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The influence of two wildfires and biological control agents on the population dynamics of *Melaleuca quinquenervia* in a seasonally inundated wetland

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Abstract

The potential of *Melaleuca quinquenervia* (Cav.) S.T. Blake to reinvoke cleared areas was evaluated over a 13-yr period that included two wildfires and the introduction of biological control agents. The first wildfire occurred in 1998 and was followed by a mean of 591.5 recruited seedlings m^{-2} . Recruits from that fire were cleared 7 yr later in July 2005 for a second experiment to evaluate seedling recruitment into cleared areas. Seed rain, seedling recruitment and mortality, and sapling growth rates were measured in four plots located around individual large reproductive trees. A second natural wildfire in 2007 burned through those plots, leading to increases in seed rain followed by a pulse in recruitment of 21.04 seedlings m^{-2} , 96.5% fewer than after the 1998 fire. Recruits in half of the plots around each tree were then treated with regular applications of an insecticide to restrict herbivory by biological control agents, while herbivory was not restricted in the other half. There was no difference in seedling mortality between treatments 1,083 d post-fire (2007) with 96.6% seedling mortality in the unrestricted herbivory treatment and 89.4% mortality in the restricted herbivory treatment. Recruits subjected to the restricted herbivory treatment grew taller than those in the unrestricted herbivory treatment, 101.3 cm versus 37.4 cm. Many of the recruits were attacked by the biological control agents, which slowed their growth. Although solitary *M. quinquenervia* trees retain some capacity to reinvoke areas under specific circumstances, there was a downward trend in their overall invasiveness at this site, with progressively smaller recruitment cohorts due to biological control agents. Land managers should prioritize removing large reproductive trees over treating recently recruited populations, which can be left for many years for the biological control agents to suppress before any additional treatment would be needed.

Introduction

The Australian tree *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtaceae) has been the target of a multidecade management effort that utilized a combination of chemical, biological, physical, and cultural tactics (LaRoche 1998). This integrated approach was guided by the Melaleuca Management Plan developed by the South Florida Water Management District, the Florida Exotic Pest Plant Council, USDA-ARS, and others in 1990 and revised in 1994 and 1999 (Florida Exotic Pest Plant Council 1999). During this period, *M. quinquenervia* was transforming large areas of greater Everglades landscape from a mosaic of sawgrass [*Cladium mariscus* ssp. *jamaicense* (Crantz) Kük] prairies, pine (*Pinus* sp.) flatwoods, and wet prairies into dense monotypic forests of *M. quinquenervia*. This led to disruptions of native communities from changing fire regimes, alterations to nutrient cycles, modifications of hydrology, and suppression of native plant species (Center et al. 2012; Gordon 1998; Martin et al. 2009; Rayamajhi et al. 2009).

One of the original challenges in managing this species was its large seedbank, held in permanent serotinous capsules within the canopy, with the seed released synchronously in response to perturbations such as treatments by herbicides or wildfires (Center et al. 2012). Following the desiccation of seed capsules, massive amounts of seeds were deposited near the tree that eventually recruited dense populations of seedlings (Woodall 1982). This species is intermediately serotinous, whereby some seeds are continually released to take advantage of favorable, yet unpredictable, germination microsites (Lamont et al. 1991). A few seed capsules (about 12% per year) desiccate and open continuously, producing a lighter but constant seed rain (Tipping et al. 2012; Woodall 1982). Seeds are very small, which aids their penetration of leaf litter to form a short-lived soil seedbank with a half-life of about 1 yr (Van et al. 2005). Although

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Management Implications

The invasive capacity of *Melaleuca quinquenervia* may be reduced as evidenced by a greater than 95% reduction in the size of recruitment cohorts following wildfires in 1998 and 2007 in the same area. In the past, before the implementation of classical biological control in 1997, mass recruitment events post-fire promoted this species to dominate landscapes. Today, seedlings, saplings, and large trees are now attacked continuously in Florida by three biological control agents. The density of the 1998 recruits was reduced by 96.3%, and none had produced seed capsules by 2005. In addition to reducing the aerial seedbanks of reproductive trees, the biological control agents reduced the rate of growth and height of the recruited seedlings following the second fire in 2007. After 3 yr, the natural mortality of new recruits (89.4%) increased slightly to 96.6% when attacked by the biological control agents. Recruits were 63% taller during the same period when protected from the agents using insecticides. There was no recruitment during the next 3 yr despite seed rain and periodically favorable hydrological conditions. Newly recruited seedlings face not only high levels of natural mortality, but also constant herbivory from biological control agents, the combination of which will reduce their numbers, slow their growth, and inhibit the survivors from achieving the capacity to reproduce for many years. Based on the results of this study, land managers should target mature reproductive trees rather than cohorts of recruits to exert maximum suppression on *M. quinquenervia* populations.

only about 9% of the seeds are viable, a single large tree located within a dense stand retains up to 9 million viable seeds within its canopy (Rayamajhi et al. 2002). Recruited seedlings are highly susceptible to drought or flooding (Lockhart et al. 1999; Tipping et al. 2012).

The original role envisioned for the biological control portion of the Melaleuca Management Plan was to reduce this seed production and retard the growth of recruits. This goal was eventually accomplished with the establishment of three biological control agents that reduced seed production and plant growth rates, while increasing the susceptibility of saplings and smaller trees to wildfires and herbicides (Tipping et al. 2008, 2017). The first agent, *Oxyops vitiosa* Moore (Coleoptera: Curculionidae), was released in 1997 and proved to be highly effective in areas that are not permanently inundated (Center et al. 2000; Tipping et al. 2009). This agent appears to promote a resource-regulation phenomenon that maintains a higher level of agent attack while reducing resources for reproductive tissues (Tipping et al. 2015). As a result of repeated defoliation, seed production is reduced by 80% to 100%, depending on conditions, and this loss of seed pressure appears to have influenced *M. quinquenervia* population dynamics to the point where the plant's invasiveness is now reduced in certain areas (Tipping et al. 2008, 2012).

The second agent, released in 2002, was *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), an agent unaffected by hydrology and with the demonstrated potential to suppress saplings and cause older trees to drop leaves (Morath et al. 2006; Purcell et al., 1997). This species established quickly and dispersed rapidly throughout the range of *M. quinquenervia* in Florida (Center et al. 2006). It appears to be temperature sensitive, with larger populations developing during the cooler dry season and smaller populations during the warmer rainy season (Chiarelli et al. 2011).

The third agent was *Lophidoplosis trifida* Gagne (Diptera: Cecidomyiidae), a galling fly that was released in 2008 (Purcell et al. 2007). It also established readily and spread quickly, and its gall-forming activities can reduce sapling height by 10%, leaf biomass by 42%, woody biomass by 42.7%, and root biomass by 30.3% (Pratt et al. 2013; Tipping et al. 2016).

These combined cooperative efforts by multiple state and federal agencies using chemical, biological, physical, and cultural tactics have reduced *M. quinquenervia* infestations in both scale and density, leading to reductions in management costs, with concomitant increases in native plant diversity in formerly infested areas (Rayamajhi et al. 2009). The impact of biological control on larger trees (>5-m height) growing in lower densities remains uncertain, given the difficulty in establishing true herbivory controls on trees of this size class, but flowering and seed production are often apparent in these trees. Some of these larger trees remain on the landscape in reduced densities and have led some land managers to target them out of concern they might serve as foci for reinvansion. These efforts can be expensive because of the need to deploy helicopters or ground crews to locate and kill isolated trees using herbicides.

The primary objective of this study was to evaluate the potential of these larger, solitary trees to serve as a seed source that might spur a reinvansion in areas largely cleared with chemical, biological, cultural, and mechanical methods. Secondarily, we measured the change in recruitment patterns following fires in 1998 and 2007 and the fate of recruited seedlings exposed to herbivory by the three biological control agents.

Materials and Methods

As part of an earlier experiment in 1998, 90 plots (0.5 m^{-2}) were established within a 20-ha site in the Belle Meade section of Picayune State Forest (26.1023°N , 81.6422°W) to evaluate the impact of the recently released *O. vitiosa* on *M. quinquenervia* seedlings and saplings. The plant communities at this site, soil types, biogeochemistry, and hydrology were described by Martin et al. (2009). Researchers counted the number of recruits following the fire in December 1998 before the larger experiment was vandalized and subsequently abandoned.

In July 2005, six large solitary *M. quinquenervia* trees (mean height + SE: $12.4 \pm 1.2 \text{ m}$) growing in the same area with apparent capsule clusters visible in their canopies were selected for another experiment. Four plots (4 m^2) were established within the seed shadow of each tree in cardinal directions, and all existing *M. quinquenervia* saplings (recruited after the 1998 fire) were counted, removed, and measured for above- and belowground biomass. A seed trap was installed adjacent to each quadrat to capture seed rain according to the design of Tipping et al. (2012). Once a month, the following data were collected from each plot: (1) number of seeds in seed traps, (2) the number and height of recruited seedlings in the quadrats, (3) water depth, and (4) soil moisture. Four soil samples (5-cm depth) were taken adjacent to the quadrats, weighed, and then dried to a constant weight to estimate soil moisture. During this experiment, *O. vitiosa* and *B. melaleucae* were common at this site, while *L. trifida* spread into the plots near the end of the experiment.

In April 2007, the Great Balsa fire burned through all the plots and, for the first time since the 1998 fire, seedling recruitment occurred at the Belle Meade site, which led the researchers to modify the original experimental design to better evaluate the event (Florida Department of Forestry n.d.). A total of 975 post-fire



Figure 1. Recruited *Melaleuca quinquenervia* seedling from the 2007 fire marked with a metal stake and tag.

recruited seedlings across all existing quadrats were numbered with a small metal stake and measured for height (Figure 1). The original quadrats around the reproductive trees were randomly assigned to one of two treatments so that half were sprayed with the insecticide acephate (OS-dimethyl acetylphosphoramidothioate) applied with a hand-pressurized backpack sprayer at a concentration of 0.367% ai (v/v) until wet (restricted herbivory) and the other half with water (unrestricted herbivory) every 4 to 6 wk. The data captured post-fire remained the same, with the addition of recording the number of surviving recruits and their heights periodically. If a seedling could not be located next to a numbered stake, it was considered dead, and the stake was removed. The study ended in May 2010, and all surviving recruits were harvested, separated into component parts (leaves, wood, roots, etc.), and dried to determine dry weight (DW) biomass.

Data Analysis

Data were tested for normality and homogeneity of variance and transformed using square-root transformation as needed before analysis. The mean mortality and height of the recruited cohort were calculated and used in a general linear model, with herbivory treatment as a fixed effect and sample date and sample tree as random effects (SAS Institute 2009). Direct comparisons of treatment effects on these final parameters were conducted with *t*-tests. The soil seedbank was estimated by assuming it was zero at the beginning of the experiment and cumulatively adding the seed rain, while subtracting recruited seedlings. Seed that fell into the plots was assumed to be nonviable after 2 yr and was subtracted from the estimated soil seedbank. Harvest biomass data from the 2007 cohort were subjected to one-way ANOVA, and the means between restricted and unrestricted herbivory treatments were separated using *t*-tests (SAS Institute 2009).

Results and Discussion

The mean number of recruits following the 1998 fire was $561.5 + 36.7$ seedlings m^{-2} (TD Center, unpublished data) and by July 2005, the mean density (+SE) of the surviving saplings had declined 96.3% to $20.4 + 1.7$ saplings m^{-2} , none of which had any evidence of seed capsules. As mentioned earlier, these were

then hand pulled to set up the second experimental plots around the individual trees. Following the establishment of the new plots, a total of two seedlings were recruited across all plots from July 2005 through March 2007 despite an average of 0.49 viable seeds $m^{-2} d^{-1}$ falling into the quadrats and periodically favorable hydrologic conditions (Figure 2). Seed rain appeared to increase beginning in May 2007, likely as a result of seed capsules desiccating after the fire and releasing seeds (Figure 2). Despite this, no seedlings were recruited for the next 5 mo until October 2007, when soil moisture and water levels increased to stimulate germination (Figure 2). After that pulse of recruitment between the end of September 2007 through mid-October 2007, no new recruitment occurred during the remaining 34 mo of the experiment, despite regular and progressively heavier seed rains (Figure 2) and an increasing estimated soil seedbank (Figure 3).

The initial mean densities of the 2007 cohorts were equivalent in their assigned unrestricted and restricted herbivory treatments at $12.4 + 2.6$ and $8.56 + 2.0$ seedlings m^{-2} , respectively ($t = 1.13$, $df = 21$, $P = 0.26$). Over the experimental duration of 1,083 d, the mortality trends of seedlings in both treatments were similar, and there was no difference in the final seedling mortality, with $96.6 + 1.3\%$ of seedlings dying in the unrestricted herbivory treatment (water) and $89.4 + 4.9\%$ dying in the restricted herbivory treatment (insecticide) ($t = 1.47$, $df = 21$, $P = 0.15$) (Figure 4). At the end of the experiment, the mean densities were also not different between treatments, with $0.27 + 0.07$ saplings m^{-2} present in the unrestricted herbivory treatment and $0.97 + 0.44$ saplings m^{-2} in the restricted herbivory treatment ($t = 1.13$, $df = 21$, $P = 0.12$). Those seedlings/saplings protected from herbivory grew taller than unprotected plants, with final mean heights of $101.3 + 2.2$ cm under restricted herbivory and $37.4 + 6.9$ cm under unrestricted herbivory ($t = 8.15$, $df = 11$, $P = 0.0001$) (Figure 5). Herbivory by the biological control agents reduced individual plant biomass by 90.1%, with a final mean DW biomass of $51.8 + 9.8$ g under restricted herbivory versus $5.1 + 2.04$ g under unrestricted herbivory ($t = 5.04$, $df = 11$, $P = 0.0004$). No flowers or seed capsules were produced by any of the recruits.

The insecticide regime in this study was effective at controlling all three agents, including the more difficult to manage *L. trifida*, for which gall production was reduced by more than 87% ($P = 0.02$). Although some of the protected plants were stimulated to form galls, it is likely the flies within were killed by the insecticide treatment (Tipping et al. 2016). The surviving recruits in the unrestricted herbivory treatment weighed 90.1% less ($P = 0.0001$) and were 63% shorter ($P = 0.0001$) than those protected with insecticides, but despite the apparent damage inflicted on the unprotected recruits by the biological control agents, they survived at the same level as protected recruits ($P = 0.15$).

Although the large *M. quinquenervia* trees in this study continued to disperse seeds between fires, the numbers were insufficient to recruit new populations without the intervention of a major perturbation like a fire. This is a common strategy in serotinous species, whereby wildfires influence both the quantity of available seeds plus improve the quality of the seedbed by burning off organic material to expose more mineral soils (Johnston and Elliott 1998). Organic materials may promote high diurnal temperature fluctuations and lead to rapid drying of the soil surface (Johnstone and Chapin 2006). At seasonally inundated sites like the Belle Meade site, a dark-colored muck layer is left on the surface of the soil after the water recedes, and this layer dries out and forms a crust that oxidizes over time. The underlying mineral soils are typified by loamy, siliceous, hyperthermic Arenic Glassoqualfs

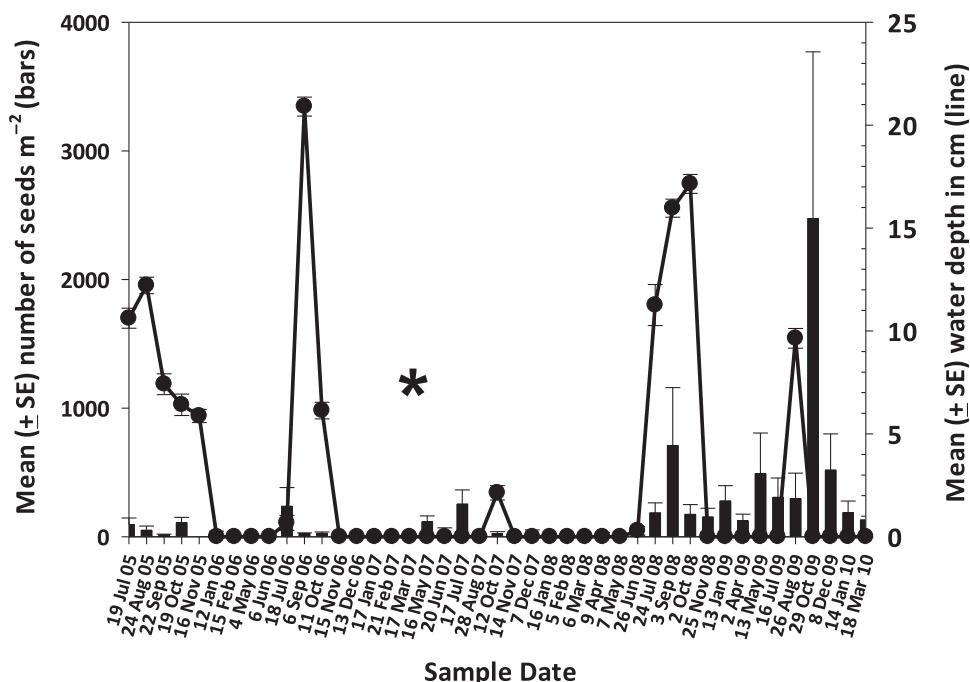


Figure 2. Mean seed rain (bars) from experimental *Melaleuca quinquenervia* trees with associated mean water depths (line) from July 2005 through March 2010 in the Belle Meade section of Picayune State Forest, Florida. The asterisk (*) indicates the approximate date of the 2007 Great Balsa fire.

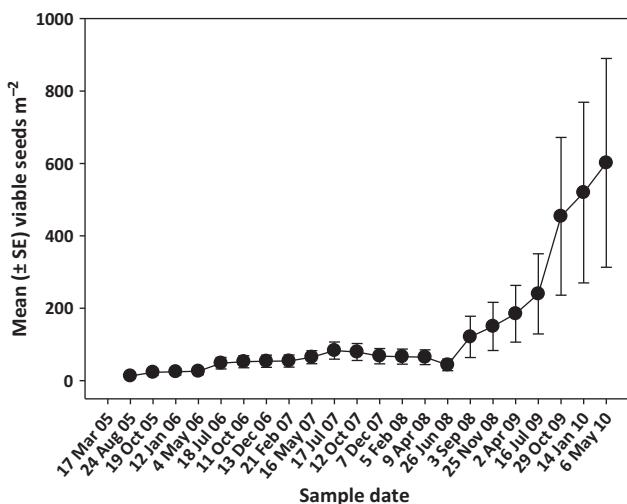


Figure 3. Mean estimated viable soil seedbank for *Melaleuca quinquenervia* from August 2005 through May 2010.

(Pineda series), which can moderate temperatures while wicking moisture from subsurface layers to relieve the moisture limitation of seedlings like *M. quinquenervia* that are vulnerable to dry conditions (Johnstone and Chapin 2006; Martin et al. 2010). Seedlings recruited atop this crust are likely to be at increased risk of drought stress as the crust dries, which may reduce their survival.

Before seed production was curtailed by *O. vitiosa*, *M. quinquenervia* trees maintained a large aerial seedbank that responded rapidly to perturbations like wildfires and exploited more favorable recruitment environments. With the 2007 fire, there was still a time lag of 5 mo until water levels were more favorable for seed germination before substantial recruitment occurred, and the recruitment window was relatively narrow, lasting only 2 mo.

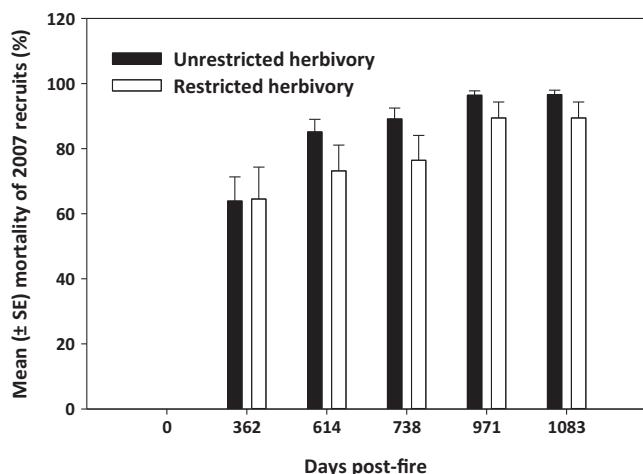


Figure 4. Mean cumulative mortality of *Melaleuca quinquenervia* seedlings recruited after the 2007 fire and subjected to unrestricted and restricted herbivory by biological control agents.

A characteristic feature of fire-prone environments is the tendency for recruitment to be concentrated in the first year following fire, at a time when resource availability is likely to be at its maximum (light, nutrients, soil moisture) and competition from established plants at its minimum (Lamont and Enright 2000). Previous studies at this site demonstrated the vulnerability of young seedlings to fluctuations in water stage, either from drying out or being drowned before they attained sufficient size (Tipping et al. 2012). Thus, although biological windows still exist whereby reproductive *M. quinquenervia* can recruit seedlings following the combination of a perturbation and the right soil moisture conditions, the reservoir of seeds in the aerial seedbank appears to be much smaller, most likely as a result of years of herbivory by biological

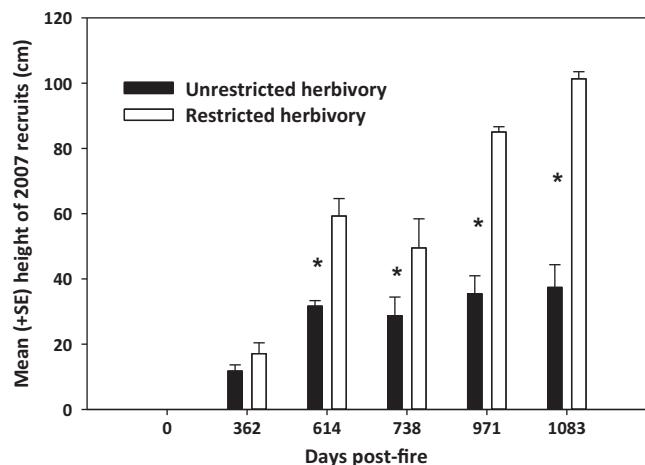


Figure 5. Mean periodic heights of *Melaleuca quinquenervia* seedlings recruited after the 2007 fire and subjected to unrestricted and restricted herbivory by biological control agents. *Treatment means within date are significantly different at $P = 0.05$.

control agents. The estimated soil seedbank at this site appeared to be increasing almost a year after the 2007 fire, which may be explained by a pulse of nutrients that were scavenged by the large trees post-fire and eventually converted into reproductive biomass that resulted in an increase in inter-fire seed rain. Even though smaller seeds can penetrate inter-fire litter more easily and facilitate establishment, smaller seeds are often short-lived (Witkowski et al. 1991). In areas with more frequent fires (<20-yr intervals), serotiny has an advantage over soil storage, in which only a proportion of seeds will germinate, even if conditions are ideal (Lamont and Enright 2000). Where conditions are suitable for inter-fire establishment (such as the appearance of small gaps, exceptionally wet years), some spontaneous seed release may be advantageous (Lamont and Enright 2000). However, that did not appear to be the case at this site, where only two seedlings were recruited during the inter-fire portions of the experiment.

Factors that promote post-fire germination and seedling establishment may include the reduction or elimination of herbivore populations (Hanley and Fenner 1997; Lamont et al. 1991). Although a number of studies, including this one, have identified the overall impact of herbivores on post-fire seedling populations using herbivore exclusion techniques, this kind of approach sheds little light on the actual mechanisms involved, including the early development and expression of seedling chemical or physical defenses (Hulme 1996; Karban and Thaler 1999). Regardless of the circumstances, it was clear in this case that the specialized herbivores were able to quickly locate and attack newly recruited seedlings.

Despite the post-fire pulse of recruitment in 2007, more than 96% of recruits were dead after about 3 yr, and the survivors will probably not flower for years to come, as evidenced by the recruitment cohort from 1998, for which none of the survivors had produced seed capsules after 7 yr. Plants protected from herbivory can reproduce within a year or two (Meskimen 1962). Comparing differences in growth rates between appropriate experimental cohorts provides a rough estimate of 15 yr before any new recruits will achieve reproductive status because of the current levels of herbivory from biological control agents.

Seedling mortality from 1998 to 2005 matched that from 2007 to 2010 (93.6%), with only a slight increase in mortality between protected and unprotected seedlings. Another study at the Belle Meade site determined that 99.2% of the recruited seedlings died

after 3 yr (Tipping et al. 2012). Edwards and Crawley (1999) and others have argued that any seedling losses from herbivory contribute little to the plant community structure because of density-dependent mortality from intraspecific competition as a seedling cohort undergoes self-thinning. If this is true, the real impact of herbivory is not with seedling mortality but rather seed reduction and storage in reproductive *M. quinquenervia*, along with a delay between the emergence of a seedling and its development into a reproductive tree. The longer-term population-level implications of these differences are unknown but may suggest that the biological control agents will inhibit or delay the development of saplings to reproductive trees, as evidenced by the lack of seed capsule clusters on the 7-yr-old saplings/trees that were recruited after the 1998 fire. Another experiment conducted nearby during 2002 to 2007 using this same cohort found that trees began flowering about a year after the start of regular applications of insecticides, while no unsprayed trees ever flowered (Tipping et al. 2009). There has been an overall decline in *M. quinquenervia* density at this site, as recruitment events have contracted in scale and scope, while the mortality of recruits remains high. This density reduction is concurrent with declines in seed production by individual trees caused by attack from biological control agents (Tipping et al. 2008). Land managers can consider this new reality when prioritizing management decisions; namely, high levels of seedling/sapling mortality without regular replacement and extended periods before *M. quinquenervia* recruits become reproductive because of herbivory by biological control agents.

Similar recruitment events have occurred nearby since this experiment, most recently in Big Cypress National Preserve, which is located east of the site of this experiment. In that case, areas adjacent to a few reproductive trees recruited seedlings following the 24,685 hectare Buzzard Fire (25.9762, 80.9408) that was sparked by lightning on April 10, 2018. As in this experiment, the seedlings were quickly attacked by biological control agents despite the low density and isolated nature of the mature *M. quinquenervia* (M Smith, personal communication). This confirms once again the ability of biological control agents to find isolated populations of seedlings and saplings and quickly build up their numbers.

Land managers at this preserve and Everglades National Park have used a variety of methods to control isolated *M. quinquenervia*, including spraying trees with herbicides delivered by drop nozzles slung under helicopters. Although this method requires specialized equipment and is expensive upfront (helicopter rental is about US\$1,500 h^{-1}), it reduces the overall costs of treatments in several ways, including reducing negative environmental impacts to the area by ground crews who must create or reopen paths to the infestations; it increases the likelihood of locating isolated trees; and it allows more areas to be treated more effectively in less time. For example, recent treatments in Big Cypress Preserve and Everglades National Park cost anywhere from US\$18 to US\$125 per tree, far less than the cost of a five-person ground crew at US\$2,000 to US\$3,000 h^{-1} , assuming that ground crews could even access these areas and find the trees in the difficult terrain and dense vegetation. In the more heavily forested and roadless landscapes of Big Cypress National Preserve, a typical ground crew can normally locate and treat two sites a day (W Snyder, personal communication). In comparison, a helicopter with a drop nozzle can locate and spot-treat *M. quinquenervia* trees in an area as large as 5,666 ha in 2 d (H Cooley, personal communication; W Snyder, personal communication).

Although recently recruited *M. quinquenervia* populations may cause concern to land managers, prioritizing the elimination of

reproductive trees may be the best use of scarce management dollars rather than spraying or burning recently recruited populations of seedlings/saplings, because the normally high levels of natural mortality from abiotic factors are no longer offset by seed rain, coupled with constant herbivory from biological control agents that retards the survivors' growth and development toward reproductive capability. Any newly recruited sites can be mapped and left to the biological agents for at least a decade or longer before any trees that survive and produce seeds would need to be treated.

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