

# Suppression of growth and reproduction of an exotic invasive tree by two introduced insects

Philip W. Tipping<sup>a,\*</sup>, Melissa R. Martin<sup>b</sup>, Paul D. Pratt<sup>a</sup>,  
Ted D. Center<sup>a</sup>, Min B. Rayamajhi<sup>a</sup>

<sup>a</sup> USDA-ARS, Invasive Plant Research Laboratory, Ft. Lauderdale, FL, USA

<sup>b</sup> University of Florida, Department of Soil and Water Sciences, Gainesville, FL, USA

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## Abstract

The invasive tree *Melaleuca quinquenervia* experienced substantial declines in growth and reproduction in response primarily to chronic herbivory by the defoliating weevil *Oxyops vitiosa*. Herbivory was mediated on individual trees using regular applications of the insecticide acephate during a 2-year period to minimize populations of *O. vitiosa* and later the phloem-feeding psyllid, *Boreioglycaspis melaleucae*. Half of the trees also received drip irrigation to evaluate the influence of water on plant responses to herbivory. Insecticide-protected trees grew in height nearly six times faster and became 108% taller. In contrast, unprotected trees produced only 19% as much woody biomass, 13% as much leaf biomass, and 0.9% as much seed as protected trees. The mean ( $\pm$ SE) of total above ground biomass was  $873.1 \pm 191.4$  g in unsprayed trees and  $3856.2 \pm 491.5$  g in sprayed trees. Unprotected trees produced more stem tips per unit of height, resulting in a more bushy structure. Greater amounts of water increased leaf biomass, but all other plant variables were influenced most by herbivory. The seed-fueled invasive capacity of melaleuca will probably be reduced in areas favorable to the biological control agents, especially *O. vitiosa*.

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## 1. Introduction

*Melaleuca quinquenervia* (Cav.) S.T. Blake (melaleuca) is a widespread and abundant conservation weed of southern Florida wetland communities. This large tree (25–30 m tall) is native to coastal areas of eastern Australia (11–34°S), southern New Guinea, and New Caledonia where it occurs typically along freshwater streams and swamps, but also grows in brackish habitats behind mangrove swamps (Boland et al., 1987). It was introduced into southern Florida in 1886 (Dray et al., 2006), originally for sale as an ornamental, but later was used for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen, 1962; Stocker and Sanders, 1981; Bodle et al., 1994).

Rapid growth rates and early reproductive maturity (Meskimen, 1962) combined to promote melaleuca monocultures which replaced woody species including slash pine (*Pinus elliottii* Engelm.) in pine flatwood communities, sawgrass (*Cladium jamaicensis* Crantz) in wet prairies, and virtually all native flora in all freshwater environments in southern Florida, eventually infesting about 0.61 million ha (Bodle et al., 1994).

It was recognized early on that the magnitude of seed produced by melaleuca played a pivotal role in its invasive nature. The melaleuca seed crop is held primarily in the canopy in sessile capsules that are arranged in discrete clusters of 30–70 capsules (hereafter capsule clusters) with each capsule containing an average of 264 seeds (Rayachhetry et al., 2002). Although viability is only about 9%, a single 21 m tall tree may hold up to 9 million viable seeds (Rayachhetry et al., 2002). Events such as fire or stem damage

\* Corresponding author. Fax: +1 954 476 9169.

E-mail address: [ptipping@saa.ars.usda.gov](mailto:ptipping@saa.ars.usda.gov) (P.W. Tipping).

can disrupt the vascular activity of the branches thereby causing seed capsules to dehisce and release seed, often in one synchronous event (Rayachhetry et al., 1998). Fires can also disproportionately damage or kill native plant species while improving the seedbed by incinerating understory plants and producing a layer of higher nutrient ash. Consequent melaleuca recruitment usually overwhelms the native species because of the massive pulse of seed rain from opened seed capsules on fire damaged trees. In the process natural plant communities with relatively few reproductive melaleuca trees are quickly replaced with even-aged, dense monocultures of melaleuca (Van et al., 2002).

Mechanical, chemical, and biological controls have been applied to this weed problem. The history of mechanical and herbicidal approaches to melaleuca was summarized by Serbesoff-King (2003). The first classical biological control agent considered was the weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), initially collected north of Brisbane in Queensland, Australia (Balciunas et al., 1994). Adults feed on buds and leaves while larvae feed voraciously on either leaf surface consuming the leaf tissue through to the opposite cuticle and creating characteristic elongate window-like scars that turn brown after a few days (Purcell and Balciunas, 1994). Larvae are coated with a thick viscous coating consisting of essential oils sequestered from melaleuca which provides a potent anti-predator defense (Wheeler et al., 2002). Adults feed less voraciously producing recognizably shorter and narrower scars and perforations on the leaf, which also turn brown (Balciunas et al., 1994). Pupation occurs in the soil, a behavior which limits the abundance of the beetles in permanently inundated areas (Center et al., 2000). The first releases were conducted in 1997 and Center et al. (2000) considered this species established in some areas by 1998. Today, the beetles are found throughout southern Florida wherever melaleuca occurs (P.W.T. personal observation).

A second agent, *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae) was released in 2002 and has established throughout southern Florida (Center et al., 2006). Both adults and nymphs are free-living phloem feeders and complete their life cycle on the plant, thereby avoiding the problem of inundated habitats faced by *O. vitiosa*. Attack by *B. melaleucae* results in premature leaf drop from seedlings and saplings (Morath et al., 2006). Third through fifth instar nymphs secrete a white, waxy flocculence which covers groups of nymphs (Purcell et al., 1997; Wineriter et al., 2003). The presence of flocculence facilitates the detection of the nymphs in the field. The primary objective of this research was to assess quantitatively the impact and influence of *O. vitiosa*, and to a lesser extent that of *B. melaleucae*, on the growth and reproduction of small and medium sized melaleuca trees growing under two experimental water regimes.

## 2. Materials and methods

Melaleuca saplings (1–1.5 m height) were planted in field plots during Dec. 1999 at the USDA-ARS Invasive Plant

Research Laboratory in Ft. Lauderdale, Florida. Plants originated from seedlings grown in trays in a screenhouse which were transplanted into larger pots before finally being placed in the field. The prevailing soil type at the field site was a Margate fine sand, siliceous hyperthermic Mollic Psammaquent, with less than a 1% slope. Initially, trees were fertilized and irrigated until they were firmly established.

The experimental design was a complete  $2 \times 2 \times 6$  factorial arranged in a randomized complete block with two herbivore treatments, two irrigation treatments, and six blocks, with the tree as the experimental unit located in the center of each square 56.25 m<sup>2</sup> plot. Herbivore treatments consisted of a control where herbivory by *O. vitiosa* and later *B. melaleucae* was not impeded, and an insecticide treatment where regular applications of acephate (OS—dimethyl acetylphosphoramidothiote), a broad spectrum systemic insecticide, were applied to reduce or eliminate herbivory.

Plots were located directly adjacent to other plantings of melaleuca which supported high densities of both species of agents. Experimental trees were continually colonized from insects that originated from these populations, as well as from the experimental trees themselves. Trees were scouted weekly for *O. vitiosa* eggs and small larvae and acephate was applied as needed at a concentration of 0.367% ai (v/v) until runoff using a hand pressurized backpack sprayer. Control trees were not sprayed. The insecticide concentration and application frequencies neither inhibited nor stimulated plant growth (Tipping and Center, 2002).

Irrigation treatments consisted either of natural rainfall or of natural rainfall plus continuous irrigation using drippers that provided a mean flow rate of ca 7.5 l h<sup>-1</sup> applied to a spot on the soil directly next to the trunk, resulting in continually saturated soils under the dripline of the tree. Precipitation and other abiotic data were captured daily by an automated weather station directly adjacent to the plots.

Every 4–6 weeks over a 2-year period measurements were made of: the number of branch tips; the number of ‘suitable’ branch tips, i.e. those that contained 2–5 distal leaves that were fully formed but remained supple and soft, a stage which is used much more extensively by *O. vitiosa* larvae than the older hardened leaves (Wheeler, 2001); tree height; canopy width; and trunk diameter measured halfway between the soil surface and the lower edge of the crown. The location where trunk diameter measurements were made was marked to ensure consistency. The first measurements were made in October 2001 and the last in October 2003.

At the same time notes were made of the presence or absence of *O. vitiosa* eggs; the number of small (instars 1–3) and large larvae (instars 4–5) and adults; and a larval damage rating based on the percentage of suitable leaves that exhibited larval feeding ranked as: (0) no damage, (1) up to 25%, (2) 25–50%, (3) 50–75%, (4) 75–99% and (5) 100% damaged. We recorded the number of colonies

of *B. melaleuca* as indicated by discrete flocculent masses after their appearance in the plots during July 2002. No obvious damage could be attributed to *B. melaleuca* because of the intensity of damage caused by *O. vitiosa*. Representative samples of these masses were collected on melaleuca in adjacent plots and dissected to record the number of *B. melaleuca* nymphs and adults to provide

an estimate of insect density. To avoid worker exposures to the insecticide, trees were sampled up to two days before each spray application.

The trees were maintained according to their herbivory and irrigation treatments until January 2004 when they were felled by cutting just above the soil surface. The trees were partitioned into trunks (>2.5 cm diameter), branches (1–2.5 cm diameter), twigs (<1 cm diameter), leaves, flowers, and capsule clusters and weighed to determine fresh biomass. A sample of each biomass component was dried at 50 °C for 6 weeks to obtain percent moisture in order to determine total dry weight biomass for each component. Capsule clusters were further partitioned into primary and secondary clusters and a sample of 25 capsule clusters from each was measured for length and the number of capsules per cluster. Primary capsule clusters occupy the most distal position on a branch with successively older (secondary, tertiary, etc.) clusters occupying progressively more proximal positions along the same branch (Rayachhetry et al., 1998). Seeds were extracted from capsules and weighed and the number of seeds produced was estimated by dividing the total seed biomass per treatment by the mean weight of an individual seed.

The harvested tree biomass was analyzed using two-way ANOVA with interaction and, in some cases (e.g., plant height) with analysis of covariance (ANCOVA) with the

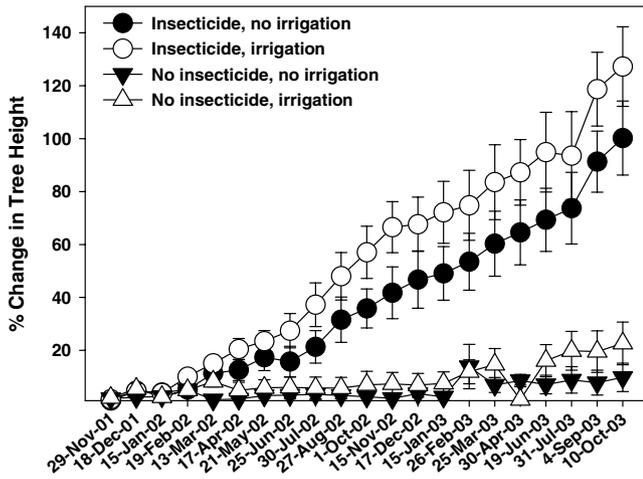


Fig. 1. Mean ( $\pm$ SE) percentage changes in heights during each sample date of *M. quinquenervia* test trees subjected to experimental herbivory and irrigation treatments.

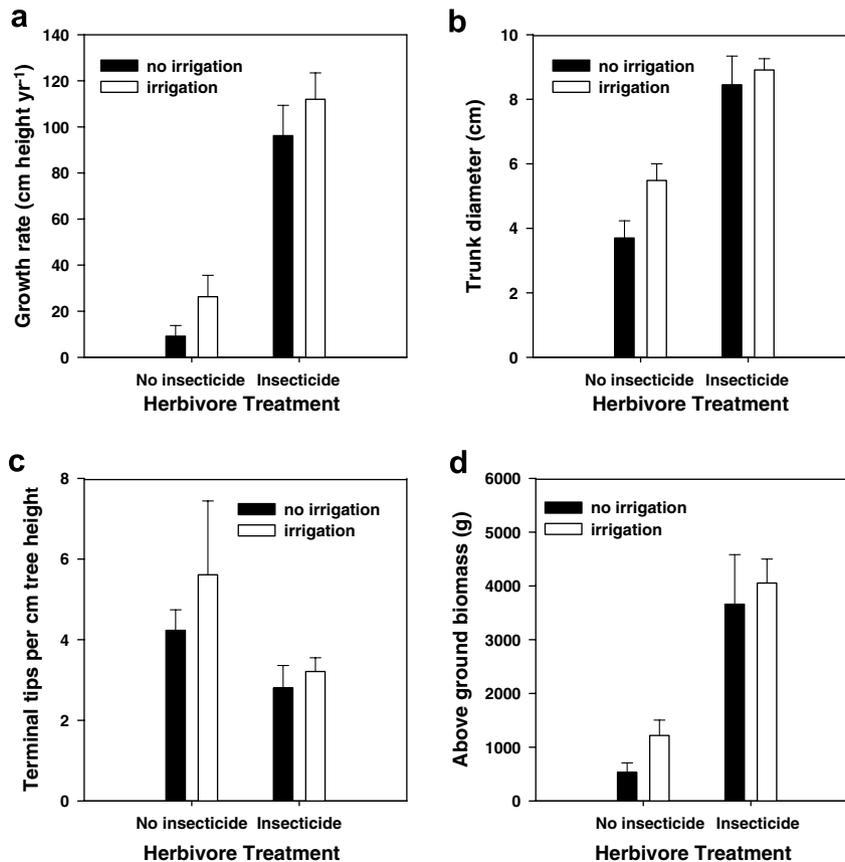


Fig. 2. Means ( $\pm$ SE) of growth rates (a), trunk diameter (b), numbers of terminal tips per tree height (c), and total above ground biomass (d) of *M. quinquenervia* test trees subjected to experimental herbivory and irrigation treatments.

initial measurements as the covariate (SAS, 1999). Means were transformed using square root transformation for non-normal data or when variances were heterogeneous and back-transformed for presentation.

### 3. Results

Acephate provided temporary protection from *O. vitiosa* and *B. melaleuca* herbivory as indicated by the damage ratings and numbers of insects or insect colonies. Overall, the mean ( $\pm$ SE) *O. vitiosa* larval damage rating for unsprayed trees was  $3.43 \pm 0.08$  while the rating for sprayed trees was  $1.68 \pm 0.05$  ( $F = 305.5$ ;  $df = 1, 20$ ;  $P < 0.001$ ). Although insecticide treatment reduced the mean number of large larvae on trees ( $F = 51.83$ ;  $df = 1, 23$ ;  $P < 0.001$ ), it did not reduce small larvae ( $F = 0.35$ ;  $df = 1, 23$ ;  $P = 0.55$ ) or adults ( $F = 1.81$ ;  $df = 1, 23$ ;  $P = 0.14$ ). Adults were apparently less deterred or less affected by the insecticide than larvae and were present throughout the course of the study as evidenced by the presence of eggs on at least one tree at every sample date. Deposition of eggs after insecticide treatment undoubtedly led to a steady recruitment of young larvae which were encountered during the surveys before subsequent insecticide applications, accounting for the low damage ratings recorded on sprayed plants. However, the small larvae rarely developed into large larvae on sprayed trees because

they were regularly killed by the next insecticide application, which would explain the difference in the number of large larvae found between treatments. This is reflected in the different demographics of the larval populations on sprayed as opposed to unsprayed trees. For example, the mean ( $\pm$ SE) percentage of small larvae comprised  $78.4 \pm 3.6\%$  of all larvae on sprayed trees and  $57.4 \pm 2.9\%$  on unsprayed trees. The reduction in late-instar larvae on sprayed trees would account for the lower damage ratings on these trees because the final instars consume cumulatively much more than the early instars (Reavey, 1993). The psyllid was substantially suppressed by the insecticide and rarely recolonized trees before *O. vitiosa*.

Herbivory caused significant biological and structural changes in melaleuca. Sprayed plants grew taller (mean final height:  $F = 59.65$ ;  $df = 1, 15$ ;  $P < 0.0001$ ) (Fig. 1) and at a faster rate (cm height  $\text{yr}^{-1}$ :  $F = 81.16$ ;  $df = 1, 15$ ;  $P < 0.0001$ ) (Fig. 2a). In addition, protected trees had wider canopies (mean canopy width:  $F = 4.36$ ;  $df = 1, 15$ ;  $P = 0.049$ ) and larger trunks (trunk diameter:  $F = 42.21$ ;  $df = 1, 15$ ;  $P = 0.001$ ) (Fig. 2b). Unsprayed plants were shorter but they had the same number of tips as sprayed plants and, therefore, experienced a change in architecture by becoming bushy with more tips per unit of tree height than sprayed trees ( $F = 7.16$ ;  $df = 1, 15$ ;  $P = 0.0145$ ) (Fig. 2c). Removal of dominant meristems through herbivory can stimulate increased meristematic activity at

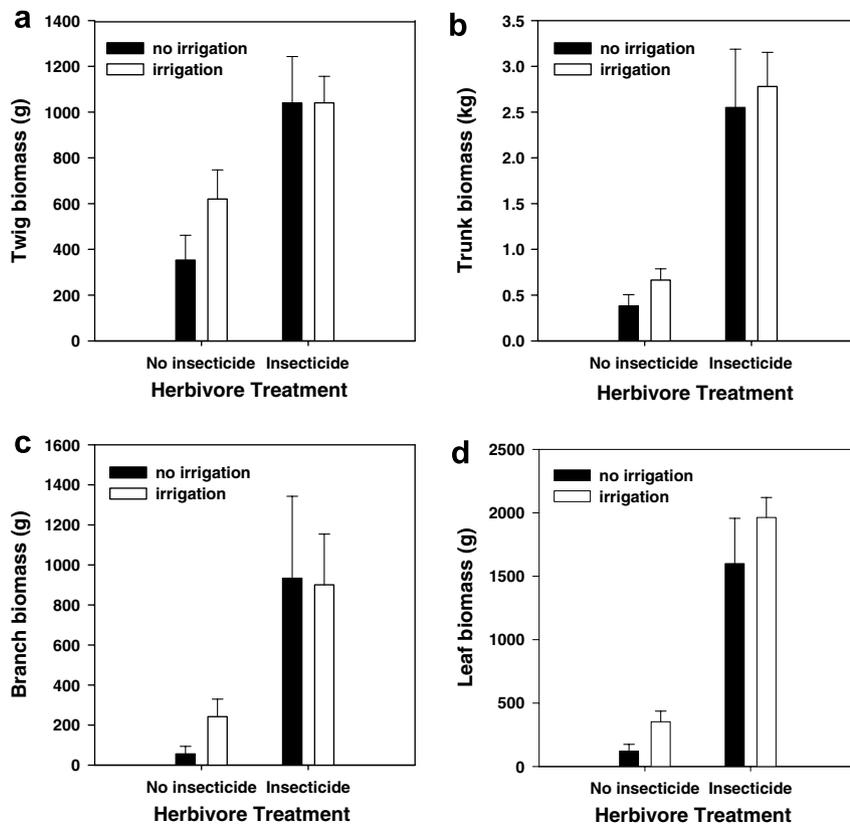


Fig. 3. Means ( $\pm$ SE) of dry weight biomass vegetative components including twig (a), trunk (b), branch (c), and leaf (d) of *M. quinquenervia* test trees subjected to experimental herbivory and irrigation treatments.

non-apical locations, leading to increased branching (Harris, 1974; Benner, 1988; Doak, 1991). Pratt et al. (2005) also found increases in branching following short-term augmented and artificial herbivory.

Total above ground biomass (Fig. 2d) and every vegetative component thereof were reduced substantially on unsprayed trees: twig biomass by 53.2% (Fig. 3a), trunk biomass by 80% (Fig. 3b), branch biomass by 83.8% (Fig. 3c), and leaf biomass by 86.7% (Fig. 3d). Herbivory was the primary influence on these variables (leaf biomass:  $F = 88.88$ ;  $df = 1, 15$ ;  $P < 0.0001$ ; twig biomass:  $F = 19.57$ ;  $df = 1, 15$ ;  $P = 0.0005$ ; branch biomass:  $F = 17.95$ ;  $df = 1, 15$ ;  $P = 0.0007$ ; trunk biomass:  $F = 56.01$ ;  $df = 1, 15$ ;  $P < 0.0001$ ), although irrigation increased the production of leaf biomass ( $F = 5.75$ ;  $df = 1, 15$ ;  $P = 0.03$ ) (Fig. 3d). The percent moisture found in leaf, twig, branch, and trunk biomass was unaffected by the herbivory or irrigation treatments.

Unsprayed trees produced <1% as many primary capsule clusters per tree as sprayed trees and no secondary capsule clusters (primary:  $F = 37.12$ ,  $df = 1, 15$ ,  $P < 0.0001$ ) (Fig. 4a). However, only a few secondary capsule clusters were produced on sprayed trees (means  $\pm$  SE:  $0.67 \pm 0.34$ ). In addition, primary capsule clusters on unsprayed trees were shorter in length ( $F = 75.44$ ,  $df = 1, 15$ ,  $P < 0.0001$ ) (Fig. 4b), with fewer capsules per cluster ( $F = 20.98$ ,  $df = 1, 15$ ,  $P = 0.0004$ ) (Fig. 4c). Finally, her-

bivory suppressed total seed production substantially ( $F = 27.69$ ,  $df = 1, 15$ ,  $P < 0.0001$ ) (Fig. 4d). If we assume seed viability to be 9% according to Rayachhetry et al. (2002), then only about 39 viable seeds were produced on unsprayed trees vs. more than 6500 on sprayed trees, a reduction greater than 99%.

The mean percentage of biomass allocated to reproduction (biomass of reproductive structures/total biomass) was  $0.04 \pm 0.03\%$  and  $3.5 \pm 0.9\%$  for unsprayed and sprayed trees, respectively ( $F = 27.91$ ;  $df = 1, 15$ ;  $P < 0.0001$ ). Rayachhetry et al. (2001) reported reproductive biomass allocations of 0.7%, 1.5%, and 3.8% for unattacked trees growing in dry, seasonally flooded, and permanently flooded habitats, respectively.

The amount of water available to the trees played a minor role in vegetative and reproductive variables despite the large disparity of water delivered to irrigated and non-irrigated trees. The monthly mean ( $\pm$ SE) of natural precipitation was  $12.2 \pm 2.1$  cm as measured at the weather station which was equivalent of applying 122 l of water to one  $m^2$ . In comparison, irrigation provided  $2424.3 \pm 189.1$  l of water per month as measured from the dripper orifice. However, these values are not comparable directly since irrigation water spread laterally and vertically through the soil from a single point source. Margate fine sandy soils are highly permeable and, therefore, this dispar-

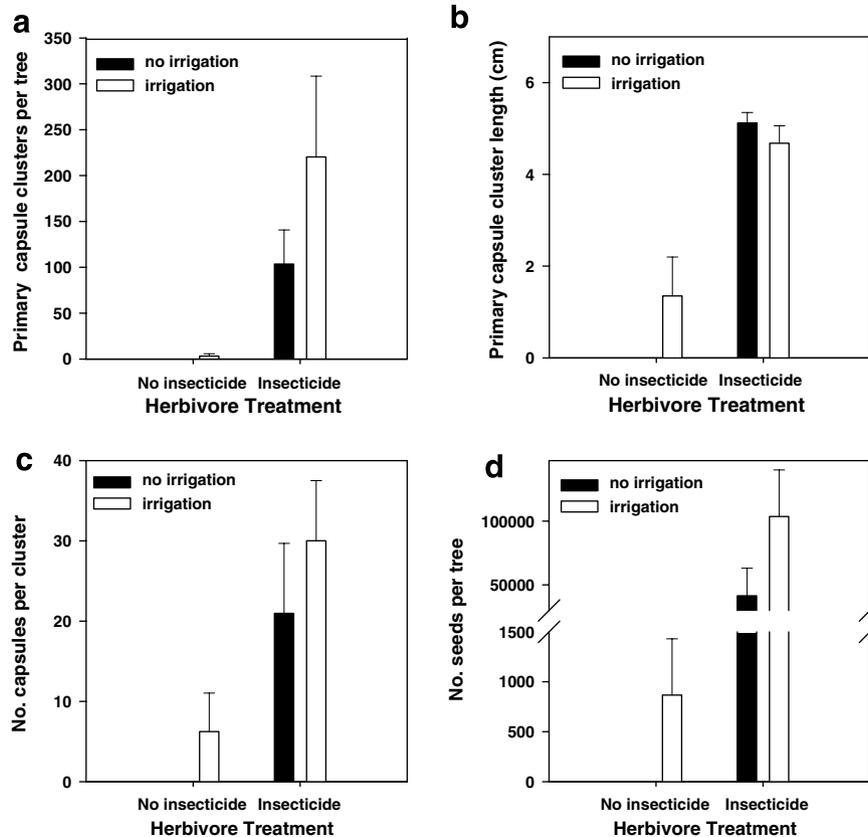


Fig. 4. Means ( $\pm$ SE) of primary capsule clusters (a), capsule cluster length (b), the number of capsules in each cluster (c), and the total amount of seed (d) produced on *M. quinquenervia* test trees subjected to experimental herbivory and irrigation treatments.

ity manifested itself primarily as periodically dry soil in the non-irrigated plots versus constantly wet soil which was never inundated in the irrigated plots.

#### 4. Discussion

Successful biological control of melaleuca was predicated on significant reductions in the tree's reproductive potential, thereby inhibiting its ability to spread throughout the landscape. Although reproductive structures often become the strongest sinks following partial defoliation (Kahn and Sager, 1969), the lack of such a reproductive sink usually results in new tissues acting as stronger sinks for carbon resources (Ryle and Powell, 1975; Vranjic and Gullan, 1990; Whigham, 1990). This reallocation of assimilates is temporary if the replacement tissue provides for its own internal carbon needs (Trumble et al., 1993; Ryle and Powell, 1975). However, *O. vitiosa* attacks new leaf tissue preferentially and relentlessly, thereby contributing to continuous refoliation and defoliation cycles on representative tree branches. Thus, because complete recovery of leaf tissue is rare, the usual temporary reallocation of plant assimilates to leaf production may become virtually permanent. This study confirms that melaleuca compensated for natural levels of defoliation by *O. vitiosa* by replacing foliage at the cost of reproductive structures with reductions exceeding those reported by Pratt et al. (2005).

The amount of moisture played only a minor role in this study compared with herbivory but it did promote more leaf production. This may partially explain perceived regional differences in melaleuca appearance wherein trees growing in wetter locations with higher organic soils typical of the east coast of Florida appear less stressed than those growing in the dryer, lower organic soils of the west coast.

Quantifying the relative suppressive contribution of each insect species in this study is difficult. However, the mean percent reduction in growth rate based on tree height was 84.4% prior to the appearance of *B. melaleucæ* and 85.7% thereafter, indicating that herbivory by *O. vitiosa* contributed most to suppression of this plant variable. It's possible that *B. melaleucæ* had a greater impact on other plant variables such as leaf biomass.

All the elements appear to be in place for reducing the seed-fueled invasiveness of melaleuca by *O. vitiosa*: a highly damaging, host-specific species, no significant seasonality to reduce growth, and a host plant that compensates preferentially for lost foliage at the expense of reproductive tissue. This may change the status of melaleuca from an invasive to a fixed-in-place tree which can be removed at leisure without concern that it will serve as a seed source for future infestations. The contribution of *B. melaleucæ* to this process is not well understood but seedlings and saplings growing in more protected understory habitats appear to be more readily attacked by this insect (P.W.T. personal observation).

Although the herbivore pressure reported in this study negatively affected individual plant fitness, extrapolating

this result to plant populations has not proven predictive because of the universe of interrelated and poorly understood variables that determine structure in plant communities (Crawley, 1989). Evidence of change is beginning to appear, however, as reported by Rayamajhi et al. (2006) who documented changes in the structure of melaleuca populations over time that corresponded with the appearance and relative abundance of *O. vitiosa*, *B. melaleuca*, and two other inadvertently-introduced exotic herbivorous species. The original project goal of constraining further population expansion of melaleuca appears achievable and may have already occurred in those areas most favorable to *O. vitiosa* growth and development.

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