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Resource regulation of an invasive tree by a classical biological control agent

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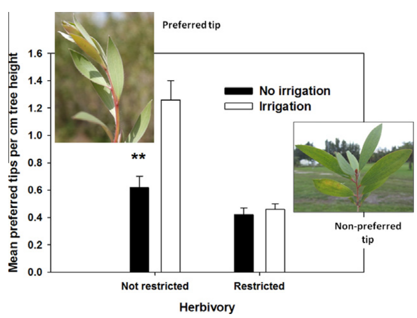
HIGHLIGHTS

- We evaluated the Resource Regulation Hypothesis in a weed biological control project.
- Feeding by *Oxyops vitiosa* increases the amount of resources for subsequent generations.
- A positive feedback loop was induced by *O. vitiosa* and mediated by water.
- *O vitiosa* appears to be controlling *Melaleuca quinquenervia* resources.

GRAPHICAL ABSTRACT



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ABSTRACT

The invasive tree *Melaleuca quinquenervia* experienced substantial declines in growth and reproduction in response to chronic herbivory by the defoliating weevil *Oxyops vitiosa*. Plants subjected to unrestricted defoliation replaced leaves that were more suitable for feeding by the next generation, a process envisioned by the Resource Regulation Hypothesis which posits that attack by one generation increases the amount of the preferred host resources for the next, resulting in a positive feedback loop for the herbivore. The production of juvenile replacement leaves stimulated additional bouts of oviposition and feeding by *O. vitiosa*, which ultimately produced positive effects for the herbivore with negative consequences for the plant. The addition of water resources to the plant prolonged the positive feedback loop such that more than twice as many insects were produced on irrigated versus non-irrigated trees. In a more simple, reassembled food web on *M. quinquenervia*, the lack of biotic constraints like parasitoids may have prevented the earlier termination of the feedback loop and thus increased the impact of the biological control agent on the target. The overall effectiveness of this classical biological control program can be attributed, in part, to the phenomenon of the target plant's induced susceptible response to a herbivore.

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1. Introduction

Plants respond to herbivory in a multitude of ways including changes in phenology (Marquis, 1985), reproduction (Kraft and Denno, 1982), architecture (Tipping et al., 2008), and plant chemistry (Edwards and Wratten, 1983). In some cases, induced plant responses can result in reduced resource quality because of chemical factors such as the accumulation of secondary plant compounds, or physical factors such as increased leaf toughness (Karban and Baldwin, 1997; Schultz and Baldwin, 1982). In contrast, improvements in resource quality can also occur as a result

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of defoliation events whereby plants create or maintain resources that favor continued herbivory by the same herbivore or their progeny via feedback loops (Rockwood, 1974; Williams and Myers, 1984). This type of induced susceptibility can have positive, negative, or neutral impacts on both plant and herbivore fitness in either a symmetric or asymmetric fashion. One type of induced susceptible response, termed resource regulation by Craig et al. (1986), produces a positive feedback loop for the herbivore whereby their feeding maintains or increases resource quality for their progeny or the next generation of conspecifics on the same plant. For example, when a stem galling sawfly, *Euura lasiolepis* Hartig (Hymenoptera: Tenthredinidae), attacked the willow *Salix lasiolepis* Benth. (Salicaceae), the plant responded by producing more of the type of shoot that promoted attack by the next generation of *E. lasiolepis* (Craig et al., 1986). Craig (2010) proposed three mechanisms that occur with cases involving resource regulation: (1) juvenilization whereby herbivory induces dormant bud growth, (2) resource manipulation of source–sink relations, and (3) nutritional or chemical changes caused by herbivory. Positive feedback cycles may result in increasing herbivore density until plant damage exceeds plant compensation, whereupon the cycle is terminated (Craig, 2010).

Melaleuca quinquenervia (Cav.) S.T. Blake (Myrtaceae) is a serious ecological weed of southern Florida, USA wetland communities. It was introduced into the U.S. in 1886 from Australia for a variety of purposes including as an ornamental, for erosion control, as a forestry crop, and as an agricultural windrow plant (Meskimen, 1962; Bodle et al., 1994; Dray et al., 2006). Rapid growth rates and early reproductive maturity combined to promote *M. quinquenervia* densities to levels that outcompeted native woody species like slash pine, *Pinus elliottii* Engelm. (Pinaceae), in pine flatwood communities and sawgrass, *Cladium jamaicense* Crantz (Cyperaceae) in wet prairies (Meskimen, 1962). Eventually this species infested up to 0.61 million ha in southern Florida (Bodle et al., 1994).

Oxyops vitiosa Pascoe (Coleoptera: Curculionidae) is also native to Australia and was first collected north of Brisbane in Queensland, Australia for evaluation as a classical biological control agent for *M. quinquenervia* in Florida (Balciunas et al., 1994). Approval for general release was granted following the completion of host range studies that proved *O. vitiosa's* fidelity to *M. quinquenervia* and the first releases were conducted in 1997 (Center et al., 2000). The insect readily established and its current range generally matches that of *M. quinquenervia* (P.W.T. personal observations). *O. vitiosa* is a flush feeder that begins to lay eggs once new growth begins on *M. quinquenervia*, typically during the late winter, early spring time period in southern Florida. These new leaves are preferred by both the adults and larvae primarily because of their softer texture, but become less attractive as they increase in toughness over time (Wheeler, 2001). In response to defoliation, trees produce new leaves which, in turn, stimulate more oviposition by adults and more feeding by larvae, leading to additional bouts of defoliation and re-foliation, thus creating what appears to be a positive feedback loop for the insect (Tipping et al., 2008). Despite this, Wheeler and Ordung (2006) found no chemical, physical, or bioassay evidence of induced resistance for *O. vitiosa* on plants previously defoliated by *O. vitiosa*.

Craig (2010) suggested that resource regulation was widespread in the plant kingdom as the assumptions for these phenomena were common to many plants including (1) damaged plants often respond with vigorous juvenile growth, (2) increased herbivore preference and performance on this juvenile growth, and (3) repeated herbivore attack on the same individual plants. Our objective was to determine if there was evidence of an induced susceptibility feedback system as proposed in the Resource Regulation Hypothesis and to quantify its impact on plant parameters and herbivore densities. The current reconstructed and relatively simple food web associated with *M. quinquenervia* in Florida makes this phenomenon relatively accessible for study. Two separate null hypotheses were posited in the study: (1) A symmetrical feedback loop was not present in this system; and (2) abiotic factors, temperature and water, did not influence any feedback loops that did develop.

2. Materials and methods

M. quinquenervia saplings (1–1.5 m height) were planted in common garden plots during Dec. 1999 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. Initially, trees were fertilized and irrigated until they were firmly established. The experimental design was a complete $2 \times 2 \times 6$ factorial arranged in a randomized complete block with two herbivore treatments, two water treatments, and six blocks, with the tree as the experimental unit located in the center of each 56.25 m^2 plot. Herbivore treatments consisted of an insecticide control where herbivory by *O. vitiosa*, and later another introduced agent *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), was restricted by regular applications of an insecticide, and a treatment where herbivory was not restricted by spraying the trees with water. *Borelioglycaspis melaleucae* appeared later in the experiment and was not considered to be a major factor since it is a phloem feeder with different resource preferences than *O. vitiosa* (Center et al., 2006). Trees were scouted weekly for *O. vitiosa* eggs and small larvae and the insecticide acephate was applied to foliage as needed at a concentration of 0.367% a.i. (v/v) until runoff using a hand pressurized backpack sprayer. The insecticide concentration and application frequencies neither inhibited nor stimulated plant growth (Tipping and Center, 2002).

Water resources consisted of either natural rainfall or continuous irrigation plus natural rainfall. In the irrigated treatment, drippers provided a mean flow rate of ca 7.5 L per hour applied to a spot on the soil directly next to the trunk. This produced continually saturated soils under the drip line of the tree compared with the natural rainfall treatment where soils were periodically dry or saturated. Precipitation and temperature data were captured daily by an automated weather station directly adjacent to the plots.

Plants were evaluated every 4–6 wk from October 2001 through October 2003 for plant and insect variables including tree height, the number of terminal branch tips, the number of preferred branch tips, and the number of *O. vitiosa*. Preferred branch tips contained 2–5 distal leaves that were fully formed but still supple and soft and appear during normal development of the plant at certain times of the year, or as replacement leaves following defoliation events. Plant variables like the final biomass of leaves and the number of seeds produced were measured at the end of the experiment.

Repeated measures analysis of variance was used to measure the impact of biotic and abiotic treatments on plant variables (SAS, 1999). Variables like the number of *O. vitiosa* per cm of tree height and the number of preferred tips per cm of tree height were calculated to take into account changes in tree growth. Means were transformed using square root transformation for non-normal data or when variances were heterogeneous and back-transformed for presentation. Nonlinear regression was used (PROC NLIN) to examine relationships between insect and plant parameters and analysis of covariance was used to compare regression lines (SAS, 1999). Variables that appeared to influence the number of preferred tips per cm of tree height were further subjected to forward stepwise