



## Invasion of a West Everglades wetland by *Melaleuca quinquenervia* countered by classical biological control

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### ABSTRACT

The population dynamics of *Melaleuca quinquenervia* were monitored over a 5-year period in a cypress-pine wetland while subjected to two levels of herbivory. The trees had been recruited during 1998–1999 after a destructive crown fire. Half of 26 experimental plots were sprayed every 4–6 weeks with an insecticide to reduce herbivory by the biological control agents *Oxyops vitiosa* and *Boreioglycaspis melaleucaae*. After only 1-year melaleuca density increased by 26% in sprayed plots and by 7% in unsprayed plots. However, over the entire 5-year period melaleuca density increased in sprayed plots by 0.1% while decreasing by 47.9% in unsprayed plots when compared to initial densities. Annual mortality of melaleuca never exceeded 6% in any year in sprayed plots but ranged from 11% to 25% in unsprayed plots. There was a significant year by treatment interaction indicating the importance of the environment on tree mortality. Limited seed production occurred on sprayed trees but never on unsprayed trees. Mean tree height increased by 19.6% in sprayed plots while declining by 30.6% in unsprayed plots. Coverage by native vegetation did not increase with decreasing melaleuca density. This is the first study with controls that quantifies the population level regulation of melaleuca by introduced biological control agents and corroborates other correlative studies that documented significant changes in melaleuca communities after the introduction and establishment of biological control agents.

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### 1. Introduction

Exotic plant species which successfully invade and dominate ecosystems cause a multitude of environmental and economic problems (Vitousek, 1990). These include modifying geomorphology (Graf, 1978; Blackburn et al., 1982), hydrology (Mueller-Dombois, 1973), nutrient cycles and productivity (Harcombe et al., 1993; Garcia-Moneil and Binkley, 1998), disturbance regimes (Mack and D'Antonio, 1998), and biodiversity (Schooler et al., 2006). The mechanisms whereby species become invasive are debatable and include the role of intrinsic biological characters (Daehler, 1998; Rejmánek, 1996), relative ecosystem resistance (Myers, 1983; Pimm, 1989; Rejmánek, 1989), frequencies of introductions (Rejmánek, 2000), and the release of the invaders from growth and reproduction constraints imposed by natural enemies that existed in their native range (Keane and Crawley, 2002).

The sheer scale or locations of many infestations often precludes labor intensive control methods, such as cutting or pulling, and makes herbicides the most practical technique. However, concerns over side effects of herbicides limits their use in some areas. Classical biological control provides an alternative control method which can be integrated with other methods or used alone. This procedure aims to reunite invading plant species with host specific natural enemies so as to restore some level of top-down regulation, thereby preventing or restraining the invasive species from dominating plant communities. The goal is the sustainable suppression of the invasive species, leading eventually to the passive or active rehabilitation of degraded ecosystems (Huffaker, 1951).

Evaluating the impact of biological control beyond the scale of the individual plant is uncommon because of the difficulty in maintaining experimental controls in the face of agent dispersal and funding the cost of longer term, community level, post-release evaluation studies. Our objective was to evaluate the impacts of two introduced biological control agents on the population level dynamics of a large cohort of *Melaleuca quinquenervia* (Cav.) S.T. Blake (hereafter “melaleuca”) under field conditions while maintaining experimental controls over a 5-year period.

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## 2. Materials and methods

### 2.1. The target weed

Melaleuca is an Australian tree which reached 25–30 m in height in Florida prior to the deployment of biological control agents (Rayachhetry et al., 2002). It originates from coastal areas of eastern Australia (11–34°S), southern New Guinea, and New Caledonia where it occurs typically along freshwater streams and swamps (Boland et al., 1987). The plant was introduced into southern Florida in 1886 (Dray et al., 2006) and by 1994 had infested about 0.61 million ha (Bodle et al., 1994).

Reproductive melaleuca exhibits serotiny where seeds are held in sessile capsules that are arranged in clusters of 30–70 capsules with a 21 m tall tree holding up to 9 million viable seeds (Rayachhetry et al., 2002). Constant propagule pressure via a continuous seed rain from the canopy has facilitated the extensive recruitment of melaleuca into native plant communities. Woodall (1982) estimated the weekly seed rain at 2260 seeds m<sup>-2</sup>. However, the rate and intensity of melaleuca invasion accelerates following disturbances, especially fires which reduce interspecific competition by disproportionately damaging native plants and improving the seedbed with a layer of higher nutrient ash. Fire damage to melaleuca branches interrupts vascular activity causing seed capsules to dehisce and synchronously release seeds (Rayachhetry et al., 2002). The result is high density recruitment of melaleuca seedlings which grow rapidly, and replace the native community with a virtual monoculture of melaleuca (Van et al., 2002). Succession in communities invaded by melaleuca has been unidirectional and rapid, leading to melaleuca domination of every freshwater plant community in southern Florida (Bodle et al., 1994).

### 2.2. Biological control agents

Two insects have been released and established on melaleuca: *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) in 1997 and *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae) in 2002. Both species were tested thoroughly prior to their release in order to determine their physiological host ranges (Balciunas et al., 1994; Wineriter et al., 2003).

Adult *O. vitiosa* feed on buds and leaves while the larvae prefer newly flushing leaves (Balciunas et al., 1994). The larvae cause most of the damage by consuming the leaf tissue through to the opposite cuticle, thereby creating characteristic elongate window-like blemishes (Purcell and Balciunas, 1994). Larvae become coated with a thick viscous coating derived from the plant which provides a potent anti-predator defense (Wheeler et al., 2002). Pupation occurs in the soil, a factor which constrains the insect in permanently inundated areas (Center et al., 2000). This species is now established throughout southern Florida (P.W.T. personal observation).

Adults and nymphs of *B. melaleucae* are phloem feeders and complete their life cycle on the plant. Third through fifth instar nymphs secrete a white, waxy flocculence which may repel predators and, or, conserve moisture (Purcell et al., 1997; Wineriter et al., 2003). This species is also now established and occurs throughout the range of melaleuca in Florida (Center et al., 2006).

### 2.3. Study site

Experimental plots were located in a 19 ha section of the Belle Meade Tract (ca. 6700 ha) within the Picayune State Forest (29,000 ha) located near Naples, Florida. This area consists of nearly-level, poorly-drained, low-fertility soils which are loamy, siliceous, hyperthermic Arenic Glossoqualfs. The top 5 cm of soil in the plots contained 4.1% organic matter, 18.5 mg g<sup>-1</sup> carbon,

0.8 mg g<sup>-1</sup> nitrogen, and 18.1 µg g<sup>-1</sup> phosphorus with a pH of 5.3 (Martin, unpublished data). This area is inundated each year typically from June through January to a maximum depth of 60 cm (Tipping, unpublished data).

The Belle Meade tract within the Forest is comprised of cypress strands, wet prairies, and pine flatwood communities which predominate in lowland sloughs while subtropical hardwood hammocks dominant upland ridges. Important native species include slash pine (*Pinus elliotii* var. *densa* Little and Dorman), pond cypress (*Taxodium ascendens* Brongn.), cabbage palm (*Sabal palmetto* [Walt.] Lodd. ex. J.S. Schult. and J.H. Schult.), saw palmetto (*Serenoa repens* [Bartr.] Small), waxmyrtle (*Myrica cerifera* L.), and sawgrass (*Cladium jamaicensis* Crantz).

Melaleuca has invaded this area over the years and replaced many of the native communities with large monocultures of various-aged trees, a process expedited by several successive canopy fires. A large fire in 1998 resulted in a major recruitment event where seedling densities exceeded 1000 m<sup>-2</sup> (Center, unpublished data) and formed the cohort of plants on which we based our research to evaluate the impact of the introduced biological control insects on melaleuca population dynamics.

### 2.4. Experimental design

Four permanent transects were established in March 2002 radiating out in cardinal directions from a central location. Pairs of 9 m<sup>2</sup> plots, separated by at least 10 m, were demarcated at the central location and at 30, 60, and 100 m intervals in each direction ( $n = 26$ ). There were no obvious environmental gradients along any combination of direction and distance from the center. The configuration of the transects was chosen initially to assess the establishment and spread of *B. melaleucae*. However, because the insect quickly spread beyond the limits of the transects, the plots were used to assess the impact of the introduced agents (Center et al., 2006).

Two herbivory treatments were assigned randomly to each pair of plots: (1) an insecticide control where herbivory by *O. vitiosa* and *B. melaleucae* was impeded by foliar applications of acephate (OS—dimethyl acetylphosphor-amidothiote), and (2) a biological control treatment where the trees were not sprayed and there were no constraints on herbivory. A concentration of 0.367% ai (v/v) acephate was applied to all plant foliage until runoff every 4–6 weeks during 2003 through 2007 using a hand pressurized backpack sprayer.

### 2.5. Insecticide selection

No one method of excluding insect herbivores from plants is exempt from potential artifacts (Adair and Holtkamp, 1999). Using insecticides usually requires an extensive commitment of resources because of the need to constantly retreat the plants, especially in a subtropical environment that lacks a dormant period over winter. Applicator safety and the safe disposal of containers must be considered. Results may be confounded where several species of herbivores are present (Crawley, 1989). However, the herbivorous insect fauna on exotic invasive weeds is often depauperate, with the released agents the only specialist herbivores present (Agrawal et al., 2005; Carpenter and Cappuccino, 2005; Vilà et al., 2005; Wolfe, 2002). Costello et al. (2003) witnessed only a few generalist insect herbivores feeding on melaleuca in Florida whereas Balciunas et al. (1995) listed 409 invertebrate herbivores attacking melaleuca in Australia.

We chose acephate, a broad spectrum organophosphate insecticide, because it has low mammalian toxicity and an antidote is readily available (Crisp and Look, 1982; Singh, 1984; Behera and Bhunya, 1989). At the selected application concentration and frequencies, acephate neither inhibits nor stimulates melaleuca

growth (Tipping and Center, 2002) while effectively controlling both species of biological control agents (Tipping et al., 2008). Acephate is systemic and is ingested by the phloem feeding *B. melaleuca* which would otherwise be protected within closed terminal leaf clusters. Bouchard and Lavy (1982) reported that less than 25% of acephate remained on the leaf surface 24 h after application.

Acephate has a half life of <3 d and 6 d in aerobic and anaerobic soils, respectively (Thomson, 1982). Aerial application of acephate on snap beans and associated weeds did not increase honey-bee mortality (Erickson et al., 1994). Repeated soil applications of acephate did not reduce nitrification, sulfur oxidation, respiration rates, or population levels of actinomycetes, bacteria, and fungi (Focht and Joseph, 1974). It's unlikely that applications of acephate would have a significant fertilizing effect since each molecule contains a single atom of N which, when applied at the rates in this study, would add only  $13.6 \text{ mg N m}^{-2} \text{ year}^{-1}$  to treated plots. Sprays were directed at foliage and, therefore, drift to soils was minimized. Watering effects were also negligible since foliage received ca  $28 \text{ ml m}^{-2}$  of water and insecticide every 4–6 weeks, a trivial amount compared to the normal rainfall amounts and periodically flooded conditions that prevailed at the site.

One concern with acephate is its solubility in water which increases its potential mobility in soils, especially those low in silt and clay components (Sanchez-Camazano et al., 1993). Acephate moves more readily in moist soil conditions than dry (Suzuki, 2000). However, Yen et al. (2000) found that the soil mobility of acephate was slower than expected and predicted it would not lead to contamination of groundwater under normal agricultural operations in subtropical areas where much higher amounts of the insecticide were applied than in this study. Our sites were inundated for at least 6 months each year so the impact of acephate on aquatic organisms was also a consideration. Geen et al. (1981) concluded that impacts of acephate on aquatic fauna and sediment were limited and localized after making controlled releases of acephate in a stream. Although acephate was rapidly taken up by fish, sediments, insect nymphs, and larvae, no mortality was observed and acephate residues in animals and sediments declined to trace or non-detectable levels after 24 h (Geen et al., 1981).

### 2.6. Evaluation of treatments

Plots were monitored annually during February when the following measurements were made in a permanent  $1 \text{ m}^2$  subplot located in the center of each plot: number and height of live melaleuca trees, number of capsule clusters, percent cover of non-melaleuca vegetation, the number of dead melaleuca trees and leaf damage using the rating of Tipping et al. (2008). To estimate levels of control achieved, the number of *O. vitiosa* larvae and *B. melaleuca* colonies were counted in the plots before herbicide treatments commenced in 2003 and again after the last treatment in 2004.

Saplings were considered dead if they had no leaves and stems broke off at the soil surface with minimal pressure. The height of plants was recorded by measuring from the soil surface to the tallest portion of the plant with live buds or leaves on the first 10 plants located along a haphazardly chosen diagonal transect within the central subplot.

Two observers visually estimated the percentage cover of all non-melaleuca plants within each subplot starting in 2004. Species which were present included *Cladium jamaicense* (Crantz), *Drosera brevifolia* Pursh, *Agalinis purpurea* (L.) Pennell, *Viola lanceolata* L., *Xyris* sp., *Cyperus retrorsus* Chapman, *Dichromena latifolia* Baldwin ex Elliott, *Andropogon glomeratus* (Walt.) Britton, Stern and Poggenburg, *Lachnocaulon anceps* (Walt.) Morong, *Hypericum* sp., *Utricularia cornuta* Michaux, and several unidentified grasses.

In 2006 and 2007, leaf residue was collected on the ground from the central subplot in six plots from each treatment ( $n = 12$ ). Samples

were bulked within plots and recognizable leaf litter was separated into component species, namely melaleuca, *P. elliotii*, *M. cerifera*, and *T. ascendens*, dried at  $70^\circ \text{C}$  and weighed.

Data on plant parameters were analyzed using analysis of covariance for repeated measures (SAS, 2003). Initial measurements of plant variables served as the covariate. Treatment means for leaf residue were separated using *t*-tests. Linear regression was used to examine the effects of treatments and duration on plant height. The capsule cluster data were not distributed normally and consisted of many zero values. In order to determine the effects of the herbivore treatment on seed production, the numbers of capsule clusters per subplot were converted to a binary response variable and analyzed with logistic regression (PROC GENMOD) with repeated measures (Allison, 1999).

### 3. Results

Melaleuca populations responded negatively to herbivory from biological control agents over the 5-year period of this study. Damage from herbivory was higher in unsprayed plots ( $F_{1,18} = 145.6$ ,  $P < 0.0001$ ) with a mean ( $\pm \text{SE}$ ) rating of  $4.1 \pm 0.1$  compared to  $1.7 \pm 0.1$  for sprayed plots, confirming the efficacy of the insecticide. The rating of 4 corresponds to 75–99% of the suitable leaves on a plant being damaged (Tipping et al., 2008). Damage ratings were unobtainable in 2003, 2005, and 2006 because frosts 'burned' the foliage and obscured the herbivore damage. There was no effect of year ( $F_{1,18} = 3.07$ ,  $P = 0.09$ ) but there was a year by treatment interaction ( $F_{1,18} = 12.49$ ,  $P = 0.002$ ) indicating the importance of the environment on this variable.

The pre- and post-spray assessments of insect control showed that there were fewer *O. vitiosa* larvae ( $F_{1,18} = 3.7$ ,  $P = 0.06$ ) and *B. melaleuca* nymphs ( $F_{1,18} = 10.5$ ,  $P = 0.004$ ) on sprayed trees. Tipping et al. (2008) found that *B. melaleuca* nymphs were disproportionately suppressed by acephate as compared to *O. vitiosa* which often recolonized trees within a few weeks after a spray. In this study, densities of *B. melaleuca* colonies decreased  $98.9 \pm 0.8\%$  on sprayed trees and increased of  $49.9 \pm 46.4\%$  on unsprayed trees. The response of *O. vitiosa* varied by life stage where densities of young larvae (instars 1–3) increased  $19.0 \pm 6.3\%$ , old larvae (instars 4–5) decreased  $54.9 \pm 14.0\%$ , and adults increased  $58.6 \pm 21.1\%$  on sprayed trees. This phenomenon was observed by Tipping et al. (2008) where a lower proportion of older larvae was the only demographic difference between *O. vitiosa* densities on sprayed and unsprayed trees. They concluded that feeding by older, larger larvae had the greatest impact on melaleuca growth and reproduction. Although the data were highly variable, the density of older larvae were significantly suppressed by the insecticide treatment ( $F_{1,18} = 7.99$ ,  $P = 0.01$ ).

Tree mortality was always greater in unsprayed plots ( $F_{1,18} = 54.1$ ,  $P < 0.0001$ ) with an annual mean ( $\pm \text{SE}$ ) of  $12.9 \pm 1.5\%$  compared with  $2.7 \pm 0.3\%$  in sprayed plots (Fig. 1). However, the influence of year ( $F_{3,54} = 6.4$ ,  $P = 0.0008$ ) and the interaction of year with treatment ( $F_{3,54} = 7.6$ ,  $P = 0.0002$ ) indicated the importance of abiotic factors, most likely moisture and temperature.

Initial tree density declined in unsprayed plots but not in sprayed plots (Fig. 2). The downward trend in tree density after 2004 in sprayed plots may be the result of self thinning. However, after 5 years tree density remained largely unchanged in sprayed plots ( $0.1 \pm 0.4\%$ ) while decreasing  $47.9 \pm 5.0\%$  in unsprayed plots when compared to initial densities (Fig. 2).

Plant height decreased  $29.9 \pm 4.7\%$  in unsprayed plots and increased  $20.3 \pm 6.4\%$  in sprayed plots ( $F_{1,18} = 370.3$ ,  $P < 0.0001$ ) over the course of the study (Fig. 3). Unprotected saplings decreased in height as the apical portions died back, primarily as a result of herbivory, and secondarily from abiotic factors such as frost. The rate

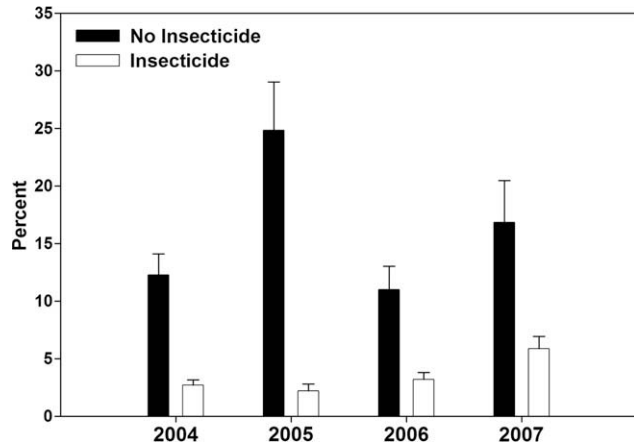


Fig. 1. Mean mortality  $m^{-2}$  of *M. quinquenervia* in unsprayed and sprayed plots from 2004 to 2007. Error bars are one standard error of the mean.

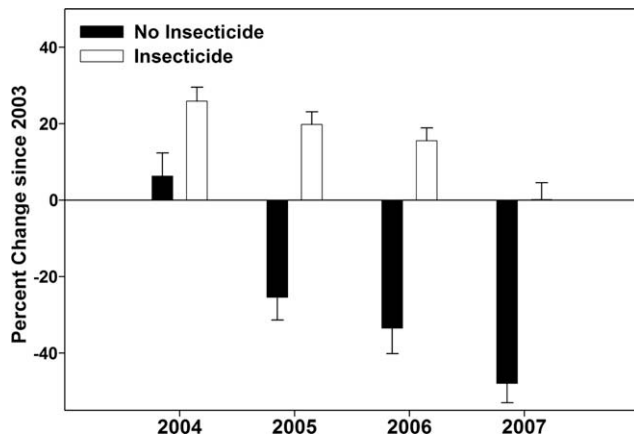


Fig. 2. Percent change in initial densities  $m^{-2}$  of *M. quinquenervia* in unsprayed and sprayed plots from 2004 to 2007. Error bars are one standard error of the mean.

of increase in plant height in sprayed plots was also probably inhibited by occasional frosts. These environmental effects were reflected by significant year ( $F_{3,54} = 9.5$ ,  $P < 0.0001$ ) and year by herbivory ( $F_{3,54} = 15.6$ ,  $P < 0.0001$ ) interactions.

Seed capsule clusters did not appear on trees in sprayed plots until 2005 and were never found in unsprayed plots ( $\chi^2 = 18.5$ ,

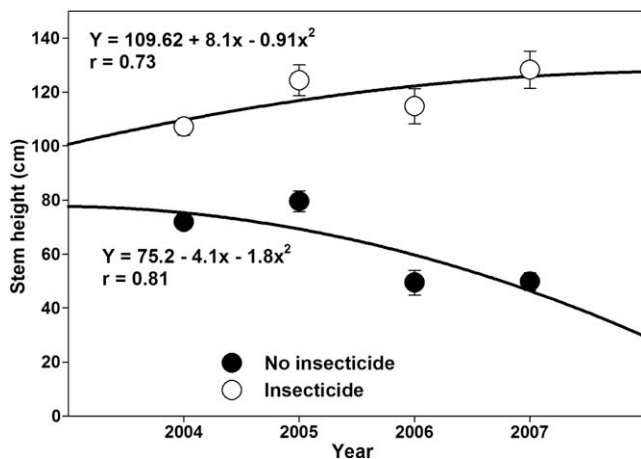


Fig. 3. Mean plant heights of *M. quinquenervia* in unsprayed and sprayed plots from 2004 to 2007. Error bars are one standard error of the mean.

$P \leq 0.0001$ ). The relatively low numbers of seed capsules in sprayed plots may be attributable to the cumulative *O. vitiosa* damage inflicted on the trees from 1998 through 2002, prior to the applications of insecticides.

The percentage of the plots covered by other plants was not related to melaleuca density or height. Vegetative cover by native species was influenced by year ( $F_{3,54} = 5.9$ ,  $P = 0.001$ ) and the interaction of year with herbivory ( $F_{3,54} = 3.2$ ,  $P = 0.02$ ) but not herbivory alone ( $F_{1,18} = 0.1$ ,  $P = 0.9$ ). Native species cover declined steadily in unsprayed plots, mirroring the decline in melaleuca (Fig. 4). However, in sprayed plots, coverage by natives declined only from 2004 to 2005 then appeared to stabilize and increase from 2006 to 2007 (Fig. 4). Although not quantified, many of the unsprayed plots in 2006 and 2007 consisted primarily of open areas with exposed mineral soil with little or no organic matter. These exposed open areas remained largely devoid of plants despite the dramatic declines in melaleuca density, primarily because of a lack of litterfall from heavily damaged plants (Table 1).

#### 4. Discussion

Significant biological suppression of melaleuca is occurring at this site on a population scale. Plants of this age would have grown much taller and produced a large quantity of seeds prior to the release of biological control agents. Tipping et al. (2008) found that growth rates in individual attacked trees were 10% of protected trees and that seed production was reduced by greater than 98%, primarily because of feeding by *O. vitiosa*. Reproductive suppression was complete at the population level probably because saplings were attacked soon after recruitment and for up to 6 years, indicating the need to consider the age of melaleuca when first exposed to herbivory when evaluating the impact of biological control. For example, older and larger, pre-biological control trees at this site still produce seed capsules regularly. Biological control impacts on the seed banks of these larger trees are uncertain but currently recruitment of seedlings within their seed shadows is uncommon. This may reflect an overall decline in their seed banks as evidenced by lower monthly seed rain (Tipping, unpublished data).

Overall, the invasion of melaleuca into the area by this 1998 cohort has been effectively checked and even reversed with respect to density, biomass, and seed production. This study supports results from correlative research by Rayamajhi (unpublished data) who documented similar changes in older melaleuca populations.

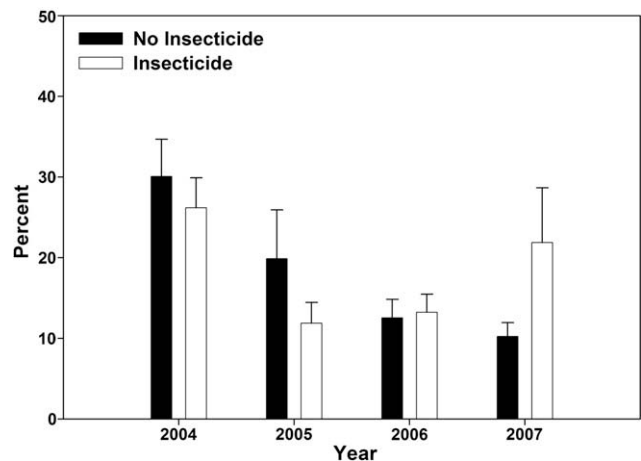


Fig. 4. Mean percentage of ground coverage  $m^{-2}$  by native plant species in unsprayed and sprayed plots from 2004 to 2007. Error bars are one standard error of the mean.

**Table 1**

Mean ( $\pm$ SE) dry weight biomass of leaf residues on the soil surface in unsprayed and sprayed plots during 2006 and 2007

Treatment	Leaf residue $\text{g m}^{-2}$	
	2006	2007
Unsprayed	19.7 $\pm$ 9.7	14.9 $\pm$ 4.6
Sprayed	101.0 $\pm$ 13.3	63.9 $\pm$ 15.5
<i>t</i>	–4.77**	2.82*

\*  $P = 0.01$ .

\*\*  $P < 0.001$ .

The influence of perturbations on recruitment remains unanswered and may depend on the degree of reduction to the canopy seed bank since the introduction of biological control. Significant reductions in the seed bank should minimize melaleuca invasive potential even with perturbations such as fires. In addition, any seedlings recruited after disturbances would now face continuous herbivory from the established insects.

Despite the decline in melaleuca populations from herbivory, there was no significant recolonization of areas by natives as open sites appeared. However, Rayamajhi (unpublished data) found increases in native plant diversity and abundance following herbivore mediated declines in older melaleuca growing in wetter, higher organic soils. The reason(s) for the lack of recolonization at Belle Meade await further study but could be related to degraded nutrient availability of microsites, insecticide effects on herbivores of native plants which promoted them even in the face of melaleuca competition, distances from reproducing native communities, soil moisture losses from evaporation due to the lack of a litter layer, and unknown legacy effects of melaleuca. These results may indicate a need for a longer time scales in order to detect changes in plant communities or perhaps a need for more active restoration efforts that include replanting of native vegetation. Unfortunately, continuing this study will not be possible because the entire area was burned again in a large fire in March 2007.

The role of insect herbivores in structuring plant communities remains an open question in natural systems (McEvoy, 2002). However, as more and more “natural” systems acquire exotics, classical weed biological control offers a sustainable alternative to mechanical and chemical programs. Most post-release evaluations of biological control programs are correlative in nature and, while often compelling, remain open to misinterpretation because of the lack of experimental control treatments. This study provides conclusive evidence that classical biological control is providing sustainable suppression of melaleuca at a population scale and corroborates other correlative research on this topic. It also highlights the need to prioritize and budget long term evaluation components for each biological control project in order to measure progress and quantify success. The design of the evaluation will necessarily differ by project and system but establishing and maintaining true experimental controls, where possible, often provides the most dramatic and irrefutable evidence of efficacy.

## References

- Adair, R.J., Holtkamp, R.H., 1999. Development of a pesticide exclusion technique for assessing the impact of biological control agents for *Chrysanthemoides monilifera*. *Biocontrol Science and Technology* 9, 383–390.
- Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W., Klironomos, J., 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86, 2979–2989.
- Allison, P.D., 1999. *Logistic Regression using SAS: Theory and Application*. SAS Institute and John Wiley and Sons, Inc., Cary, NC.
- Balcunas, J.K., Burrows, D.W., Purcell, M.F., 1994. Field and laboratory host ranges of the Australian weevil, *Oxyops vitiosa* (Coleoptera: Curculionidae), a potential biological control agent the paperbark tree, *Melaleuca quinquenervia*. *Biological Control* 4, 351–360.

- Balcunas, J.K., Burrows, D.W., Purcell, M.F., 1995. Australian insects for the biological control of the paperbark tree, *Melaleuca quinquenervia*, a serious pest of Florida, USA, wetlands. In: Delfosse, E.S., Scott, R.R. (Eds.), *Proceedings of the Symposium on Biological Control of Weeds, 2–7 February 1992*, Lincoln University, Canterbury, New Zealand, pp. 247–267.
- Behera, B.C., Bhunya, S.P., 1989. Studies on the genotoxicity of asataf (acephate), an organophosphate insecticide, in a mammalian in vivo system. *Mutation Research* 223, 287–293.
- Blackburn, W.H., Knight, R.W., Schuster, J.L., 1982. Saltcedar influence on sedimentation in the Brazos River. *Journal of Soil and Water Conservation* 37, 298–301.
- Bodle, J.M., Ferriter, A.P., Thayer, D.D., 1994. The biology, distribution and ecological consequences of *Melaleuca quinquenervia* in the Everglades. In: Davis, S.M., Ogden, J.C. (Eds.), *Everglades: The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, FL, pp. 341–355.
- Boland, D.J., Brooker, M.I.H., Chippendale, C.M., Hall, N., Hyland, B.P.M., Johnson, R.D., 1987. *Forest Trees of Australia*. Nelson Wadsworth Publisher, Melbourne, Australia.
- Bouchard, D.C., Lavy, T.L., 1982. Fate of acephate in the cotton plant. *Journal of Economic Entomology* 75, 921–923.
- Carpenter, D., Cappuccino, N., 2005. Herbivory, time since introduction and the invasiveness of exotic plants. *Journal of Ecology* 93, 315–321.
- Center, T.D., Van, T.K., Rayachhetry, M.B., Buckingham, G.R., Dray, F.A., Wineriter, S.A., Purcell, M.F., Pratt, P.P., 2000. Field colonization of the melaleuca snout beetle (*Oxyops vitiosa*) in south Florida. *Biological Control* 19, 112–123.
- Center, T.D., Pratt, P.D., Tipping, P.W., Rayamajhi, M.B., Van, T.K., Wineriter, S.A., Dray Jr., F.A., Purcell, M., 2006. Field colonization, population growth, and dispersal of *Boreioglycaspis melaleucæ* Moore, a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake. *Biological Control* 39, 363–374.
- Costello, S.L., Pratt, P.D., Rayamajhi, M.B., Center, T.D., 2003. Arthropods associated with above-ground portions of the invasive tree, *Melaleuca quinquenervia* in South Florida, USA. *Florida Entomologist* 86, 300–322.
- Crawley, M.J., 1989. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: Bernays, E.A. (Ed.), *Insect-Plant Interactions*. CRC Press, Boca Raton, FL, pp. 45–71.
- Crisp, C.E., Look, M., 1982. Effect of esterification and side-chain alkylation on alteration of translocation characteristics of methamidophos. *Xenobiotica* 12, 469–479.
- Daehler, C.C., 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. *Biological Conservation* 84, 167–180.
- Dray, F.A., Bennett, B.C., Center, T.D., 2006. Invasion history of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. *Castanea* 71 (3), 210–225.
- Erickson, E.H., Erickson, B.J., Wyman, J.A., 1994. Effects on honey-bees of insecticides applied to snap beans in Wisconsin—chemical and biotic factors. *Journal of Economic Entomology* 87, 596–600.
- Focht, D.D., Joseph, H., 1974. Microbial activity in soils treated with acephate and monitor. *Journal of Environmental Quality* 3, 327–328.
- Garcia-Moneil, D.C., Binkley, D., 1998. Effect of *Eucalyptus saligna* and *Albizia falcata* on soil process and nitrogen supply in Hawaii. *Oecologia* 113, 547–556.
- Geen, G.H., Hussain, M.A., Oloffs, P.C., McKeown, B.A., 1981. Fate and toxicity of acephate (Orthene) added to a coastal B.C. stream. *Journal of Environmental Science Health—Part B Pest Food Contamination and Agricultural Wastes* 16, 253–271.
- Graf, W.L., 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Geological Society of America Bulletin* 89, 1491–1501.
- Harcombe, P.A., Cameron, G.N., Glumac, E.G., 1993. Above-ground net primary productivity in adjacent grassland and woodland on the coastal prairie of Texas, USA. *Journal of Vegetation Science* 4, 521–530.
- Huffaker, C.B., 1951. The return of native perennial bunchgrass following the removal of Klamath weed (*Hypericum perforatum* L.) by imported beetles. *Ecology* 32, 443–458.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17, 164–170.
- Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13, 195–198.
- McEvoy, P.B., 2002. Insect-plant interactions on a planet of weeds. *Entomologia Experimentalis et Applicata* 104, 165–179.
- Mueller-Dombois, D., 1973. A non-adapted vegetation interferes with water removal in a tropical rain forest area in Hawaii. *Tropical Ecology* 14, 1–18.
- Myers, R.L., 1983. Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *Journal of Applied Ecology* 20, 645–658.
- Pimm, S.L., 1989. Theories of predicting success and impact of introduced species. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M. (Eds.), *Biological Invasions: A Global Perspective*. John Wiley and Sons, New York, NY, pp. 351–367.
- Purcell, M.F., Balcunas, J.K., 1994. Life history and distribution of the Australian weevil *Oxyops vitiosa* (Coleoptera: Curculionidae), a potential biological control agent for *Melaleuca quinquenervia* (Myrtaceae). *Annals Entomological Society of America* 87, 867–873.
- Purcell, M.F., Balcunas, J.K., Jones, P., 1997. Biology and host-range of *Boreioglycaspis melaleucæ* (Hemiptera: Psyllidae), potential biological control agent for *Melaleuca quinquenervia* (Myrtaceae). *Environmental Entomology* 26, 366–372.
- Rayachhetry, M.B., Van, T.K., Center, T.D., Goolsby, J.A., Pratt, P.D., Racelis, A., 2002. Biological attributes of the canopy-held *Melaleuca quinquenervia* seeds in Australia and Florida. *Journal of Aquatic Plant Management* 40, 87–91.

- Rejmánek, M., 1989. Invasibility of plant communities. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M. (Eds.), *Biological Invasions: A Global Perspective*. John Wiley and Sons, New York, NY, pp. 369–388.
- Rejmánek, M., 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* 78, 171–181.
- Rejmánek, M., 2000. Invasive plants: approaches and predictions. *Australian Ecology* 25, 497–506.
- SAS Institute, 2003. *SAS/STAT User's Guide*, SAS Institute, Cary, NC.
- Sanchez-Camazano, M., Gonzalez-Pozuelo, J.M., Sanchez-Martin, M.J., Crisanto, T., 1993. Adsorption and mobility of acephate in soils. *Ecotoxicology and Environmental Safety* 29, 61–69.
- Schooler, S.S., McEvoy, P.B., Coombs, E.M., 2006. Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. *Diversity and Distributions* 12, 351–363.
- Singh, A.K., 1984. Improved analysis of acephate and methamidophos in biological samples by selective ion monitoring gas-chromatography–mass spectrometry. *Journal of Chromatography* 301, 465–469.
- Suzuki, S., 2000. Leaching of several pesticides in andosol upland fields under natural rain conditions. *Journal of Pesticide Science* 25, 1–9.
- Thomson, W.T., 1982. *Insecticides, Acaricides, and Ovicides*. Agricultural Chemicals. Book I. Thomson Publications, Fresno, CA.
- Tipping, P.W., Center, T.D., 2002. Evaluating acephate for insecticide exclusion of *Oxyops vitiosa* (Coleoptera: Curculionidae) from *Melaleuca quinquenervia*. *Florida Entomologist* 85, 458–463.
- Tipping, P.W., Martin, M.R., Pratt, P.D., Center, T.D., Rayamahji, M.B., 2008. Suppression of growth and reproduction of an exotic tree by two introduced insects. *Biological Control* 44, 235–241.
- Van, T.K., Rayachhetry, M.B., Center, T.D., Pratt, P.D., 2002. Litter dynamics and phenology of *Melaleuca quinquenervia* in south Florida. *Journal of Aquatic Plant Management* 40, 22–27.
- Vilà, M., Maron, J.L., Marco, L., 2005. Evidence for the enemy release hypothesis in *Hypericum perforatum*. *Oecologia* 142, 474–479.
- Vitousek, P.M., 1990. Biological invasions and ecosystem processes: towards and integration of population biology and ecosystem studies. *Oikos* 57, 7–13.
- Wheeler, G.S., Massey, L.M., Southwell, I.A., 2002. Antipredator defense of biological control agent *Oxyops vitiosa* is mediated by plant volatiles sequestered from the host plant *Melaleuca quinquenervia*. *Journal of Chemical Ecology* 28, 297–315.
- Wineriter, S.A., Buckingham, G.R., Frank, J.H., 2003. Host range of *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), a potential biological control agent of *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtaceae), under quarantine. *Biological Control* 27, 273–293.
- Wolfe, L.M., 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalist* 160, 705–711.
- Woodall, S.L., 1982. Seed dispersal in *Melaleuca quinquenervia*. *Florida Scientist* 45, 81–93.
- Yen, J.H., Lin, K.H., Wang, Y.S., 2000. Potential of the insecticides acephate and methamidophos to contaminate groundwater. *Ecotoxicity and Environmental Safety* 45, 79–86.