



The ecological host range of an intentionally introduced herbivore: A comparison of predicted versus actual host use

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ABSTRACT

An underlying assumption of weed biological control asserts that laboratory-based host specificity testing accurately predicts the realized host range of herbivorous arthropods. We tested this assumption by comparing predicted host specificity with the realized host range of the introduced weevil *Oxyops vitiosa* (Pascoe). Laboratory host specificity tests showed that the weevil can complete its development on only a small group of species in the *Melaleuca* genus, including the target host *Melaleuca quinquenervia* (Cav.) Blake. Three years after its release, adult weevils readily emigrated from the surrounding *M. quinquenervia* trees into replicated common gardens but only a small proportion occurred within the canopies of non-*Melaleuca* species. Adults remained within the canopies of *Melaleuca* congeners longer than non-*Melaleuca* and the former recruited 98% of all individuals dispersing from neighboring test plant species. Oviposition was predicted to occur on seven of the 19 species planted in the common gardens but was realized on only four exotic species. Consistent with the prerelease assessments, larvae were observed on four plant species but larval development was limited to *Melaleuca* congeners. These results lend support to the premise that risk assessments based on physiological host ranges, as characterized by laboratory testing, are conservative when compared to the realized ecological host ranges that occur under field conditions. We conclude that the ecological host range of *O. vitiosa* is highly restricted and there will be no colonization of species other than the target weed in the adventive range.

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1. Introduction

The premise that a herbivore's ecological or realized host range can be predicted from data collected during laboratory-based prerelease testing has been met with skepticism (McEvoy, 1996; Louda et al., 2005). In nature, herbivore host finding behaviors typically proceed in a stepwise fashion from dispersal to habitat location, identification of host patch, plant finding, alighting, and locating the suitable plant part that elicits feeding or oviposition stimuli (Schoonhoven et al., 1998). Due to inherent artificiality, laboratory studies standardize environmental conditions and interfere with sequences in host finding behaviors, which may influence the incidence and intensity of herbivory by natural enemies among plant species (Louda et al., 2005).

The underlying assumption that laboratory-based host specificity testing accurately predicts the realized host range of herbivorous arthropods after release remains largely unconfirmed for most biological control systems (Louda et al., 2005). The few studies that have investigated this assumption have employed differing approaches. Some have monitored sentinel non-target plants within existing weed populations for use by biological control agents

after introduction (Blossey et al., 2001; Schooler et al., 2003; Dudley and Kazmer, 2005; Breiter and Seastedt, 2007). Alyokhin et al. (2001), for instance, observed no use when surveying for the fly *Acinia picturata* (Snow) in flower heads of seven non-target species in the Asteraceae that had overlapping distributions with the closely related target weed *Pluchea odorata* (L.) Cass. In addition, *a posteriori* hypothesis testing using retrospective analyses based on literature reviews and expert opinions have provided insights into general patterns of realized host specificity and evolution (Fowler et al., 2000; Pemberton, 2000; Sing et al., 2005). Alternatively, experimental designs that incorporate replicated and interspersed plantings of species predicted to be suboptimal or non-hosts during host range testing also provide insight into the scalability of physiological host ranges (Stiling and Simberloff, 2000). We adopted the latter approach using a common garden experiment to investigate the ecological host range of *Oxyops vitiosa* Pascoe, an intentionally introduced natural enemy of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake.

The Australian tree *M. quinquenervia* has been internationally disseminated over the course of the last century for ornamental, re-vegetation, and agroforestry purposes (Turner et al., 1998; Serbesoff-King, 2003; Dray et al., 2006). It was introduced into California, Texas, and Louisiana, but has not been reported as an invasive pest in these areas of the United States. In contrast,

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M. quinquenervia was widely planted in Florida, Puerto Rico, Hawaii, Cuba, and the Bahamas (Dray et al., 2006; Pratt et al., 2005b, 2007), where the tree has naturalized and proven to be a superior competitor to most, if not all, native vegetation in forested and sawgrass dominated systems (Pratt et al., 2005b; Turner et al., 1998). After its introduction in Florida, *M. quinquenervia* spread at an estimated rate of 2850 ha/yr (Laroche and Ferriter, 1992) and now dominates ca. 200 000 ha of Everglades ecosystems, with dense stands of up to 132 000 saplings and trees/ha (Rayachhetry et al., 2001). These *M. quinquenervia* wetland forests typically form dense monocultures characterized by continuous upper canopies with sparse understories (Rayamajhi et al., 2002).

To mediate negative ecological impacts caused by the tree's invasion, explorations for natural enemies of *M. quinquenervia* were conducted in eastern Australia (Burrows and Balciunas, 1999). The curculionid weevil *O. vitiosa* was then selected for quarantine-based risk assessments (Purcell and Balciunas, 1994). Host range testing indicated that *O. vitiosa* only completes development on a small group of species in the *Melaleuca* genus, of which there are no native representatives in the New World. Based on this narrow host range, the weevil was permitted for release in Florida during the spring of 1997 and readily became established in *M. quinquenervia* dominated habitats (Center et al., 2000; Pratt et al., 2003).

In this study we tested whether quarantine-based host specificity testing of *O. vitiosa* accurately predicted the herbivore's ecological host range. To address this question, we conducted a series of common garden experiments to: (1) determine whether *O. vitiosa* demonstrated similar tendencies to feed, oviposit, and develop on test plant species predicted in quarantine tests to be non- or suboptimal hosts, (2) assess residency time, feeding, and oviposition of adult weevils when placed on test plants, and (3) quantify utilization of test plants after the normal host was removed locally.

2. Materials and methods

2.1. Study species

In its native range, *M. quinquenervia* occurs along Australia's northeastern coast from Sydney in New South Wales to the tip of Cape York Peninsula in northern Queensland, in New Guinea, and in New Caledonia (Boland et al., 1987). Multiple introductions of *M. quinquenervia* were made on both the eastern and western coasts of south Florida during the 1880s through early 1900s (Dray et al., 2006). These evergreen trees produce new foliage and flowers during winter (dry season) although some individuals do so at unpredictable intervals (Meskimen, 1962). Inflorescences are indeterminate and arranged in bottlebrush-like spikes, which give rise to persistent capsular fruits arranged in a series of clusters (Meskimen, 1962; Holliday, 1989). Capsules contain 200–350 seeds each and the canopy of a mature tree (380 mm diameter at breast height and 12 m tall) may hold up to 1.4 kg of seeds (about 56 million seeds) (Rayamajhi et al., 2002). Because of the massive seed release, dense, monospecific *M. quinquenervia* stands are common (Hofstetter, 1991; Van et al., 2000).

Oxyops vitiosa is native to eastern Australia and is a specialist herbivore on species in the *Melaleuca leucadendra* species complex, of which *M. quinquenervia* is the southern-most member (Balciunas et al., 1994). In its introduced range, oviposition occurs mainly during daylight hours from October to March (Center et al., 2000). Eggs are deposited on the surface of expanding foliar buds, young leaves, or elongating stems. A hardened coating of frass and glandular secretions covers each egg (Purcell and Balciunas, 1994). Adult weevils feed indiscriminately and superficially on *M. quinquenervia* foliage whereas larvae are specialized feeders, consuming

only newly-developed, expanding leaves which are ephemeral produced in seasonal flushes at branch apices (Purcell and Balciunas, 1994; Pratt et al., 2004). Larvae are ectophages, feeding on one side of the leaf through to the cuticle on the opposite side, producing a window-like feeding scar. They complete five instars then drop to the forest floor where they pupate in the soil. Larvae are uncommon during summer months (April–September) when suitable leaves are scarce and only found on damage-induced regrowth (Center et al., 2000; Pratt et al., 2005a). Adult weevils can live in excess of 1 year and females produce ca. 350 eggs during their life time (Wheeler, 2005).

2.2. Study sites

We conducted our experiments in Broward County, Florida, USA, which experiences distinct wet and dry seasons with warm temperatures year round. The average low temperature in January is 10.9 °C, the average high 24.6 °C, and average precipitation 63 mm. In July, the average low temperature is 21.5 °C, the average high is 32.9 °C, and the average precipitation is 197 mm. The mean annual rainfall based on normal patterns for the period of 1971–2000 is 1302 mm, with 60% falling in June through September (NOAA, 2002).

Two study sites were chosen. The first study site, Andytown, consisted of a 1 ha *M. quinquenervia* dominated wetland occurring in the Everglades Buffer Strip (N 26.035483; W –80.43495). Trees in the study area form part of a larger *M. quinquenervia* stand that extends N to S and is surrounded by a short hydroperiod sawgrass wetland. Land managers cut *M. quinquenervia* trees near their bases prior to 1997, resulting in multi-stemmed coppices sprouting from the stumps. At the onset of the study, *M. quinquenervia* trees within the site were 2–5 m tall and occurred at a density of 2517 trees/ha. Trees were growing in soils of high organic content with seasonal summer flooding over a 2–3 month period. In the summer of 1997 over 450 adult *O. vitiosa* weevils were liberated near the center of the study site, resulting in a self-sustaining population (Pratt et al., 2002).

The second study site was located at the Invasive Plant Research Laboratory (IPRL) in Davie, Florida (26.085, –80.2414). A 0.7 ha study plot was delineated within an open field that supported a ruderal herbaceous ground cover growing on an arenaceous soil substrate. In March 2000, four *M. quinquenervia* saplings (~1 m tall) were randomly planted in each of 11 rows, with individuals separated by 7.6 m within and between rows. Supplemental water was provided continuously through a drip irrigation system. Adult *O. vitiosa* from nearby sources began exploiting the trees soon after planting.

2.3. Herbivore recruitment and damage

A common garden was established at the Andytown site in May 2000. For this study, eight plant species were selected from among those evaluated during host range testing so as to provide a range in the level of use (oviposition, feeding, and larval development) by the herbivore as predicted under laboratory conditions. In addition, test plants varied in phylogenetic relatedness and represented both native as well as adventive exotic species (Table 1). Five plants of each species were purchased from local nurseries, except *M. quinquenervia*, which was obtained from a stock of plants maintained at the IPRL. The test plants were not subjected to any insecticides prior to their purchase. In addition, plants purchased as *Melaleuca rigidus* R.Br. from local nurseries were determined to be an ornamental variety of *Melaleuca viminalis* (Sol. Ex Gaertn.) Byrnes but, to be consistent with the industry and as these plants exhibited a growth habit and phenology distinctly different from the other variety of *M. viminalis*, we refer to the selection hereafter

Table 1
Plant species used to compare the predicted and realized host range of *Oxyops vitiosa*.

Species ^a	Site ^b	Origin ^c	Host use under laboratory conditions		
			Adult ^d feeding	Oviposition	Larval development
<i>Calyptanthes pallens</i>	1, 2	Native, FT	1	–	–
<i>Calyptanthes zuzygium</i>	1	Native, FE	1	–	–
<i>Eugenia axillaris</i>	1,2	Native	1	–	–
<i>Eugenia confusa</i>	2	Native, FE	1	–	–
<i>Eugenia foetida</i>	1,2	Native	1	–	–
<i>Eugenia rhombea</i>	1,2	Native, FE	1	–	–
<i>Melaleuca quinquenervia</i>	1,2	Exotic	3	+	+
<i>Melaleuca (rigidus)</i>	1,2	Exotic	3	+	+
<i>Melaleuca viminalis</i>	1,2	Exotic	3	+	+
<i>Melaleuca viminalis</i> var. 'Little John'	2	Exotic	3	+	–
<i>Myrcianthes simpsonii</i>	1,2	Native, FT	2	+	–
<i>Myrciaria cauliflora</i>	2	Exotic	1	–	–
<i>Myrica cerifera</i>	1,2	Native	3	+	–
<i>Pimenta dioica</i>	2	Exotic	NT	NT	NT
<i>Pimenta racemosa</i>	2	Exotic	NT	NT	NT
<i>Psidium guajava</i>	2	Exotic	2	+	–
<i>Psidium longipes</i>	2	Native, FT	2	–	–
<i>Syzygium jambos</i>	2	Exotic	1	–	–
<i>Syzygium malaccense</i>	2	Exotic	NT	NT	NT

^a All species are in the family Myrtaceae except *M. cerifera*, which belongs to Myricaceae.

^b Common garden: 1 = Andytown, 2 = Invasive Plant Research Lab.

^c Exotic or native to Florida, U.S. Species considered threatened or endangered in Florida are designated as FT and FE, respectively.

^d Adult *O. vitiosa* feeding categories described by (Balciunas and Buckingham, 1996): 0 = no feeding; 1 = light feeding on a few leaves; 2 = noticeable feeding, but over small area; 3 = feeding similar to that observed on *M. quinquenervia*. Feeding predictions represent the highest damage level observed during testing. NT = not tested.

as *M. (rigidus)*. A single plant of each test species was planted into five, 3 × 5 m plots in a randomized block design. These test plots were delineated near the center of the study site and watered weekly until July, when seasonal rains provided sufficient moisture to ensure survival. Beginning in July 2000, each test plant within the five study plots was examined at monthly intervals and the numbers and stages of *O. vitiosa* per plant were recorded. As *O. vitiosa* larvae only exploit newly developing, expanding leaves, the phenological development of foliar buds on each test plant was also monitored.

To quantify herbivore pressure surrounding the common garden, *O. vitiosa* populations were monitored at 10 m intervals along eight transects oriented east to west and spaced 10 m apart throughout the stand (Center et al., 2000; Pratt et al., 2004). Every month between July 2000 and June 2001, four *M. quinquenervia* trees were sampled at 20 randomly selected transect points using the quarter method of Krebs (1999). The area surrounding each point was divided into quadrats (NE, SE, SW, and NW) and the nearest tree to the sample point in each sector was inspected to determine the number of *O. vitiosa* individuals (all stages) per plant. Resource availability was quantified on a 5-point scale based on a visual estimation of the percentage of branch apices that possessed leaves that would support larval development: 0 – no expanding leaves; 1 – <25% of the apices possessed suitable foliage; 2 – 26% to 50%; 3 – 51% to 75%; 4 – 76% to 100% of the apices had expanding leaves.

A common garden was also planted at the IPRL study site, in which rows of test species alternated with rows of *M. quinquenervia* trees. In May 2002, four sets of 18 test species were planted in a randomized block design among the *M. quinquenervia* rows (Table 1). The inclusion of 10 additional test species provided a wider range of species, in terms of taxonomic relatedness and predicted host use, than the Andytown study. A row of nine randomly selected test plants was established between each *M. quinquenervia* row, with two test plant rows comprising a block. Test plants were separated by 1.5 m within the row and 3.5 m from *M. quinquenervia* between rows. All plants in the study were provided supplemental irrigation as described above. Each test plant and *M. quinquenervia* tree was inspected at monthly intervals and the

numbers of *O. vitiosa* adults and larvae and the incidence of eggs were recorded until July 2003. As feeding damage from both larvae and adults is distinct from other herbivores in the system (Pratt et al., 2003), the level of damage that was attributable solely to the introduced herbivore was assessed on each test plant using a 5-point scale based on a visual estimation of percentage of the leaves attacked by the herbivore: 0 – no damage; 1 – less than 25%; 2 – 26% to 50%; 3 – 51% to 75%; 4 – 76% to 100% of the leaves damaged.

2.4. Residency time

In this experiment we placed adult weevils directly into the canopies of test plants and monitored their dispersal over time. On 28 June 2001, 400 adult weevils were collected at a release site near Estero, Lee County, Florida (26.035483, –80.43495). The adults were sexed according to morphological characteristics and 100 ♀/♂ pairs were individually placed into separate cylindrical clear plastic cages (80 mm diam × 150 mm tall), each containing a single 60–80 mm *M. quinquenervia* branch held in a water-filled vial to maintain leaf turgor. Weevils were monitored for 48 h for signs of oviposition. Gravid females, and their accompanying males, were marked by placing multiple patches of paint on the elytra in a unique combination of colors to differentiate genders, assigned test plant species and block. On 5 July 2001 the weevils were transported to the Andytown study site and two females and two males were placed near the canopy center of each test species. Test plants as well as the adjacent *M. quinquenervia* plants outside the study blocks were inspected at 3, 8, 25, 32, and 45 h after release and the location of the marked weevils was recorded. Residency time, calculated as the number of hours that each individual was observed on the assigned test plant, was averaged for all blocks.

2.5. Host plant removal

To investigate the behavior of *O. vitiosa* under resource shortages, the recruitment and impact of adult weevils on the test plants was monitored at the Andytown site after *M. quinquenervia* was re-

moved locally. To do this, weevil density was quantified in the *M. quinquenervia* stand surrounding the Andytown study plot on 14 August 2001 as described earlier. Over the subsequent 72 h all trees within the stand (>2500 individuals), excluding those in the study blocks, were felled and left in the field to desiccate. Weevil densities, levels of herbivory, and oviposition on test plants were measured on 4 September in the same manner as described earlier. The removal of the *M. quinquenervia* plants was timed so that the majority of the test plants possessed both newly developed, expanding leaves as well as older foliage.

2.6. Data analysis

Due to the correlation of herbivore densities observed on the same test plant over time, we used repeated measures analysis of variance to compare the number of *O. vitiosa* adults and larvae recruited to the study species as well as damage levels in the common garden studies (von Ende, 1993; Littell et al., 2002). The Huynn–Feldt adjustment was used when the covariance matrix of the data did not meet the assumption of sphericity (von Ende, 1993; SAS Institute, 1999). Linear regression was used to test for a numerical response of *O. vitiosa* adults as a function of oscillations in resource availability (Schenk and Bacher, 2002). Least square means averaged over the 12 censuses were used to compare differences among plant species. Repeated measures logistic analysis of variance (ANOVA) was used to compare the ovipositional incidence and residency time among species (PROC GENMOD, Littell et al., 2002). The inverse link function was used to convert the logit to the predicted probability of oviposition and converted standard errors from the link function scale to the inverse link scale using the delta rule (Littell et al., 2002). Orthogonal contrasts were used to compare among species specific probabilities. The influence of plant origin (exotic versus native) and phylogenetic relatedness to the target species (*Melaleuca* species versus all others) on incidence of adult and larvae recruitment to the test plants were also compared with logistic ANOVA as described above (Littell et al., 2002).

3. Results

3.1. Herbivore recruitment and damage

3.1.1. Andytown site

Resources available for consumption by *O. vitiosa* in the *M. quinquenervia* stand surrounding the common garden fluctuated tem-

porally (Fig. 1). As reported for other stands of the invasive tree in Florida, expansion of foliar buds was greatest during fall and winter but some suitable foliage was present year round (Fig. 1). Adult *O. vitiosa* were also continually present. Their densities fluctuated over time, although not in direct response to resource availability ($F_{1,11} = 0.23$; ns). The proportion of trees bearing weevil eggs, in contrast, ranged from 94% in February to 2.5% in June and was highly correlated with flushes of new foliage ($F_{1,11} = 21.64$; $P = 0.0009$) (Fig. 1). A numerical response to pulses in newly developed leaves was also observed for total larvae, with greatest increases in larval densities during October, November, and February ($F_{1,11} = 2.66$; $P = 0.0237$). Larval stages were also present throughout the study, although the proportion of adults to immature stages was higher during resource limited periods.

The location of immigrating adults within the common garden was influenced by plant species ($F_{8,37} = 6.54$; $P < 0.0001$), with 92% of the individuals occurring on *Melaleuca* hosts (Fig. 2). Adult densities were highest on *M. (rigidus)*, intermediate on the other congeners, and lowest on the non-*Melaleuca* species (Fig. 2). Adult densities increased in response to increases in suitable stages on the *Melaleuca* species over time ($F_{68,117} = 1.54$; $P = 0.019$). In contrast, phenological variation among the non-*Melaleuca* species did not affect adult densities ($F_{85,242} = 0.51$; ns). On *Melaleuca* species, adult densities were highest during spring (January–May), which corresponded with maturation of larvae in the surrounding *M. quinquenervia* stand (Fig. 1).

Egg distribution patterns were consistent with those of adult densities, although more conservative. While adults alighted on 78% of the test plant species in the common garden, oviposition was restricted solely to *Melaleuca* species. Among the *Melaleuca* species, egg densities were greatest for *M. (rigidus)* ($\chi^2_1 = 10.43$, $P = 0.0012$) and were 1.17 times greater than on the other *Melaleuca* species (95% Wald confidence interval: 0.458–1.873). There was no difference in egg numbers on *M. quinquenervia* and *M. viminalis* ($\chi^2_1 = 0.89$, $P = 0.3458$).

Melaleuca quinquenervia supported greater larval densities (sum of all stages) than all other plants tested ($F_{8,38} = 5.01$; $P < 0.001$). There was no significant difference in larval densities on *M. (rigidus)*, *M. viminalis*, and the remaining non-*Melaleuca* species (Fig. 2b) but all larval stages were only observed on *M. (rigidus)* and *M. viminalis* in addition to *M. quinquenervia*. As in the surrounding stand (Fig. 1), larval density increases were greatest during early spring (Fig. 2b). During this phase of high larval densities on nearby hosts, 4th instar larvae were seen wandering within the canopies of individual *Eugenia axillaris* (Sw.) Willd., *Eugenia foetida*

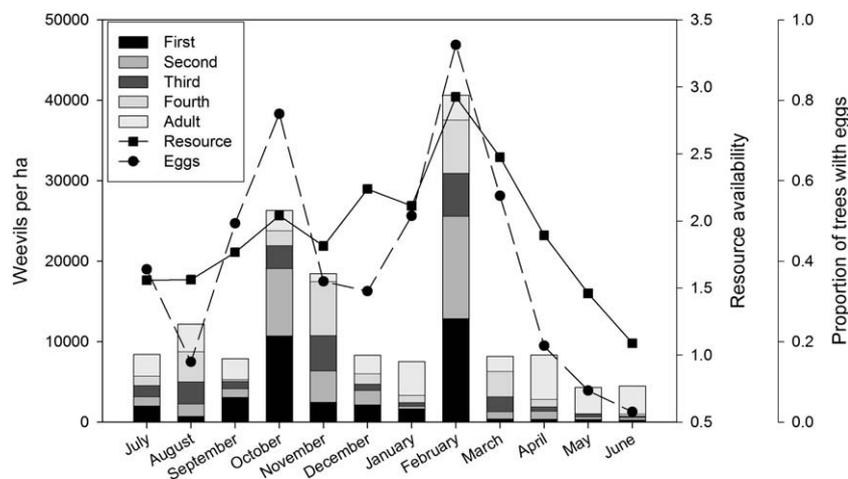


Fig. 1. Population densities of the introduced herbivore *Oxyops vitiosa* within the *Melaleuca quinquenervia* stand surrounding the Andytown common garden.

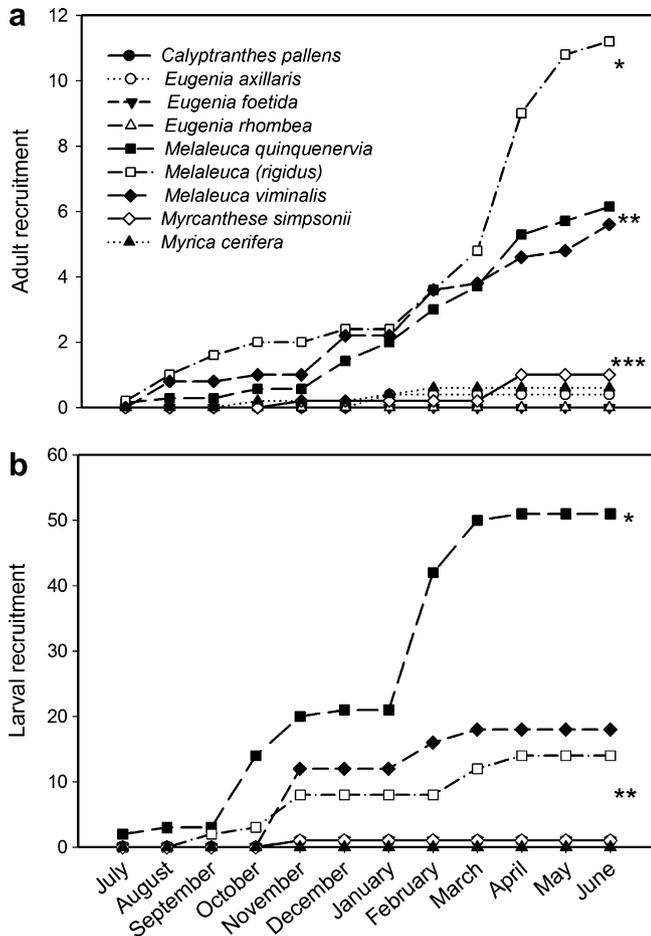


Fig. 2. Cumulative recruitment of *Oxyops vitiosa* adult and larval stages among test species at the Andytown common garden. Cumulative levels of recruitment followed by differing number of stars are significant at $P < 0.05$ based on orthogonal contrasts.

Pers., *Calyptanthes pallens* Griseb., and *Myrcianthes fragrans* (Sw.) McVaugh plants but no feeding damage was observed.

3.1.2. IPRL site

Consistent with our previous findings, the distribution of adult weevils at the IPRL common garden was also species-dependent ($F_{18, 77} = 8.05$; $P < 0.0001$). Adults were observed within the canopies of 11 test species during the study (Table 2), although the majority (287 or 79% of observed individuals) occurred within the canopies of *M. quinquenervia* ($F_{18, 77} = 25.0$; $P < 0.0001$). Fewer adults were observed on *Psidium guajava* L. (13%), *M. (rigidus)* (6%), and *M. viminalis* (2%). Adult counts on native species were not significantly different from zero.

Eggs were only found on four of the 19 test species, including three *Melaleuca* species and *P. guajava* (Table 2). There is limited evidence to suggest that oviposition frequency varied among these four species ($\chi^2_3 = 6.45$, $P = 0.0915$). Interspecies comparisons indicate, however, that the probability of observing eggs on *M. quinquenervia* was greater than on the pooled data for the congeners *M. (rigidus)* and *M. viminalis* ($\chi^2_1 = 6.15$, $P = 0.0131$), but intermediate for *P. guajava* ($\chi^2_1 = 0.85$, $P = 0.3558$) (Table 2).

The occurrence of larvae on test plant species reflected the ovipositional trends described above ($F_{18, 77} = 14.62$; $P < 0.0001$). All stages of *O. vitiosa* larvae occurred on the three *Melaleuca* species while 1st instar larvae were not able to complete development on *P. guajava*. Mean larval densities (all stages) averaged over the 12-month study period were greatest on *M. quinquenervia*, which

hosted 92% of all larvae observed within the common garden. The mean larval densities occurring within the canopies of all other test species were not significantly different from zero.

Herbivory levels on the *M. quinquenervia* trees within the common garden averaged 3.3 (95% C.I. = 3.13–3.47), corresponding with 51–75% defoliation (Table 2). The herbivory level for this species ranged from 2.8 in January to 3.7 in July. Within the common garden, foliar damage varied between species ($F_{18, 77} = 51.43$; $P < 0.001$) (Table 2). Levels of herbivory when measured over the entire experiment were greatest on *M. quinquenervia*, intermediate on the other *Melaleuca* species and *P. guajava*, and lowest on the remaining species.

3.2. Residency time of adult weevils

Residency time varied among plant species ($\chi^2_8 = 51.80$, $P = < 0.0001$). Experiment-wise weevil residency time was greatest for *M. quinquenervia*, intermediate for *M. (rigidus)*, *M. viminalis*, and *Myrcianthes simpsonii*, and lowest for the remaining species (Table 3). Three hours after release, for instance, 75% of the assigned weevils remained on *M. quinquenervia*, 80% on *M. (rigidus)*, 55% on *M. viminalis*, 40% on *M. simpsonii*, and 25% on *M. cerifera*, with the remaining species harboring <15% of the original cohort. The probability of adults remaining on their assigned test plant over the entire 45 h assessment followed similar trends as described above (Table 3). While weevils dispersed from all test plants, there is weak evidence to suggest that residency time is shorter for males as compared to females ($\chi^2_1 = 2.98$, $P = 0.084$). The within-plot destination of weevils dispersing from assigned plants was also influenced by plant species ($F_{8, 32} = 8.40$; $P < 0.001$). *Melaleuca* species recruited 98% of all recovered weevils, with *M. viminalis* harboring 36%, *M. (rigidus)* 35%, and *M. quinquenervia* 28% (Table 3). Among the non-*Melaleuca* species, four of the 172 weevils dispersing within the plot were observed within the canopies of *E. axillaris* and *Eugenia rhombea* Krug & Urb. ex Urb, respectively.

3.3. Host plant removal

Prior to felling, *M. quinquenervia* harbored 0.9 (SD \pm 1.24) adults per tree or ca. 2100 individuals per ha in the stand surrounding the Andytown common garden. Following host plant removal, adult weevils numbers differed among test species ($F_{8, 44} = 10.93$; $P < 0.001$). Consistent with previous results, *Melaleuca* species attracted the greatest number of adults, with *M. quinquenervia*, *M. (rigidus)*, and *M. viminalis* harboring 5.2 (\pm 1.6), 4.0 (\pm 2.3), and 4.6 (\pm 1.4) individuals within their respective canopies. Two adult weevils were also observed on *M. simpsonii* and one individual on *C. pallens*. No feeding damage was associated with weevil presence on the non-*Melaleuca* species. The numbers of adult weevils on *Melaleuca* species after local host removal were three times greater than those observed during the previous monthly surveys ($F_{1, 32} = 11.16$; $P < 0.002$), while the remaining species showed no increase.

4. Discussion

Of the pest management tactics employed to mitigate the ecological impacts of invasive species, few have generated more reaction in the current scientific literature than weed biological control. One commonly cited concern relates to the largely untested assumption that forms the basis of risk assessments: laboratory-based specificity tests accurately predict the ecological host range of an introduced herbivore (Louda et al., 2005). We compared host test predictions to the realized ecological host range of *O. vitiosa*, with emphasis on those species considered suboptimal

Table 2

Recruitment and herbivory of *Oxyops vitiosa* on test plants at the Invasive Plant Research Lab common garden. Means (SE) averaged across all dates are presented except for oviposition, which is the probability (SE) of observing eggs on test plants.

Species	Adult density	Oviposition	Larval density	Herbivory level ^a
<i>Calyptanthes pallens</i>	0	0	0	0.30 (0.07)
<i>Calyptanthes zuzygium</i>	0.04 (0.03)	0	0	0.44 (0.09)
<i>Eugenia axillaris</i>	0	0	0	0.34 (0.68)
<i>Eugenia confusa</i>	0.02 (0.02)	0	0	0.14 (0.57)
<i>Eugenia foetida</i>	0	0	0	0.22 (0.59)
<i>Eugenia rhombea</i>	0	0	0	0.16 (0.05)
<i>Melaleuca quinquenervia</i>	6.33 (1.14)	0.66 (0.70)	39.97 (5.16)	3.30 (0.08)
<i>Melaleuca (rigidus)</i>	0.46 (0.15)	0.26 (0.06)	0.34 (0.23)	1.74 (0.11)
<i>Melaleuca viminalis</i>	0.16 (0.07)	0.24 (0.07)	1.29 (0.17)	1.24 (0.12)
<i>Melaleuca viminalis</i> var. 'Little John'	0	0	0	0.12 (0.05)
<i>Myrcianthes simpsonii</i>	0.12 (0.05)	0	0	0.34 (0.07)
<i>Myrciaria cauliflora</i>	0.02 (0.02)	0	0	0.30 (0.07)
<i>Myrica cerifera</i>	0.12 (0.05)	0	0	0.73 (0.08)
<i>Pimenta dioica</i>	0	0	0	0.10 (0.05)
<i>Pimenta racemosa</i>	0.02 (0.02)	0	0	0.16 (0.05)
<i>Psidium guajava</i>	0.98 (0.26)	0.48 (0.11)	1.30 (0.55)	1.14 (0.13)
<i>Psidium longipes</i>	0	0	0	0.16 (0.52)
<i>Syzygium jambos</i>	0.04 (0.03)	0	0	0.12 (0.05)
<i>Syzygium malaccense</i>	0	0	0	0.26 (0.07)

^a See Section 2 for grades used.

Table 3

Residency time for *Oxyops vitiosa* adults when placed on test plants.

Species	Residency time ^a	Slope of logistic regression	Residency probability (SE)	df	χ^2	P-value ^b	Recruitment
<i>Calyptanthes pallens</i>	0.6 (0.2)	-3.21 (0.59)	0.04 (0.02)	1	29.94	<0.0001	–
<i>Eugenia axillaris</i>	0.6 (0.2)	-3.50 (0.73)	0.03 (0.02)	1	23.07	<0.0001	0.4 (2.4)
<i>Eugenia foetida</i>	0 (0)	-2.73 (1.01)	0.06 (0.06)	1	7.25	0.0071	–
<i>Eugenia rhombea</i>	0 (0)	-3.50 (0.76)	0.03 (0.02)	1	21.34	<0.0001	0.4 (0.2)
<i>M. quinquenervia</i>	21.0 (0.7)	-0.03 (0.26)	0.51 (0.06)	1	0.01	0.9100	9.6 (3.8)
<i>Melaleuca (rigidus)</i>	17.8 (0.8)	-0.29 (0.29)	0.43 (0.07)	1	0.99	0.3196	12.2 (3.1)
<i>Melaleuca viminalis</i>	2.4 (0.2)	-1.17 (0.36)	0.19 (0.05)	1	10.31	0.0013	12.6 (3.1)
<i>Myrcianthes simpsonii</i>	2.2 (0.4)	-1.61 (0.38)	0.17 (0.05)	1	17.67	<0.0001	–
<i>Myrica cerifera</i>	0.6 (0.2)	-2.97 (0.42)	0.05 (0.02)	1	49.81	<0.0001	–

^a Mean (SE) number of hours before half of adult weevils dispersed from test plants.

^b Tests the null hypothesis that the probability of adult weevils remaining versus dispersing from the test plant = 0.

hosts in prerelease studies. We observed substantial symmetry between the predicted and realized host range of *O. vitiosa* following its introduction in Florida. Adult weevils readily immigrated to common garden plots but few were observed within the canopies of non-*Melaleuca* species (8% at the Andytown and 4% at the IPRL common gardens). Although differing scales complicate direct comparisons, there were no cases in which adult herbivory levels exceeded those predicted from host range tests and in at least four instances levels were lower than predicted. Similarly, *O. vitiosa* was predicted to oviposit on seven of the 19 plant species tested but realized oviposition was restricted to four, suggesting that these plants lie outside the herbivore's ovipositional host range under field conditions.

The probability of a herbivore encountering and exploiting a potential host is likely to be influenced by the relative abundance of the plant species in a given community. We assume herein that the absence of *O. vitiosa* on native plants represents discrimination rather than a random host selection process. In the nearly-mono-specific stand of *M. quinquenervia*, however, there is expected to be a low probability of dispersing *O. vitiosa* adults alighting on the few test plants in the common garden at the Andytown site. Indeed, one may hypothesize that *O. vitiosa* would have exploited more species if there had been a higher encounter rate. When placed directly into canopies of test species or when local hosts were removed, however, *O. vitiosa* adults resided on *Melaleuca* congeners longer than other species and recruited 98% of all dispersing individuals. These findings have relevance for the use of re-

gional herbicide treatments that selectively kill entire *M. quinquenervia* stands while leaving sympatric native species, including many of those tested herein, as the only remaining vegetation within local patches. The findings indicate that *O. vitiosa* will not utilize the native species included in the tests, despite experiencing local resource shortages.

The "spill over" of herbivory from *M. quinquenervia* to *P. guajava* is expected to be localized, temporary and carries little ecological relevance as *P. guajava* is also considered an exotic invasive plant (Langeland and Burks, 1998). In contrast, the Florida native and sympatric *M. cerifera* was also predicted to be at risk from wandering *O. vitiosa* late instar larvae (Wheeler, 2005). As *O. vitiosa* larvae overexploit local resources, they wander or drop from *M. quinquenervia* canopies in search of food. Simulating encounters of larvae with native plants under controlled laboratory conditions, Wheeler (2005) determined that, although none of the neonates fed on *M. cerifera*, 20% of *O. vitiosa* larvae survived to pupation when reared first on *M. quinquenervia* and then transferred as 3rd instars to *M. cerifera* leaves. These encounters between late instar larvae (3rd and 4th instars) and non-*Melaleuca* species, including *M. cerifera*, were also observed at the Andytown site but no signs of larval herbivory occurred on non-target species throughout the experiment. The incongruity between results of Wheeler (2005) and those reported herein is likely explained by differences in physiological versus ecological host ranges: a small proportion of confined late instar larvae can complete development on the native *M. cerifera* but this event is rare in nature. Our results show that the ecological

host range of *O. vitiosa* is highly restricted and there is extremely low risk of colonization of non-target species in the adventive range. These results also lend support to the premise that risk assessments based on physiological host ranges, as characterized by laboratory testing, are conservative when compared to the realized ecological host ranges that occur under field conditions (McEvoy, 1996; van Klinken and Heard, 2000; van Klinken and Edwards, 2002; Littlefield and Buckingham, 2004).

A growing body of literature indicates that a herbivore's physiological host range is unlikely to expand in the adventive environment (see van Klinken and Edwards, 2002; Pemberton, 2000). However, the level to which a herbivore exploits those within the ecological host range is subject to selection in the adventive region, which may lead to changes in acceptance or increased use (adult feeding, oviposition, larval feeding) of suboptimal hosts (Thompson, 1998; Schaffner, 2001; van Klinken and Edwards, 2002). The likelihood that rapid evolution will lead to enhanced herbivore performance on a given suboptimal host is related, in part, to the genetic changes needed to overcome the physiological or behavioral factors that defined the host's suboptimal status upon introduction (Thompson, 1998; van Klinken and Edwards, 2002). Herein, for instance, we observed similar levels of adult recruitment and oviposition on the optimal host *M. quinquenervia* and *M. (rigidus)* but the latter species was considered suboptimal due to the markedly lower larval survival and associated herbivory levels (Fig. 2b; Wheeler, 2005). The genetic change required to enhance survivorship of *O. vitiosa* larvae when exploiting *M. (rigidus)* is expected to be relatively small compared to *P. guajava*, which supports adult recruitment and oviposition but not larval development (Table 2, Fig. 4). The greatest disparity in herbivore performance occurred between *M. quinquenervia* and the native *M. cerifera*, which supported development of late instars under controlled conditions (Wheeler, 2005) but recruited few *O. vitiosa* adults, did not induce oviposition or support early-instar development. These observations indicate that rapid evolution leading to improved herbivore performance on *M. cerifera* is unlikely considering the suite of genetic constraints that govern physiological and behavioral factors currently limiting *O. vitiosa* performance. Quantitative genetics studies may be helpful to elucidate whether variation in larval survival or performance when feeding on these hosts is genetically based (Futuyma et al., 1995; Schaffner, 2001).

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