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An abundant biological control agent does not provide a significant predator subsidy

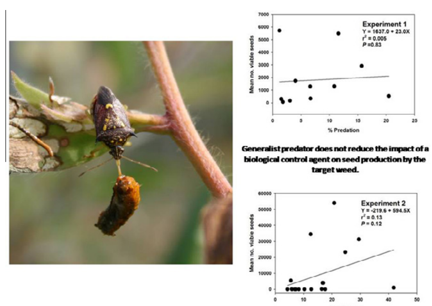
Philip W. Tipping [a,*], Melissa R. Martin [b], Paul D. Pratt [a], Min B. Rayamajhi [a], Ted D. Center [a]

[a] USDA-ARS, Invasive Plant Research Laboratory, Ft. Lauderdale, FL, USA
[b] ARM Loxahatchee Wildlife Refuge, Delray Beach, FL, USA

HIGHLIGHTS

- Chemically defended biological control agent experienced low predation.
- Predation effects did not cascade down to producer level.
- Predation events did not increase despite increases in prey populations.
- Hence, an abundant biocontrol agent did not promote a significant predator subsidy.

GRAPHICAL ABSTRACT



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ABSTRACT

Classical weed biological control agents, regardless of their effectiveness, may provide subsidies to predators and parasites. The chemically defended weevil *Oxyops vitiosa* Pascoe is a successful agent that was introduced to control the invasive tree *Melaleuca quinquenervia*. Two consecutive small plot experiments that lasted two and three years, respectively, examined the population dynamics of *O. vitiosa* while subjected to predation by *Podisus mucronatus*, a native generalist predator. During this time the estimated mean (±SE) percent predation of *O. vitiosa* larvae was 7.2 ± 1.7% per sample date in the two year study and 8.4 ± 0.8% in the three year study. There was no relationship between the number of larvae per tree and the number that were predated in either experiment. Consumer losses from predation did not cascade down to the producer level and influence any plant variable in either experiment. Time series analysis found no autoregressive processes for predation in either experiment while there were strong first through fourth-order auto-correlations for live larvae in both experiments, indicating the presence of strong trends in prey density. If longevity was a gauge of the relative importance of a predator subsidy, then any provided by *O. vitiosa* was negligible because predation was unlikely to increase over two consecutive sample periods despite increasing prey populations. The benign presence of sustained populations of a biological control agent provides a tailored counter argument to studies that imply inevitable and perilous linkages between introduced agents and community food webs.

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1. Introduction

Classical weed biological control programs aim to reunite exotic invasive weeds with natural enemies in order to re-establish some level of top-down suppression in the invaded range (Mc Fadyen, 1998; Müller-Schärer and Schaffner, 2008). During the process of establishing and acclimating, populations of approved agents are

* Corresponding author. Address: USDA-ARS Invasive Plant Research Laboratory, 3225 College Ave., Ft. Lauderdale, FL 33314, USA. Fax: +1 954 476 9169.
E-mail address: philip.tipping@ars.usda.gov (P.W. Tipping).

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subject to demographic, environmental, and genetic processes with outcomes ranging from local extinction to maintenance of outbreak densities (Fauvergue et al., 2012). Predicting these population trajectories and linking them to the target plant population dynamics remains a formidable challenge. The reasons why agents fail to provide effective control are poorly understood but are often attributed to climatic mismatches, population-level compensation of the plant, top-town forces like predation, or bottom up forces like plant quality (Paynter, 2004; Thomas and Reid, 2007; Garren and Strauss, 2009; Center and Dray, 2010; Manrique et al., 2011).

Agents that do establish sustainable populations will inevitably provide temporary or permanent subsidies to generalist predators or stenophagous parasitoids (Paynter et al., 2010; Veldtman et al., 2011). Critics argue that such subsidies influence food web interactions unpredictably, resulting in indirect effects that range from apparent competition to risks to human health (Willis and Memmott, 2005; Pearson and Callaway, 2006). However, a number of studies have observed that food web interactions are generally weak in natural systems (Fagan and Hurd, 1994; Power et al., 1996; Kokkoris et al., 1999). Indirect effects are also widespread in natural systems, unique to their own sets of organisms and communities, and likely to be dynamic processes whose ecological significance will remain open to interpretation (Yodzis, 1988; Polis and Strong, 1996). For example, although Carvalheiro et al. (2008) did document declines in native seed herbivores from apparent competition with an abundant biological control agent, there were also positive effects on native plant abundance. Weighed against these largely theoretical risks are the very concrete and negative consequences to plant, animal, and human communities from the unfettered growth and spread of some exotic plants (Headrick and Goeden, 2001).

The objectives of this study were to (1) characterize the population dynamics of a biological control agent subjected to predation by a generalist predator, (2) determine if consumer losses from predators cascaded down to the producer level, and (3) evaluate the relative importance of the predator subsidy.

2. Materials and methods

2.1. The weed

Melaleuca quinquenervia (Cav.) S.T. Blake is a tall evergreen tree that has historically occupied tropical to subtropical wetland sites along the eastern coast of Australia (Kaufman and Smouse, 2001). The plant was introduced into southern Florida in 1886 and by 1994 had infested about 200,000 ha (Bodle et al., 1994; Dray et al., 2006). Its invasive attributes are due in part to its reproductive capacity wherein the canopy of a 21 m-tall tree can hold up to 9 million viable seeds (Rayachhetry et al., 2002). In addition to constant propagule pressure via continuous seed rain from a canopy-held seed bank, episodic perturbations like fires cause seed capsules to dehisce and release seeds, usually in one synchronous event. This has led to high density recruitment of *M. quinquenervia* seedlings, which grow quickly and dominate the area (Van et al., 2002).

Infestations of *M. quinquenervia* can alter plant and animal community structure and diversity, nutrient storage and cycling, and ecosystem response to disturbance (O'Hare and Dalrymple, 1997; Martin et al., 2009, 2010, 2011). The scale of the problem led to the creation of a long term, integrated management plan using chemical, mechanical, and biological methods which ultimately proved successful in reducing the abundance and impact of the plant (Laroche, 1998). The resulting landscape level reductions in *M. quinquenervia* acreage are credited with reducing the home-range size requirements for the endangered Florida panther, *Puma concolor coryi*, because of overall improvements to habitat quality (Julian et al., 2012).

2.2. The biological control agent

The first agent released against *M. quinquenervia* was *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) in 1997 (Center et al., 2000). Adults feed on buds and leaves while larvae feed on either leaf surface and consume the leaf tissue through to the cuticle on the other side (Purcell and Balciunas, 1994). This species probably produces 3–5 generations per year in southern Florida, depending on the temperature (Purcell and Balciunas, 1994). Larvae are coated with a thick viscous layer of essential oils sequestered from the plant which provides a potent defense to most predators (Wheeler et al., 2002; Wheeler et al., 2003). This species is considered to be an effective biological control agent at both the individual and plant population levels where it has reduced seed production by up to 99% and sapling densities by up to 47% in the field (Tipping et al., 2008; Tipping et al., 2009).

2.3. The predator

Podisus mucronatus Uhler (Hemiptera: Pentatomidae) is a common but little studied component of the southern Florida fauna and has been the most apparent predator in areas where *O. vitiosa* has established (Christensen et al., 2011). Costello et al. (2002) described this species in greater detail and tested several nymphal diets for suitability, including one that included *O. vitiosa.* A well studied and presumably similar congener, *Podisus maculiventris* (Say), has a host range of over 50 prey species, a consistently low attack rate and, unlike other, more specialized penatomid predators like *Perillus* sp., is found in many habitats (Evans, 1982a; McPherson, 1982; O'Neal, 1988). *Podisus maculiventris* typically spends more time resting than searching even at higher prey densities (Wiedenmann and O'Neil, 1991). Other ambush-style predators in the Anthocoridae and Lygaeidae are known to conserve energy with relatively long resting periods (Evans, 1976; Cohen, 1984, 1985). Females usually accumulate and begin ovipositing only in the presence of dense aggregations of soft bodied larvae in the Lepidoptera, Hymenoptera (sawflies), and Coleoptera (Warren and Wallis, 1971; Evans, 1982b).

2.4. Sampling design

Saplings of *M. quinquenervia* (1–1.5 m height) were planted in two adjacent field plots during December 1999 (experiment 1) and in March 2003 (experiment 2) at the USDA-ARS Invasive Plant Research Laboratory in Ft. Lauderdale, Florida. The prevailing soil type was a Margate fine sand, siliceous hyperthermic Mollic Psammaquent, with less than a 1% slope. Trees were fertilized and irrigated until they were firmly established. For the purposes of this study, the experimental designs were complete 2×6 (experiment 1) and 2×12 (experiment 2) factorials arranged in a randomized complete block with two irrigation treatments and six or 12 blocks with the tree as the experimental unit located in the center of each 56.25 m^2 plot. Hurricane Wilma blew over many trees in experiment 2 on October 24, 2005 which prevented their inclusion in the final analyses.

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