca domes. The pattern in the rate of decrease of absolute densities in peripheral, transitional, and central positions during PNEI period was –1.4%, –10.3% and –7.1% per year, respectively; though the

stand DBH and basal area, which is mainly contributed by the trees of larger dimensions, continued to increase. Thus, the negative changes in absolute densities of the central (with larger trees) and transitional (with medium-sized trees) positions indicated that the most demographic changes in the stands have occurred due to loss of the trees of smaller stature, which contributed least to stand DBH and basal area. These overall changes in melaleuca densities during PNEI period in our study approximate decreases (–1.9% to –9.9%) reported for mixed deciduous and gallery forests of Nicaragua (Marin et al. 2005) and other plant communities (Lawson et al. 1999).

Insect and disease outbreaks in forests are historically more pronounced in pure stands, possibly due to resource concentration and apparentness of susceptible hosts (Feeny 1976; Schowalter 2000). In our study, all research sites were monocultures, so any difference in tree mortality due to biological control agents could be attributed to the predominant size of the trees in the stands. This was reflected by the highest periodic annual loss in melaleuca densities between PNEI and NEI periods among peripheral (with proportionally higher number of small trees) compared

to those in central and transitional (with proportionally larger trees) sections of the stand. The higher mortality of smaller melaleuca trees reflects the larger populations of biocontrol agents and higher levels of damage on individuals of smaller stature as compared to those of larger stature at the same location. This is further supported by previous reports of the greater impact of herbivory among melaleuca individuals of smaller size classes (Franks et al. 2006; Morath et al. 2006).

Although they were released in 1997, the weevils remained undetected in litter trap samples until 2000, although damaged leaves were present as early as 1999. Not surprisingly, leaf damage was a more sensitive indicator of a weevil population in the canopy than was the presence of the actual insects. However, the maximum weevil numbers observed on the traps preceded the maximum proportion of damaged leaves (2003 and 2005) by 1–2 years. This year-to-year variation observed in the proportion of damaged leaves may be attributable to the reductions in leaf availability. The decreasing weevil numbers with increasing proportions of weevil-damaged leaves suggests that fewer weevils were damaging proportionately more leaves. Psyllid impact on melaleuca canopies was evident visually within a year after their release in the research plots, but it was difficult to quantify their damage using litter trap samples because the damaged leaves showed no physical evidence of psyllid feeding. On the other hand, rust disease impact was detected soon after the first detectable level of weevil damage. Similar impacts by herbivores and pathogens in forest systems (Gibson 1956; Ayres and Lombardo 2000; Kosola et al. 2001) and other perennial invasive plants (Palmisano and Fox 1997) have been documented in the literature. Repeated defoliations by the gypsy moth (*Lymantria dispar* L.), for instance, have been reported to affect the morphology and physiology (reduced tree growth, increased top dieback, and reduced non-structural carbohydrate allocation in roots, trunks, and twigs) of the poplar tree *Populus canadensis* Moench var. *eugenei* (Simon-Louis) Schelle (Kosola et al. 2001). Declines in total nonstructural carbohydrates have also been reported in other systems (Wargo et al. 1972; Parker and

Patton 1975) where repeated defoliations have occurred. Such a decline in allocation of carbon to root systems may result in decreased growth, increased mortality, declines in nitrate and ammonium ion uptake, and reduced mycorrhizal colonization of root systems (Kosola et al. 2001). These effects may also expose structural roots to attack by otherwise mildly pathogenic soil microbes as reported for the *Acer saccharum* Marsh-*Armillaria mellea* (Vahl.) Quell. system (Wargo 1972). As noted by Harper (1977), plants in high density stands are generally less vigorous and hence are more prone to diseases that may result in large scale mortality of individuals in a given plant population.

Thus, the mechanisms leading to the enhanced mortality of melaleuca trees during the NEI are attributed to the impact of natural enemies through leaf damage and defoliation. Abundance of damaged melaleuca leaves in the litter traps as well as on felled trees in our study lends support to the premise that the natural enemies, *O. vitiosa*, *B. melaleucae*, *P. psidii*, and *P. lobata lobata*, contributed to density-independent mortality. *B. melaleucae* causes premature abscission of mature leaves (Morath et al. 2006) and *P. psidii* causes abscission of immature leaves carrying rust pustules (Rayachhetry et al. 2001). As a result, infested trees appear progressively denuded. This accentuates the effects of the weevils which defoliate young foliage from stem tips. Similar defoliation impacts have been reported for *Personia borbonia* (L) Spreng. attacked by a leaf-galling psyllid, *Trioza magnoliae* (Ashmeade) (Leege 2005). Attack of foliage and stem tissues by plant pathogens causes defoliation and mortality of lateral branches (Maguire 1994) which eventually results in crown thinning and reduced leaf to stem ratio. Reduced leaf to stem ratio and sustained damage of live leaves may negatively impact photosynthesis to respiration rates which in general may have negative affect in allocation of nonstructural carbohydrates to the root systems (Morath et al. 2006). This phenomenon was observed in an experiment where quantities of nonstructural carbohydrates in the sap of melaleuca leaves were reduced following attack by the melaleuca psyllid (*B. melaleucae*) as compared to plants protected from the herbivore (Van,

unpublished data). Waring and Pitman (1980) have hypothesized that the tree vigor is related to the carbohydrate production, and reserves in the host and any factor that affects this process will also affect the resistance of the host tree to bark beetle attack. This hypothesis is also applicable to melaleuca system in our study, in which introduced natural enemies may have caused tremendous reduction in total carbohydrate production and storage through defoliation and dieback of tree crown (Pratt et al. 2005). Therefore, the accelerated decline in melaleuca stand density during the NEI period in our study could be attributed mainly to the natural-enemy impact. Such declines and mortalities of trees due to various biotic and abiotic causes have also been reported among red and scarlet oak populations (Staley 1965).

The periodic annual increment (PAI) of the DBH during PNEI [0.6 (± 0.1), 0.7 (± 0.2), and 0.4 (± 0.1) mm per tree in central-, transitional, and peripheral-stand positions, respectively] and NEI [2.8 (± 0.4), 1.3 (± 0.3) and 0.6 (± 0.1) mm per tree in central, transitional, and peripheral stand positions, respectively] periods of our study was within the range (1.4–2.0 mm/tree/year) reported for mature trees in mixed-species stands in the Brazilian Amazon region (da Silva et al. 2002) but remarkably lower than DBH increment range (1.4–12.1 mm/tree/year) for mature trees in Nicaraguan forest systems (Marin et al. 2005). The overall increase in melaleuca DBH in a given stand position was relatively greater in NEI- than in PNEI-period. This is also reflected in the significant periodic annual increment in stand DBH during NEI over the PNEI period. In general, mortality of smaller diameter trees in a stand results in increases in mean tree diameter. Similarly, reduced stand-density has also been reported to be associated with increased average tree diameter in *Eucalyptus* sp. (Schonau and Coetzee 1989) and *Pinus palustris* Mill. (Moser et al. 2002). Overall, natural-enemy impacts in our study appeared to enhance mean diameter increment. However, this DBH increment is attributable to the loss of small trees and the failure of newly recruited seedlings to survive. Secondarily, enhanced growth due to reduced intraspecific competition following mortality of

smaller individuals may have contributed towards the substantial increases in the DBH of surviving individuals during the NEI period.

Stand basal area provides a more holistic measure of the impact of natural enemies on melaleuca populations in south Florida. Overall basal area in a stand reflects both DBH and tree density it provides a more meaningful representation of productivity. Therefore, if basal area loss due to tree mortality in the stand exceeds the basal area increment due to radial growth of surviving individuals and newly recruited individuals, then the annual basal area increment rate in the stand becomes negative. The periodic annual rate of basal area change during the PNEI period in our study was positive in all three sections of our study stands. However, it was significantly negative in central (-6.2 m²/ha/year) and transitional (-2.4 m²/ha/year), but slightly positive (1.7 m²/ha/year) in peripheral sections of the stand due to a one-time surge in growth during 2002. As in absolute densities, the basal area changes in the three sections of melaleuca stands in this study were clearly affected by the herbivorous insects and pathogenic rust fungi. This is evidenced by increasing trends of basal area in all (central, transitional, and peripheral) sections of the stands until 2001 (prior to natural-enemy impact) and subsequent declining trends into 2005 (after the natural-enemy impact). This demonstrates a significant impact of natural enemies on overall productivity of melaleuca stands regardless of the prevalent tree stature. Herein, mortality of larger trees led to major losses of basal area although mortality of smaller trees accounted for the major loss in absolute densities in the stand.

Conclusion

A few studies (Paynter 2005, 2006) have reported the dynamics of invasive plants both before and after the implementation of biological controls. The study presented herein was designed to evaluate the impact of biological control agents within central (predominantly larger trees), transitional (predominantly medium sized trees), and peripheral (predominantly smaller trees) sections of the melaleuca-dominated stands. Overall annual

decrements in absolute density of melaleuca in all three portions of the stands resulted from self-thinning prior to 2001. This decline intensified after natural-enemy populations increased in abundance. The resultant foliage damage, defoliation and twig dieback led to 16% annual mortality of trees. This density decrement was highest in peripheral segments of the stands where the majority of trees were smaller compared to those in the central and transitional sections. Mean diameter of melaleuca trees in all three sections of the stands increased significantly as smaller trees died leading to greater representation of large individuals. The periodic annual rate of basal area change was positive in all three sections of the stand until 2001, but became negative in central and transitional sections afterward due the impact of natural enemies. The stand level impact of herbivorous insects and plant pathogen led to massive mortality and crown thinning in our study areas through rapid defoliation. This trend of decreasing stand density and gradual opening of the melaleuca canopy is facilitating development of mixed plant communities in stands previously dominated by melaleuca monocultures (Rayamajhi et al. unpublished data).

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