

Herbivory by Introduced Insects Reduces Growth and Survival of *Melaleuca quinquenervia* Seedlings

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ABSTRACT We studied the influence of herbivory by two introduced insect herbivores on the survival and performance of seedlings of *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae), an invasive tree that threatens the Florida Everglades ecosystem. *Boreioglycaspis melaleuciae* (Moore) (Homoptera: Psyllidae) nymphs and *Oxyops vitiosa* (Pascoe) (Coleoptera: Curculionidae) larvae were transferred onto *Melaleuca* seedlings within replicated 0.25-m² caged plots in Palm Beach County, FL. The treatments included three densities of *Boreioglycaspis* first instars at 1, 15, and 50 nymphs per seedling, one treatment of a single first *Oxyops* larval instar per seedling, another treatment of both one *Oxyops* larva and one *Boreioglycaspis* nymph per seedling, and caged and uncaged controls. Herbivory by *Oxyops* did not affect *Melaleuca* seedling height, leaf number, or survival. Feeding by *Boreioglycaspis* decreased survival, height, and leaf number, with these measures of plant performance ≈50% lower in the high and medium densities compared with controls. In a field plot adjacent to the experimental area, we measured growth, survival, and naturally occurring insect density and damage on 1,100 seedlings. Although insect densities were on average lower in the field plot than in the experiment, mortality and growth rates of the seedlings were comparable with those in the experiment. The results indicate that, above a threshold density, *Boreioglycaspis* herbivory may be effective in reducing growth and survival of *Melaleuca* at the potentially critical seedling life stage. It also seemed that effects of the insects were independent rather than antagonistic or synergistic.

KEY WORDS competition, Florida Everglades, insect interactions, invasive species, weed biological control

INVASIONS BY EXOTIC PLANTS pose one of the greatest threats to natural and economically important ecosystems (Cox 1999, Pimentel et al. 1999, Mooney and Hobbs 2000, Rossman 2001). Classical weed biological control has the potential to be a highly effective and sustainable component of an invasive plant management program (DeBach and Rosen 1991, Bellows and Fisher 1999). However, biological control also has potential risks to nontarget organisms, with possible unanticipated negative effects (Follett and Duan 2000, Louda et al. 2003). It is thus essential to implement biological control programs that both maximize the effect of the agents on the target species while also minimizing the risks to nontarget organisms (Cofrancesco 2000).

One method of enhancing the efficacy of a biological control program is by introducing organisms that affect plant life stages that have the greatest impact on population growth rates (McEvoy and Coombs 1999). If the biological control agents have a large impact on the target species but not at a critical life stage, agents

may not be effective at reducing the population growth rate of the target species (Shea and Kelly 1998). For example, Hoffmann and Moran (1991) found that herbivory by the introduced weevil *Trichapion lativentre* (Béguin-Billecocq) (Coleoptera: Apionidae) resulted in a 98% reduction in *Sesbania punicea* (Cavanille) Benth (Fabaceae) seed production, yet these reductions did not result in concomitant decreases in mature plant densities. Similarly, Noble and Weiss (1989) predicted that seed predation of the shrub *Chrysanthemoides monilifera* L. T. Norlindh (Asteraceae) must reach 95% of total seed production to halt population growth of the invasive plant. In contrast, the transition from seed to juvenile plant stages in seed-limited systems has been identified as an important demographic phase of many species, including invasive plants (Lonsdale et al. 1995, Rees and Paynter 1997, Shea and Kelly 1998). For invasive woody species, seedlings have substantially less leaf area and reserve carbon storage and may be far more vulnerable to attack by biological control agents than mature adults. Some invasive woody plants have been shown to have high densities of seeds in seed banks (Lonsdale et al. 1988) and of seedlings (Lonsdale and Abrecht 1989). Whether or not inva-

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sive woody plants are seed- or seedling-limited is currently uncertain, but reduction in growth and mortality at the seedling stage may translate into reduced population growth and spread of seed-limited invasive species, reducing their ability to reestablish after adult individuals have been damaged or removed in a given area. Effective control of seedling recruitment in these systems should help to reduce the need for expensive and potentially environmentally damaging chemical or mechanical treatments after control or elimination of adults.

In many biological control programs, multiple species are used in an attempt to maximize impact on the target species (Denoth et al. 2002). Because biological control agents are generally studied and released one at a time, little is usually known about interactions among the species (McEvoy and Coombs 1999, Center et al. 2005). Depending on the species and the environmental circumstances, the effects of biological control organisms could be independent, antagonistic, or synergistic. If the effects are independent, different species would not affect each others' performance. This may be especially likely if the species occupy different feeding guilds, differ in life cycle timing, or otherwise have minimal overlap in niche parameters. Species could also interact antagonistically, making each less effective than they would be alone through competition, activation of inducible defenses, or some other mechanism of interference (Ehler and Hall 1982). Finally, species could act synergistically, making the combined effects greater than the sum of the independent effects. Synergistic interactions would be likely if there is some threshold damage level that leads to target mortality that neither species can achieve alone but that can be achieved when the agents are acting in concert.

There is currently some debate as to how many species to release in an optimal biological control program, with most scientists agreeing that a parsimonious release of as few agents as necessary is desirable (McEvoy and Coombs 1999, Denoth et al. 2002). However, knowing how many and which species will be most effective has proven difficult in practice. A better understanding of interactions among biological control agents would aid in determining the optimal number of agents to be introduced and in increasing our general understanding of interactions among organisms (Center et al. 2005).

In this study, we examined the effects of two biological control insect herbivore species on seedlings of the invasive tree, *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae) (hereafter referred to by genus). Our objectives were to (1) determine the effects of herbivory on the performance of *Melaleuca* seedlings, (2) determine the effect of density of one insect species on *Melaleuca* seedling damage, and (3) determine if the effects of the two insect species are independent, antagonistic, or synergistic. We conducted a field experiment using an existing population of *Melaleuca* seedlings, applying biological control insects at different density levels and species combinations to caged seedlings. Also, in spring of 2002 and again in spring of

2003, we sampled an unmanipulated area of *Melaleuca* seedlings adjacent to the experimental site to determine the response of a natural population of seedlings to the biological control insects.

Materials and Methods

Study Species. *Melaleuca quinquenervia* is an Australian tree that was introduced into southern Florida in the late 1800s (Dray 2003). *Melaleuca* is considered one of the most problematic invasive species in the Florida Everglades ecosystem (Rayamajhi et al. 2002a). The ecology and management of *Melaleuca* is reviewed in Turner et al. (1998) and Serbesoff-King (2003). Populations of *Melaleuca* in Florida are generally found south of Lake Okeechobee, and major infestations occur in Lee, Collier, Hendry, Palm Beach, Broward, and Dade counties (Turner et al. 1998). The trees, which occur in both dry and flooded habitats, can grow in height at rates of up to 2 m/yr (Alexander and Hofstetter 1975), can reach sexual maturity in <2 yr (Meskimen 1962), and can flower several times per year. A flower spike in its introduced range can produce 30–70 sessile capsules, and up to 7 consecutive capsule clusters have been recorded from *Melaleuca* branches (Rayachhetry et al. 1998). These serotinous capsules release seeds when vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (Woodall 1982). Capsules contain 200–350 seeds each (Meskimen 1962), yet only 9% of these seeds are viable, and seed survivorship in the soil is <2 yr (Rayachhetry et al. 1998). This low percentage of viable seeds and short-lived soil seed bank may render *Melaleuca* seed- or seedling-limited in Florida, especially in areas where the canopy has been disturbed. The canopy of a mature tree (38 cm diameter at breast height [dbh] and 12 m tall) may hold upward of 56 million seeds (Rayamajhi et al. 2002b), and areas where *Melaleuca* has been treated or naturally disturbed can become covered with a dense cohort of seedlings. This high level of seed production ability and seedling densities has been identified as one factor leading to the invasiveness of this species (Turner et al. 1998) and is thus a prime target for biological control efforts.

Oxyops vitiosa (Pascoe) (Coleoptera: Curculionidae) is native to eastern Australia and feeds exclusively on species in the *M. leucadendra* species complex, of which *M. quinquenervia* is the southernmost member (Balciunas et al. 1994). *Oxyops* were released in Florida in 1997 as the first biological control agent of *Melaleuca* (Center et al. 2000). Larvae feed on one side of the leaf through to the cuticle on the opposite, producing a window-like feeding scar. After the completion of five instars, larvae drop to the forest floor and pupate in the soil. In the absence of suitable phenological stages of its host, larvae are uncommon during summer months (April to September) unless damage-induced regrowth is present (Center et al. 2000). Adult weevils can live in excess of 1 yr, and

females produce ~350 eggs during their life time (Wheeler 2003).

Boreioglycaspis melaleuca (Moore) (Hemiptera: Psyllidae) was imported from Australia and released in South Florida in 2002 in an effort to control *Melaleuca* (Pratt et al. 2004). *Boreioglycaspis* are host-specific sap feeders (Hodkinson 1974, Purcell et al. 1997). Adult and nymph *Boreioglycaspis* feed on *Melaleuca*, but only nymphs have been found to cause substantial damage (Purcell et al. 1997). First instars are mobile, but later stages are more sessile and congregate on leaves or stems, secreting copious amounts of white, waxy filaments from glands located on their dorsum. Both adults and nymphs feed on *Melaleuca* by inserting their stylets through stomatal pores to gain access to the phloem (Woodburn and Lewis 1973, Purcell et al. 1997). The nymphs are flush-feeders and are generally found on new *Melaleuca* leaves, probably because of a higher concentration of soluble nitrogen in this fresh tissue (Hodkinson 1974). *Boreioglycaspis* and *Oxyops* both prefer young leaves, but the psyllids readily exploit fully expanded, mature leaves. Thus, *Boreioglycaspis* and *Oxyops* belong to different feeding guilds but may overlap somewhat in resource use.

Experimental Design. The study was conducted in the Loxahatchee Slough in Palm Beach County, FL (N 26.82, W 80.21). The site is now completely dominated by *Melaleuca* but was formerly a slash pine/saw palmetto community typical of this area of southern Florida, as evidenced by remaining fragments of this vegetation. The soils are high in sand content, and the area is seasonally flooded, with a water depth of ~10 cm from May to September. The climate is typical for south Florida, with winter dry and summer rainy seasons and warm temperatures year round. The average low temperature in January is 10.9°C, the average high is 24.6°C, and average precipitation is 6.3 cm. In July, the average low temperature is 21.5°C, the average high is 32.9°C, and average precipitation is 19.7 cm (http://www.coaps.fsu.edu/climate_center/data.html). A wildfire burned the area several years before initiation of the experiment, producing a dense cohort of seedlings. Neither *Oxyops* nor *Boreioglycaspis* was released directly into the experimental site, and neither species was present at the initiation of the experiment. By the termination of the experiment, both species had colonized the area and become widespread.

For the insect addition experiment, we selected an area with seedlings $\approx 26.1 \pm 0.13$ cm tall at densities of 125–564 individuals per 0.25 m². Forty 0.5 by 0.5-m plots were chosen for the experiment, and existing seedlings were thinned to six individuals per plot. Thinning was necessary to prevent transfer of insects onto other plants, and while thinning could have reduced competitive effects among the seedlings, this impact is expected to be minimal over the short-term duration of this study. Only seedlings without visible insect damage were used. Plots were randomly assigned the following treatments: *Boreioglycaspis* addition (1, 15 or 50 first-instar nymphs per seedling), *Oxyops* addition (1 first larval instar per seedling), *Boreioglycaspis* + *Oxyops* addition (1 individual of

each species per seedling), caged controls (cages with no insects added) and no-cage controls with 5 replicate plots per treatment for all treatments except for caged controls, which had 10 replicate plots. For the insect treatments, insects were directly transferred onto live leaves on each plant in the plot using paint brushes. For the *Oxyops* treatments, only one *Oxyops* density was used because one *Oxyops* larva per seedling was the maximum number observed in the adjacent plot and the average number of larvae per seedling was substantially less than one (see Results). Also, there is not enough leaf tissue on one seedling to support the development of more than one *Oxyops* larva (Wheeler 2003), so a treatment of more than one larva would have only lead to *Oxyops* mortality and not produced any more damage than that done by one larva. All insect treatments and the caged controls were enclosed in cages measuring 50 by 50 cm wide and 75 cm tall constructed of PVC frames and insect-exclusion screen (No-Thrips Insect Screen; BioQuip, Rancho Dominguez, CA). We placed yellow sticky cards in all insect addition plots to trap out adults and maintain consistent insect densities. No adults of either species were observed in any of the plots except attached to the sticky cards, so the cards appeared to be effective. The plots were established in November 2002, and insects were added in December 2002, February 2003, and April 2003, with insect additions as described as above for each addition date. We recorded seedling survival, height, number of leaves at monthly intervals, and leaf, stem, and root mass at final harvest. Baseline data on one harvested seedling per plot were taken before the insect addition treatments.

Analyses were performed on data for the mean of all of the seedlings in each plot, because plot is the experimental unit. The effects of insect treatments on percent survival was analyzed with a mixed model analysis of variance (ANOVA) using the procedure MIXED in SAS (version 8.0). Survival was arcsine square root transformed. Proportional change in height and leaf number were calculated as $\ln([final - initial]/initial)$, and the effects of treatments were analyzed with ANOVAs using the GLM procedure. Biomass and root:shoot ratios were transformed with the natural logarithm and analyzed with ANOVAs using the GLM procedure. For all dependent variables, differences among the levels of *Boreioglycaspis* densities were analyzed with REGWQ (SAS Institute 1985) post hoc tests. Means reported are \pm SE.

We established a long-term seedling observation plot adjacent to the experimental area in March 2003. The plot is 0.25 by 2 m and contains seedlings of the same approximate height and density as in the experimental area. We recorded initial diameter (at 5 cm above the soil level) for each seedling, and in March–April 2004 we recorded plant survival, diameter, height, number of *Oxyops* larvae, number of *Boreioglycaspis* colonies, and leaf damage by each insect species. The effect of damage on seedling growth was analyzed with a mixed model ANOVA.

Table 1. ANOVA table for the effects of *Boreioglycaspis* (BOR) and *Oxyops* (OXY) treatments and their interaction on *Melaleuca* seedling survival, change in height, change in no. of leaves, and total final biomass

	df	Survival		Height		No. leaves		Biomass	
		MS	F	MS	F	MS	F	MS	F
BOR	3	1.34	13.1 ^a	0.02	15.5 ^a	0.07	3.36 ^b	1.13	7.48 ^a
OXY	1	0.01	0.04	0.00	1.92	0.00	0.05	0.09	0.61
BOR × OXY	1	0.01	0.04	0.00	3.21	0.00	0.00	0.00	0.00
Residual	34	0.01		0.00		0.02		0.15	

^a $P < 0.001$; ^b $P < 0.05$.

Results

There were no differences in plant survival, height, or leaf number between the caged and uncaged controls (all $P > 0.05$), indicating that experimental artifacts caused by cage effects were unlikely. The caged and uncaged controls were thus pooled for the remainder of the analyses. *Boreioglycaspis* caused a significant decrease in plant survival (Table 1). Plots with no *Boreioglycaspis* or with one *Boreioglycaspis* per plant had survival at or near 100%, whereas plots with 15 or 50 *Boreioglycaspis* per plant were at or below 50% (Fig. 1). Survival was significantly lower in the 15 or 50 *Boreioglycaspis* per plant treatments than in the control treatments with zero *Boreioglycaspis* nymphs per plant, but there was no difference between the controls and the one *Boreioglycaspis* per plant treatment (Table 2). There was no effect of *Oxyops* on plant survival and no statistical interaction between the *Oxyops* and *Boreioglycaspis* treatments (Table 1).

Boreioglycaspis significantly affected plant biomass (Table 1). Compared with the control seedlings with zero nymphs per plant, seedlings with 15 or 50 nymphs per plant had significantly less biomass (Table 2). This effect on total biomass was caused by effects on leaf mass ($F_{3,32} = 22.41$; $P < 0.0001$), number of leaves ($F_{3,34} = 3.36$; $P < 0.05$), stem mass ($F_{3,32} = 8.20$; $P < 0.01$), and root mass ($F_{3,32} = 2.97$; $P < 0.05$). For

example, seedlings with zero or one nymph per plant had an average of 4.62 leaves per plant, whereas seedlings with 15 or 50 nymphs per plant had an average of 1.92 leaves. Seedlings with 15 or 50 nymphs per plant lost more leaves than control seedlings (Table 2). *Boreioglycaspis* treatments did not change biomass allocation patterns, with no effect of *Boreioglycaspis* treatment on root:shoot ratio. *Boreioglycaspis* also had a significant effect on seedling height (Table 1). Plants with 15 or 50 larvae per plant were significantly shorter than plants with 0 or 1 larvae per plant (Table 2). The effects of the *Boreioglycaspis* treatment on plant height did not become apparent until 4 mo after the initiation of the treatments (Fig. 2). There was no effect of *Oxyops* on plant biomass or leaf number and no statistical interaction between the *Oxyops* and *Boreioglycaspis* treatments for biomass and leaf number (Table 1).

In the unmanipulated, observational plot, *Melaleuca* seedlings were at an initial density of 2,394 seedlings/m². Of the seedlings alive in the first year of sampling, 58.8% survived to the second year. Insect damage and densities were not recorded in the first year, so the amount of this mortality that can be attributed to herbivory is uncertain. The seedlings were an average of 1.98 ± 0.04 cm diameter at 5 cm height in year 1 and 2.54 ± 0.05 cm diameter in year 2. In the second year of sampling, there were an average of 0.03 ± 0.01 *Oxyops* larvae and 1.70 ± 0.11 *Boreioglycaspis* colonies (≈32 nymphs per colony) observed per seedling on the census date. The percent of seedlings with damage caused by *Boreioglycaspis* and *Oxyops* was 54.1 and 32.7%, respectively. Damage by the two insect species co-occurred on 18% of the seedlings, whereas 26% were damaged by *Boreioglycaspis* only, 12% were damaged by *Oxyops* only, and 44% were undamaged. There was a significant effect of damage by *Boreioglycaspis* ($F_{1,653} = 18.67$; $P < 0.0001$) and by *Oxyops* ($F_{1,653} = 23.92$; $P < 0.0001$) on growth (change in diameter from year 1 to year 2) in the seedlings, but no interaction between *Boreioglycaspis* and *Oxyops* ($F_{1,653} = 1.36$; $P > 0.05$). Seedlings with *Boreioglycaspis* and *Oxyops* damage in year two had grown more than undamaged plants (Table 3.)

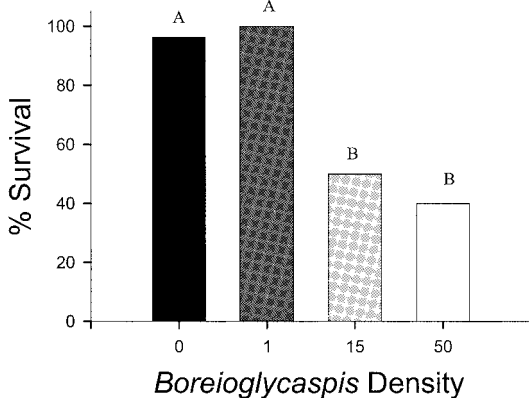


Fig. 1. Percent seedling survival in each of the four levels of the *Boreioglycaspis* treatments. This result is pooled across levels of the *Oxyops* treatment, which had no significant effect on survival. Different letters indicate significantly different means according to a REGWQ post hoc test ($\alpha = 0.05$).

Discussion

In the experimental plots, there was a significant impact of herbivory by *Boreioglycaspis* nymphs on growth and survival of *Melaleuca* seedlings. This is the

Table 2. Means \pm SE for proportion survival, change in height (cm), change in numbers of leaves, and final biomass (g) for *Boreioglycaspis* at 0, 1, 15, and 50 nymphs per seedling densities in the experimental plots

<i>Boreioglycaspis</i> density	Survival		Height		Leaves		Biomass	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
0	0.96A	0.027	3.90A	0.247	-4.71A	0.630	6.53A	0.093
1	1.00A	0.000	2.89A	0.475	-4.04A	0.691	6.47A	0.107
15	0.40B	0.170	0.30B	0.318	-8.63B	2.188	5.87B	0.164
50	0.50B	0.177	0.22B	0.594	-8.59B	1.859	5.68B	0.168

Identical letters show means not significantly different from each other according to REGWQ post hoc tests ($\alpha = 0.05$).

first study to show an effect of *Boreioglycaspis* herbivory on *Melaleuca* seedling performance in the field. Only approximately one half of the seedlings in the high-density *Boreioglycaspis* treatments (15 or 50 nymphs per seedling) survived compared with nearly 100% survival in the low (0 or 1 nymph per seedling) treatments. Of the surviving seedlings, those in the high-density *Boreioglycaspis* treatments had 11.4% less biomass and fewer than one half as many leaves as those in the low-density treatments. Thus, it seems that *Boreioglycaspis* herbivory has a substantial impact on *Melaleuca* seedling survival and performance, but that this impact is only apparent at high densities (15 or 50 nymphs per seedling). The fact that effects of *Boreioglycaspis* were found at 15 and 50 but not 1 nymph per seedling indicates that there seems to be a threshold of somewhere between 1 and 15 nymphs for *Boreioglycaspis* to have a detectable effect on *Melaleuca* seedling survival and performance. Management strategies may thus benefit by maintaining *Boreioglycaspis* densities above this threshold level, but densities far above this threshold level are unlikely to have a proportionally greater impact on seedlings, according to these results. Other studies have also shown increasing impacts of herbivory with increasing insect density. For example, Bacher and Schwab (2000) found that performance of the creeping thistle

Cirsium arvense L. Scopoli (Asteraceae) decreased with increasing numbers of experimentally applied shield beetle [*Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae)] larvae. However, the effect of insect density on plant performance is still unknown for many systems.

In contrast to the results for *Boreioglycaspis*, there was no detected effect of *Oxyops* herbivory on *Melaleuca* seedling survival or performance in the experimental plots. This result differs from several previous studies that have shown heavy damage by *Oxyops* on *Melaleuca* plants under field conditions (Pratt et al. 2005). Additionally, nearly one third of the seedlings in the observational plot in this study suffered from *Oxyops* damage. There are several possible reasons for the lack of a detected effect of *Oxyops* in our experiment. Most previous studies of *Oxyops* have been on trees or larger saplings, so seedlings may not be as susceptible to herbivory by *Oxyops*. *Oxyops* larvae prefer newly flushed leaf tips and require 0.5 g leaf material to complete development (Wheeler 2003), and this amount of material may not have been available on most seedlings. While one *Boreioglycaspis* nymph per plant was also too low of a density to detect an effect, it was predicted that one *Oxyops* larva would have a greater impact because *Oxyops* larvae are more than an order of magnitude larger than *Boreioglycaspis* nymphs.

In the observational plot, there was substantial damage by *Boreioglycaspis* and *Oxyops* and high levels of mortality (nearly 50%), which is comparable with that found in the experiment. In contrast to the experimental results, the plants that were damaged in the second year had actually grown larger than undamaged plants since the first year. This result may be because of the fact that insects were choosing larger plants. Thus, the negative effect of insect herbivory could only be detected in the experimental plots,

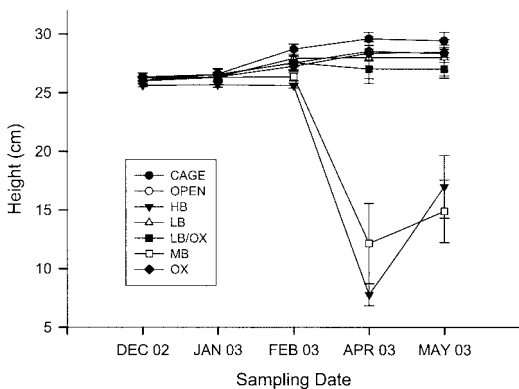


Fig. 2. The effect of treatments on seedling height at each sampling time during the experiment. The treatments are coded as follows: CAGE, caged controls; OPEN, uncaged controls; HB, 50 *Boreioglycaspis* per seedling; MB, 15 *Boreioglycaspis* per seedling; LB, 1 *Boreioglycaspis* per seedling; OX, 1 *Oxyops* per seedling; LB/OX, 1 *Boreioglycaspis* + 1 *Oxyops* per seedling. Shown are means \pm SE.

Table 3. Means \pm SE for seedling growth (change in diam in mm from year 1 to year 2) by type of insect damage in the observational plot

Damage type	Growth	SE
NONE	0.3297	0.0423
BOR	0.6758	0.0556
OXY	0.7117	0.0808
BOR+OXY	0.9107	0.0671

Types include *Boreioglycaspis* only (BOR), *Oxyops* only (OXY), *Boreioglycaspis* plus *Oxyops* (BOR+OXY), and undamaged (NONE).

where insect preference and damage were not confounded.

There was no statistical interaction between the *Boreioglycaspis* and *Oxyops* treatments for any measurement of plant performance in both the experimental and observational plots. This finding supports the hypothesis that the effects of the insects are independent rather than antagonistic or synergistic. However, this could be because of the fact that there was only one level of the *Oxyops* treatment and no effect of the insects at this density level. If more levels of *Oxyops* density and more combinations of *Oxyops* and *Boreioglycaspis* levels were used, it is possible that an interaction could be detected. Alternatively, because *Boreioglycaspis* and *Oxyops* occupy different feeding guilds (sap-feeder and leaf-chewer, respectively), it is possible that interactions between the insect species are minimal.

In reviewing the literature on interactions among phytophagous insects, Denno et al. (1995) found that of 193 pairwise interactions, evidence for competition was found in 76% of the cases. They found that competition was more likely if the insects were introduced and aggregative, as is the case for *Oxyops* and *Boreioglycaspis*. Competition was also more likely if the insects were related and sessile, which *Oxyops* and *Boreioglycaspis* are not. Competition seems to be widespread among phytophagous insects and may be important in structuring insect communities. However, competition may not be prevalent among insects used in biological control programs. Denoth et al. (2002) found that, for biological control projects with weeds as the target species, the success of the project increased with an increasing number of agents released, and control is usually attributable to one agent. Thus, competition does not seem to be often important, possibly because of the variable success of insect introductions. Their finding supports a lottery model (Myers 1985) of success in weed biological control, in which agents do not directly interact, and increasing the number of agents increases the likelihood of success by increasing the chances that an effective agent will establish. However, based on the risks associated with releasing multiple control agents, Denoth et al. (2002) recommend releasing as few agents as possible in biological control programs.

Regardless of interactions among the biological control insects, they will only have an impact on the population dynamics of the target species if the insects affect plant performance at a critical life stage. Seedlings likely represent a sensitive transitional stage in the life cycle of *Melaleuca*. Herbivory by *Boreioglycaspis* reduced seedling survival and performance, although it remains unclear how these effects would translate into reductions in population growth rates and spread of invasions of *Melaleuca*. The lack of a long-lived soil seedbank (Rayamajhi et al. 2002b), however, makes *M. quinquenervia* particularly vulnerable to herbivore-mediated reductions in fitness and delays in reproductive maturation. Because canopy-held seedbanks continue to diminish over time, seedling suppression is predicted to have direct, long-term

effects on plant density. To test this prediction, future research will examine how herbivores affect stage-specific demographic transitions of *Melaleuca* and quantify the effects of herbivory in the context of the entire plant life cycle (Doak 1992, Shea and Kelly 1998).

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