8 Australian Paperbark Tree (Melaleuca)

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PEST STATUS OF WEED

The exotic tree *Melaleuca quinquenervia* (Cav.) Blake (commonly referred to as melaleuca or paperbark tree) aggressively invades many south Florida ecosystems (Fig. 1), including the Everglades (Hofstetter, 1991; Bodle *et al.*, 1994). It was introduced during the early 1900s or late 1800s (Gifford, 1937; Meskimen, 1962; Dray, pers. comm.). *Melaleuca quinquenervia* displaces native vegetation, degrades wildlife habitat, creates fire hazards, and causes human health problems (Morton, 1962; Diamond *et al.*, 1991). Florida state laws enacted in 1990 and 1993 prohibit the sale, cultivation, and transportation of *M. quinquenervia.* It was placed on the United States Department of Agriculture's Federal Noxious Weed List in 1992 (Bodle *et al.*, 1994; Laroche, 1994).

Although *M. quinquenervia* is a major pest in south Florida, it is considered threatened in its native Australia. Therefore, conservation groups in Australia advocate its protection. *Melaleuca quinquenervia* habitat in Australia comprises low-lying, high-rainfall areas, primarily in coastal regions (Resource Assessment Commission, 1992). Most of the remaining and remnant *M. quinquenervia* woodlands in Australia are located on private land, where clearing for commercial development continues.

Nature of Damage

Economic damage. *Melaleuca quinquenervia* flowers several times a year producing large amounts of pollen, allegedly a mild respiratory allergen (Morton, 1962; Lockey *et al.*, 1981; Stanaland *et al.*, 1986), from which as much as 20% of the population may suffer allergic reactions (Diamond *et al.*, 1991). In addition, *M. quinquenervia* trees burn with extremely hot crown fires due to high foliar concentrations of essential oils. These fires are difficult to extinguish, often threatening buildings near *M. quinquenervia*-infested areas and causing local municipalities to incur additional fire fighting costs (Diamond *et al.*, 1991).

Melaleuca quinquenervia infested areas become less attractive and monocultures become impenetrable to tourists, hikers, boaters, and other recreational users. Such impacts result in decreased revenues for parks and harm the economies of surrounding communities that rely on tourism associated with wilderness areas (Diamond *et al.*, 1991).

Ecological damage. Prolific seed production, tolerance of brackish water, flooding, and fire enable *M. quinquenervia* to aggressively invade various wetland habitats and diminish the value of these habitats for native plant communities and associated wildlife (Meskimen, 1962; Crowder, 1974; Myers, 1975; Hofstetter, 1991). *Melaleuca quinquenervia* may accelerate loss of groundwater due to increased evapotranspiration (Alexander *et al.*, 1977), although this view has been challenged (Allen *et al.*, 1997). Trees produce allelopathic chemicals (Di Stefano and Fisher, 1983), which may enhance their ability to displace native flora. *Melaleuca quinquenervia* invasion has resulted in significant (60 to 80%) losses of biodiversity in freshwater herbaceous marsh communities in south Florida (Austin, 1978).

Extent of losses. The extent of the *M. quinquenervia* infestation in southern Florida (the area south of Lake Okeechobee) has been estimated at 0.20 to 0.61 million ha of the total 3.04 million ha (7 to 20% of the total) in the region (Bodle *et al.*, 1994). It has been suggested that many of the remaining natural areas within this region will be overtaken by uncontrolled growth of *M. quinquenervia* within 30 years (Bodle *et al.*, 1994).

The National Park Service, the U.S. Fish and Wildlife Service, the U.S. Army Corps of Engineers, and the South Florida Water Management District repeatedly conduct costly and labor-intensive operations to control *M. quinquenervia*. Mechanical removal of a moderately thick stand (about 988 trees/

Figure 1a.

Figure 1b.

Figure 1c.

Figure 1. *Melaleuca quinquenervia* in Florida: (a) Flowering sapling representing early invasion stage in seasonally flooded habitat; (b) A well-established mature stand in a permanently flooded sawgrass habitat in the Everglades, note the tree stand is surrounded by sawgrass; (c) Vertical section of a stand in seasonally flooded site in the Everglades. (Photographs by M. Rayamajhi and W. Durden.)

ha) cost $2,080/ha (McGehee, 1984), whereas ground herbicide treatment using tree injection techniques cost $1,330/ha (Laroche *et al.*, 1992). Aerial treatments are less expensive but less effective and cause more damage to non-target plant species. Additionally, seed release is accelerated among trees stressed by herbicides and new infestations are created by dispersal of these seeds (Laroche and Ferriter, 1992). This regeneration of treated stands necessitates repeated herbicidal applications, which compromises environmental preservation. According to a recent estimate, the South Florida Water Management district alone spent more than $13 million from 1991 to 1998 for *M. quinquenervia* control in water conservation areas, Lake Okeechobee, and Loxahatchee Wildlife Refuge (Laroche, 1999). Millions of dollars also have been spent by other agencies such as Loxahatchee National Wildlife Refuge, Big Cypress National Preserve, Everglades National Park, Lee County, Miami-Dade County, and Palm Beach County.

Melaleuca quinquenervia trees benefit Florida's beekeeping, chip, mulch, lumber, and pulp industries. However, *M. quinquenervia* honey is less valuable than that from fruit tree sources. Furthermore, access to *M. quinquenervia* infestations limits commercial utilization. Failure to control expanding *M. quinquenervia* infestations would result in an estimated loss of $168.6 million/year in revenue from reduced ecotourism of the Florida Everglades (Schmitz and Hofstetter, 1999).

Geographical Distribution

Native range. *Melaleuca quinquenervia* is the southern-most member of the *M. leucadendra* complex. It is distributed within a 40-km-wide zone along Australia's northeastern coast from Sydney in New South Wales to the tip of Cape York peninsula in northern Queensland; in New Guinea; and in New Caledonia (Fig. 2) within the range of 11 to 34° S latitude (Boland *et al.*, 1987). Its altitudinal range is from sea level to about 100 m, sometimes up to 165 m (Boland *et al.*, 1987). It occurs in coastal wetlands that are at least seasonally inundated, such as freshwater swamps, stream banks, and in brackish water behind mangrove swamps. The center of diversity for the *M. leucadendra* complex is on the Cape York Peninsula in northern Queensland (Turner *et al.*, 1998). Barlow

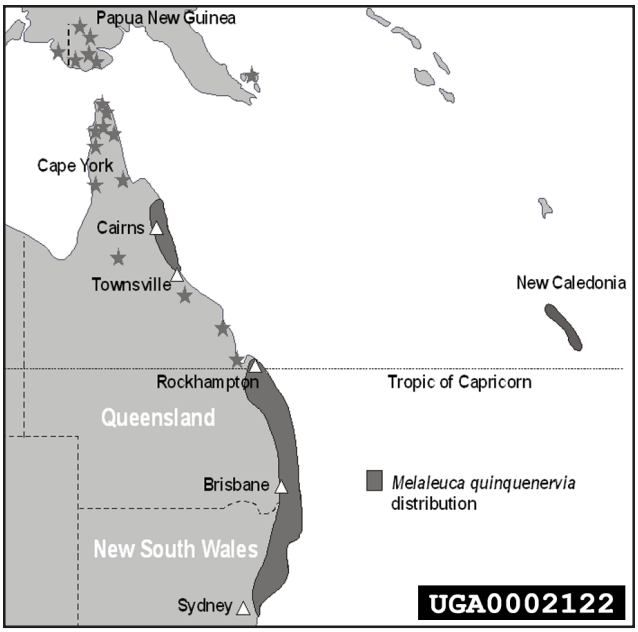

Figure 2. *Melaleuca quinquenervia* distribution in Australia and neighboring islands. Solid black colors and stars represent continuous and relatively isolated *M. quinquenervia* forests, respectively. (Map by D. Johnston.)

(1988) noted the genus *Melaleuca* to be of northern Australian (tropical) origin, with the high diversity in temperate areas representing a secondary area of species radiation.

Florida. The main infestations of *M. quinquenervia* exist along both coasts of southern Florida with scattered infestations in between (Fig. 3). The northernmost records (ca. 30° N latitude) are in Gainesville (Turner *et al.*, 1998).

BACKGROUND INFORMATION ON PEST PLANT

Taxonomy

The taxonomic position of *M. quinquenervia* according to Cronquist (1988) is as follows: class Magnoliopsida (Dicot), subclass Rosidae, order Myrtales, family Myrtaceae, subfamily Myrtoidea, tribe Leptospermae, genus *Melaleuca,* species *quinquenervia* (Cav.) Blake. Synonyms include *M. leucadendra* L., *M. viridiflora* var. *angustifolia* (L.f.) Byrnes, *M. viridiflora* var. *rubiflora* Brong. and Gris., and *Metrosideros quinquenervia* Cav.

Linnaeus coined the genus name *Melaleuca* (Greek *melas* = black and *leucos* = white), probably in reference to the fire-charred white bark (Holliday, 1989). The genus contains at least 219 and perhaps more than 250 species (Craven and Lepschi, 1999) and is the third largest angiosperm genus in Australia (Barlow, 1986). *Melaleuca quinquenervia* is a member of the *M. leucadendra* (L.) L. group, 15 species that are mostly large shrubs or trees and occur primarily in northern and northeastern Australia (Boland *et al.*, 1987; Craven, 1999).

Biology

Holliday (1989) and Bodle *et al.* (1994) describe *M. quinquenervia* as being erect trees up to 25 m tall with multi-layered, thick white or grayish papery bark that insulates the trunk and branches. Leaves are lanceolate-elliptical to oblanceolate with five prominent longitudinal veins; up to 3 cm broad and 10 cm long; and flat, stiff, and leathery when mature. In general, woody biomass constitutes a major portion (83 to 96%) of dry weight across habitats (non-flooded, seasonally flooded, and permanently flooded), with the remaining portion (4 to 17%) being comprised of foliage and seed capsules (Rayachhetry *et al.*, 2001).

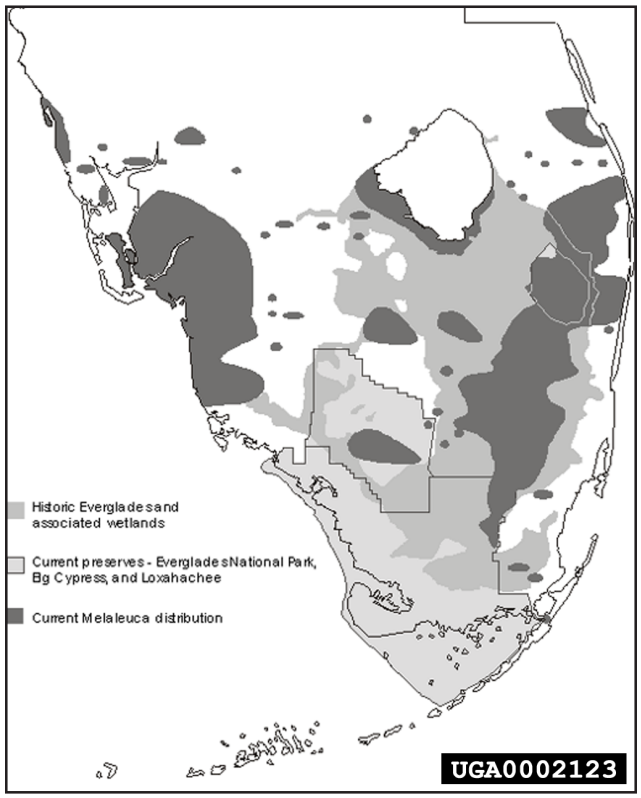

Figure 3. *Melaleuca quinquenervia* distribution in Florida. Note stand concentrations along east and west cost of central and south Florida and scattered stands in between. (Map by D. Johnston.)

In Florida, some *M. quinquenervia* trees become reproductive within a year of germination, and flowering events occur several times a year (Meskimen, 1962). Inflorescences are indeterminate, 2 to 5 cm long, and arranged in bottlebrush-like spikes (Holliday, 1989). Flowers are white or cream colored, with tripartite ovaries surrounded by five sepals. Five petals surround 30 to 50 stamens, and a pistil. Capsular fruits are persistent, arranged in the series of clusters, and may remain attached to the trunks, branches, or twigs for several years (Meskimen, 1962). In Florida, a flower spike can produce 30 to 70 sessile capsules (Meskimen, 1962). In excess of seven linearly occurring capsule clusters (each separated by series of leaves) have been recorded from *M. quinquenervia* branches (Rayachhetry *et al.*, 1998). Seed capsule biomass (dry weight) on trees in permanently flooded habitats is two-fold greater compared to seasonally flooded habitats (3 to 4% vs. 2% of total biomass). These serotinous capsules release seeds when their vascular connections are disrupted by increased bark thickness or stresses such as fire, frost, mechanical damage, herbicide treatments, or self-pruning of branches (Woodall, 1982; Hofstetter, 1991). The canopy of a mature tree (38 cm diameter at breast height and 12 m height) may hold up to 1.4 kg of seeds (about 56 million seeds) (Rayachhetry, unpub. data). While massive, synchronous seed release occurs in response to various stresses, some capsules open successively in a non-synchronous manner, resulting in a light but constant seed rain (Woodall, 1982; Hofstetter, 1991). In Florida, capsules contain 200 to 350 seeds each (Meskimen, 1962) and each seed weighs ca. 25 g (Rayachhetry, unpub. data). Only about 15% of the canopy-held seeds in Florida are filled (embryonic). Overall, about 9% of seeds are viable and 7% can germinate, suggesting that ca. 2% remain dormant (Rayachhetry *et al.*, 1998). Enforced dormancy under field conditions is suggested by the fact that a small proportion of buried seeds remain germinable for more than two years (Van, unpub. data). Forest fires reduce competition, prepare ash-enriched forest floors, and promote establishment and rapid growth of seedlings, provided the soil remains wet and the canopy is open. Seed germination occurs in both shade and sun, as well as under submerged conditions (Meskimen, 1962; Lockhart, 1995). However, prolonged submergence (six to 12 months) and fire can kill smaller seedlings (Myers, 1975; Woodall, 1981).

Because of the massive seed release from mother trees, extremely dense (more than 250,000/ha of 3- to 4 m-tall trees) *M. quinquenervia* stands are common (Hofstetter, 1991; Van *et al.,* 2000). Standing biomass of 129 to 263 metric ton/ha has been reported for *M. quinquenervia* in the United States and Australia (Van *et al.,* 2000). *Melaleuca quinquenervia* is fire adapted (Stocker and Mott, 1981; Ewel, 1986). It has layers of thick, spongy bark; dormant epicormic buds on trunks that regenerate new shoots; and is capable of sprouting from roots (Turner *et al.*, 1998).

Analysis of Related Native Plants in the Eastern United States

The Myrtaceae is a large, diverse plant family with approximately 100 genera and 3,000 species worldwide (Stebbins, 1974). It is almost entirely tropical in distribution. The group achieves maximum diversity in Australia, where several hundred species are known, but it is also quite diverse in the New World tropics. The family was formerly divided into two groups (the Myrtoideae and Leptospermoidae) based upon characteristics of the fruit. The Myrtoideae, which are centered in tropical America, produce berries whereas the Leptospermoideae, which are centered in Australia, produce serotinous capsules. Eight indigenous species of Myrtoideae occur in the continental United States and Florida (Tomlinson, 1980), including the genera *Eugenia*, *Calyptranthes*, *Psidium*, and *Myrcianthes,* commonly referred to as "stoppers." Some species such as red stopper (*Eugenia rhombea* Krug and Urban) and long-stalked stopper (*Psidium longipes* [Berg] McVaugh) are rare and considered endangered. All native Florida species are threatened by loss of habitat to development. At least 30 non-native species of *Eugenia* (*sensu latu*), as well as species in other Myrtoideae genera, are cultivated in Florida for their edible fruits and for ornamental uses (Menninger, 1958). Besides *M. quinquenervia*, about 56 additional *Melaleuca* species have been imported to Florida, of which at least 16 and 14 species were common in California and Florida, respectively, during the first decade of the 20th century (Dray, pers. comm.). Current status of these additional *Melaleuca* species in both states is not known. No native species of Leptospermoideae occur in North America. Besides *Melaleuca*, the only representatives of Leptospermoideae present in Florida are a few species of Australian native *Callistemon* (bottlebrush, some of which have been recently transferred to the

genus *Melaleuca*). These have been widely planted as landscape ornamentals.

HISTORY OF BIOLOGICAL CONTROL EFFORTS IN THE EASTERN UNITED STATES

Area of Origin of Weed

Australia is clearly the center of origin for the genus *Melaleuca,* but a few tropical species within this genus extend into New Guinea, New Caledonia, Malaysia, and Burma (Holliday, 1989; Craven, 1999). The *M. leucadendra* group consists of broad-leaved *Melaleuca* species, including *M. quinquenervia* and 14 closely related species (Craven, 1999). This group is widespread along the eastern coast of Australia, from Sydney to Cape York. It also occurs in New Caledonia and the southern parts of Papua New Guinea and Irian Jaya (Blake, 1968). In Australia, *M. quinquenervia* is more common in the southern part of its range, mainly growing along streams and in swamps (Holliday, 1989), or in seasonally inundated, low-lying areas. Five separate sources (Nice, France; Ventimiglia, Italy; Tamatave, Madagascar; Sydney, Australia; and Burringbar, Australia), mostly botanical gardens or plantations, have been identified for the *M. quinquenervia* seeds that were introduced into Florida (Dray, pers. comm.).

Areas Surveyed for Natural Enemies

Preliminary surveys to locate biological control agents for *M. quinquenervia* were conducted in New Caledonia and southeastern Queensland in 1977 (Habeck, 1981). The United States Department of Agriculture, Australian Biological Control Laboratory (USDA ABCL), started a long-term exploration program in 1986. Surveys have been conducted from south of Sydney in New South Wales, along the eastern seaboard of Australia, to Cape Flattery in northern Queensland. Searches for biological control agents on other broad-leaved *Melaleuca* spp., closely related to *M. quinquenervia*, also were conducted near Darwin in the Northern Territory, and in southern Thailand. During November 1999, several species in the *M. leucadendra* complex were surveyed for pathogens in southern and northern Queensland and northeastern New South Wales in Australia. A number of microorganisms have been found associated with *M. quinquenervia* in Florida and in Australia.

Natural Enemies Found

More than 450 plant-feeding insect species have been collected from *M. quinquenervia* in Australia, and an additional 100 species have been collected from closely related *Melaleuca* spp. (Balciunas *et al.*, 1994a, 1995). Of the major herbivores (Table 1), seven species have been intensively studied, but only five have been introduced into domestic quarantine facilities. Only the melaleuca snout beetle (leaf weevil), *Oxyops vitiosa* Pascoe, and the melaleuca psyllid, *Boreioglycaspis melaleucae* (Moore), have been released. The bud gall fly, *Fergusonina* n. sp. Malloch, is currently undergoing host range testing. The melaleuca defoliating sawfly, *Lophyrotoma zonalis* (Rohwer), is being tested for vertebrate toxicity. The mirid bug *Eucerocoris suspectus* Distant and the tip wilting bug, *Pompanatius typicus* Distant, though very damaging (Burrows and Balciunas, 1999) were found to be insufficiently host specific for introduction. Other insects, including a leaf-galling cecidomyiid (*Lophodiplosis indentata* Gagné), several flower-feeding tortricids (*Holocola* sp., *Thalassinana* species group), and the tube-dwelling pyralid moth *Poliopaschia lithochlora* (Lower), are currently undergoing preliminary host range testing in Australia.

Previously, a few fungal species had been reported from *M. quinquenervia* and its allies in Florida, Australia, and some other parts of the world (Alfieri *et al.*, 1994; Rayachhetry *et al*., 1996ab, 1997). Four additional fungal species (*Fusarium* sp., *Pestalotiopsis* sp., *Phyllosticta* sp., *Guignardia* sp.) have recently been found to be associated with *M. quinquenervia* and its close relatives in Australia (Rayachhetry, unpub. data).

Host Range Tests and Results

Three herbivorous insect species (*O. vitiosa*, *L. zonalis*, and *B. melaleucae*) have been subjected to intensive host specificity tests. These host range studies have shown *O. vitiosa, L. zonalis,* and *B. melaleucae* to be specific to *M. quinquenervia*. Small amounts of feeding and development through only one generation in the laboratory were found on a few test plant species, mostly *Callistemon* spp. (Balciunas *et al.*, 1994b; Buckingham, 2001; Center *et al.,* 2000;

Table 1. Insects under Investigation for Biological Control of *Melaleuca quinquenervia*

Scientific Name	Unofficial Common Name	Impact/Current Research Status
Agents Released and Established		
Oxyops vitiosa (Coleoptera: Curculionidae)	Snout beetle	Foliage on growing branch tips grazed; tip dieback/field impact evaluation
Boreioglycaspis melaleucae (Hemiptera: Psyllidae)	Melaleuca psyllid	Foliage and stems wilt, saplings killed; quarantine studies completed
Agents Introduced into U.S. Quarantine		
Lophyrotoma zonalis (Hymenoptera: Pergidae)	Melaleuca defoliating sawfly	Complete defoliation of trees; quarantine studies completed, found to be host specific and vertebrate toxicity testing underway
Fergusonina sp. (Diptera: Fergusoninidae)	Bud-gall fly	Floral and vegetative buds galled; growth and reproduction retarded; further quarantine studies underway
Eucerocoris suspectus (Hemiptera: Miridae)	Leaf-blotching bug	Young foliage blotched and distorted resulting in leaf drop; attacks bottlebrushes; dropped from further consideration
Agents under Evaluation in Australia		
Holocola sp., Thalassinana species group (Lepidoptera: Tortricidae)	Inflorescence axis borer	Flower buds aborted; immature flowers and foliage damaged
Lophodiplosis indentata (Diptera: Cecidomyiidae)	Pea-gall fly	Young foliage distortion
Careades plana (Lepidoptera: Noctuidae)	Defoliating noctuid	Stem and branch defoliation
Paropsisterna tigrina (Coleoptera: Chrysomelidae)	Defoliating chrysomelidae	Stem and branch tip defoliation
Poliopaschia lithochlora (Lepidoptera: Pyralidae)	Tube-dwelling moth	Shoots webbed; defoliated
Agents with Questionable Specificity or are Poorly Known		
Pomponatius typicus (Hemiptera: Coreidae)	Tip-wilting bug	Wilting of stem and branch tips; rejected due to low host specificity
? *Acrocercops* sp.(Lepidoptera: Gracillariidae)	Leaf blister moth	Young foliage mined and blistered
Haplonyx multicolor (Coleoptera: Curculionidae)	Flower weevil	Damage of flowers and foliage
Cryptophasa spp. (Lepidoptera: Oecophoridae)	Branch fork moth	Defoliation; weakening of branch forks
Rhytiphora sp.(Coleoptera: Cerambycidae)	Stem boring longicorn beetle	Branches and stems killed
Pergaprapta sp. (Hymenoptera: Pergidae)	Gregarious sawfly	Defoliation of growing branch tips
*Acanthoperga cameroni*i (Hymenoptera: Pergidae)	Sapling sawfly	Defoliation of growing branch tips, especially of saplings

Wineriter and Buckingham, 1999). However, extensive field studies in Australia determined that *Callistemon* spp. are not host plants of *O. vitiosa, L. zonalis,* or *B. melaleucae* (Balciunas *et. al*., 1994b; Burrows and Balciunas, 1997; Purcell *et al.,* 1997). Currently, federal authorities are preparing biological and environmental assessments for the field release of *B. melaleucae*. Australian host range studies have demonstrated that the bud-gall fly, *Fergusonina* sp., also is highly specific to *M. quinquenervia* and it is undergoing further host specificity testing at the quarantine facilities in Florida.

Botryosphaeria ribis (a canker fungus) and *Puccinia psidii* (a rust fungus) were evaluated in south Florida as potential *M. quinquenervia* biological control agents. *Botryosphaeria ribis* appeared to be a plurivorous pathogen (Smith, 1934) that attacked stressed plants (Punithalingham and Holiday, 1973; Rayachhetry *et al.*, 1996c,d), while *P. psidii* attacked vigorously growing *M. quinquenervia* branch tips (Rayachhetry *et al.*, 1997) and had a host range restricted to the family, Myrtaceae (Rayachhetry *et al*., 2001b).

Releases Made

Of the five insects imported into Florida quarantine, only *O. vitiosa* and *B. melaleucae* have been released (Center *et al.,* 2000). Adults and/or larvae of *O. vitiosa* were released during spring 1997 at both permanently and seasonally flooded habitats. By winter 2000, more than 47,000 adults and 7,000 larvae had been released at more than 97 locations in south Florida. *Oxyops vitiosa* established at all but the permanently flooded sites. Even small releases of 60 adults successfully produced viable populations when site conditions were favorable (Center *et al.,* 2000). However, populations have dispersed slowly. Ease of establishment and slow dispersal suggested an optimal introduction strategy of numerous small releases at carefully selected but widely dispersed sites. Currently, the distribution of *O. vitiosa* is limited compared to the vast area occupied by *M. quinquenervia*. Therefore, concerted establishment and redistribution efforts are ongoing to ensure the widespread colonization of *M. quinquenervia* in south Florida. *Boreioglycaspis melaleucae* was first released during Spring 2002 but it is not yet certain whether populations have established.

BIOLOGY AND ECOLOGY OF NATURAL ENEMIES

Oxyops vitiosa (Coleoptera: Curculionidae)

Oxyops vitiosa larvae prefer to feed on relatively new foliage (Fig. 4a), while adults feed on both young (Fig. 4b) and old (Fig. 4c) foliage. The resultant damage stunts growth of saplings and reduces foliage production in older trees. Larvae are most damaging, feeding on one side of a leaf through to the cuticle on the opposite side, which produces a window-like feeding scar (Fig. 4a). This damage may persist for months, ultimately resulting in leaf drop (Fig. 5). Adult feeding on young and mature leaves is characterized by holes (Fig. 4b) and narrow scars along the leaf surfaces (Fig. 4c), respectively. Oviposition occurs mainly during daylight hours from September to March in Florida (Center *et al*., 2000). Eggs are laid singly, or in small clusters, on the surface of young leaves, usually near their apex, or on stems of young shoots. A hardened black-to-tan coating of frass and glandular materials covers individual eggs. In Florida, larvae are absent or uncommon from April to August unless damage-induced regrowth is present (Center *et al*., 2000). Pupation occurs in the soil, usually beneath the host plant. Egg-to-adult development requires about 50 days. Females survive up to 10 months and can produce more than 1,000 eggs. Adults can be collected year round.

Boreioglycaspis melaleucae (Homoptera: Psyllidae)

The melaleuca psyllid, *B. melaleucae*, severely damages *M. quinquenervia*, especially in the absence of its predators and parasites. Nymphs are parasitized by *Psyllaephagus* sp. (Hymenoptera: Encyrtidae) and preyed on by coccinellids (Coleoptera) and lygaeids (Hemiptera) in Australia. This psyllid was collected in northern and southeastern Queensland and northern New South Wales during field surveys in Australia. Collection records also exist for Western Australia and the Northern Territory. Psyllids, both adults and nymphs, reportedly feed on phloem sap through the stomata (Clark, 1962; Woodburn and Lewis, 1973); however, nymphs cause the most damage by inducing defoliation and sooty mold growth on excreted honeydew. Populations of *B. melaleucae*

Figure 4a.

Figure 4b.

Figure 4c.

Figure 4. *Oxyops vitiosa* on *Melaleuca quinquenervia*: (a) Two larvae and typical larval feeding damage on a twig tip, note feeding scars on young leaves; (b) Adults aggregated on young tips, note typical adult feeding holes on young leaves; (c) Note an adult and feeding scars on fully mature leaves at the tip of a twig. (Photographs by W. Durden and G. Buckingham.)

Figure 5. Severely defoliated (bare twigs) upper crown of *Melaleuca quinquenervia* trees. Such branch defoliation and twig dieback is caused by severe larval and adult feeding damages. (Photograph by T. Center.)

grow rapidly, causing moderate leaf curling, discoloration, defoliation, and plant mortality.

Adults of *B. melaleucae* mate throughout the day and the male grasps the female with large abdominal claspers (parameres) before mating. Females oviposit on leaves or stems of host plants and lay an average of 78 eggs. Each egg is attached to the leaf by a pedicel that is inserted into the plant tissue to absorb water (White, 1968). Most eggs hatch within 18 days. Nymphs of *B. melaleucae* congregate on leaves and secrete white, flocculent threads, which can completely cover the nymphs. These secretions facilitate easy detection at field sites. Like all psyllids, *B. melaleucae* has five instars (Hodkinson, 1974) and development from egg to adult takes 28 to 40 days. Purcell *et al.*, (1997) present a complete biology of *B. melaleucae*.

Lophyrotoma zonalis (Hymenoptera: Pergidae)

The defoliating melaleuca sawfly, *L. zonalis*, was the most damaging insect observed on *Melaleuca* spp. in Australia. It was collected from Mackay in central Queensland to the Daintree River in north Queensland, and near Darwin in the Northern Territory. Records also indicate its presence in New Guinea (Smith, 1980). Larvae are voracious leaf feeders and dense populations cause complete defoliation. Defoliation stresses trees and reduces flowering during subsequent years (Burrows and Balciunas, 1997). Adults do not feed on the plant tissue. They are frequently observed swarming around the bases of trees.

Larvae burrow into the papery bark of *M. quinquenervia* to pupate, unlike many other pergid sawflies that pupate in soil. It therefore should be an excellent agent for use in wetter areas, where other agents are less effective. Females are parthenogenic, producing all males when unmated, while mated females produce both males and females.

Burrows and Balciunas (1997) provide a detailed description of the life history of *L. zonalis*. The life cycle from egg to adult takes approximately 12 weeks. Females insert eggs into the tissue along the edges of leaves using their saw-like ovipositors. The subsequent egg batches form a line along the leaf margin, and harden and turn brown with age. Females oviposit up to 140 eggs in their lifetime, which are heavily parasitized in Australia. The neonate larvae feed gregariously, forming a feeding front across the leaf; later instars become solitary feeders. Three unidentified fly species (Diptera: Tachinidae) and one wasp species (Hymenoptera: Ichneumonidae) parasitize larvae. The final instar, or prepupa, does not feed and burrows into the bark of the trunk and lower branches to excavate a chamber in which it enters the pupal stage. In Australia, *L. zonalis* is mainly found during the summer months and a resting, possibly diapausing, prepupal stage occurs during winter. Larval outbreaks also occasionally occur during cooler months.

The toxic peptides lophyrotomin and pergidin, which have been reported in three other sawflies from around the world (Oelrichs *et al.*, 1999), have recently been detected in *L. zonalis* larvae (Oelrichs, pers. comm.). Consumption of large quantities of larvae of a related sawfly from *Eucalyptus* sp. causes cattle mortality in Australia, although *L. zonalis* has never been implicated in livestock or wildlife poisonings (Oelrichs *et al.*, 1999). Therefore, the decision to release *L. zonalis* in Florida awaits assessment of the risk of this insect to wildlife and livestock.

Fergusonina sp. (Diptera: Fergusoninidae)

The *M. quinquenervia* bud-gall fly, *Fergusonina* sp., forms galls in vegetative and reproductive buds of *M. quinquenervia* in a unique, mutualistic association with nematodes of the genus *Fergusobia* Currie (Nematoda: Tylenchida: Sphaerulariidae). Preliminary data indicate that the nematode initiates gall production (Giblin-Davis *et al*., 2001). *Fergusonina* sp. have been reared from most broad-leaved *Melaleuca* spp. in Australia, although the flies on each plant species appear to be unique (Taylor, pers comm.). Galls on *M. quinquenervia* vary greatly in size and color, depending on growth stage and type of buds being attacked, and on developmental stage of the gall. They have the potential to impede branch and foliage growth, and retard flower formation resulting in reduced seed set. These galls also may act as nutrient sinks, reducing plant vigor (Goolsby *et al.*, 2000). However, the gall production is seasonal, with highest densities occurring during periods of maximum leaf bud production, usually during winter and spring (Goolsby *et al.,* 2000). The flies are heavily parasitized by several species of parasitic Hymenoptera in Australia.

Botryosphaeria ribis (Pleosporales: Botryosphaeraceae)

Grossenbacher and Duggar (1911) first described *B. ribis* from currants (*Ribes* sp.) in New York. Taxonomy, biology, and ecology of this fungus are discussed in Punithalingam and Holliday (1973), Morgan-Jones and White (1987), and Rayachhetry *et al.* (1996a). It belongs to a group of fungi that produce conidiospores (asexual spores) in stromatic pycnidia and/or ascospores in ascomata on the surface of stems, leaves, and fruits. The mode of entry into stem tissues is assumed to be through wounds, frost-induced cracks, sun-scorched bark, lenticels, or branch stubs. Stems of healthy plants callus rapidly, and the fungus may remain latent under the callus tissues, causing perennial cankers when trees are stressed. Stems and branches of stressed trees are girdled quickly due to the plants' inability to callus and compartmentalize the fungus. Infected plants may die back, show vascular wilt, or crown thinning. Affected vascular tissues usually appear brown to black in color (Rayachhetry *et. al*., 1996d).

Puccinia psidii (Uredinales: Pucciniaceae)

Puccinia psidii, commonly known as guava rust, has been reported on 11 genera and 13 species in the family Myrtaceae in Central America, Caribbean Islands, and South America (Laundon and Waterston, 1965; Marlatt and Kimbrough, 1979). In 1996, *P. psidii* was found to attack healthy new growth of *M. quinquenervia* (Rayachhetry *et al.*, 1997). Figueiredo *et al.,* (1984) studied the life cycle of *P. psidii* on *Syzygium jambos* (L.) Alston, and reported three spore stages (uredospore, teliospore, and

basidiospore) in its life cycle. Only uredinial pustules have been observed on *M. quinquenervia* in Florida, but other stages also may exist. No alternate host has been discovered and it is assumed to be autoecious (Figueiredo *et al.*, 1984). Guava rust attacks both foliage and succulent stems of vigorously growing *M. quinquenervia* saplings. Rust disease on *M. quinquenervia* is usually severe during winter and spring. Severe infections cause foliage distortion, defoliation, localized swellings on twigs, and tip diebacks (Rayachhetry *et al*., 2001b).

EVALUATION OF PROJECT OUTCOMES

Establishment and Spread of Agents

Oxyops vitiosa is now established at many locations in south Florida where larvae or adults were released; however, rate of spread is limited (Center *et al.,* 2000). Slowly expanding *O. vitiosa* populations now exist in Dade, Broward, Lee, Collier, Palm Beach, Martin, Monroe, Sarasota, and Glades Counties. Habitats with short hydroperiods, dry winter conditions, and abundant young foliage favor growth and development of *O. vitiosa*. *Oxyops vitiosa* populations did not establish in permanently aquatic sites because of the soil requirement for pupation (Center *et al.,* 2000). Dispersal occurs more rapidly at sites where the trees are scattered savannah-like in open areas. Other factors such as geographical location, hydroperiod, wind direction, life stage released, or date of release do not affect the rate of overall dispersal (Pratt, unpub. data). Also, adults seem to move from unsuitable trees (tall, dense stands with a paucity of young foliage) onto trees that provide acceptable foliage (smaller, bushier, open-grown trees with an abundance of young foliage) (Center *et al.,* 2000).

Suppression of Target Weed

Oxyops vitiosa adults feed on both old and new foliage as well as on emerging vegetative and reproductive buds (Fig. 4). Early instars feed only on young succulent foliage, while late instars are less discriminating (Fig. 4a). Adults feed on both young and mature leaves (Figs. 4b, c). Severe adult or larval feeding results in tip dieback and defoliation (Fig. 5). Repeated damage of growing tips removes apical dominance and induces lateral growth from axillary buds. Subsequent new growth acts as a nutrient sink and sustains continual adult and larval weevil populations. Foliar damage, and the subsequent diversion of photosynthetic resources to the development of new foliage, appears to limit reproductive performance of *M. quinquenervia*. In preliminary studies, flowering of severely damaged *M. quinquenervia* trees was reduced more than 90%, (Pratt, unpub. data).

Repeated defoliation weakens the trees' defense mechanisms, predisposing them to attack by other insects and pathogens. As a result, existing populations decline as their regenerative capabilities become reduced. The diverse community of insects that damage *M. quinquenervia* in Australia probably suppresses the regenerative potential of native melaleuca forests. For example, the number of seed-capsules per unit of infructescense length is three and eight capsules/cm in Australia and Florida, respectively. Similarly, the viability (9.1 vs. 3.3%) and germinability (in 14 days, 7.8 vs. 2.8%) of *M. quinquenervia* seeds are significantly higher in the United States than in Australia. The reduction in seed production, and thus the invasibility of *M. quinquenervia*, is the primary objective of the biological control program. While removal of existing stands may be best accomplished by other means (herbicides and mechanical removal), a reduction in canopy seed production through biological control should enhance the efficacy of the overall management program (Laroche, 1999).

Recovery of Native Plant Communities

The diversity and abundance of native plant species in areas invaded by *M. quinquenervia* should begin to recover as *M. quinquenervia* canopies open due to crown thinning and/or tree mortality resulting from feeding by biological control agents. Long-term monitoring programs have been initiated by establishing permanent plots in *M. quinquenervia*-infested sites to document such events in dry, seasonally inundated, and aquatic habitats.

Economic Benefits

The containment and/or elimination of *M. quinquenervia* monocultures should produce economic benefits by sustaining the tourist industry, permitting the recovery of native flora and fauna, decreasing the risk to human health, and reducing the fire hazard to urban areas near highly flammable *M. quinquenervia* stands.

RECOMMENDATIONS FOR FUTURE WORK

Currently, the *M. quinquenervia* biological control program is focused on procuring additional biological control agents. Additional quarantine space is needed to improve and accelerate host testing of additional agents. Construction of a new facility designed for this purpose began at Fort Lauderdale during December 2001. The primary focus of the Fort Lauderdale Invasive Plant Research Laboratory has been the release of new agents as they become available, and the evaluation of those agents that establish. To combat the *M. quinquenervia* invasion and successfully reduce its impact, state and federal agencies will need to (1) continue foreign exploration for new biological control agents, with special emphasis on those that will complement the effects of existing agents; (2) continue to evaluate host specificity and efficacy of promising agents; (3) import selected agents into quarantine for further evaluation; (4) accelerate release programs through development of efficient testing facilities and reduction of avoidable delays; (5) develop a thorough understanding of the biology and ecology of the host as well as the candidate biological control agents, both in Florida and Australia, to enhance agent selection and subsequent establishment; (6) acquire necessary permits for field release of the bud-gall fly into *M. quinquenervia* populations in south Florida; (7) continue to monitor field populations of established agents and redistribute them to new locations as needed; and (8) monitor the impact of released agents at individual plant, community, and landscape scales.

Because *M. quinquenervia* is a large perennial tree, the effect of biological control agents likely will be slow and cumulative over an extended period of time. In addition to *O. vitiosa*, and *B. melaleucae* which have already been released, other insects are either waiting for field-release permission or undergoing evaluation in Australia or in U.S. quarantine. Therefore, evaluation of the performance of released agents in the field and their relationship with predators and pathogens in Florida should continue with special emphasis on (1) measuring changes in the reproductive potential of existing trees and monitoring for signs of population decline and habitat recovery; (2) assessing the impact of predators, parasitoids, and pathogens on the released biological control agent populations; (3) monitoring other plant species to validate host specificity research and determine whether non-target effects occur; and (4) developing and integrating selected fungal agents into the suite of herbivorous biological control agents.

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