BioControl (2012) 57:151–165
DOI 10.1007/s10526-011-9390-6

Biological control of *Melaleuca quinquenervia*: an Everglades invader

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Received: 8 April 2011 / Accepted: 27 June 2011 / Published online: 29 July 2011

Abstract A massive effort is underway to restore the Florida Everglades, mainly by re-engineering hydrology to supply more water to the system at appropriate times of the year. However, correcting water flow patterns alone will not restore the associated plant communities due to habitat-transforming effects of invasive species, in particular the Australian wetland tree *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtales, Myrtaceae), which has invaded vast areas and transformed sawgrass marshes into dense, biologically impoverished, structurally altered forest habitats. To address this threat, an invasive species reduction program was launched that combined mechanical removal and herbicidal control to remove mature trees with the release of specialized insects to suppress seed production and lower seedling survival. Melaleuca has now been removed from most public lands while biological control has limited its ability to regenerate and reinvade from nearby infestations often located on unmanaged privately held lands. This case illustrates how restoration of highly modified ecosystems may require both restoration of physical conditions (water flow), and suppression of high impact or transformative invaders, showing well the need to integrate biological control into conservation biology.

Keywords Wetlands · Weed biological control · Ecosystem restoration · Transformer species · Herbivory · Florida

Description of the everglades, a threatened ecosystem

Located in a transition zone between temperate and tropical ecosystems (Gunderson 1994), the Florida Everglades is a 500,000 ha subtropical freshwater wetland (Craft et al. 1995), unique in character and stunning in its beauty. With an average water depth of only about 10 cm, it has been described as "a river of grass." Its conservation and preservation has long been a national conservation priority, yet paradoxically it has been ditched, drained and extensively manipulated for water management to serve human needs. It has also been invaded by alien species that are highly damaging to the ecosystem. The Australia tree *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtales, Myrtaceae) is arguably the most important among these because of its power to physically transform the nature of the habitat and adversely affect biodiversity (Austin 1978). Here we describe an integrated control project targeting this tree, which has been conducted within the context of a larger re-engineering project aimed at restoring more natural water flows to the region.

Handling Editor: Roy van Driesche

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The Everglades are part of a larger watershed that originates near Orlando in central Florida, USA and flows through Lake Okeechobee to the southern tip of the peninsula. It now occupies a basin approximately 170 km long by 65 km wide (Rader and Richardson 1992) inclusive of most of the southern tip of Florida. The topography is flat with a slight elevation change from the north to the south of only about 3–5 cm km^{-1} creating a slowly southward flowing system (ca. 0.8 km d^{-1}) emanating from the southern end of Lake Okeechobee and terminating in the mangrove estuaries of Florida Bay (George 2008; Kushlan 1990). It is geologically young with the oldest soils only about 5000 years old (Gleason and Stone 1994). It encompasses one of the largest freshwater marshes on the North American continent and the largest single body of organic soils in the world (Loveless 1959; Stephens 1956). It is composed of a variety of habitats including marshes, sloughs, wet prairies, and tree islands. The global importance of the Everglades is reflected in its designations as an International Biosphere Reserve, a World Heritage Reserve, and a Wetland of International Importance (Maltby and Dugan 1994).

Everglades plant communities contain elements of tropical (primarily Caribbean) and temperate floras, along with numerous endemic species (Gunderson 1994). These communities are largely defined by their hydrology, i.e., the depth and duration of inundation (hydroperiod), which is governed by slight differences in elevation. Sawgrass (*Cladium jamaicense* Crantz), the quintessential Everglades plant community, covers about 70% of the area either as monocultures or intermixed with other emergent species (Loveless 1959). The average hydroperiod for a sawgrass marsh is about ten months, ranging from less than six months to continuous (Lodge 2004). Shallow-water sloughs, which traverse sawgrass marshes, are flooded year round and are dominated by floating and emergent aquatic species. Tree islands (bayheads, willow heads, and cypress heads) are interspersed within a matrix of shorter vegetation, primarily sawgrass prairie (Rader and Richardson 1992). Upland, drier habitats include tropical hardwood hammocks and pinelands (Gunderson 1994).

The climate of the Everglades region is characterized by long, hot, wet summers and mild, dry winters (Rader and Richardson 1992). Historically, Everglades habitats were drier in winter and wetter in summer. Drainage and water conservation programs, however, have largely reversed this pattern by retaining water during dry periods and discharging water through drainage canals during high rainfall events to meet urban and agricultural needs (Rader and Richardson 1992). This has had profound negative effects on the associated flora and fauna and has increased susceptibility to invasion by non-indigenous species (Doren et al. 2009; Duever 2005).

Adjacent urban neighborhoods provide staging areas for the invasion of numerous alien species, both plants and animals, into Everglades systems (Bodle et al. 1994; Cox 1999; Gordon 1998). Over 400 introduced plant species have naturalized in south Florida. As a result, 26% of the 840 plant species in Everglades National Park are not native (LaRosa et al. 1992). While many of these invaders are seemingly benign (see Williamson and Fitter 1996), some are truly transformer species capable of altering the structure and functioning of the afflicted systems (Williamson and Fitter 1996). The Australian tree *M. quinquenervia* is one such example due to its ability to alter ecosystem structure and functioning (Gordon 1998).

Melaleuca: the target invader and its ecological impacts

Melaleuca quinquenervia is native to north-eastern Australia, parts of New Guinea, and New Caledonia. It is a member of a larger group of 10–15 allied broad-leaved species that show evidence of genetic introgression among these species (Barlow 1988; Blake 1968; Brown et al. 2001; Cook et al. 2008). These are often referred to as the "*Melaleuca leucadendra*" complex with a center of diversity in northern Queensland. It has been present in south Florida since the late ninteenth century (Dray et al. 2006), but exhibits substantial genetic heterozygosity and geographic population structuring (Dray et al. 2009). Invasion of natural areas by this tree apparently began soon after the first trees attained seed-bearing size. Dispersal was assisted by nurserymen who are believed to have deliberately spread seeds into natural areas as a cheap and easy means of propagation (Austin 1978; Dray et al. 2006; Meskimen 1962). The US Army Corps of Engineers planted trees in the marshes of Lake Okeechobee during 1938–1941 to create offshore tree islands to protect the southern levee from erosion (Dray et al. 2006). Altered hydrology from flood control and drainage projects during the 1950s undoubtedly contributed to its invasion. Stand coverage proceeds exponentially after initial colonization of suitable habitat (Laroche and Ferriter 1992) so by the late 1990s, it infested about 400,000 ha and the Everglades was at risk of being totally overwhelmed (Laroche 1998).

Although data are scant and some of the putative effects are dubious [e.g., increased transpiration (Allen et al. 1997)], *M. quinquenervia* clearly alters fire regimes, soil elevations, water table depth, surface flows, nutrient mineralization, disturbance regimes, vertical structure of plant communities, recruitment of native species, light availability, and nutrient availability (Gordon 1998; Turner et al. 1998). One of the important impacts of melaleuca has been its effects on Everglades fire regimes. Sawgrass marshes are shallow-water communities that are well adapted to fire. They recover quickly after burning so long as water levels are not too deep and the organic soils do not burn (Kushlan 1990; Lodge 2004). However, *M. quinquenervia*, by virtue of its thick corky bark, also resists fire. Fires fueled by stands of this tree are very different in character from those fueled by sawgrass. In dense *M. quinqueneriva* stands, flames are quickly and explosively carried into the canopy as volatile essential oils in the foliage ignite (Flowers 1991). The resultant fires are extremely hot and often ignite the underlying muck soils, which can burn for weeks. The intense heat kills sawgrass and other native plants that normally survive the cooler ground fires that often occur in sawgrass dominated areas. Fires induce massive seed release from *M. quinquenervia*, which retains seeds in persistent serotinous capsules on branches with individual trees storing as many as nine million viable seeds (Rayamajhi et al. 2002). Burning induces the capsules to open a few days after a fire discharging massive quantities of seeds onto the enriched mineral soil (Wade 1981). Devoid of competition and surface litter, the dense carpets of *M. quinquenervia* seedlings that emerge prevent establishment of other plant species (Wade 1981). These initial recruitment events often evolve into nearly pure stands of mature trees achieving densities of up to 10,000 mature trees ha^{-1} (Rayamajhi et al. 2006b; Rayamajhi et al. 2009) and standing biomasses (dry) of 129–263 MT ha^{-1} (Van et al. 2000). Seeds in the soil can remain viable for up to 2.3 yrs (Van et al. 2005) if conditions for germination are not immediately suitable.

Community transformation by melaleuca in long hydroperiod areas is driven by its ability to accelerate soil accretion. As mentioned above, slight elevation differences determine hydroperiod durations and lead to large differences in plant communities. In contrast, *M. quinquenervia*, once established, is not much affected by hydroperiod (Woodall 1981a). Individual *M. quinquenervia* trees growing in flooded environments produce adventitious 'water' roots surrounding the base of the trunks up to the water line (Gomes and Kozlowski 1980; McJannet 2008; Myers 1983). These directly add to the organic accumulation at the base of the tree while also binding soil and trapping sediments (McJannet 2008). In addition, litterfall adds as much as 4–10 MT year^{-1} to the organic layer in a mature forest (Rayamajhi et al. 2006b). Unlike the subsiding exposed muck soils of reclaimed Everglades marshes (Stephens 1956), this material decomposes slowly (Greenway 1994). Consequently 12–25 MT ha^{-1} of undecomposed organic matter accumulates on the forest floor (Rayamajhi et al. 2010a), leading to increased soil elevation. The mulching effect inhibits germination of native plant seeds while providing a moist substrate for germination of the slow, steady rain of *M. quinquenervia* seeds (Woodall 1982). Seedlings grow best on moist sediments (Myers 1983) so, as the organic layer builds, conditions for recruitment at the periphery become more favorable allowing for expansion of stands, which coalesce with outlying populations and become ever more extensive (Woodall 1981b). Soil accretion inevitably produces shorter hydroperiods over extensive areas thus creating conditions conducive to further invasion. This 'legacy effect' persists long after the trees are removed so that while site rehabilitation may be possible, full restoration to a pre-invasion status may be difficult.

Components of an everglades restoration plan

Alarm over the deterioration of the Everglades led to a widespread desire to preserve and restore the system. Re-establishment of hydrological regimes was widely recognized by engineers as the essential foundation of restoration. However, biologists argued that correcting water flow patterns alone would not restore ecosystem functioning (Weaver 2000) without addressing the invasive species problem (Doren et al. 2009). Chief among these was the need to reduce the effects of *M. quinquenervia*. Accordingly, a task force was assembled during the late 1980s to formulate a plan to reduce infestations of *M. quinquenervia*. This plan included biological control as one component within an overall management strategy (Center et al. 2008; Laroche 1998). The plan called for traditional weed control measures (e.g., herbicide applications and mechanical harvesting) to remove the massive standing biomass and thus eliminate the tree from infested areas. However, anything done to kill the trees caused capsules to desiccate resulting in mass seed releases thus exacerbating the problem. To impede the reinvasion of cleared areas and to slow the rate of spread to new areas, a biological control program was designed with a primary goal of inhibiting stand regeneration.

The high seed production of melaleuca is rooted in several of the plant's characteristics. Saplings are able to produce flowers quite early, within a year or two after germination (Meskimen 1962). Flowers are produced on indeterminate stem tips involving the direct conversion of the stem axis into a flower cluster (Tomlinson 1980). Thus, each stem axis can produce flowers many times, even during the same year (Rayachhetry et al. 1998). Each flowering cluster produces 30–70 persistent capsules and each capsule holds about 250 seeds (Hofstetter 1991). Even though viability is low (7–8%) massive numbers are produced [as many as 51 million seeds on a single mature tree (Rayachhetry et al. 1998)]. While synchronous seed release occurs in response to various stresses, there is also a lighter, continuous seed rain of ca. 40–120 viable seeds m^{-2} d^{-1} (Hofstetter 1991; Rayamajhi et al. 2006b; Woodall 1982).

The biological control program (described below), therefore required agents that could prevent flowering or seed production or increase mortality of seedlings and saplings. Finding agents that attacked stem tips, thus preventing formation of flowers either directly by destroying apical meristems, or indirectly by inhibiting allocation of photosynthate to reproduction, was an early priority of the project. Alternatively, it was posited that attack on the foliage might also reduce seed production by forcing the plant to redirect resources. This seemed plausible because of its leaf characteristics (scelerophyllous, defended with essential oils, and long-lived). The leaves persist 2–4 years (Van et al. 2002) and are therefore assumed to be metabolically costly to produce (Chabot and Hicks 1982; Johnson and Tieszen 1976). This suggested that defoliators might divert resources from reproduction by forcing compensatory foliage production. Sustained defoliation pressure should then deplete carbohydrate reserves and reduce tree performance (Hudgeons et al. 2007; Kosola et al. 2001).

Selection of prospective biological control agents

Faunal surveys

Preliminary surveys to find suitable candidate species for introduction against melaleuca begun in 1986 built upon a brief 1977 survey in Australia and New Caledonia (Balciunas and Center 1991; Habeck 1980). The later surveys were conducted mainly out of Townsville and Brisbane, Queensland. Collaborators at both laboratories were engaged primarily on research of other weeds, so the survey intensity began low and escalated as funding increased. Faunal inventories continue, although at a more-or-less opportunistic level, to this day (2011). The most intensive faunal studies were done from 1989 to 1995 when more than 400 species of plant-feeding insects were recorded from the *M. leucadendra* species complex (Balciunas 1990; Balciunas et al. 1993a, b; 1995a, b, c; Burrows et al. 1994, 1996; Gagné et al. 1997; Gagné and Boldt 1995; Knihinicki and Boczek 2003; Purcell and Goolsby 2005). This large potential pool of candidates was then narrowed down using a variety of filters.

Agent selection

Housecleaning filter

Many of the species associated with *M. quinquenervia* were known generalists, transients, not damaging, or not encountered with enough regularity to be available for study and were therefore of no interest. Several other species had unknown immature stages and were impossible to rear under laboratory conditions and were not further studied. Subsequent observations were made on about 61 species but only 26 species were considered further (Table 1). We voluntarily disqualified one of the most promising species, the defoliating sawfly *Lophyrotoma zonalis* Rohwer (Hymenoptera: Pergidae) when it was discovered that its larvae contained toxins (Oelrichs et al. 1977, 1999, 2001), even though it was fully tested, its host range was sufficiently narrow, and it defoliated large *M. leucadendra* (L.) L. trees in its native range (Buckingham 2001; Burrows and Balciunas 1997). All of the other pergid sawfly species were rejected on the same basis.

Species selected for further consideration were those whose feeding patterns affected the growth of the stem tips or buds. These were expected to reduce flower and seed production either by destroying meristematic tissues or by stressing the plant (e.g., by way of defoliation) forcing it to divert resources to essential but non-reproductive structures (Silvers et al. 2008). Flower feeders were not considered due the difficulty of maintaining a supply of flowers for rearing and testing purposes. Persistence of these species in Australia likely depends on asynchronous flowering of alternate hosts. The intermittent availability of flowers in Florida (Van et al. 2002) suggested that such species would have difficulty persisting.

Host range filter

Subsequent vetting narrowed the list to 15 species, four of which were disqualified as it became apparent that laboratory studies would be unable to clearly define the host range or that critical species might be at risk. The mirid *Eucerocoris suspectus* Distant seemed promising because it attacked new growth causing stem tips to wilt (Burrows and Balciunas 1999), but it was dropped from consideration due to its unacceptably broad host range (Buckingham et al. 2011) despite initial promising results (Burrows and Balciunas 1999). The tube-dwelling moth *Poliopaschia lithochlora* (Lower) seemed an effective defoliator and was of interest because of its preference for wetter habitats (Galway and Purcell 2005). However, it also fed and developed on bottlebrush (*Melaleuca viminalis* (Sol. Ex Gaertner)) (Purcell, unpub. data), a widespread ornamental species in the southern and western US. Likewise, the coreid bug *Pomponatius typicus* Distant was rejected because it readily accepted *M. viminalis* (Burrows and Balciunas 1998). Similarly, the twig girdling weevil *Haplonyx multicolor* Lea has recently been found to utilize *M. viminalis* and *M. citrina* (Curtis) Dum. Cours (another ornamental bottlebrush) as fully as *M. quinquenervia*. It will likely be disqualified.

Four species not rejected based on the above considerations were subsequently released and two remain of interest. Host ranges were validated in field studies for two important species, *O. vitiosa* and *B. melaleucae* after they were released (Center et al. 2007; Pratt et al. 2009). This substantiated the predictive value of the laboratory host range assessments made on these species (Balciunas et al. 1994; Purcell et al. 1997; Wineriter et al. 2003).

Efficacy filter

Ideally, one would release only species able to have a significant effect on the target plant. However, reliable methods for making such predictions have not been developed. From our initial list of species seen in field surveys, only those perceived to be potentially effective based on field, laboratory and glasshouse observations of damage to vital plant tissues were considered for intensive investigation. Departing from suggestions in recent literature (e.g., McClay and Balciunas 2005), we placed emphasis on which plant tissues agents damaged rather than just agent *per capita* consumption of plant tissue. Observations of mortality in glasshouse plants were also important in electing high priority species. However, agent selection in this program was an exercise in “adaptive management” inasmuch as knowledge gained after the release of the first of these agents shaped later decisions. As the established suite of introduced agents grew, we used direct observation of their effects to guide choice of additional agents, with the hope of developing a guild of agents with complementary biologies in terms of the timing of their effects, plant parts damaged, and habitat choice (especially habitat hydrology).

Although some insecticide exclusion studies were done in Australia (the native range) (Balciunas and Burrows 1993), they failed to simulate a realistic biological control scenario wherein only a select few species (as opposed to dozens of species, including generalists, that are limited by parasitoids) would

Table 1 Prospective biological control agents from the complete faunal inventory (Balciunas et al. 1995b)

Order: Family	Candidate species	Feeding guild	Disposition
Released			
Coleoptera: Curculionidae	**Oxyops vitiosa* Pascoe	Leaf feeder	Released 1997; established; effective
Diptera: Cecidomyiidae	**Lophodiplosis trifida* Gagné	Stem galler	Released 2008; established; effective
Diptera: Fergusoninidae	**Fergusonina turneri* Taylor	Bud galler	Released 2005; failed to establish
Hemiptera: Psyllidae	**Boreioglycaspis melaleucae* Moore	Sap feeder	Released 2002; established; effective
Testing underway			
Diptera: Cecidomyiidae	**Lophodiplosis indentata* Gagné	Leaf galler	Host range studies initiated
Homoptera: Pseudococcidae	*'*Sphaerococcus*' *ferrugineus* (Froggatt)	Bud galler	Unable to colonize in quarantine, but still of interest
Lepidoptera: Nolidae	**Chora plana* Warren	Defoliator	Of interest; difficult to rear
Tested-non specific			
Coleoptera: Cerambycidae	Sub-family Strongylurini	Stem borer	Unable to colonize; field host range unsuitable
Coleoptera: Curculionidae	**Haplonyx multicolor* Lea	Twig girdler	Imported; unsuitable host range; difficult to rear
Hemiptera: Coreidae	**Pomponatius typicus* Distant	Sap feeder	Unsuitable host range
Hemiptera: Miridae	**Eucerocoris suspectus* Distant	Sap feeder	Imported; unsuitable host range
Lepidoptera: Noctuidae	*Characoma vallata* (Meyrick)	Flower feeder and tip binder	Unsuitable host range (*Eucalyptus*)
Lepidoptera: Pyralidae	**Poliopaschia lithochlora* (Lower)	Defoliator	Unsuitable host range (ornamental *Melaleuca* spp.)
Low efficacy or potentially toxic			
Hemiptera: Cicadellidae	*Hishinomus melaleucae* (Kirkaldy)	Sap feeder	Not damaging
Hemiptera: Eurymelidae	*Ipo conferata* Kirkaldy	Sap feeder	Not damaging
Hemiptera: Eurymelidae	*Ipoides melaleucae* Evans	Sap feeder	Not damaging
Hymenoptera: Pergidae	*Acanthoperga cameronii* (Rohwer)	Defoliator	Possibly toxic
Hymenoptera: Pergidae	**Lophyrotoma zonalis* (Rowher)	Defoliator	Contains toxins; disqualified
Hymenoptera: Pergidae	*Pergagrapta* sp.	Defoliator	Possibly toxic
Hymenoptera: Pergidae	*Pterygophorus insignis* Kirby	Defoliator	Unsuitable host range; possibly toxic
Lepidoptera: Pyralidae	*Syntonarcha irastis* Lucas	Flower feeder	Insufficient information; damage questionable
Lepidoptera: Tortricidae	*Strepsicarates semicanella*	Flower feeder and tip binder	Insufficient information; damage questionable
Unable to colonize			
Coleoptera: Cerambycidae	**Rhytiphora* spp.	Stem borer	Unable to rear pending artificial diet

Table 1 continued

Order: Family	Candidate species	Feeding guild	Disposition
Diptera: Cecidomyiidae	**Lophodiplosis bidentata* Gagné	Tip galler	Unable to colonize
Lepidoptera: Gracillaridae	*Acrocercops* sp.	Leaf miner	Not damaging; difficult to rear
Lepidoptera: Xyloricidae	*Clerarcha poliochyta* Turner	Stem borer and leaf feeder	Unable to rear

Species designated with an asterisk (*) were ranked highly for further evaluation

attain higher than normal population levels in habitats similar to those likely to be encountered in Florida. Indeed, the most abundant species in that study appeared to be generalists, such as white-flies (Homoptera: Aleyrodidae) and scale insects (Homoptera: Coccoidea). None of the species that proved ultimately to be of greatest interest were represented. While this demonstrated some vulnerability of the plant to herbivory, it did little to aid in the selection of prospective candidates.

Limited efficacy trials shown in laboratory studies done in Australia did not eliminate potential agents from further evaluations, but demonstrations of substantial impact were used to prioritize insects for introduction into US quarantine facilities. These included the two gall midges *Lophodiplosis trifida* Gagné and *Lophodiplosis indentata* Gagné. The former species was released and appears to be very effective (pers. obs.) and the latter species is under study in quarantine.

Climatic filters

Climatic filters proved of limited value in selecting agents because of the restricted native and adventive ranges of *M. quinquenervia* and the climatic similarity between the two areas (coastal Queensland and southern Florida).

Agents released

Five biological control agents have been released against melaleuca in Florida: the weevil *Oxyops vitiosa* Pascoe, the psyllid *Boreioglycaspis melaleucae* Moore, the gall fly *Fergusonina turneri* Taylor (along with a mutualistic nematode *Fegusobia melaleucae* Davies & Giblin Davis), and the gall midge *Lophodiplosis trifida* Gagné.

The melaleuca weevil

The weevil *O. vitiosa* (Coleoptera: Curculionidae) was released in 1997 (Center et al. 2000). It had been highly ranked because of its ability to defoliate young foliage and kill stem tips (Balciunas et al. 1994; Center et al. 2000), thus potentially reducing the reproductive potential of *M. quinquenervia*. Also, populations attained high densities in the native range despite high rates of parasitism. Foliage and flowering were markedly reduced on trees persistently attacked by this weevil in Australia (Purcell and Balciunas 1994). However, its behavior of pupating in the soil suggested it might be limited to sites with short hydroperiods. Oviposition occurs on emerging buds of actively growing tips. Early instars feed on the youngest, expanding leaves while older larvae exploit progressively older, but mainly immature, foliage. Larvae coat themselves with a slimy defensive secretion that contains essential oils sequestered from the host plant (Montgomery and Wheeler 2000; Wheeler et al. 2003). Fully grown larvae drop from the tree and enter the soil to pupate. Pupation occurs in a spherical cocoon covered with soil particles. Larvae that drop from the trees at inundated sites usually drown.

The melaleuca psyllid

The psyllid *B. melaleucae* was of interest because it seemed unaffected by hydroperiod. It was elevated in rank when it erupted as a pest of the trees grown in greenhouses in Australia (Purcell, pers. obs.), which suggested that populations were highly regulated by natural enemies and would benefit from "enemy release". It was released in Florida during 2002 (Center et al. 2006). Females oviposit on leaves or stems. All stages are free-living but late instars usually remain in one spot, possibly by attaching and feeding through stomata. It is a sap-feeder and completes its life cycle entirely on the plant (Purcell et al. 1997).

The gall fly and nematode

The mutualistic nematode, *Fergusobia melaleucae*, and gall fly *Fergusonina turneri*, induce galling of vegetative and reproductive tissues (Davies and Giblin-Davis 2004; Giblin-Davis et al. 2001a, b, 2004; Taylor 2004). These two species were ranked highly because of their potential to terminate stem growth and reduce flowering. Together, they form multi-chambered galls that compromise both vegetative and reproductive meristems, thereby curtailing growth of stems and reproduction of the plant. Flies deposit juvenile nematodes while inserting their eggs into vegetative and reproductive buds. Nematodes initiate gall formation inducing hypertrophied plant tissue before the fly eggs hatch. The fly maggots then feed on the primed nutrient-rich tissues while presumably inducing further enlargement of the galls. Meanwhile, the parthenogenetic nematodes produce a second sexual generation. The mated female nematodes invade the hemocoel of fully grown female (3rd instar) fly larvae. They produce juveniles that invade the rudimentary ovaries of pupating female flies. The adult fly then emerges from the gall with juvenile nematodes in her ovaries. All female flies contain nematodes, which are deposited in buds during oviposition allowing the cycle to begin anew. Molecular analyses of related *Melaleuca* species and host range studies demonstrated extreme host fidelity of both species (Scheffer et al. 2004; Ye et al. 2007). They were released in south Florida beginning in 2005 and temporarily colonized release sites, but disappeared completely after about three generations. The more recent release and establishment of another gall former, the midge *Lophodiplosis trifida* Gagné (see following section), precluded the need for further efforts with this pair of organisms. Nonetheless, this is the first time that a mutualistic combination of two agents has been approved and attempted for use in a weed biological control program.

The gall midge

The stem-galling midge *L. trifida* (Diptera: Cecidomyiidae), in contrast to *O. vitiosa*, prefers wet, humid conditions (Purcell et al. 2007; Wineriter Wright and Center 2008). It was released during 2008 and has established widely (Pratt, pers.obs.). Females oviposit on leaf, stem, and bud surfaces (Wineriter Wright and Center 2008). Larvae penetrate actively growing tissue and form galls on young shoots (Purcell et al. 2007). The lignified multilocular galls (Gagné et al. 2009) were expected to compromise stem elongation, distort growth, and reduce flower production.

Impact of released agents on target plant

Predictions made concerning efficacy

The leaf weevil *O. vitiosa* was expected to establish at drier sites, attack new growth, and defoliate stem tips, thereby forcing allocation of photosynthate towards refoliation and reduce flowering (Purcell and Balciunas 1994). Adults were thought to be capable of moving from adjacent dry sites to trees in inundated areas, possibly in sufficient numbers to become damaging, but populations were not expected to persist in permanently wet habitats. Larvae require young foliage (Purcell and Balciunas 1994; Rayamajhi et al. 2006a; Wheeler 2001) so we predicted abundance to be affected by the phenology of the plant because young foliage became available mainly during winter and spring (Van et al. 2002). Some data also suggested that plant chemotype could be limiting (Dray 2003; Dray et al. 2004; Wheeler 2006).

The psyllid *B. melaleucae* completes development entirely on the host plant (Purcell et al. 1997) so it was expected to establish over a broader range of habitat types, including permanently flooded areas (Wineriter et al. 2003). It was also thought to be less sensitive to tree chemotype than *O. vitiosa* (Chiarelli et al. 2011; Wheeler and Ordung 2005). Large populations were expected to develop quickly, forcing psyllids to feed on stems as well as young and mature foliage (Wineriter et al. 2003) causing premature leaf drop and mortality of smaller plants. However, high temperatures and possibly rainfall seemed detrimental so it was thought that summer conditions might be limiting (Chiarelli et al. 2011).

The gall fly *F. turneri* (with the nematode *Fergusobia quinquenerviae*) was expected to infest flower and stem buds and curtail flowering and stem elongation. Galls were also expected to act as moderately powerful metabolic sinks (Goolsby et al. 2000). It was anticipated that galling of meristems would pre-empt stem elongation and inhibit flowering.

The stem gall midge *L. trifida* was expected to infest seedlings and small saplings, curtailing growth, sometimes leading to the death of small plants (Purcell et al. 2007). It also seemed capable of galling stem tips of young shoots on mature trees (Purcell, pers. obs.) possibly reducing seed production. It was expected to establish quickly if plants with suitable tips were present. However, it was thought that it would be confined to low-growing seedlings and saplings and lower branches of trees because of its need for high humidity, being found mainly in low-lying areas near the ground in its native range (Purcell, pers. obs.). It was also thought to prefer young growth and thereby likely to be influenced by host phenology, becoming most abundant during winter and spring (Purcell et al. 2007; Van et al. 2002).

Post-release validation of efficacy

Oxyops vitiosa established readily at dry and seasonally wet sites but establishment failed at permanently flooded sites (Center et al. 2000). It dispersed relatively slowly (Pratt et al. 2003) but is now widely distributed (Balentine et al. 2009) and even occurs in the Bahamas (Pratt et al. 2008). Populations increased at rates comparable to other effective weed biological control agents but were influenced by availability of young shoots (Pratt et al. 2002, 2004). Damage to the stem tips virtually eliminated flowering and seed production (Pratt et al. 2005; Tipping et al. 2008). However, the accompanying defoliation caused buds to erupt at other times of the year thus extending feeding opportunities. Coppicing from stumps was severely curtailed, especially when the adventive rust fungus (*P. psidii* G. Wint.) also infected the shoots (Rayamajhi et al. 2006a, b). Growth of saplings was dramatically reduced and termination of apical growth produced a bushier habit (Tipping et al. 2008). However, larvae became abundant mainly during winter and spring coincident with seasonal production of young foliage (Center et al. 2000). This allowed some ‘escape’ at other times of the year. After attainment of large populations, weevils regularly moved into flooded sites causing significant damage. Although many fully grown larvae drowned, some managed to find pupation sites allowing small populations to persist (Center, pers. obs.). There is no evidence from field studies that chemotype influenced their abundance or distribution (Tipping & Pratt, unpub. data). A common garden study suggested that Florida plants were not less resistant to herbivory than Australian plants (Franks et al. 2008a, b).

The psyllid *B. melaleucae* established quickly (Center et al. 2006) and dispersed rapidly throughout the range of *M. quinquenervia* in Florida. Enormous populations developed during the spring dry season in all habitat types but populations declined during the summer rainy season. This was probably more of an effect of high temperatures rather than of precipitation (Chiarelli et al. 2011). Psyllids caused high mortality of seedlings and premature leaf drop from mature trees (Franks et al. 2006; Morath et al. 2006). Mortality of coppicing stumps also increased in conjunction with infestations of *O. vitiosa* and the rust (Center et al. 2007; Rayamajhi et al. 2010b). Populations spread at a rate of approximately 7 km year^{-1} and are now widely distributed (Balentine et al. 2009). Melaleuca psyllids have recently been found on *M. quinquenervia* in Puerto Rico, more than 1600 km from the nearest known release (Pratt et al. 2006).

The gall fly/nematode mutualistic pair (*Fergusonina turneri*/*Fergusobia quinquenerivae*) failed to establish. Rearing was difficult so only small numbers were available for release. Galls imported from Australia were heavily parasitized and produced insufficient numbers for large releases. Establishment temporarily occurred at one site but numbers progressively dwindled and disappeared after about three generations.

The stem-galling midge *L. trifida* was initially released at 24 sites distributed throughout southern Florida in *M. quinqueneriva* stands of varying sizes and hydrology. Both small and large numbers of individuals were used in an attempt to determine an optimal release strategy. Establishment was universally successful (Pratt, unpub. data). Areas where *M. quinquenervia* stands were regenerating from seed or coppicing stumps were heavily galled with a high percentage of the plants being killed, possibly due to interactions with fire or frost. While galls occurred most abundantly in the lower strata, near ground level, they were also found as high as 13 m in the upper canopy (Pratt & Rayamajhi, unpub. data). Dispersal is occurring at a rate estimated to be 20 km year^{-1} (Pratt, pers. obs.).

Adventive species not deliberately released

An adventive rust fungus (*Puccinia psidii* G. Winter) was discovered infecting young leaves of *M. quinqueneriva* in Florida during spring 1996 (Rayachhetry et al. 1997). It was initially most common during flushes of new foliage but became more prevalent at other times after the introduction of *O. vitiosa*. This was thought to be related to the non-seasonal production of new foliage induced by defoliation, which extended the time that innocula remained present.

Interaction of biological control with other management efforts

The processes followed in the successful implementation of a biological control program for *M. quinquenervia* serve as a model for future and existing biological control projects. Achievable goals were set at the beginning of the project after extensive consultation with all relevant stakeholders. Progress was maintained through continued consultation with these stakeholders and their committed investment in this project. A thorough inventory of all potential agents throughout the native range of *M. quinquenervia* in Australia was compiled and agents for further study were prioritized through a tiered screening process as outlined above. Comprehensive demographic studies in both the native and introduced range confirmed that curtailing seed production was the key to controlling invasive *M. quinquenervia*. Agents chosen for release specifically addressed this criterion and proved to be very effective at reducing the reproductive capacity of this tree resulting in reductions in flowering, seed production, foliage, seedling recruitment, stand densities and tolerance to fire and herbicide treatment. Importantly, although some minor transitory feeding occurred on non-target plants growing adjacent to melaleuca trees, no significant non-target damage has occurred. The reduced control measures required to arrest the invasiveness of this tree as well as the restoration of native plants in ecosystems previously invaded by *M. quinquenervia* (Rayamajhi et al. 2009) is testament to the success of this project.

Biological control, however, was not expected to remediate infestations of mature *M. quinquenervia* trees over large areas. The total biomass at these sites has been estimated at 129–263 MT ha^{-1}, most of which is wood (Rayachhetry et al. 2001; 2008; Van et al. 2000). Even if insects had killed these large trees, tremendous quantities of standing biomass would remain to be removed or left to decay. Therefore, removal of large stands was accomplished using herbicidal treatments and/or mechanical harvesting (Silvers et al. 2007). As a result, lands held by the South Florida Water Management District have been largely cleared through the prodigious efforts of extremely effective contractors (Laroche 1998). The combination of biological, herbicidal, and mechanical control efforts has yielded an Everglades Protection Area that is now largely free of *M. quinquenervia*. The original infestions, which occupied over 200,000 ha, have been reduced to about 110,000 ha most of which are on private lands (Ferriter et al. 2008; Silvers et al. 2007).

Infestations adjacent to cleared sites previously provided seed sources for reinvasion and were often inaccessible to land managers. The character of the trees has changed, however, due to the chronic herbivory that they now experience. They are now much less invasive (Tipping et al. 2009). Insecticide exclusion studies (done prior to the establishment of *L. trifida*) showed decreases in tree density following recruitment after a fire and greatly reduced seed production. Saplings grow more slowly, attain smaller stature, and develop a bushier habit with a much reduced canopy (Tipping et al. 2008). The trees are more susceptible to natural and manmade disturbances (e.g., frost, fires, and herbicide treatments). Herbivory also now interferes with the ability of the trees to recover from such disturbances. Overall control efforts in areas cleared by the South Florida Water Management District have been reduced to maintenance activities and biological control has assisted by making this a much more manageable situation.

In 2001, the USDA/ARS established The Area-wide Management and Evaluation of *M. quinquenervia* (TAME Melaleuca) to facilitate the landscape level adoption and integration of biological control with conventional control tactics (Silvers et al. 2007). The TAME Melaleuca program was primarily an outreach effort, which culminated in a series of training workshops and field tours that were held at demonstration sites throughout southern Florida. Field tours facilitated the side by side comparison of various conventional control tactics when integrated with biological control as well as areas impacted solely by the introduced insects. Representatives responsible for invasive species control efforts on >1.4 million acres from >40 public agencies, private companies and non-governmental organizations attended the events. In addition, over two million biological control agents (*O. vitiosa* and *B. melaleucae*) were redistributed throughout the melaleuca infested regions of the state to augment their natural dispersal and promote biologically based management on private lands. Information produced during the lifetime of the TAME Melaleuca project is archived electronically (http://tame.ifas.ufl.edu/) as a lasting resource on sustainable melaleuca management for land and resource managers.

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