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

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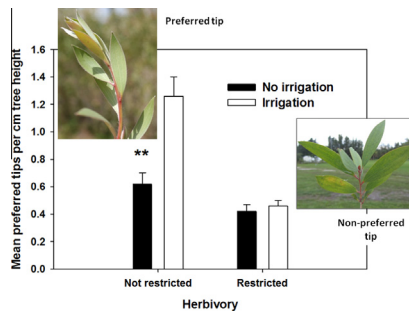[a] USDA-ARS Invasive Plant Research Laboratory, Davie, FL, USA
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HIGHLIGHTS

- 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

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. *Boreioglycaspis 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

regression (entry level into the model = 0.15) when herbivory was restricted and unrestricted (SAS, 1999).

3. Results

Regular applications of acephate reduced defoliation by *O. vitiosa* as reported by Tipping et al. (2008). The monthly mean (±SE) of natural precipitation was 12.2 ± 2.1 cm as measured at the automated weather station adjacent to the plots which was equivalent to 122 L of water per m². In comparison, irrigation provided 2424.3 ± 189.1 L of water per month as measured from the dripper orifice. Although these values cannot be compared directly, this disparity manifested itself primarily as periodically dry soil in the non-irrigated plots versus continually wet soils in the irrigated plots.

The number of preferred tips per cm of tree height was influenced primarily by date and secondarily by herbivory and water (Table 1). There was a date × herbivory interaction which was caused by a change in magnitude whereby unrestricted herbivory both regularly and episodically resulted in greater numbers of preferred tips per tree (Fig. 1). There was also a herbivory × water interaction which resulted from a difference in magnitude whereby the number of preferred tips was greater in irrigated treatments when herbivory was not restricted (Fig. 2).

There was an overall positive relationship between the number of *O. vitiosa* per cm of tree height with the percentage of preferred tips, and this relationship was stronger when herbivory was not restricted (Fig. 3A) than when it was (Fig. 3B). Two weak but significant relationships were also present between the number of preferred tips and abiotic variables, namely the mean monthly temperatures which were inversely related ($r = -0.20$, $N = 258$, $P < 0.0001$), and the mean monthly precipitation, which was positively correlated ($r = 0.16$, $N = 258$, $P = 0.0002$). Adding water resources via irrigation resulted in more than twice as many *O. vitiosa* per cm of tree height (0.12 ± 0.01 and 0.05 ± 0.01 for irrigated and non-irrigated, respectively) ($t_{131} = 2.95$, $P < 0.0001$).

Tree height, which could be measured non-destructively during the experiment, was influenced primarily by herbivory, but also by the date with a date × herbivory interaction that was explained by a difference in magnitude whereby trees subjected to restricted herbivory grew taller over time than those subjected to unrestricted herbivory. Other plant parameters such as leaf biomass and seed production were measured when the experiment was harvested and these were affected primarily by herbivory but not by water ($P = 0.15$) (Table 1). In general, higher densities of *O. vitiosa* resulted in less leaf biomass and seed production by *M. quinquenervia* (Fig. 4A and B).

Stepwise regression analysis found that the lower densities of *O. vitiosa* found in the restricted herbivory treatment, along with mean temperature, contributed little to the production of preferred tips, with water not contributing at all (Table 2). In contrast, the higher densities of *O. vitiosa* found in the unrestricted herbivory treatment explained a large percentage of the variation in the
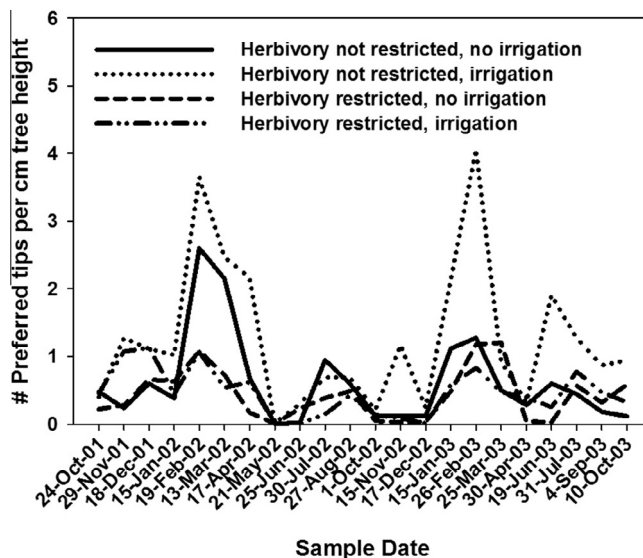

Fig. 1. Mean preferred tips per cm of tree height for *M. quinquenervia* across sample dates as influenced by different herbivory and water treatments.
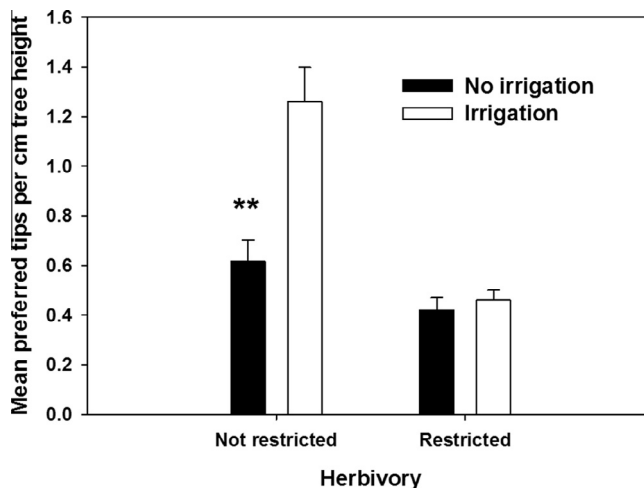

Fig. 2. Total mean (±SE) preferred tips per cm of tree height for *M. quinquenervia* subjected to experimental herbivory and water treatments.

number of preferred tips that were produced. The amount of water also explained some of this variation, albeit to a relatively minor degree (Table 2).

4. Discussion

Mechanisms that promote the continued availability of suitable or preferred host tissue for herbivore feeding may act to prolong

Table 1
Results of ANOVA for *Melaleuca quinquenervia* parameters with date, herbivory, and water as main factors.

Variable	Date (D)		Herbivory (H)		Water (W)		D × H		D × W		H × W		D × H × W	
	df	TSS (%)[a]	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)
Preferred tips	21	22.3**	1	4.9**	1	2.3**	21	7.9**	21	2.8	1	1.8**	21	2.6
Plant height (cm)	20	20.3**	1	31.5**	1	0.3*	20	12.6**	20	0.3	1	0.1	20	0.1
Leaf biomass tree⁻¹	–		1	72.5**	1	2.7	–		–		1	0.1	–	
No. seeds tree⁻¹	–		1	32.2**	1	6.1	–		–		1	5.8	–	

[a] Presented are the degrees of freedom (df) and the rounded percentage of variance explained by a factor (TSS) calculated using the formula: TSS = 100 × (factor SS/total SS).
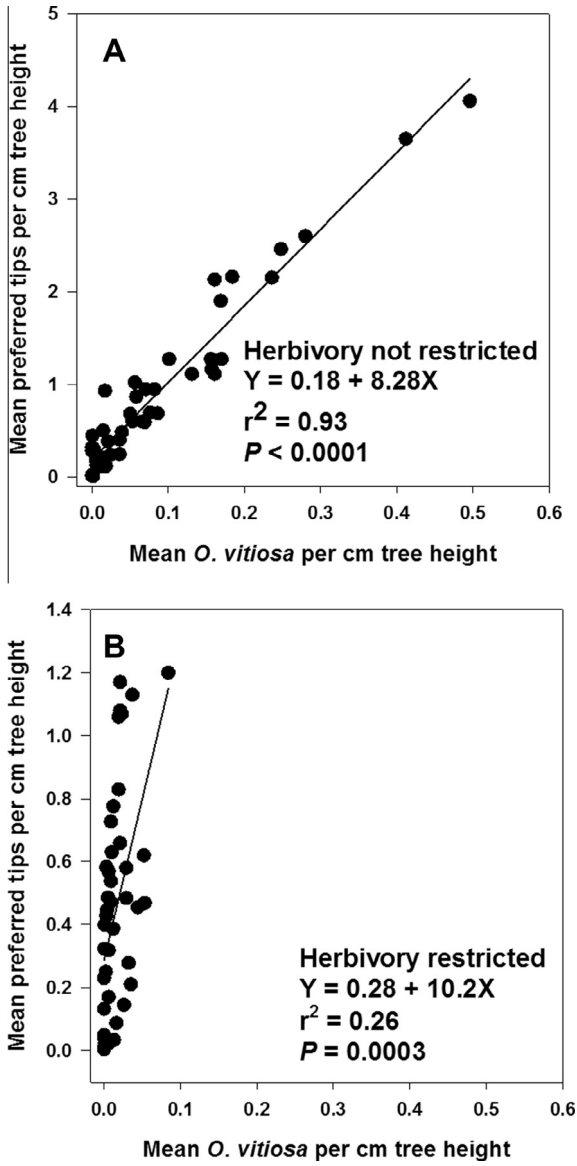* $P = 0.05$.
** $P = 0.01$.

Fig. 3. (A) Relationship between the mean number of *O. vitiosa* per cm of tree height with the mean number of preferred tips per cm of tree height when herbivory by *O. vitiosa* was not restricted. (B) Relationship between the mean number of *O. vitiosa* per cm of tree height with the mean number of preferred tips per cm of tree height when herbivory by *O. vitiosa* was restricted.
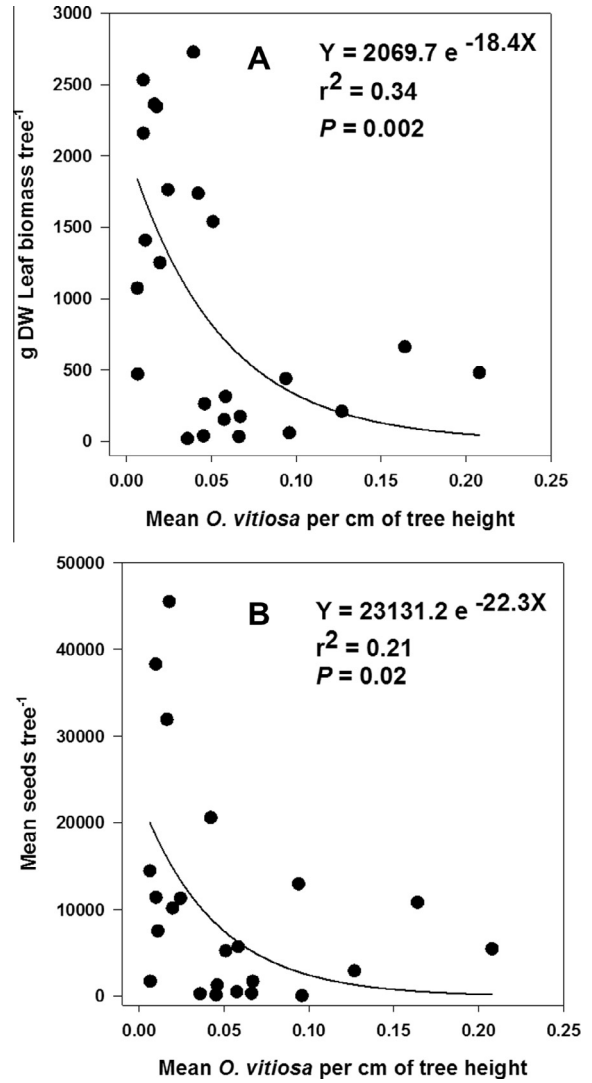

Fig. 4. (A) Relationship between the mean number of *O. vitiosa* per cm of tree height with mean leaf biomass per tree. (B) Relationship between the mean number of *O. vitiosa* per cm of tree height with the mean number of seeds per tree.

their attack, potentially increasing the amount of damage inflicted on the host. Contrary to the first null hypothesis, *M. quinquenervia* compensated for larval defoliation by producing additional preferred tips, which were consumed in turn, triggering more compensation. In general, more larvae meant more defoliation, leading to re-foliation and subsequent enhanced resource (juvenile leaf tissue) availability for the next generation. In this way, *O. vitiosa* appears to be controlling *M. quinquenervia* resources by inducing a positive feedback loop that helped to maintain a higher level of attack. Although *M. quinquenervia* normally produces a flush of new growth with preferred tips during the lower temperature months of January and February, the magnitude of this seasonal peak was greatest when more water was available and herbivory was not restricted as evidenced by greater numbers of preferred tips when trees were irrigated (Fig. 5A and B) thus disproving the second null hypothesis that abiotic factors had no effect on preferred tip production feedback loops. Price and Hunter (2005) noted a strong correlation between the amount of

Table 2
Stepwise forward regression of the number of preferred tips per cm of tree height with independent abiotic and biotic variables with restricted and unrestricted herbivory.

Dependent	Herbivory	Step	Independent variable	r^2	P	Slope
Preferred tips per cm tree height	Restricted	1	Mean *O. vitiosa* per cm tree height	0.05	0.0001	1.89
		2	Mean temperature	0.07	0.01	−0.03
	Unrestricted	1	Mean *O. vitiosa* per cm tree height	0.85	0.0001	7.23
		2	Mean water	0.86	0.0026	0.0001

Presented are the explained cumulative variance (r^2), the level of significance of each added variable, and the slope.

water available to plants with the densities of natural enemies, and found that drought conditions effectively ended a resource regulation feedback cycle. The interactions in this study appear
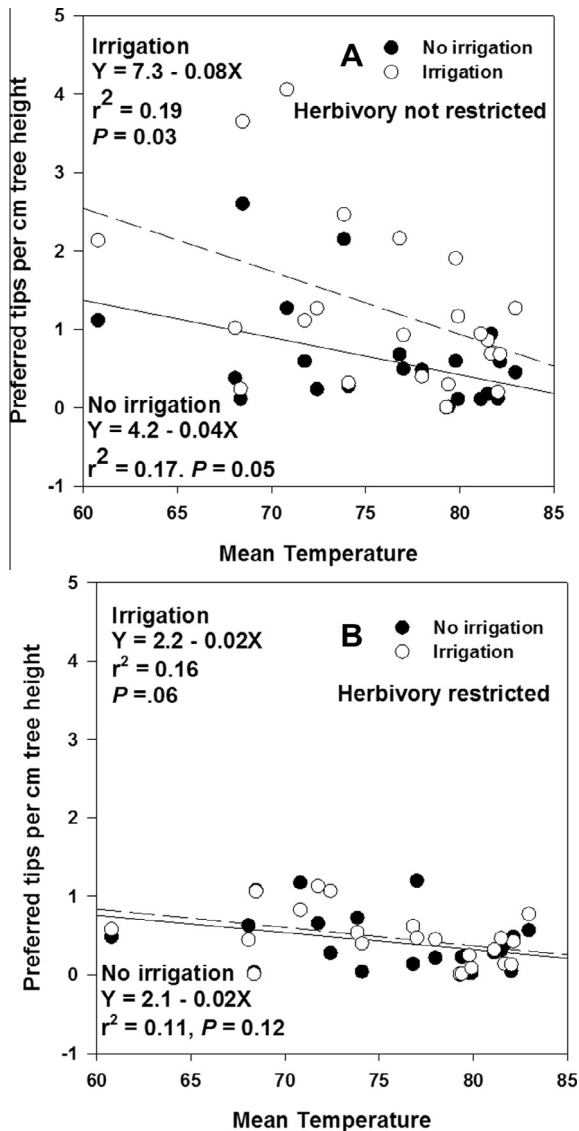
Fig. 5. (A) Relationships between the mean temperature with the number of preferred tips per cm of tree height with irrigation (dashed line) and without irrigation (solid line) when herbivory was not restricted. The slopes of the regression lines were not different from each other ($F_{1, 260} = 1.6$, $P = 0.19$) while the Y intercepts were different ($F_{1, 261} = 15.6$, $P = 0.0001$). (B) Relationships between the mean temperature with the number of preferred tips per cm of tree height with irrigation (dashed line) and without irrigation (solid line) when herbivory was restricted. Neither the slopes of the regression lines ($F_{1, 222} = 0.04$, $P = 0.83$) nor the Y intercepts were different from each other ($F_{1, 242} = 0.33$, $P = 0.56$).

to support the Resource Regulation Hypothesis, including the mediating influence of abiotic forces such as temperature and water availability on preferred host resources.

In Australia, *O. vitiosa* is distributed sporadically and occurs at low densities, but can be found readily at sites were *M. quinquenervia* has been damaged, either mechanically or by defoliation by the *Melaleuca* sawfly *Lophyrotoma zonalis* Hohwer (Hymenoptera: Pergidae) (Purcell and Balciunas, 1994). This may suggest that *O. vitiosa* plays a relatively minor role in regulating this plant in its native range and that any positive feedback loops that occur may be of shorter duration. Normally, positive feedback loops are constrained by an array of biotic and abiotic factors including natural enemies, lower nutrient quality of replacement foliage, physical changes in host quality, shortages of host availability, or some combination thereof which act to inhibit population cycles

(Anderson and May, 1980; Berryman, 1987; Umbanhowar and Hastings, 2002). The presence of several parasitoid species that attack *O. vitiosa* larvae may be one such constraining factor (Purcell and Balciunas, 1994). In Florida, *O. vitiosa* faces no specialist natural enemies, only a few generalist predators, no induced plant defenses based on previous herbivory by conspecifics and, thus far, a relative abundance of hosts (Wheeler and Ordung, 2006; Costello et al., 2002; Tipping et al., 2013). These differences may explain, in part, why this insect achieves chronic and high densities on *M. quinquenervia* throughout its new range.

Ultimately, in order for plant population regulation to occur, natural enemy populations must attain densities that suppress critical plant parameters to the point where population level changes can occur. The mechanisms whereby this happens are varied but the compensatory actions of *M. quinquenervia* to direct resources into replacing foliage at the expense of reproductive tissues ensures that high value resources will continue to be available for herbivores while, at the same time, plant reproduction will be curtailed (Fig. 4). Although reproductive structures often become the strongest sinks following partial defoliation (Kahn and Sager, 1969), the lack of such a sink usually results in new tissues acting as stronger sinks for carbon resources (Ryle and Powell, 1975; Vranjic and Gullan, 1990). The feedback loop documented in this study is clearly asymmetric, with a positive outcome for herbivore density, coupled with a concomitant negative outcome for the growth and reproduction of *M. quinquenervia*. Repeated defoliation can reduce seed production by 80–100%, depending on conditions and the resulting reductions to the seed bank of *M. quinquenervia* may be directly attributed to resource regulation by *O. vitiosa* (Pratt et al., 2005; Tipping et al., 2008, 2009). The phenomenon of resource regulation may have provided the framework whereby herbivory by *O. vitiosa* could fundamentally alter the population dynamics of *M. quinquenervia* to a point where its invasiveness is now reduced in certain areas (Tipping et al., 2012).

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