



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

P.D. Pratt \*, M.B. Rayamajhi, T.D. Center, P.W. Tipping, G.S. Wheeler

USDA/ARS, Invasive Plant Research Laboratory, 3225 College Ave., Fort Lauderdale, FL 33314, USA

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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,

\* Corresponding author. Fax: +1 954 976 9169.

E-mail address: [Paul.Pratt@ars.usda.gov](mailto:Paul.Pratt@ars.usda.gov) (P.D. Pratt).

*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

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