Combining biological and mechanical tactics to suppress *Melaleuca quinquenervia*

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ABSTRACT

A four year common garden study was initiated using once-cut *Melaleuca quinquenervia* trees that were subsequently subjected to a full factorial of treatments that included reduced versus unrestricted herbivory from biological control agents, a mechanical treatment (trees were not cut or were cut every 6 m), and an irrigation treatment (trees were irrigated or not). Repeated cutting reduced the total tree biomass by 76.4%, herbivory alone reduced total biomass by 58.7%, and the combination of cutting and herbivory reduced total biomass by 80.1%. Unrestricted herbivory reduced the seed biomass per tree by 93.9% in uncut trees while repeated cutting eliminated all seed production regardless of herbivory. Uncut trees subjected to unrestricted herbivory allocated an average of 8.8% of their biomass to reproductive tissue, while those exposed to restricted herbivory allocated an average of 15.8%. Unrestricted herbivory by biological control agents on uncut trees also reduced the total number of seed capsule clusters by 79.2%, the number of capsules per cluster by up to 20.8%, and the individual seed weight by up to 58.9%. Repeated cutting did reduce the amount of damage to regrowth by one biological control agent, *Oxyops vitiosa* (Coleoptera: Curculionidae), but did not reduce the abundance another, *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae). Trees that were only cut once at the initiation of the study exhibited vigorous regrowth, including increased height and seed production. The mortality of trees was lower compared with other studies, highlighting the influence of localized biotic and abiotic factors on the cumulative suppressive effects of cutting and herbivory on *M. quinquenervia*.

1. Introduction

Integrating different weed management tactics is often more effective in suppressing weeds than individual tactics employed alone or in a piecemeal fashion (Tipping, 1991; Kluth et al., 2003; Paynter and Flanagan, 2004). Classical weed biological control using arthropods, differs from more conventional tactics like chemical, mechanical, and cultural methods because it harnesses the inherent evolutionary capacities of natural enemies to locate, attack, and respond to their plant hosts (Culliney, 2005; Holt and Hochberg, 1997). A common outcome is a transformation of the weed to a less vigorous state compared with the fundamental "kill or no kill" outcomes from more conventional tactics (Van Driesche and Bellows, 1996). Thus, classical biological control represents the foundation of any integrated weed management system (Müller-Schärer et al., 2000). Despite this, actively integrated programs are rare; most employ a passive approach that relies on the ability of

vagile agents to locate infested sites that were skipped or were inaccessible by the primary conventional tactics employed, i.e., areas that can't be mowed or sprayed or burned.

The counter to the strictly passive approach is a purposeful, systematic, and actively integrated program like the one developed to manage the exotic tree *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtaceae) in southern Florida, which stands as a strong example of how to suppress a problematic weed on a landscape scale. The original melaleuca management plan was developed in the 1990s and has been updated several times as needed (Laroche, 1998). The general approach involved an initial reliance on herbicides, cutting, and burning in larger monotypic stands while biological control agents were under development. These agents were envisioned as follow-on controls to the more conventional methods to inhibit both the spread and re-infestation of previously treated areas by suppressing the considerable reproductive capacity of this tree (Center et al., 2012). Several studies have

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documented changes in the weed caused by chronic herbivory where *M. quinquenervia* has become less invasive in some habitats (Center et al., 2012; Tipping et al., 2009; Tipping et al., 2012). Currently, this weed is approaching maintenance control levels and overall spending using conventional methods like herbicides and cutting has declined (Rodgers, 2016).

One of the tactics employed routinely against *M. quinquenervia* in some areas is cutting down the trees and treating the stump with herbicides to prevent regrowth (Laroche and Ferriter, 1992). However, herbicide applications to stumps are not always done, or done effectively and, as a result, the trees can re-grow vigorously with multiple stems to resemble coppices as intentionally practiced in some forestry methods (Sims et al., 2001). In certain species, cutting can release plants from limitations imposed by the accumulation of old and dead tissue, overriding the negative effects of biomass loss (Oesterheld and McNaughton, 1991). In the case of *M. quinquenervia,* this re-growth can be of higher quality for the biological control agents *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae)*, Borelioglycaspis melaleucae* Moore (Hemiptera: Psyllidae), and *Lophidoplosis trifida* Gagné (Diptera: Cecidoymiidae) (Wheeler, 2001). The last species, *L. trifida*, had not been released by the time the research described herein was conducted. Herbivory by these agents may help counter the plant compensation that can occur after cutting such as increased net photosynthetic rate, higher relative growth rate, and increased branching or tillering following release from apical dominance (Strauss and Agrawal, 1999).

Two previous studies examined different aspects of herbivory and cutting on *M. quinquenervia* but did not quantify the contribution of regular cutting over time on plant factors in the presence and absence of herbivory by biological control agents (Center et al., 2007; Rayamajhi et al., 2010). These studies also raised questions regarding the potential for substituting herbivory by biological control agents for herbicides after cutting. The primary objective of this study was to quantify the relative contributions of cutting treatments and herbivory by combinations of biological control agents on suppressing the growth and development of small trees (< 5 m in height) of *M. quinquenervia*.

2. Materials and methods

2.1. Experimental design

A small plot insecticide-check study was conducted on small trees of *M. quinquenervia* during 2001–2003 after which all the trees were harvested by cutting them at the soil surface (Tipping et al., 2008). The regrowth that occurred was incorporated into this study which was conducted from November 2004 to February 2008 to elucidate the relative influences of biological control and single or repeated cuttings of smaller *M. quinquenervia* trees (< 5 m in height) on multiple plant factors.

The experimental design was a $2 \times 2 \times 2$ factorial arranged in a randomized complete block with six replications. Treatments included: 1) an herbivory treatment where trees were sprayed with either insecticide or water, 2) a cutting treatment where trees were either cut down to the soil surface every 6 months or left uncut following initiation of the experiment, and 3) an irrigation treatment where trees were not provided supplemental water beyond natural rainfall or continuously irrigated according to Tipping et al. (2008). The same herbivory and irrigation treatments from Tipping et al. (2008) were applied to the same trees during this study. The insecticide control treatment was attained by applying acephate (OS – dimethyl acetylphosphor-amidothioate) every 4–6 w at a concentration of 0.367% ai (v/v) to all plant foliage until it was wet.

2.2. Sampling design

Prior to each cutting, all trees were assessed for height, *O. vitiosa* damage, and *B. melaleucae* abundance. Plant height was estimated by measuring the height of the five tallest stems and averaging. The amount of damage from *O. vitiosa* was estimated using the damage rating from Tipping et al. (2008) namely, 0 = no damage, 1 = 1–24% of leaves damaged, 2 = 25–49% damaged, 3 = 50–74% damaged, 4 = 75–99% damaged, and 5 = 100% damaged. A four scale rating of abundance was employed for *B. melaleuca*e with 0 = none found after a 5 min search, 1 = rare (present but not easily found), 2 = common (easily found after a brief search), and 3 = abundant (easily seen from any point). The biomass from each cut was weighed to obtain fresh weight biomass, and then dried to a constant weight at 50 °C to determine percent moisture in order to calculate dry weight biomass.

At the end of the experiment, all trees were harvested by cutting them at the soil surface and partitioning them into trunk (> 2.5 cm diameter), branch (1–2.5 cm diameter), twig (< 1 cm diameter), leaf, flower, and capsule clusters for biomass measurements. The capsule clusters are structures formed following flowering events; each inflorescence can produce an infructescence of 30–70 serotinous capsules with each capsule containing an average of 264 seeds (Rayamajhi et al., 2002). Capsule clusters were characterized by class as primary, secondary, or tertiary, similar to the method of Rayachhetry et al. (1998) that was based on their relative position from a branch tip. Primary clusters were the youngest and were located in the most distal position on branches, while tertiary clusters occupied the most proximal location on the same branch. A sample of five clusters of each class, if available, was selected without bias from each tree and used for additional measurements. Most of the trees in the uncut treatment had at least five primary clusters, but some had only secondary or tertiary clusters. In those cases, all the harvested clusters were measured per tree and were processed by recording their length, fresh weight biomass, and the number of capsules in the cluster followed by drying and re-weighing as described above. A bulked subsample of seeds (1–2 mg) from each cluster was weighed and the number of seeds counted to calculate an average seed weight. Remaining seeds were extracted from all clusters and weighed to obtain the total seed biomass produced per tree.

2.3. Statistical analysis

The data were subjected to analysis of covariance with the original stump diameter at the beginning of the experiment as the covariate. To test if the trees regrew more vigorously after being cut once, the mean relative growth rate (MRGR; mm height day^{-1}) for tree height was compared with the MRGR for height from the previous experiment in the herbivory treatments using a two-sample T-test. The formula for MRGR was:

$$\text{MRGR} = (\ln \text{height}_2 - \ln \text{height}_1)/(t_2 - t_1) \tag{1}$$

where height$_1$ and height$_2$ are the tree height at the beginning (t_1) and end (t_2) of the sampling period, and ln is the natural logarithm. The production of capsule clusters was also compared between experiments using a two-sample T-test. Repeated measure analysis of variance was used to measure the impact of repeated cutting on tree and insect variables (SAS, 2009). Means were transformed using square root transformation for non-normal data or when variances were heterogeneous and back-transformed for presentation. Simple linear regression was used to examine the effect of multiple cuttings and herbivory on the amount of regrowth produced after each cut. Analysis of covariance was used to determine if the slopes or Y – intercepts were different on trees subjected to unrestricted or restricted herbivory.

3. Results and discussion

Herbivory, cutting, and the initial size of the tree influenced *M. quinquenervia* biomass but irrigation did not (Table 1). Cutting had a greater influence on all biomass components than did herbivory but there were significant interactions between the two tactics whereby *M.*

Table 1
Results of ANOVA for *Melaleuca quinquenervia* parameters with cutting, herbivory, and water as main factors and the initial stem diameter of the tree as a covariate. Parameters include the cumulative amount of biomass from each cutting.

Biomass	Initial Diameter		Cutting (C)		Herbivory (H)		Water (W)		C × H	
	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)
Trunk	1	5.1*	1	32.9**	1	0.8	1	0.9	1	7.5**
Branch	1	0.7	1	49.3**	1	3.2	1	0.4	1	4.0*
Twig	1	2.1	1	43.1**	1	1.5	1	0.2	1	5.3*
Leaf	1	5.9*	1	31.9**	1	1.2	1	< 0.001	1	7.5**
Capsule clusters	1	0.7	1	30.6**	1	6.9**	1	< 0.001	1	14.6**
Seeds per tree	1	1.8	1	22.6**	1	6.9**	1	0.01	1	3.9**
Reproductive allocation (%)	1	3.4*	1	60.5**	1	8.0**	1	< 0.001	1	4.5*

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). There were no significant C × W, H × W, or C × H × W interactions. Asterisks indicate significance level, *: $P = 0.05$, **: $P = 0.01$.
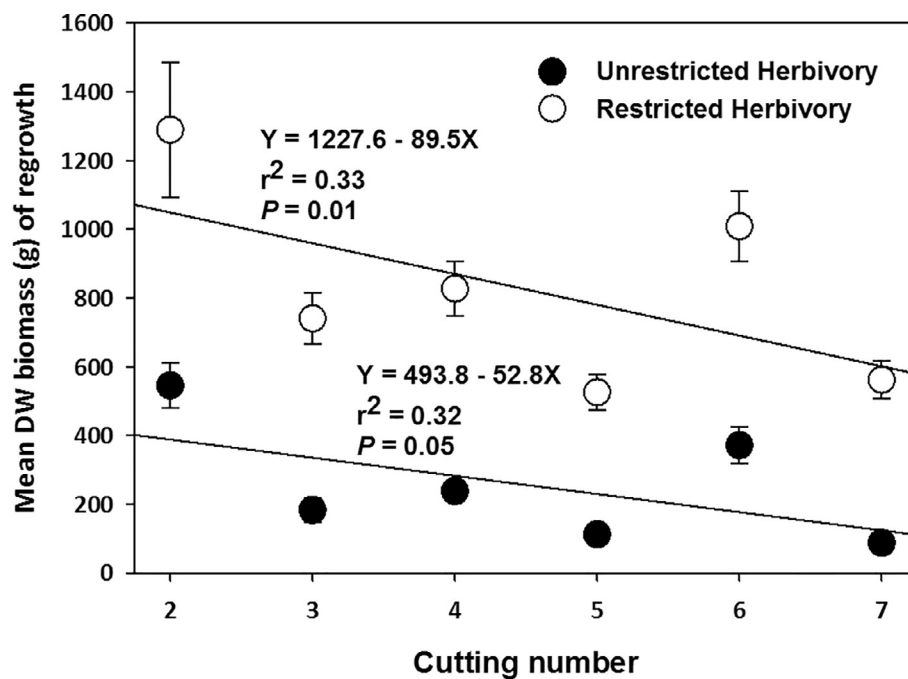

Fig. 1. Relationships between the amount of regrowth biomass collected at consecutive cuts to *M. quinquenervia* trees subjected to unrestricted and restricted herbivory by biological control agents.

quinquenervia parameters were reduced more with unrestricted herbivory (Table 1). Herbivory did directly influence the reproductive components of the biomass, albeit to a minor degree. Although repeated cuttings resulted in an overall decline in the amount of biomass that was replaced over time regardless of herbivory ($F_{6, 137} = 0.26$, $P = 0.95$), trees subjected to unrestricted herbivory replaced less biomass following each cut than did trees subjected to restricted herbivory ($F_{1,143} = 385.6$, $P = 0.0001$) (Fig. 1).

Repeated cutting with restricted herbivory reduced the mean total biomass by 76.4%, unrestricted herbivory alone reduced the mean total biomass by 58.7%, while the combination of cutting and unrestricted herbivory reduced total biomass by 80.1%. Unrestricted herbivory alone on uncut trees reduced the mean seed biomass per tree by 93.9% while repeated cutting eliminated all seed production. These data add to a growing body of literature that demonstrates the importance of herbivory in regulating reproductive performance of *M. quinquenervia* (Pratt et al., 2005; Tipping et al., 2008, 2009). Uncut trees subjected to unrestricted herbivory allocated an average of 8.8% of their total biomass to reproductive tissue, while uncut trees exposed to restricted herbivory allocated an average of 15.8%. More primary and secondary seed capsule clusters were produced on trees with restricted herbivory; no tertiary clusters were found on trees with unrestricted herbivory

(Table 2). The overall primary capsule cluster length and the number of capsules per cluster were reduced in the unrestricted herbivory treatment as was seed weight in primary and secondary capsule clusters (Table 2). Seed weights were generally lower in the primary capsule cluster because many of the seeds were immature. There was no difference between the herbivory treatments in the numbers of seeds per cluster in primary and secondary cluster types (Table 2).

Cutting repeatedly did reduce the amount of *O. vitiosa* damage to regrowth (Fig. 2A) but it did not reduce the average abundance *of B. melaleucae* (Fig. 2B). This may reflect a lag in the re-appearance of larval damage from *O. vitiosa* as adults re-colonized the re-growth and resumed ovipositing following each cut. In contrast, *B. melaleucae* appeared to re-colonize the regrowth quickly.

There was an increase in the mean relative growth rate for plant height when compared with results from the study by Tipping et al. (2008). This may indicate that, at least initially, that the trees responded with more vigorous growth when cut. For example, the MRGR for tree height in the unrestricted herbivory treatment was more than 12 times greater than that found by Tipping et al. (2008) ($t_{22} = 30.7$, $P = 0.0001$), while in the restricted herbivory treatment, the MRGR for height was more than twice as great ($t_{22} = 22.4$, $P = 0.0001$). An even greater increase occurred in the number of seed capsule clusters

Table 2
Means (±SE) of *Melaleuca quinquenervia* seed related parameters from trees cut once at the beginning of the experiment and subject to restricted and unrestricted herbivory.

Variable	Herbivory		
	Unrestricted	Restricted	t^1
No. Capsule clusters			
Primary	1007.9 + 237.4	4470.6 + 702.5	4.6**
Secondary	33.4 + 14.4	398.0 + 109.9	3.2**
Tertiary	0 + 0	10.9 + 6.0	1.8
Cluster length (cm)			
Primary	4.9 + 0.2	5.6 + 0.2	2.2*
Secondary	5.1 + 0.2	6.4 + 0.6	1.9
Tertiary		5.6 + 0.8	–
No. Capsules per cluster			
Primary	31.1 + 1.8	39.3 + 2.0	3.0**
Secondary	31.1 + 2.0	37.3 + 3.0	1.7
Tertiary		27.3 + 7.6	–
Seeds per capsule			
Primary	337.4 + 42.8	251.8 + 8.2	1.9
Secondary	226.8 + 6.5	262.3 + 15.6	2.1
Tertiary	–	239.2 + 14.0	–
Individual seed weight (mg)			
Primary	0.016 + 0.003	0.039 + 0.001	6.7**
Secondary	0.179 + 0.045	0.016 + 0.003	3.1**
Tertiary		0.061 + 0.032	–

[1] t score using two sample *t*-test comparing variable means from unrestricted and restricted herbivory treatments. Asterisks indicate significance level, *: $P = 0.05$, **: $P = 0.01$.

produced following the single cut that preceded and signaled the beginning of the this study with an average (± SE) of 1041.4 ± 247.1 and 4879.6 ± 782.1 capsule clusters produced per tree in unrestricted and restricted herbivory treatments, respectively. By comparison, the original parent trees used by Tipping et al. (2008) produced an average of 1.5 ± 1.3 and 161.9 ± 48.8 capsule clusters per tree for the same herbivory treatments. This increase in reproductive structures could also be a function of the relative differences in tree size and age between the study by Tipping et al. (2008) and this study, namely that larger trees generally produce more seed (Greene and Johnson, 1994).

A total of four trees died (8.3%) during the study; all were subjected to the cutting treatment but only two were exposed to unrestricted herbivory. Despite the presence of significant herbivory, the combination of repeated cutting and herbivory did not produce the levels of mortality noted in a study by Center et al. (2007) who reported a decline of 70% in the number of coppicing (regrowth) *M. quinquenervia* from small trees (ca. 3 m in height) in a regularly mowed cattle pasture in southwest Florida following release and establishment of *O. vitiosa*. Later, after the site was colonized by *B. melaleucae*, another 35% of the coppices died within 10 months (Center et al., 2007). Rayamajhi et al. (2010) conducted three consecutive cuttings 12 months apart of *M. quinquenervia* trees (< 4 m in height in controls following regrowth) growing in an existing mature stand of *M. quinquenervia* and reported 34.5% mortality of the stumps in an equivalent restricted herbivory treatment and 87.3% in an unrestricted herbivory treatment. In both of those studies it was not possible to disentangle the potential influence of abiotic and biotic factors including intra- and interspecific plant competition, shading, water, the history of herbivory on the parent tree, and trampling by livestock from the contributions of biological control and cutting on the decline of *M. quinquenervia* (Mitchell and Kirby, 1990; Goldberg and Barton, 1992; Suzuki et al., 2003). Under the relatively favorable environmental conditions present in this study (adequate water, no intra-specific competition, no shading, no cattle trampling, etc.), repeated cutting had a significantly greater suppressive effect than did the biological control agents, but an additive, albeit modest, suppressive effect occurred with the combination of both tactics. In cases where trees are growing under less than optimal growing conditions, as described in the aforementioned studies by Center et al.
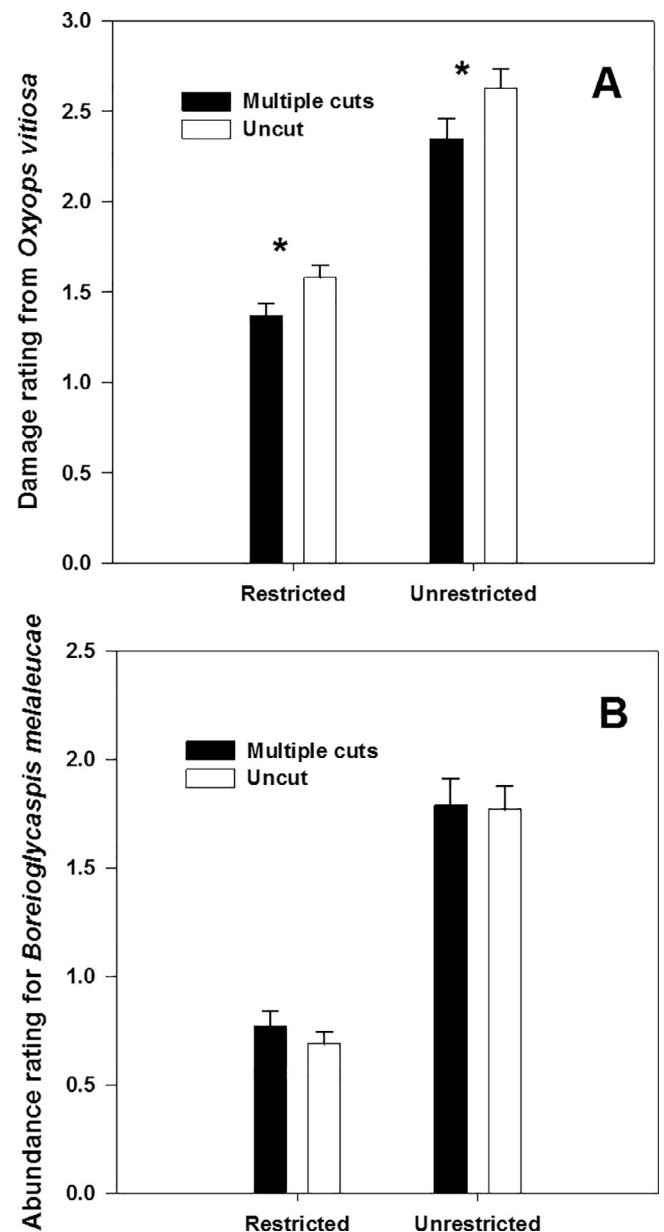

Fig. 2. Effect of cutting treatments on insect attack or presence on regrowth A) damage rating of *O. vitiosa*, B) abundance rating for *B. melaleucae*. *, $P = 0.05$.

(2007) and Rayamajhi et al. (2010), such an additive effect would likely be magnified. Maschinski and Whitham (1989) noted that plant responses to herbivory varied with local conditions that included competition, nutrient availability, and timing.

Although repeated cutting was effective at reducing biomass of treatment trees, it is not normally done at the frequency used in this study in most areas where *M. quinquenervia* invades. *Oxyops vitiosa* and *B. melaleucae* are now found throughout the landscape in southern Florida so land managers that repeatedly or occasionally cut smaller trees without treating the stumps with herbicides may expect that the vigorous plant regrowth will be offset to some degree by continual herbivory from biological control agents that, over the long term, will likely reduce plant fitness while providing managers longer intervals between re-treatments.

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