Chapter 29

Successful Melaleuca Biological Control in the Florida Everglades

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NON-TECHNICAL SUMMARY

Non-native plant invasions are often the result of intentional introductions through the horticulture trade. Beginning in the early 1800s, extensive effort was made to explore the world in search of plants for use in ornamental horticulture. *Melaleuca quinquenervia* (Myrtaceae) is one such plant that was brought into south Florida beginning in 1886 for use as a landscape tree.

During the next fifty years (1905–1955), *M. quinquenervia* (or melaleuca) was used to reforest edges of swamps where cypress and pine had been removed by settlers, planted extensively in urban settings, used to stabilize dikes for large U.S. Army Corps of Engineers projects, and seeded from planes in an attempt to make Florida wetlands more hospitable for development. Gradually, however, the landscape melaleuca was invading, especially in the Everglades which became an icon for imperiled North American ecosystems. Soon thereafter in the 1960s, Florida and the federal government began large-scale efforts to preserve this unique subtropical wetland. A major cause of the degradation of the Everglades was the invasion of plant species, especially melaleuca, but also others such as Brazilian pepper tree (*Schinus terebinthifolia*), Old World climbing fern (*Lygodium microphyllum*), and air potato (*Dioscorea bulbifera*).

Over the past forty years or so (1980–2022), extensive efforts to introduce biological control agents against melaleuca (to reduce further expansion and prevent regrowth by limiting reproduction) and to integrate those agents with mechanical and chemical removal reduced the size of the melaleuca-dominated area from 400,000 ha (988,000 acres) to less than 100,000 ha (247,000 acres). Melaleuca control is currently in a maintenance mode in south Florida. Fire appears to spur new seedling recruitment events, but most large, mature stands are dwindling or have been treated and have not returned due to the ability of biological control agents to drastically reduce recruitment of new seedlings.

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HISTORY OF INVASION

Melaleuca quinquenervia (Myrtaceae) is an evergreen subtropical tree from Queensland and New South Wales, Australia (Blake, 1968). In Australia, *M. quinquenervia* (hereafter melaleuca) grows in wet swampy environments adjacent to various species of gum (*Eucalyptus*) and acacia (*Acacia*) trees. Melaleuca is emblematic of the horticultural expansion in Florida during the late 1800s through the early 1900s, when plant collectors such as Dr. David Fairchild in Miami and the Reasoner Brothers of Royal Palm Nursery in Manatee County began importing new taxa that could survive in Florida's subtropical climate (Dray et al., 2006). Several initial introductions and subsequent dispersal efforts using melaleuca seeds and seedlings took place throughout the early 1900s, including by the U.S. Department of Agriculture (USDA), the U.S. Army Corps of Engineers, the Koreshan Unity (a utopian society in southwest Florida), and several nurseries (Dray et al., 2006).

While the initial introductions were made in central Florida, the introductions along the east and west coasts of southern Florida appear to be the source of the invasion and where the bulk of the impacts were later felt. By the 1920s, twenty years after the USDA imported melaleuca into the Miami test station, it had escaped from cultivation (Dray et al., 2006). Melaleuca is now widespread throughout the Greater Everglades ecosystem and affects important conservation areas such as Everglades National Park, Big Cypress National Preserve, and Picayune Strand State Forest, which collectively support a unique subtropical/temperate flora and fauna (**Fig. 1**).

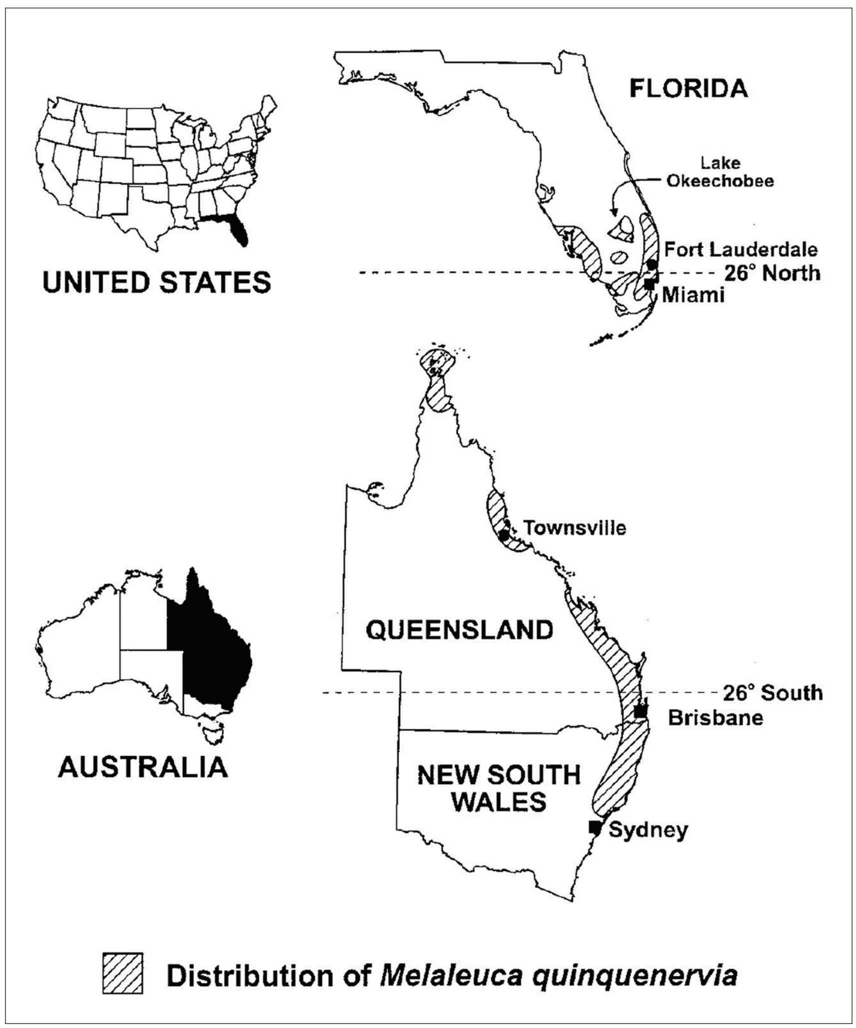

Figure 1. Distribution of melaleuca, *Melaleuca quinquenervia*, in Florida and Australia. (reproduced with permission from Turner et al., 1997)

THE NATURE AND ECOLOGY OF THE PROBLEM

Melaleuca's impact may be limited geographically to southern Florida and several nearby islands (e.g., Bahamas, Cuba, Puerto Rico), but its invasion has important ecological consequences for south Florida's natural ecosystems and human inhabitants. Melaleuca outcompetes and displaces native vegetation, alters fire frequency and severity, and changes the hydrology within the Greater Everglades ecosystem (Martin et al., 2011). By reducing water flow through increased evapotranspiration and loss of any intercepted rainfall, melaleuca effectively reduces the laminar flow over the coral cap rock that is fundamental to the physical basis of the Everglades (Lodge, 2016). Melaleuca reduces both the available surface water and the inputs into the region aquifer that supplies water to the growing human population of south Florida (Chin, 1998).

Fire, water, climate, and topography are the chief natural environmental factors that determine the ecology and structure of the Everglades ecosystem (Lockwood et al., 2003). Based on char in the soil record, fire historically occurred in the region every 2–3 years in some habitats and every 10–15 in others (Lockwood et al., 2003). But the advent of major hydrological diversion projects changed the spatial structure, timing, and intensity of fires in the southern tip of the Floridian peninsula. The expansion of melaleuca and its conversion of grass and sedge marshes to swamp forests further changed the fire dynamics and brought more severe fires closer to the wildland-urban interface. Restoration of the Everglades was initially focused on "Getting the Water Right," but that focus quickly widened to embrace restoration of both the fire and water regimes, as well as efforts to undo the large-scale plant invasions that affect both factors (Sklar et al., 2005).

WHY CONTROL THIS INVASIVE SPECIES?

The Greater Everglades ecosystem extends from the Kissimmee River south to Florida Bay, and it encompasses most of the east-west expanse from the Atlantic Ocean to the Gulf of Mexico (Ogden et al., 2005). By the 1970s, melaleuca had become a severely ecologically damaging species in the Everglades. The same ecological features that produced the largest graminoid-dominated wetland in the world (fire, water, and temperature) made it particularly vulnerable to the melaleuca invasion. Melaleuca is fire-adapted and thus does well in the fire-prone Everglades; mature trees resprout after fires, and millions of seeds are released that quickly germinate in the nutrient-infused post-fire conditions (Conde et al., 1981; Turner et al., 1997). Increased fire frequency and severity create a positive feedback loop in which melaleuca germinates and grows faster and quickly suppresses shade-intolerant native species (Laroche and Ferriter, 1992).

While it is a common misconception that melaleuca was introduced to 'dry up the Everglades,' the plant has indeed had large impacts on the hydrology of the invaded wetlands, resulting in a net loss of 0.2–0.6 million ha (0.5–1.5 million acres) of wetland habitat (Bodle et al., 1994). These newly formed forested areas exclude native understory vegetation and wildlife, including migratory and wading birds such as the endangered wood stork (*Mycteria americana*) (Catling, 2005).

In addition to the well documented ecological impacts of melaleuca, its invasion incurred millions of dollars in control costs and lost economic revenue. The South Florida Water Management District alone spent $13 million ($22 million in 2022 dollars) between 1991 and 1998 attempting to control melaleuca (Serbesoff-King, 2003). Diamond et al. (1991) estimated that economic losses due to melaleuca were nearly $168 million (fire control costs and lost tourism revenue). Balciunas and Center (1991) extrapolated the costs associated with melaleuca invasions to 2010 and estimated that melaleuca would cost up to $2 billion annually if left uncontrolled.

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

In January 1990, as a response to the growing call for Everglades restoration, the Melaleuca Task Force was formed to guide efforts to control melaleuca (Laroche, 1994). In a shift from previous control efforts that relied solely on chemical and mechanical methods, the Melaleuca Task Force added biological control as a key part of the control strategy. Foreign surveys for natural enemies of melaleuca in Australia were initiated in 1986 (Laroche, 1994). Over three decades of research (1986–2022) culminated in the establishment of three insects: *Oxyops vitiosa* (Coleoptera: Curculionidae), *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae), and *Lophodiplosis trifida* (Diptera: Cecidomyiidae). A fourth insect, *Fergusonina turneri* (Diptera: Fergusoninadae) and its obligate nematode *Fergusobia quinquenerviae* (Tylenchida: Neotylenchidae) were also approved for release in 2002, but they failed to establish after several release attempts (Pratt et al., 2013). A fifth species, *Lophodiplosis indentata*, was approved for release in early 2022 and is planned for release in the fall of 2022 (Center et al., 2012; Smith et al., 2020). In addition to these releases, the sawfly *Lophyrotoma zonalis* (Hymenoptera: Pergidae) was also evaluated for host-specificity and impact, but it was ultimately dropped from further consideration due to concerns over the mammalian toxicity of sequestered plant poisons found in the larvae (Buckingham, 2001; Oelrichs et al., 2001). The melaleuca project illustrates several innovative approaches to biological control of weeds, including ranking of agents based on mode of attack and how well these insects could be integrated with other management tools (e.g., chemical, mechanical, and biological) (Tipping et al., 2018). While some biological control projects successfully suppress their target weeds solely through the agents' direct and indirect effects (e.g., projects against air potato, *Dioscorea bulbifera*, and golden wattle, *Acacia longifolia*), many others, including melaleuca, require the use of additional methods of suppression to achieve satisfactory control.

By the 1980s, surveys for herbivores and pathogens that attack *M. quinquenervia* were well underway in Australia, and these surveys culminated in the release of the melaleuca snout weevil, *O. vitiosa*, in 1997 (**Fig. 2**). This weevil quickly established at several release sites. Later, several factors were found to influence establishment and impact of this weevil (Center et al., 2000; Balentine et al., 2009). Seasonal changes in foliage growth and hydroperiod appear to have the largest influence on whether *O. vitiosa* would establish at a site (Center et al., 2000). New flushing foliage provides high quality oviposition locations and food for developing larvae and adults. However, Purcell and Balciunas (1994) observed that *O. vitiosa* requires dry soil for its pupation. Immediately after its release, *O. vitiosa* began to have a measurable impact (Pratt et al., 2005). While *O. vitiosa* is arguably the most effective of the biological control agents released against melaleuca, its inability to establish in persistently wet areas created a need for additional agents that could persist under such conditions. Foreign exploration for agents resulted in the discovery of biological control agents that do not require soil

Figure 2. (a) An adult and (b) larvae of *Oxyops vitiosa* feeding on new melaleuca foliage. (M. C. Smith, USDA-ARS)

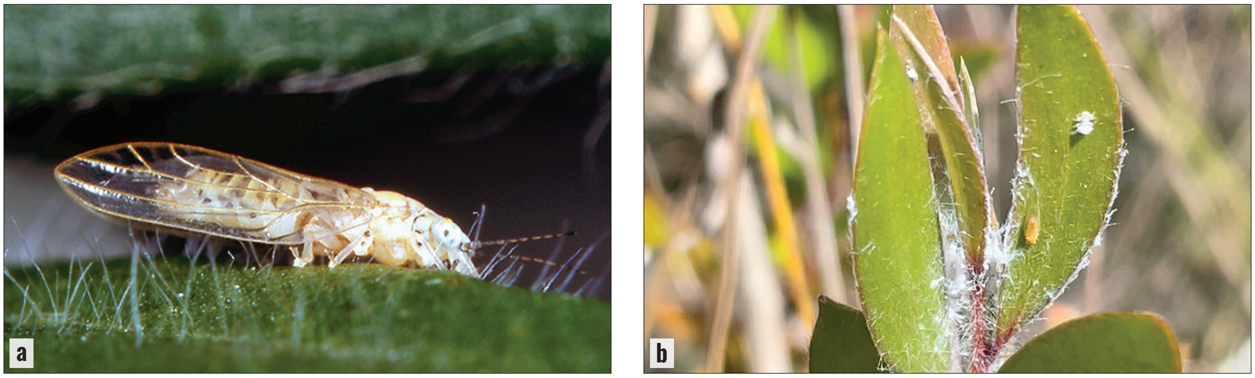

Figure 3. (a) Adult melaleuca psyllid, *Boreioglycapsis melaleucae*, and (b) adult psyllid with nymphal flocculence on a melaleuca leaf. (a: S. Wineriter-Wright, USDA-ARS; b: M. C. Smith, USDA-ARS)

for pupation, primarily the melaleuca psyllid, *B. melaleucae* (**Fig. 3**), and the melaleuca tip-galling midge, *L. trifida* (**Fig. 4a**). These agents were released in 2008 and 2012, respectively. *Lophodiplosis indentata* was issued a release permit in April 2022, and releases were anticipated to begin shortly thereafter. Both *L. trifida* and *L. indentata* are gall midges, with *L. trifida* galling buds (**Fig. 4b,c**) and *L. indentata* attacking leaves (**Fig. 4d**). Several studies in Australia showed that these species have similar impacts on saplings and seedlings, but they do not seem to compete for resources (Kumaran et al., unpub. data). The impact of *L. indentata* on mature trees may be greater than *L. trifida* due to the greater area of leaves available for attack (M. Purcell, pers comm.).

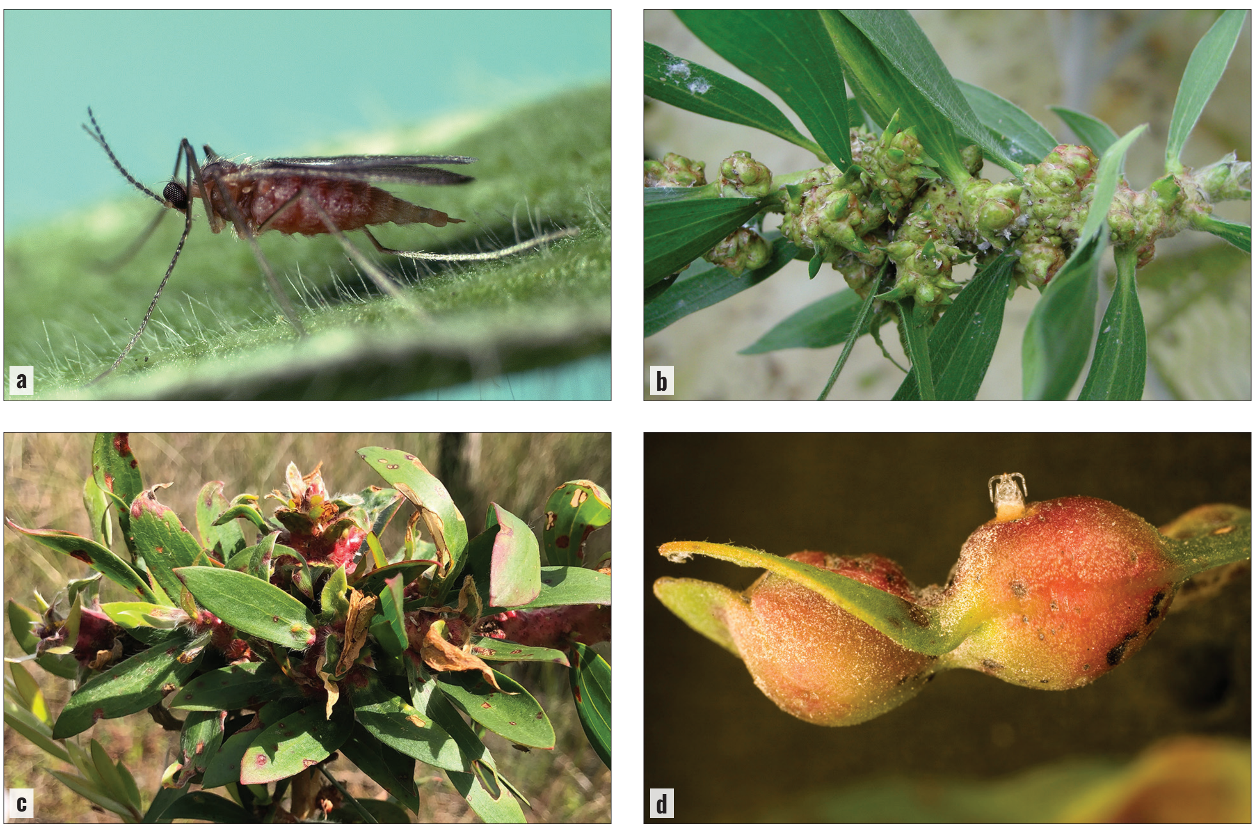

Figure 4. (a) Adult *Lophodiplosis trifida*. Females lay eggs and larvae grow in and emerge from (b) galls that become woody and cease to grow; (c) heavy *L. trifida* galling on melaleuca seedling in Big Cypress National Preserve; (d) an adult *Lophodiplosis indentata* emerges from a leaf pea-gall formed as a response to larval feeding. (a: S. Wineriter-Wright; b: M. Purcell, USDA-ARS Australian Biological Control Laboratory; c: M. C. Smith; d: P. Clark; a,c,d: USDA-ARS)

HOW WELL DID THE INTEGRATED CONTROL PROGRAM WORK?

Measurable impacts of the biological control agents individually and in combination are well documented experimentally (Pratt et al., 2005; Franks et al., 2006; Center et al., 2012; Tipping et al., 2018). *Oxyops vitiosa* attacks the seed-producing plant parts and the new growth, while *B. melaleucae* causes considerable senescence of both young and mature leaves (Franks et al., 2006). *Lophodiplosis trifida* debilitates mature trees, saplings, and seedlings by re-directing resources away from tree growth and reproduction into galls, resulting in plants with 10% less biomass, 10% shorter stature, and 40% lower leaf biomass (Tipping et al., 2016).

Turner et al. (1997) recognized early that large areas of mature trees were unlikely to be suppressed by any one method (chemical, mechanical or biological) given that the biological control agents affected tree reproduction, seedling survival, and growth while chemical and mechanical controls removed large stems effectively but had no effect on plant reproduction. Therefore, a coordinated effort to implement a program of integrated measures began in 1990 with the writing of the Melaleuca Management Plan (Thayer, 1990). The Florida Exotic Pest Plant Council (now the Florida Invasive Species Council) convened various stakeholders to create the Melaleuca Task Force (federal, state, local land managers, scientists, and others) with the goal of developing a comprehensive long-term plan for reducing and managing melaleuca in South Florida (Thayer, 1990). In 2001, The Areawide Management and Evaluation of Melaleuca (TAME Melaleuca) Project was formed and produced a handbook for integrative control of melaleuca utilizing chemical, mechanical, and biological control (Scoles et al., 2006).

The Melaleuca Task Force's objectives, as outlined in 1990, stated that controlling melaleuca would require the full complement of control tactics, including biological control, herbicides, flooding, fire, and mechanical removal (Laroche, 1994). Following this recommendation, the South Florida Water Management District (SFWMD) initiated an aggressive removal campaign focused on the Everglades Water Conservation Areas (WCA) and the Lake Okeechobee marsh. Within seven years, many of the large trees had been removed from several of the WCAs, and the sites were under maintenance control (Laroche, 1994). Manual removal alone, however, would be inadequate to control melaleuca and would need to be followed by herbicide treatment or biological control (Stocker, 1999). The melaleuca biological control insects readily attacked coppicing stumps, seedlings, and saplings, as well as new growth on mature trees (Center et al., 2012). Although areas that do not become reinvaded with melaleuca cannot be specifically attributed to the biological control agents, many of the areas that were mechanically cleared of larger melaleuca trees early on continue to remain essentially free of melaleuca (L. Rodgers, pers. comm.). Also, in areas with formerly dense, mature, melaleuca stands (e.g., Pennsucco, Florida) that were not mechanically cleared, the older trees are now beginning to die due to damage from hurricanes and attack of the biological control agents, and the native understory plants are returning, with few if any new melaleuca seedlings (Rayamajhi et al., 2009; Smith et al., unpub. data). Additionally, the melaleuca biological control agents proved particularly effective at finding and attacking difficult-to-reach melaleuca stands, attacking newly emerged seedlings (which erupt in massive numbers after fire) and reducing subsequent seed production and dispersal (Pratt et al., 2005; Balentine et al., 2009; Center et al., 2012; Tipping et al., 2018) (**Fig. 5a,b**).

Through the combination of tree cutting, herbicide applications, and the impacts of the biocontrol agents, melaleuca coverage in South Florida was reduced from nearly 400,000 ha (988,000 acres) in 2000 to just under 100,000 ha (247,000 acres) in 2015, and likely less in 2021 although this has not been directly measured because it is no longer a management priority (Rodgers et al., 2014; L. Rodgers, pers. comm.). Several invaded areas still have persistent melaleuca populations, but these have not been actively managed for decades. Additionally, areas with melaleuca trees producing seeds can still experience large seedling recruitment events such as those seen in 2018 after the Raccoon Point complex fire in Big Cypress National Preserve (**Fig. 6**). Seedling recruitment events are often very discouraging for land managers, but two separate

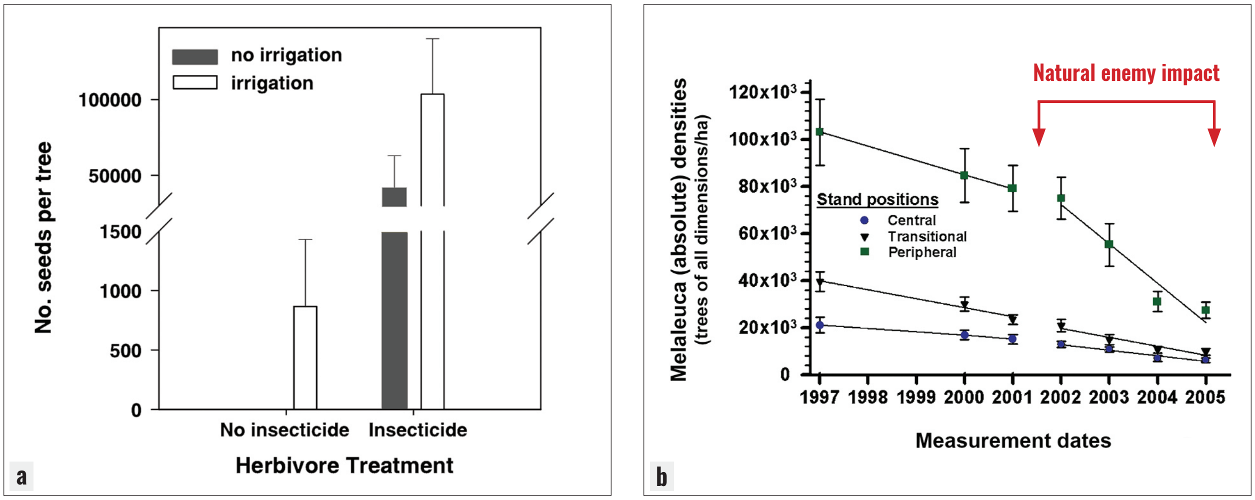

Figure 5. (a) Biological control drastically reduces seed production in mature trees. Due to this and herbivory on seedlings, we observed (b) significant decreases in stem density over time, resulting in (c) recovery of the understory with native species. Significantly lower leaf area also helps to increase light in the understory, which is a more competitive environment for native forbs and grasses. Images 1–4 illustrate transition from a dense melaleuca stand to a forest floor covered by various non-melaleuca plants due to the actions of biological control. (a: modified from Tipping et al., 2008; b: modified from Rayamahji et al., 2007; c: modified from Rayamahji et al., 2013)

experiments, one done before the *L. trifida* release and one done afterwards, illustrate two overarching findings: (1) melaleuca seedlings decline more than 90% over five years even without insect attack and (2) the biological control agents make the surviving seedlings smaller and still non-reproductive at five years after germination (Tipping et al., 2018; Smith et al., unpub. data). In areas where *O. vitiosa* cannot pupate successfully (e.g., persistently wet areas), seedlings are taller and may reach seed-production size (Center et al., 2012). This is due to a lack of persistent herbivory from the weevil. Evidence from post-fire events in these areas suggests that remnant trees are still somewhat reproductive and contribute to the melaleuca seed bank in the soil (Smith et al., unpubl. data). Combining fire with removal of individual remnant trees will likely stop the replenishment of the seed bank at these sites. Research is currently underway to determine if successive burning of these sites and removal of the remnant mature trees will exhaust the seed bank and reduce seedling recruitment events.

Figure 6. A persistent seed bank produces post-fire melaleuca seedlings in excess of 500/m^2. Biological control agents readily attack seedlings (see *Oxyops vitiosa* feeding and *Lophodiplosis trifida* galling damage visible on leaves), which increases mortality and decreases height and biomass. It also impedes the development of seedlings into reproductive trees. (M. C. Smith, USDA-ARS)

BENEFITS OF CONTROL OF MELALEUCA

Melaleuca harmed one of the most imperiled wetland ecosystems in the world, which happens to be next to one of the highest density population centers in the United States. Controlling melaleuca and increasing or restoring ecosystem function in the Everglades have both intrinsic and extrinsic values. For example, laminar water flow over the bed rock is critical for maintaining aquifer recharge and ensuring the safety of municipal water sources (Lockwood et al., 2003). Additionally, millions of people come to south Florida not just for the beaches, but also to visit Everglades National Park, Big Cypress National Preserve, and Arthur R. Marshall Loxahatchee National Wildlife Refuge. The loss in income from lower tourism was estimated in the millions at the start of the TAME melaleuca project. The direct economic costs associated with melaleuca in 2003 were more than $25 million ($39 million in 2022 dollars) (Carter-Finn et al., 2006). Based on the costs of the TAME melaleuca project and the yearly costs of funding the melaleuca biological control project, the total combined costs for biological control development and implementation for melaleuca control were estimated at $7 million. While the benefit-cost analyses for melaleuca biological control vary over time, they range from 2:1 at the start of the project to 40:1 after 15 years (Carter-Finn et al., 2006; McFadyen, 2008). Furthermore, controlling melaleuca with biological control has helped restore an ecosystem badly damaged by human disturbances.

CONCLUSIONS

Melaleuca quinquenervia is often called the 'poster child' for successful integration of biological control into a comprehensive management strategy. Biological control agents were specifically chosen not just for their specificity, but also their mode of attack, point of attack, and potential for integration with other biocontrol agents or with chemical and mechanical removal methods. Melaleuca is still present in several areas within the Greater Everglades Ecosystem, and these stands may create some new small foci of reinvasion, but most areas that received treatment now have healthy populations of native graminoids, shrubs, and forbs. Melaleuca is currently under maintenance management using aerial foliar herbicide application to reduce the stem density of melaleuca on an occasional basis, as needed. Other than prescribed burns, mechanical removal methods such as cutting are rarely used. The last biological control agent approved for release (*L. indentata*) is intended to improve control in the areas where melaleuca has persisted, especially areas where *O. vitiosa* cannot establish.

ACKNOWLEDGMENTS

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