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Post-biological control invasion trajectory for *Melaleuca quinquenervia* in a seasonally inundated wetland

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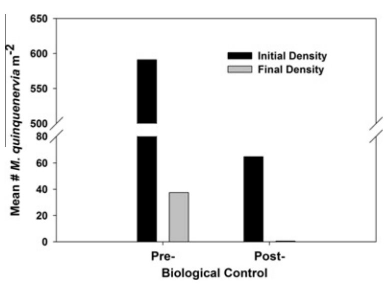
HIGHLIGHTS

- ▶ We examined the recruitment and mortality of *Melaleuca quinquenervia* in the Everglades.
- ▶ Post-biocontrol populations were 99% smaller than pre-biocontrol populations.
- ▶ Biocontrol agents did not increase mortality of weed seedlings.
- ▶ Weed invasion trajectory likely changed by depleted aerial seed banks.

GRAPHICAL ABSTRACT



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ABSTRACT

The recruitment and mortality of *Melaleuca quinquenervia* seedlings were evaluated over a 3-year period in a seasonally inundated wetland in the western Everglades region. The mean (±SE) density of seedlings/saplings m^{-1} declined from 64.8 (±4.5) to 0.5 (±0.2) over the 3 years, a population reduction of 99.2%. Four distinct water regimes characterized this site: dry, dry to wet transition, flooded, and wet to dry transition. Seedling recruitment was highest in the dry to wet transition and lowest in the flooded water regime, while mortality was highest under flooded and dry water regimes. The mean estimate of population growth (λ) across water regimes was 0.64 ± 0.05 indicating negative population growth. Elimination of introduced insect herbivores using insecticides did not reduce mortality of recruited *M. quinquenervia* seedlings/saplings indicating that direct herbivory was not responsible for the decline in seedling density. On the other hand, a mean of only 0.2 (±0.03) viable seeds m^{-2} d^{-1} fell into the plots, an amount considerably lower than in previous studies. We submit that change in the invasion trajectory *M. quinquenervia* was most likely caused by reduced seed inputs from aerial seed banks depleted by insect herbivory rather than direct herbivory on seedlings. This may indicate a fundamental alteration of *M. quinquenervia* population dynamics ultimately resulting in a less invasive and, therefore, less ecologically damaging species.

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1. Introduction

Exotic plants that successfully invade new ranges often possess a high reproductive capacity which enables them to outcompete native species by swamping available seed microsites with propagules (Reichard and Hamilton, 1997; Mason et al., 2008; Martin and Canham, 2010). A high degree of propagule pressure is considered vital for successful invasion and establishment into new habitats (Rouget and Richardson, 2003). However, the relationship between seed inputs and recruited seedlings are often non-linear (Poulsen et al., 2007) as a result of microsite limitations (Clark et al., 2007) and density-dependent factors such as intraspecific

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competition (Conduit et al., 1994). In addition to higher fecundity, exotic invasive species often exhibit early reproduction, effective seed dispersal, fast population growth, vegetative reproduction, release from natural enemies, or dependence on non-specific mutualisms (Rejmánek and Richardson, 1996; Pysek and Richardson, 2007).

Water regimes are often the most important factor in determining the spatial and temporal heterogeneity of wetland plant communities (van der Valk, 2005; Watt et al., 2007; Raulings et al., 2010). Hydrology can regularly limit seed microsites which, in turn, influence germination, seedling recruitment, and seedling mortality (Froend and Van der Moezel, 1994; Keddy and Ellis, 1985). Casanova and Brock (2000) found the duration of flooding to be more important than depth in determining plant communities, and that species were grouped according to their response to fluctuations in the water regime. Water regimes can also serve as environmental triggers for seed release from species with aerial seed banks (Hamilton-Brown et al., 2009). Triggers may be location specific; rainforest trees growing in perennially wet sites release more seed during the wet season, while trees growing in dry sites release more seed in the dry season (Russell-Smith and Setterfield, 2006).

One such non-native invasive species that invades wetlands and produced copious amounts of seeds from an aerial seed bank is *Melaleuca quinquenervia* (Cav.) S.T. Blake. The origin, natural history, and management of this tree in Florida were summarized by Serbesoff-King (2003). The intentional introduction of *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) in 1997 as part of a classical biological control project provided the first significant herbivore pressure on *M. quinquenervia* (Center et al., 2000). As a result of overcompensation to herbivory from this insect, reproduction in individual trees was reduced by 80–100% (Pratt et al., 2005; Tipping et al., 2008, 2009). In concert with reducing aerial seed banks, *O. vitiosa* also directly damages older saplings resulting in reduced population densities (Tipping et al., 2009). A second insect, *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) was released in 2002 and is now widely distributed (Center et al., 2007). The impact of this species on reproductive *M. quinquenervia* trees is unclear but appears to be relatively minor compared to *O. vitiosa* (Tipping et al., 2008).

The objective of this study was to quantify the post-biological control invasion trajectory of *M. quinquenervia* in a seasonally inundated wetland characteristic of the western Everglades area. Specifically, this included determining if reproductive *M. quinquenervia* can still serve as potential invasion source despite herbivory by *O. vitiosa* for more than a decade. A secondary objective was to measure the impact of herbivory on newly recruited seedlings. Two hypotheses were proposed: (1) post-biological control densities of recruited *M. quinquenervia* populations would be equivalent to those recruited pre-biological control, and (2) direct herbivory would have no effect on survival of recruited seedlings of *M. quinquenervia*.

2. Materials and methods

2.1. The study area

Experimental plots were located in a 19-ha section of the Belle Meade tract (ca. 6700 ha) within the Picayune Strand State Forest (29,000 ha) located near Naples, Florida. This area consists of nearly level, poorly drained, low fertility soils which are loamy, siliceous, hyperthermic Arenic Glassoqualfs. The soil series is Pineda-Boca-Hallandale which is characterized by moderately to poorly drained sands over-lying limestone bedrock at a depth of approximately 1.4 m (USDA, 1998). The top 5 cm of soil in the plots contained 4.1% organic matter, 18.5 mg g^{-1} carbon, 0.8 mg g^{-1} nitrogen, and 18.1 mg g^{-1} phosphorus with a pH of 5.3 (Martin et al., 2009). The water table fluctuates annually between greater than 15 cm below the soil surface to approximately 25 cm above. The area has a distinct wet season from approximately July to December and a dry season from January to June. Average annual rainfall in this region is approximately 1.36 m (SERC, 2007).

The Belle Meade tract is comprised of cypress strands, wet prairies, and pine flatwood communities with important native species like slash pine (*Pinus elliotii* var. *densa* Little and Dorman), pond cypress (*Taxodium ascendens* Brongn.), cabbage palm (*Sabal palmetto* [Walt.] Lodd. ex. J.S. Schult. and J.H. Schult.), saw palmetto (*Serenoa repens* [Bartr.] Small), waxmyrtle (*Morella cerifera* (L.) Small), and sawgrass (*Cladium jamaicensis* Crantz). *M. quinquenervia* has invaded this area over the years and replaced many of the native communities with large monospecific stands of various-aged trees, a process expedited by several successive canopy fires. A large fire in 1998 resulted in a major recruitment event where recruited seedling densities exceeded 591 m^{-2} (Center, unpublished data) and formed the pre-herbivory cohort of plants included in this study.

Four distinct water regimes were characterized at this site, namely (1) dry: no standing water in any plots for two consecutive sampling periods, (2) dry to wet transition: sampling periods between dry stages and flooded stages with some standing water in some plots and followed eventually by a sampling period with complete soil submergence, (3) flooded: complete submergence of soil in all plots, and (4) wet to dry transition: sampling periods between flooded stage and dry stage with some standing water in some plots followed eventually by a sampling period with no standing water. Although the boundaries of these periods were somewhat arbitrary they realistically describe field conditions as well as the direction of hydrologic change. In most cases the sequence of water regimes were unidirectional, normally transitioning from dry to flooded, and then back to dry (Fig. 1).

2.2. Sampling design

Ten reproductive *M. quinquenervia* trees (mean height ± SE: 12.5 ± 1.2 m) located at least 100 m from other reproductive trees were identified and four 1 m^2 quadrats were established in cardinal directions within their seed shadows (within 2 m from the trunk). Existing *M. quinquenervia* seedlings and saplings within each of the quadrats were counted (mean ± SE: 64.8 ± 4.5) and then removed by hand along with the leaf litter to facilitate seed germination and seedling recruitment (Fowler, 1986; Hamrick and Lee,

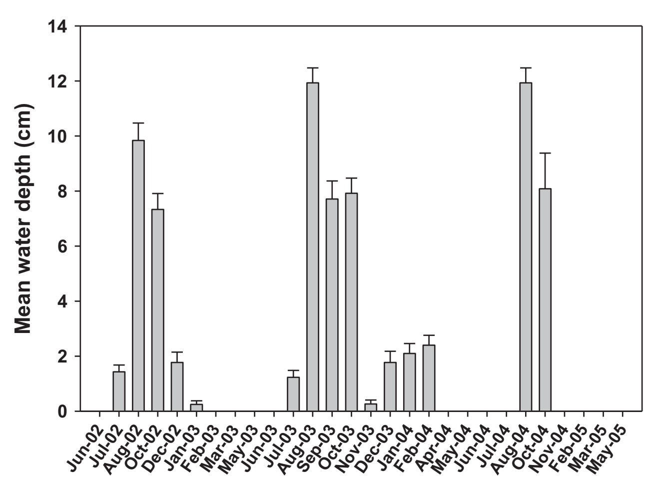

Fig. 1. Mean (±SE) water depths at the Belle Meade experimental plots.