A review of the taxonomy, biology, harmful and beneficial values, distribution and control of *Melaleuca quinquenervia* in Florida

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Abstract

Melaleuca (*Melaleuca quinquenervia* (Cav.) S.T. Blake) is a large tree, which occurs naturally throughout eastern Australia, New Caledonia, Irian Jaya and southern New Guinea. In North America, melaleuca is widely invasive in south Florida and primarily infests the Florida peninsula south of Lake Okeechobee. It is classed as a Federal Noxious Weed in the United States and as a prohibited aquatic plant and Noxious Weed in the state of Florida. In the continental United States, melaleuca is also found in Louisiana, Texas, California, and Georgia. Additionally, this tree has become moderately invasive in Hawaii. Melaleuca rapidly invades moist, open habitats, both disturbed and undisturbed, and forms dense, impenetrable forests. In general, invasion is less prominent on forested sites than marshes, however only dense hammock-type communities seem to produce enough shade to prevent invasion. Invasive characteristics of melaleuca include its evergreen habit, prolific seed production, frequent flowering and flood and drought tolerance. This tree threatens biodiversity of native flora and fauna by diminishing the value of their habitat. The large expanses of melaleuca on public lands have cost public agencies in Florida $25 million in control efforts between 1989 and 1999. Estimations of economic impacts of melaleuca on recreation, tourism, fires, loss of endangered species, and more range from $168 million annually to $2 billion over a period of 20 years.

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Various methods of control (chemical, mechanical/manual, biological and integrated) are evaluated.

Key words: Melaleuca quinquenervia, exotic invasive plant, herbicides, biological control

1. Names

Melaleuca quinquenervia (Cav.) S.T. Blake; bottlebrush tree, broad-leaved paperbark, cajeput, melaleuca, niaouli, paper-bark, punk tree (Craven 1999, Godfrey and Wooten 1981, Holliday 1989, Long and Lakela 1971, Nelson 1994). Synonymy: *Melaleuca leucadendron* (L.) L. misapplied (Wunderlin 1998). Myrtaceae, myrtle family.

2. Taxonomic Discussion

In the family Myrtaceae, about 130 genera and 3,000 species have been identified (Stebbins 1974, Watson and Dallwitz 1992). The family is found in temperate, sub-tropical, and tropical regions, however, it is chiefly centered in Australia and tropical America (Watson and Dallwitz 1992). The family Myrtaceae is comprised of trees and shrubs with simple, mostly entire, evergreen, opposite or rarely alternate leaves (Long and Lakela 1976). The plants in this family are noted for their spicy, aromatic odor caused by ethereal oils and the presence of numerous stamens (Gentry 1993, Tomlinson 1980, Zomlefer 1989). All of the genera, with slight variations, have the same basic theme for the flower branch. The flower branch has the same morphology as the vegetative shoot, with opposite pairs of leaves at each node and leaves at successive nodes at right angles to each other (Tomlinson 1980). Two subfamilies have been distinguished in the family Myrtaceae: Leptospermoideae and Myrtoideae (Tomlinson 1980). Leptospermoideae has dry fruit, woody capsules and alternate leaves. Myrtoideae, in contrast, has fleshy fruit (berry) and opposite leaves.

The family Myrtaceae is found naturally in the eastern United States only in subtropical Florida (Tomlinson 1980). Zomlefer (1989) has listed 8 genera and 18 species in the Myrtaceae family as being Florida representatives. These genera are Eugenia, Melaleuca, Rhodomyrtus, Calyptranthes, Myrcianthes, Psidium, Myrtus, and Syzygium. Additional genera found in Florida, both introduced, are Eucalyptus and Callistemon (FDEP 1994, Nelson 1994). Both of the subfamilies, Leptospermoideae and Myrtoideae, exist in Florida (Tomlinson 1980). Melaleuca is in the subfamily Leptospermoideae, which are generally thought of as "Old World" plants. The main center of these "Old World" plants is in Australia where they occur naturally (Tomlinson 1980).

3. Description and Account of Variation

(a) Physical Description

Melaleuca is a large, evergreen tree, to 33 m tall, with drooping, irregular branches. It has a slender, much branched, somewhat columnar crown. **Bark** is thick, spongy, whitish at first, exfoliating in pale cinnamon-colored, papery layers giving it a very distinctive appearance. Layers can be easily pulled apart. The bark comprises approximately 15 to 20% of its stem volume. **Leaves** are mostly 4 to 12 cm long, simple, narrowly elliptic to lanceolate-elliptic with the principal veins parallel. Leaves are very short petiolate, arranged in 5 spiral rows. Blades are first densely pubescent, becoming glabrous with age. Leaf color is dull green on both surfaces and dotted with reddish punctuations. Distinctly aromatic. **Flowers** are crowded in terminal spikes or panicles of spikes on woody axes. Stamens are especially numerous in 5 bundles opposite the petals, and conspicuous giving the inflorescence a “bottle-brush” appearance. Sepals, 5, are about 2 mm long, obtuse. Petals, 5, are 3 to 5 mm long, white, obovate to orbicular, 3 to 4 mm long. **Fruits** are 3 to 5 mm long, short cylindrical to squarish, woody capsules, dehiscing within and below the thick circular rim of the floral tube. **Seeds** are many, reddish brown and somewhat lustrous, asymmetric, long angular, vary in shape and size within a single capsule, 0.5 to 1 mm long. Description based on Chiang and Wang 1984, Godfrey and Wooten 1981, Langeland and Burks 1998, Long and Lakela 1976 and Woodall 1982.

(b) Distinguishing Features

The Melaleuca genus is characterized from others in the Family Myrtaceae by the possession of the following combinations of features (Craven 1999): “Shrubs or trees; leaves spiral, decussate or ternate, small to medium-sized, the venation pinnate to parallel; flowers in spikes or clusters or sometimes solitary, the basic floral unit being a monad, dyad or triad; sepals 5 (rarely 0); petals 5; hypanthium fused to the ovary in the proximal region only; stamens few to numerous, the filaments fused for part of their length into 5 bundles, the anthers dorsifixed (or rarely basifixed) and versatile with two parallel cells that open via longitudinal slits; ovary 3-celled, the ovules few to numerous; fruit a capsule within an usually woody to subwoody fruiting hypanthium; seeds with a thin testa, generally obovoid-oblong to obovoid, unwinged, the cotyledons planoconvex to obvolute.”

The tropical and subtropical tree species in the Melaleuca genus have collectively become known as the *Melaleuca leucadendra* group, or the broad–leaved paperbarks. Within the fifteen species included in the *Melaleuca leucadendra* group, Craven 1999, further characterizes *Melaleuca quinquenervia* as separate species through the following key features: “Calyx lobes present; staminal filaments glabrous; hypanthium distinctly hairy; leaf blade indumentum without lanuginulose or sericeous-lanuginulose hairs (the hairs sericeous, sericeous-pubescent or pubescent); *and* inflorescence up to 30 mm wide; inflorescence more than 20 mm wide; calyx lobes herbaceous in the proximal-central zone and scarious in a broad marginal band; leaves 1.3 to 9.7 times as long as wide; older leaves with the secondary venation more or less obscure *or* inflorescence more than 30 mm wide; young shoots with at least some spreading-ascending to spreading hairs; hypanthium 1.5 to 2.5 mm long; petals 2.5 to 3.5 mm long; inflorescence axis pubescent."

(c) Intraspecific Variation

Hofstetter (1991) speculated that there were genetic differences among the melaleuca present in Florida. He based his belief on melaleuca's ability to invade so many different habitats. The genetic differences may have originated from the first prominent introductions of melaleuca seeds released in the early 1900's, or, even if the seeds were genetically identical, new ecotypes may have become established in the two main subregions of Florida (southeast and southwest). His observations of phenotypic plasticity of the trees in Florida included melaleuca's architectural adaptations to sun and shade and the considerable range of soil conditions in which it grows. It appears that Hofstetter's assumptions of the genetic differentiation of melaleuca in Florida may have been correct. Recent greenhouse and laboratory studies have since demonstrated phenotypic and genetic variation in melaleuca (Laroche 1999, Kaufman 1999, 2001, Wheeler et al. 2002).

Greenhouse garden experiments conducted by Kaufman (1999) indicated genetic differences among four south Florida melaleuca populations. It was speculated that the small genetic differences among populations might enable individuals to perform somewhat better under particular environmental conditions and that the phenotypic plasticity of the species may be even more important for adaptation under highly variable field conditions, such as varying water levels and pH. Kaufman (1999) also found that the genetic differences for several traits seemed to follow a "latitudinal gradient, with leaf width and plant height increasing, from south to north [Florida]." Kaufman's (2001) next greenhouse garden experiment went even farther to confirm Hofstetter's earlier theory of genetic variation and phenotypic plasticity. The author compared seedlings grown from seeds collected from three Australian, two east Florida and two west Florida populations of melaleuca. Overall, Australian had more among-population variation than Florida. This was thought to be due to longer time for evolutionary change in Australia. However, the Australian populations had less phenotypic plasticity than Florida, possibly due to founder effects in Florida or due to "subsequent adaptive evolution of phenotypic plasticity in Florida populations."

Other scientists have conducted laboratory experiments, which have shown that 1) population differentiation is present among Florida's melaleuca populations based on early results of isozyme analysis (Laroche 1999) and 2) there are different melaleuca chemotypes that have distinct terpenoid profiles (Wheeler et al. 2002).

Based on the above greenhouse and laboratory analyses, phenotypic plasticity seems to play an important role in the adaptability of Florida's melaleuca populations with genetic differences also possibly aiding performance. Good scientific information, which helps to define the genetic and phenotypic differences of melaleuca, both in Florida and Australia, is extremely important in developing new control techniques for this species.

4. Economic Importance

(a) Detrimental Effects

Melaleuca is an aggressive, invasive weed in South Florida (Bodle et al. 1994, Laroche 1999). The massive loss of habitat contributed to melaleuca in southern Florida (peninsular area south of Lake Okeechobee) has been estimated as 0.2 to 0.61 million hectares of a total 3.04 million hectares (Bodle et al. 1994). These authors also suggested that many remaining natural areas will be overtaken by uncontrolled growth of melaleuca within 30 years. Laroche (1999) reported that the melaleuca control costs for the South Florida Water Management District alone for the time period between 1991 and 1998 was $13 million. An estimate of all control expenditures (including biological, mechanical, chemical and physical control) by participating agencies in south Florida was given at a cost of $25 million for the ten years of reporting time of the Melaleuca Task Force (Laroche 1999).

The potential economic impact of melaleuca's rampant invasion of south Florida has been estimated by many (Balciunas and Center 1991, Diamond et al. 1991, Laroche 1999). In a report by Diamond et al. (1991) and subsequently by Laroche (1999) it was speculated that the unchecked spread of melaleuca would severely restrict use of parks and recreational areas by residents and tourists and that the potential losses to the south Florida economy would be around $168 million annually. Diamond et al. (1991) further estimated that as much as 20% of the population in south Florida may suffer allergic reactions to melaleuca (Morton 1966, melaleuca is "a prime respiratory irritant in south Florida").

Another economic estimate by Balciunas and Center (1991) calculated that by the year 2010, close to $2 billion would be lost due to the expansion of melaleuca in southern Florida. The financial losses in this calculation included: $1,000 million in tourism to Everglades National

Park; $250 million in tourism to the rest of south Florida; $250 million in recreation; $250 million due to fires; $1 million in control efforts; $10 million due to loss of endangered species; and, $1 million to nursery growers. Other possible losses of money, but for which no dollar amount was given were increased water loss, storm flow and irrigation, and medical (allergies, injuries, etc.). Even though a potential economic benefit of melaleuca in Florida is its contribution to the honey industry, Balciunas and Center (1991) estimated that the resulting losses in honey production if melaleuca was eradicated would only be about $15 million a year. Their claim of financial losses due to fires has been substantiated by Diamond et al. (1991), Flowers (1991), Laroche (1999) and Wade (1981). These authors all discussed the difficulty in controlling the intense fires associated with melaleuca and the resultant problems to fire departments and property.

Melaleuca threatens biodiversity of native flora and fauna by diminishing the value of their habitat (Myers 1975, Hofstetter 1991). Once established, melaleuca forms dense, pure stands with a closed tree canopy and very little understory vegetation (Mazzotti et al. 1981, O'Hare and Dalrymple 1997). These dense stands have been shown to have very little value to the resident wetland wildlife (O'Hare and Dalrymple 1997, Ostrenko and Mazzotti 1981, Schortemeyer et al. 1981). O'Hare and Dalrymple (1997), in their field study, showed fewer crayfish and grass shrimp, fewer fishes, mainly upland birds and mix of wetland and upland mammals in dense melaleuca stands versus the wetlands replaced by those stands. Schortemeyer et al. (1981) reported that only 10% of the bird species active in melaleuca heads actually fed there and only 1.5% of bird activity involved nesting. They concluded that dense melaleuca stands would eventually eliminate adjacent essential wildlife habitats.

(b) Beneficial Effects

In parts of its native range, *Melaleuca quinquenervia* is called niaouli and is the source of the essential oil product name ‘niaouli oil’ (Craven 1999). Cochrane (1999) explored the antibacterial and antifungal qualities of melaleuca, as well as other invasive plants in Florida. The author proposed that there would be an economic incentive to harvest exotic, invasive plants if an antibiotic or other drug were developed. It was shown in this study that melaleuca exhibited antibacterial and antifungal activity, however, further studies are warranted as to its potential medicinal uses.

Many have investigated the use of melaleuca as a mulch product and as a timber product (Bodle 1998, Geary and Woodall 1990, Huffman 1980a,b, Timmer and Teague 1991). The predominant reasons for these investigations were to find a way to offset the costs of controlling melaleuca. It was found that melaleuca was suitable timber for such uses as pulp and cabinetry and that the bark also had potential uses as an amendment to plant potting mixes and in packaging and insulation (Huffman 1980a,b). However, Geary and Woodall (1990) in their silvicultural review of *Melaleuca quinquenervia* assert that it is not used in Florida or Hawaii for traditional timber products due to a high bark-to-wood ratio, small average stem diameter, and poor form. Timmer and Teague (1991) proposed that the commercial use of melaleuca for mulch would be feasible at an attractive cost in areas where tree density is high and transportation costs are low. They suggested that the proceeds from the sale of the mulch could offset a significant portion of the control cost. To date, the only widely known use of melaleuca as a timber product is as mulch. Melaleuca mulch has the double benefit of removing the invasive plant as well as providing a wetland friendly alternative to cypress and pine mulch (Bodle 1998).

Converting melaleuca to electricity has also been proposed (Tufts 1991). Tufts suggested that the biomass generated from removing melaleuca from the Everglades could be used to generate electricity without using fossil fuels. "The harvesting and conversion of Melaleuca would create a new industry for the region. This industry would generate employment and increase the tax base, as well as provide electricity for an expanding population." However, he conceded that the value of the wood would be low in comparison to the cost of the sensitive methods required when removing melaleuca in the Everglades. In addition to this disadvantage, Geary et al. (1980) points out that even though the entire tree can be used as a biomass fuel, it is more difficult to use than most other species because of its powdery, low-density bark.

One of the most noted benefits of melaleuca in Florida is to the apiary industry (Balciunas and Center 1991, Morton 1966, Robinson 1980, Sanford 1988). It has been listed as a major nectar source for bees and because melaleuca blooms several times a year it assists the Florida bees during times of "nectar death" (Sanford 1988). The honey produced from melaleuca is termed "punk honey." The nectar is considered distasteful by some, but a market does exist locally for the resultant product (Balciunas and Center 1991, Morton 1966, Robinson 1980, Sanford 1988). Balciunas and Center (1991) dispute that punk honey is a real economic boon to the apiary industry claiming that due to its low sales and poor taste there is no real commercial market for punk honey. Also, while beekeepers pay rent to place beehives in citrus groves, no one pays to rent a place to put their hives in melaleuca stands. Robinson (1980) conceded that the dollar value of melaleuca honey is a relatively unimportant share of total production of honey in Florida.

(c) Legislation

In 1992, melaleuca was added to the Federal Noxious Weed List - 7 C.F.R. 360.200 (PPQ 1999). Melaleuca is regulated as a "noxious weed," which is defined as any plant or plant product that can directly or indirectly injure or cause damage to crops (including nursery stock or plant products), livestock, poultry, or other interests of agriculture, irrigation, navigation, the natural resources of the United States, the public health, or the environment.

The Florida Department of Environmental Protection (FDEP) regulates melaleuca as a Class 1, Prohibited Aquatic plant, pursuant to Chapter 62C-52.011 Prohibited Aquatic Plants (FDEP 1996). According to this rule, plants listed as prohibited aquatic plants display one or more of the following characteristics (abbreviated from rule): a) the tendency to spread or become invasive in an ecosystem b) the propensity to invade and disrupt aquatic and wetland ecosystems in other areas or in other countries with climates similar to that of Florida; c) the ability to create dense, monospecific stands or monotypic stands which displace or destroy native habitats, inhibit water circulation, hinder navigation and irrigation, or severely restrict the recreational use of waterways; and/or d) the ability to resist effective management by present technology or available management agents. The Florida Department of Agriculture and Consumer Services (FDACS) also regulates melaleuca as a terrestrial weed pursuant to Chapter 5B-57.007, Noxious Weed List (FDACS 1996). A noxious weed is defined as any living stage, including, but not limited to, seeds and reproductive parts, of a parasitic or other plant of a kind, or subdivision of a kind, which may be a serious agricultural threat in Florida.

The North Carolina Department of Agriculture regulates melaleuca as a Class A noxious weed under Chapter 48 Plant Industry, Subchapter 48A Plant Protection, Section .1700 – State Noxious Weeds. A Class A noxious weed is defined as any noxious weed on the Federal

Noxious Weed List or any noxious weed that is not native to the State, not currently known to occur in the State, and poses a serious threat to the State. (NCDA 1996). In addition, the South Carolina Department of Agriculture regulates melaleuca as a noxious weed under Title 46, Agriculture, Chapter 23, Noxious Weeds. A noxious weed is defined as any living stage of any plant including seed or reproductive parts thereof or parasitic plants or parts thereof which is determined by the Commissioner of Agriculture to be directly or indirectly injurious to public health, crops, livestock, or agriculture including but not limited to waterways and irrigation canals (SCDA 2001).

There are also many local agencies that regulate melaleuca in Florida. In a 2000 publication for the South Florida Ecosystem Restoration Task Force, a list of all local agencies which regulate invasive plants was included for the 16 counties within the boundaries of the South Florida Water Management District (Doren and Ferriter 2000). According to this account of local regulations in south Florida, ten counties and municipalities regulate melaleuca.

5. Geographic Distribution

Melaleuca occurs naturally throughout eastern Australia, New Caledonia, Irian Jaya and southern New Guinea (Correll and Correll 1986, Craven 1999, Geary and Woodall 1990, Holliday 1989, PIER 2001).

In North America, melaleuca is widely invasive in south Florida and primarily infests the Florida peninsula south of Lake Okeechobee (Bodle et al. 1994, Morton 1966, Kaufman 1999). Wunderlin et al. (2000) has documented voucher specimens of melaleuca in nineteen counties in the state of Florida, the northernmost counties being Brevard, Orange and Hernando. Surveys conducted by SFWMD in 1992 indicate that the general distribution of melaleuca in Florida centers around the areas of original introduction, primarily southwest Broward and northern

Dade Counties (Bodle et al. 1994). In other areas of the continental United States of America, melaleuca is present and may be naturalized to some extent in California (Geary and Woodall 1990, Kaufman 1999, Morton 1966), Texas (Geary and Woodall 1990, Kaufman 1999, Morton 1966), Louisiana (USDA 2001) and possibly in Georgia (Center 2002 pers.comm.).

In the eastern United States, melaleuca may have the potential to spread farther north than its current range. The center of melaleuca distribution in Florida is around latitude 26 degrees north (approximately Fort Lauderdale) and is considered subtropical with a tropical humid or tropical savannah climate (Henry et al. 1994). The distribution of melaleuca in Australia is roughly at latitude 26 degrees south and is in areas considered tropical and subtropical with a subtropical humid or tropical humid climate. Both of these regions of Florida and Australia experience wet summers, dry winters and frequent fires (Turner et al. 1998). With the assistance of climatalogical models developed in Australia, it has been postulated that the entire Gulf coast of the United States, including valuable wetlands in southern Louisiana and eastern Texas, may provide conditions similar to the native Australian range (Bodle et al. 1994, Center 2002 pers.comm.). Woodall (1978), without the aid of models, came to same conclusion stating, "I believe that the species can become naturalized much further north than Lake Okeechobee … the capacity of melaleuca to dominate the vegetation of a region appears unlikely north of Lee and Palm Beach counties. However, the tree could become a *troublesome pest in coastal areas as far north as possibly the Panhandle*."

Melaleuca is now considered moderately invasive in Hawaii (Geary and Woodall 1990, HEAR 2000, Kaufman 1999, Sherly 2000, USDA 2001) and is listed as a potential invader on both the islands of Yap and Pohnpei, Federated States of Micronesia (PIER 2001, Sherly 2000, Space 1999). It has been noted that it is spreading slowly on the island of Yap. Melaleuca is also present in Fiji, Palau, French Polynesia (Tahiti), has been listed as moderate invader in Guam (PIER 2001, Sherly 2000) and, recently, has been documented as a potential invader in Hong Kong (Hau 2001).

Other areas of melaleuca occurrences outside of its native range, include Mexico (Sanchez-Silva 2002 pers.comm.), Puerto Rico (Geary and Woodall 1990, Kaufman 1999, USDA 2001), Cuba (Thayer 2002 pers.comm.), Jamaica (IABIN 2002), and the Bahama Archipelago, which consists of the islands of the Bahamas, Turks and Caicos (Correll and Correll 1986). In the Bahamas, melaleuca is reported to be present in Exuma, New Providence, Andros, and Grand Bahama, however it is considered unlikely to be able to establish except in the Northwestern Islands because of the salinity of the marshes and ponds in the Southern Islands (Hammerton 2002 pers.comm.).

6. Habitat

(a) Climatic Requirements

Melaleuca thrives in warm climates but is tolerant of infrequent frost (Woodall 1981b). Within its native range, frost occurs most years in coastal southern Queensland (Woodall 1981b). Sydney, which represents the southernmost distribution melaleuca in Australia, is climatically similar to New Orleans. Both are classified as "CaF" climatic types: with rainy climates and mild winters; the coolest month above 0 degrees C but below 18 degrees C; the warmest month above 22 degrees C; constantly moist conditions with rainfall of the driest month at least 60 mm. The more typical climates for the natural range of melaleuca would be those of areas in north coastal Queensland such as Mackay. It is classified as a "Caw" climate, which is similar to the

CaF climates, except that it has a winter dry season (Muller 1982). Nearly all of the southeastern U.S. lies between these two climatic types.

Woodall (1981b) noted that melaleuca survived a severe freeze during January, 1977. It also survived record-breaking freezes that occurred during late December, 1989 (Henry et al. 1994), even at inland locations around Sebring, Highlands county where temperatures reached –5 degrees C and remained below 0 degrees C for several hours (Center 2002 pers.comm.). Melaleuca trees throughout the area were severely affected. Many were completely defoliated and appeared dead for several weeks. However, epicormic sprouts formed, even on severely damaged trees, and most recovered (Center 2002 pers.comm., Geary and Woodall 1990). This suggests that the plant is more cold tolerant than expected and that its present distribution is limited more by suitable habitat and proximity of a seed source (Hofstetter 1991) than by climate.

Melaleuca occurs abundantly within zones 9a to 10b of the U. S. Department of Agriculture's plant-hardiness zone map (Cathey 1990). The coldest of these zones (9a) is characterized by minimum winter temperatures of -3.9 to -6.6 degrees C, which includes significant portions of the Gulf Coast of Louisiana and Texas. In Hawaii, growth of melaleuca occurs at mean annual temperatures from 24 degrees C to 18 degrees C (trees grow in even cooler temperatures at higher elevations) (Geary and Woodall 1990). In Hawaii, melaleuca is found from sea level up to 1,373 meters (4,500 ft) elevation. Most of southern Florida, where melaleuca readily invades, is less than 0.2 meters (25 ft) above sea level (Geary and Woodall 1990).

(b) Substratum

In Florida, melaleuca is well adapted to flooded, saturated and well drained soils and can thrive on sites that are either always or never flooded (Hofstetter 1991, Woodall 1981b). In general, soils supporting melaleuca are in the suborders Psammaquents, Aquods, and Saprists (sometimes marly) of the orders Entisol, Spodosol, and Histosol, respectively (Geary and Woodall 1990). It will survive on many local soil types, including acid sands, organic soils and alkaline marls and limestone of varied thickness (Hofstetter 1991). In order to become established, seedlings require access to a stable water supply but do well on both organic and mineral soil (Woodall 1981b). Melaleuca is purportedly tolerant of saline conditions and can establish within the mangrove zones along coastlines (Hofstetter 1991, Woodall 1981b). Plants can tolerate a wide range of pH (from 4.4 to 8.0) which encompass nearly the entire range of soil pH to be expected in Florida (Meskimen 1962, Woodall 1981b). Kaufman (1999) reported that in the Everglades, melaleuca tends to grow under pH conditions greater than 7, while in Australia, melaleuca's native habitat, the soil pH is usually 6 or less. Its ability to root deeply enables it to thrive in low nutrient soils. Seedlings, however, grow poorly in nutrient poor conditions unless recent fires have caused nutrient release from surface litter (Woodall 1981b, Wade 1981).

It grows fairly well on all Hawaiian soils, including calcareous beach sand, but does best on Inceptisols (Dystrandrepts), Ultisols, and Oxisols developed on basalt ash or lava rock of pH 4.5 to 5.5 (Geary and Woodall 1990).

(c) Communities

Melaleuca has invaded virtually all terrestrial or wetland plant community types and conditions in south Florida, including those where vegetative components appear to be healthy and presumed to be comparable to historical vigor (Hofstetter 1991, Woodall 1981b). Melaleuca has been documented in moist, undisturbed pine flatwoods, disturbed sites, sawgrass-dominated communities, cypress swamps, mangroves, savannas, and wet prairies (Abrahamson and Hartnett 1990, Hofstetter 1991, Laroche and Ferriter 1992, Nelson 1994, Woodall 1981b). In general, melaleuca invasion is less prominent on forested sites than on marshes and wet savannas (Geary and Woodall 1990) and xeric communities such as scrub tend to be resistant, but not immune to infestation (Bodle et al. 1994). Only dense hammock-type communities seem to produce enough shade to prevent invasion by melaleuca (Woodall 1981b).

In Hawaii, natural regeneration occurs at the edges of plantations, on road cuts, and in wet, sparsely vegetated openings in forests (Geary and Woodall 1990, Smith 1998). It is one of the few trees that has survived planting and reproduces naturally on the upland bogs that form in Hawaii when native forests are destroyed (Geary and Woodall 1990).

7. History

Melaleuca was apparently introduced during the 1880s by horticultural nurseries near Sarasota, Florida and San Diego, California as a landscape tree (Dray 2002 np). At least ten more introductions occurred into Florida within the subsequent forty years from botanical gardens in France, Italy, and Australia and plantations in Australia (Pritchard 1976). Dr. Henry Nehrling planted seeds in his garden near Orlando around the turn of the 20th century (Meskimen 1962). John C. Lange also claims to have made an early introduction of melaleuca in the beginning of the 1900's (Dray 2002 np). Even with these previous importations, Dr. John C. Gifford, a professor of Tropical Forestry at the University of Miami, was almost certainly the first to establish the species in south Florida. He received seeds in 1906 from Sydney, Australia, and planted his seedlings along Biscayne Bay. Specimens or seeds were later given to Frank Stirling, a nurseryman, who owned Stirling and Sons Nursery in Davie, Broward Co., Florida (Meskimen 1962). In 1912, A. H. Andrews with the Koreshan Unity introduced the plant to the west coast of Florida at Estero in Lee Co. (Meskimen 1962). The Koreshan introduction probably resulted in most of the infestations on the lower gulf coast of Florida. In 1936 Mr. Hully Stirling collected seeds from the Davie population of melaleuca and spread them by airplane in the eastern Everglades (Meskiman 1962). Further spread was caused by nurserymen who dug up saplings from the west coast populations and propagated them as ornamental landscape plants. The populations south of Lake Okeechobee were begun in 1941 when trees were planted on levees and spoil islands for erosion control by the US Army Corps of Engineers (Dray 2002 np, Stocker and Sanders 1981). Melaleuca was commonly used as ornamental landscape trees, as agricultural windrows, and as protective living "guard rails" and soil stabilizers along canals (Bodle et al 1994).

Melaleuca has been planted extensively in reforestation projects in Hawaii (HEAR 2000, Smith 1998). A million trees were planted in Hawaiian State Forest Reserves alone, but natural regeneration is considered localized and currently melaleuca is only considered a "moderate invader" (Geary and Woodall 1990, Sherly 2000).

8. Growth and Development

(a) Morphology

Melaleuca plants in Florida attain heights of 33 meters (Langeland and Burks 1998) with an average height from 15 to 21 meters (Geary and Woodall 1990). Saplings of this tree are strongly excurrent with a dominant leader, which is readily substituted if the terminal bud is damaged. However older trees generally become multi-stemmed (Tomlinson 1980). Trees that initially grow in the open have multiple, often more than a dozen, trunks that originate close to the sediment surface and diverge outward. Trees that grow in dense monocultures are self-pruning, producing tall whip-like trees generally lacking branches on the lower two thirds of its bole

(Hofstetter 1991). The root system is well-adapted to fluctuating water tables. The dense surficial roots are complemented by abundant vertical sinker roots that extend at least to the water table's deepest annual level (Geary and Woodall 1990). This plant has a strong capacity to produce a profusion of adventitious roots shortly after flooding, which provides for a very efficient water absorbing system that may prevent severe desiccation of shoots as well as aid in gas transport (Gomes and Kozlowski 1980).

(b) Perennation

Melaleuca exhibits two modes of perennation: seed dormancy and evergreen growth. Year-long leaf retention, along with south Florida's year round growing season, allows melaleuca to continue production throughout the year. As mentioned elsewhere in this review, melaleuca seeds can persist for at least ten months and up to two years in the soil (Rayachhetry et al. 2002b, Wade 1981, Woodall 1983). In addition, the retention of several years' seed production in the canopy allows for a particularly heavy seedfall even if a natural catastrophe or herbicide treatment kills off advance reproduction along with seed trees (Woodall 1982). The longevity of melaleuca in Florida is not well documented, however Hofstetter (1991) found trees in south Florida that he speculated were 70 years old and exhibiting no signs of senescence. Observations of older trees still producing seeds and the overall abundance of seeds in the canopy leads one to conclude that canopy seed retention is a major factor in the persistence of melaleuca.

(c) Physiology

A study published in 1981 by Conde et al, estimated standing crop biomass values for melaleuca in south Florida from 122 to 170 dry metric tons per hectare (dry mt/ha). This study was based on whole-harvest sampling of the above-ground biomass of the tree. Van et al. (2000)

revised this estimation with stated standing crop biomass values for the tree varying from 129 to 263 dry mt/ha. This study, conducted in south Florida, was also based on destructive sampling. Using these data, Van et al. (2000) established a predictive equation for estimating the above-ground biomass of melaleuca based on the stem diameter of the tree at breast height (dbh). They found that dbh alone is a good allometric predictor of dry weight of the overall above-ground biomass of the tree as well as for the individual components, trunk, branch, leaf, seed capsule and seed (Rayachhetry et al. 2001, Van et al. 2000). The total proportion of wood in the biomass increases with increasing values of dbh (Rayachhetry et al. 2001) and the proportion of wood in the biomass is reported as 83 to 96% (Van et al. 2002). Leaves and seeds made up the next highest percentage of the biomass with rates of 10 to 13% and 3 to 4%, respectively, in permanently flooded areas and 4 to 12% and up to 2%, respectively, in dry and seasonally flooded habitats (Van et al. 2002).

Annual litterfall at south Florida sites range from 6.5 to 9.9 t dry wt per hectare per year (Van et al. 2002). The ranges reported in this study varied from high amounts of litterfall in seasonally flooded sites, mid range litterfall in permanently flooded sites to low amounts of litterfall recorded in non-flooded sites. These reported ranges of litterfall in south Florida correspond well with a similar study conducted of melaleuca in Australia. Greenway (1994) reported annual litterfall values of melaleuca of 7.6 and 8.1 t dry wt per hectare per year at two sites of seasonally inundated forests in subtropical southeastern Australia. Greenway found that litterfall of melaleuca was lower when subjected to drought conditions because the leaves are retained longer on the tree as a drought response. In contrast, Greenway found higher productivity at seasonally flooded site similar to the conclusions reported by Van. et al. (2002) in south Florida trees. In the south Florida study, however, the researchers speculate that the lower productivity in trees in non-flooded sites (corresponding to Greenway's drought response) may be partially attributed to differences in the age of the stands studied in their research. On average Florida litter is comprised of 70% leaf fall, 14% to 18% woody material (twigs and bark) and 11% reproductive material (flowers/bracts and capsules) (Van et al. 2002). In comparison, Australia litter is comprised of 67% leaf fall, 17% twigs, 6% bark, 6% flowers/bracts and 5% capsules (Greenway 1994).

Growth rates of melaleuca trees in Florida are not well documented. Meskimen (1962) observed the aboveground growth rate of 5 seedlings (average height of 1 meter) on a mixed cypress-pine site in southwest Florida. The growth rates of these seedlings ranged from 33 cm/year to 90.5 cm/year with an overall average of 55 cm/year. Meskimen felt that the difference in the growth rates of the 5 seedlings were "related to the individual's length of growing season and probably genetic in origin." Myers (1975) in greenhouse treatments, observed aboveground growth rates of melaleuca seedlings up to 40 cm in 6 months in saturated conditions and just below 30 cm in 6 months for moist well-drained soils. When he transplanted seedlings into various field conditions, Myers observed growth rates ranging from approximately 75 cm in 9 months in burned cypress areas to approximately 40 cm in 9 months in wet prairies (Myers 1975). Data collected over a 16-month period from a melaleuca head in southeast Florida, showed an average height increase of 3.7 meters (from an average starting height of 1.3 m) during the period of the study (Alexander and Hofstetter 1975). Clearly, the wide range in reported growth rates for melaleuca in south Florida indicates the need for additional research on melaleuca productivity across various environmental gradients. This is important to determine what, if any, implications this variation may have on management of this species.

(d) Phenology

In Florida, melaleuca seedlings have been observed flowering at less than 2 years of age (Meskimen 1962). The tree is able to produce flowers throughout the year (Hofstetter 1991, Long and Lakela 1976), however its main flowering periods are in fall and winter (Van et al. 2002). In a recent two year study by Van et al. (2002) it was observed that flowering began in October and November, with peak flower production around December, and flowering essentially completed by February and March. The authors also reported new shoot growth beginning in mid winter after peak flowering, and extending into the spring. Very little new growth was observed in melaleuca forest during the summer months (May to August) in south Florida (Van et al. 2002). Their study indicates that melaleuca in south Florida follows similar seasonal patterns of flowering and growth as it does in its native range. In Australia, flowering also occurs from early autumn to late spring and new leaf growth begins mid winter immediately after flowering and extends to early summer. The authors found no seasonality in the fall of seed capsules (Van et al. 2002). No information was found on the phenology of seed germination.

9. Reproduction

(a) Floral Biology

In Florida, melaleuca trees can become reproductive within a year of germination and will flower profusely within three years of germination (Meskimen 1962). An individual tree may flower as many as five times per year and a given twig may flower three or more times per year (Godfrey and Wooten 1981, Meskimen 1962). Numerous flowers are produced on each tree and are crowded in terminal spikes or panicles of spikes on woody axes. The apices of the flowering twig resumes growth after a flowering event (Godfrey and Wooten 1981). Florida melaleuca trees are known to be self-compatible and autogamous, but also promote outcrossing (Vardaman 1994). The primary mode of reproduction for melaleuca is sexual (Hofstetter 1991).

Melaleuca is monoecious and pollination is by insects (Geary and Woodall 1990). A major pollinator of melaleuca is the introduced honey bee *(Apis mellifera L.)* (Hofstetter 1991). Hofstetter (1991) speculated that the honey bee probably has caused more fertilization to occur than if only native pollinators were present and may have played a role in the increased rate of spread of melaleuca in Florida since the 1950's.

(b) Seed Production and Dispersal

Woodall (1982), based on a 6 month study in a closed stand of mature melaleuca trees in Florida, reported a weekly seedfall of 2,260 seeds/m^2. After flowering, 30 to 70 sessile seed capsules are left on the twig and each seed capsule contains, on average, 264 seeds (Alexander and Hofstetter 1975, Meskimen 1962). The profuse flowering of melaleuca (up to 5 times per year and up to 3 times per year per twig) and the copious amounts of seed produced could potentially result in the production of over 500,000 seeds per twig in a given year. In contrast, the number of capsules and seeds/cluster are threefold less on trees from Australia (Rayachettry et al. 2002b). Melaleuca seeds are small, averaging about 30,000 seeds per gram (Meskimen 1962, Woodall 1982). The seeds vary in size and shape and weight (Woodall 1982). A mean length and diameter of 1.20 mm and 0.26 mm, respectively, has been reported for melaleuca seeds (Rayachhetry et al. 1998).

With the exception of sheer abundance and possibly flotation, there seems to be no plant or seed adaptations in melaleuca that aid in seed dispersal (Hofstetter 1991). The majority of melaleuca seeds simply fall from the tree within a short distance from the trunk of the seed tree (Meskimen 1962, Woodall 1978). Even with the aid of wind, seeds will be dispersed no farther than 8.5 times the height of the seed source (Woodall 1982). Browder and Schroeder (1981) using a predictive model, found that 99% of seeds released from one tree during an ordinary year would disperse no farther than 170 m. In the case of hurricane force winds, they found a maximum dispersal distance of 7 km, however, in the absence of hurricane force winds, no seeds traveled farther than one kilometer (Browder and Schroeder 1981). No native small mammals or birds are suspected of eating the seeds (Hofstetter 1991). However, Meskimen (1962) suggested transport of seeds on the bodies of birds may be possible dispersal mechanism. Hartman (1999) theorized that the high germination rate of melaleuca seeds that float might be important dispersal strategy for high water conditions such as are found in the Florida Everglades.

(c) Seed Banks, Seed Viability and Germination

Due to the light, continuous seed release of the melaleuca tree, fresh seeds lying on the ground are always present. However, melaleuca's profuse seed production and its ability to hold seed capsules for several years on the tree contributes enormously to a large 'above-ground' seed bank (Hofstetter 1991, Meskimen 1962, Rayachhetry et al. 1998). This above ground seed bank allows for a particularly heavy seedfall if some natural catastrophe or man induced control activity kills seed trees or fells seed-bearing branches. If the capsules remain on the tree, the seeds are typically released only after fire or some other stress interrupts phloem transport, which causes the capsules to dehisce (Rayachhetry et al. 1998). Rayachhetry et al. (2002b) estimated the above ground seed bank of a 21 m high open grown tree in Florida could contain up 100 million seeds/tree. In an earlier study of south Florida seeds, 15% of the seeds were found to contain embryos (Rayachhetry et al. 1998). Of these embryonic seeds, 62% were viable and of the viable seeds, 73% germinated in greenhouse conditions after 10 days (Rayachhetry et al. 1998). Rayachhetry et al. (1998) theorize that the remaining 27% of the viable seeds that did not germinate after 10 days may be exhibiting dormancy. Overall, based on the finding of both these studies, the hypothetical 21 m high open grown tree in Florida, with 100 million seeds/tree, could have 9 million viable seeds that were capable of producing seedlings. In Australia, the number of viable seeds/cluster was 7.5 times less than in south Florida (Rayachhetry et al. 2002b).

Germination and viability of seeds decrease significantly with capsule age (Meskimen 1962, Rayachhetry 1998). However, seeds can remain viable for months (Myers 1975, Myers 1983, Woodall 1983). Woodall (1983) found that some seeds remained viable after 10 months in the sandy soils of a well-drained saw palmetto prairie. Results of a seed burial test showed that seed viability was reduced by about 50% after 8 months in soil (Laroche 1999). A saturated soil surface is needed for germination (Woodall 1978). Seeds will germinate within 3 days of wetting (Myers 1975). Access to full sunlight is not necessary for germination but seed germination is best in open sun (Hartman 1999, Meskimen 1962, Woodall 1978). Newly fallen melaleuca seeds can resist wetting and can rest atop the surface-tension film for days (Woodall 1982). Hartman (1999) found that the germination of floating seeds was 46.6% compared to 6.6% for seeds that sank. Lockhart (1999) found that seeds could germinate underwater on soil substrate. Seed germination is favored by both alternating wet and dry cycles and continuous wet conditions (Myers 1975). Cool temperatures will inhibit germination but seems to have little residual effect on the germinablity of the seed when temperatures rise (Woodall 1978). Seeds can survive submersion in water up to 6 months and still be viable and germinate (Meskimen 1962), however after one year of submersion, seeds are not viable and do not germinate (Myers 1975).

The actual seed of melaleuca shows few adaptations for survival (Woodall 1978), but because so many seeds are produced, the chances of seedling establishment are very high. Hartman, (1999) states, "…our experiments demonstrate that the processes of seed germination and seedling establishment represent a bottleneck in the life history of melaleuca. Despite low germination and establishment rates, each tree produces millions of seeds, the likelihood of some trees establishing, therefore is high."

(d) Vegetative Reproduction and Resprouting

Melaleuca stumps sprout/coppice readily (Conde et al. 1981, Hofstetter 1991). Trees with damaged or removed stems have the ability to generate adventitious buds on roots and shoots resulting in coppicing below a cut or when the apical bud is destroyed. A tree that is uprooted and on the ground may develop into a row or trees as a result of branches on the upper side of the bole becoming individual trunks. Broken branches that fall on suitable soils may also root and grow (Hofstetter 1991).

10.Hybrids

No documentation of melaleuca hybridization was found.

11.Population Dynamics

The establishment of melaleuca in Florida has been much more robust than in Australia (Rayachhetry et al. 2002b). This is thought to be due to a combination of favorable conditions for growth and the lack of biological controls on populations. In its native range, melaleuca is found in low-lying areas that are periodically swept by fire (Laroche 1999). Low areas and frequent fires are also conditions commonly found in south Florida, making it especially suitable to the rapid establishment of this species. These favorable ecological conditions, in conjunction with human interference in natural systems, melaleuca's biological attributes and the lack of any natural population controls, are thought to be responsible for this tree's explosive invasion of

Florida habitats (Hofstetter 1991, Kaufman and Smouse 2001, Rayachettry et al. 2001, Turner et al. 1998).

Melaleuca infestation results in a strong shift in the structural and biological attributes of south Florida wetland habitats. Melaleuca does not typically invade dense tree stands, rather it invades open canopied forests (i.e. fire damaged) sparsely vegetated ecotones, wetland prairies and marshes, and fire damaged forests (Geary and Woodall 1990). As melaleuca invades a wetland marsh, it changes the system from one with low structural diversity into a savannah with open marsh and trees and a greater structural diversity. Over time, this transitional stage becomes a closed canopy forest with a sparse understory and low structural diversity (O'Hare and Dalrymple 1997). As the tree replaces low, open-canopied ecosystems, it effectively turns these systems into dense, monotypic forests, thereby greatly changing many attributes of the ecosystem (Laroche 1999). The differences in species composition and structure are great and the pace of this invasion is rapid. Laroche and Ferriter (1992) performed a time series analysis of the invasive capacity of melaleuca. In their study, they found that once an infestation of melaleuca reached 5 percent in a one square-mile area (size of study area), it only took approximately 25 years for 95 percent infestation to occur within that same area.

The rapid colonization of melaleuca is facilitated by profuse seed production. As discussed above, a single melaleuca inflorescence can produce 30 to 70 sessile capsules, each containing 200 to 350 seeds, which can remain attached to the tree for over 7 years (Meskimen 1962). Physiological mechanisms that trigger seed release from the capsules represent a major challenge to vegetation management of melaleuca. Seed capsules quickly dehisce in response to bole girdling or stem damage, resulting in massive, synchronous seed releases. A single tree, when stressed, may release as many as 20 million seeds at one time (Woodall 1981b). Because of this massive seed release from mother trees, extremely dense, even-aged stands are common, on the order of over 250,000 3 to 4 meter high trees per hectare (Alexander and Hofstetter 1975). As these dense stands mature, interspecific competition reduces the stand density to approximately 5,000 12 meter high trees per hectare (Hofstetter 1991). Recently sampled stand densities in dense, pure stands (all trees over 1.3 m counted) ranged from 11,450 to 36,275 trees per hectare (Van et al. 2002) and from 8,000 to 132,200 trees per hectare (Rayachhetry et al. 2001) with the range largely depending on site suitability.

Mature melaleuca trees are considered to be intolerant to shade (Geary and Woodall 1990). Pure stands of melaleuca with closed canopies inhibit the development of understory vegetation including melaleuca seedlings (Geary and Woodall 1990, O'Hare and Dalrymple 1997). Melaleuca seedlings require ample sunlight and are thought to be only moderately shade tolerant (Woodall 1981b). However, melaleuca germination and seedling development does occur in shade. Based on the recent study by Van et al. (2002), the authors documented the presence of a relatively high percentage of juvenile trees in mature melaleuca stands, which suggested to them a high regenerating capacity by melaleuca in south Florida.

Due to shading effects and increased evapotranspiration rates caused by dense melaleuca stands, melaleuca forests may have a long-term impact on litter decomposition rates (Laroche 1999) as well as fire regime and fire intensity (Flowers 1991). When melaleuca trees displace the wetland marsh/prairie vegetation, the ground fire fuel load is changed. Flowers (1991) proposed that this fuel load change was a result of a continuous rain of litter from melaleuca canopy that results in a rich layer of undecomposed leaf litter on the forest floor. Melaleuca's trees in pine and cypress stands can cause a fire to become a crown fire that damages melaleuca only superficially but can kill other canopy species (Wade 1981). Mature melaleuca trees are known to be fire tolerant in Florida and the tree can flower within weeks after a fire (Hofstetter 1991, Meyers 1983). In addition, the heat from a fire actually helps in the drying out of the seed capsules on the tree and a resulting massive seed release. The seed rain released by intense fires can result in dense, even-aged stands estimated to contain from 19,000 to 40,000 saplings/hectare (Meskimen 1962, Hofstetter 1991). Seedlings are also less tolerant of fires because they don't have the thick protective bark of mature trees (Woodall 1981b). Larger seedlings, however, may be able to recover from a hot surface fire by regenerating shoots from the root collar (Hofstetter 1991).

The timing and duration of flooding is a strong determinant of successful establishment and regeneration. In south Florida, mature melaleuca populations can grow under constantly flooded conditions, but the presence of seedlings is more commonly found in lower water conditions (Kaufman 1999). Myers (1975) found that that continuous submergence of seedlings would halt growth and that 6 to 12 months of continuous submergence would kill most seedlings. In a later study, Lockhart (1996) found that melaleuca seedlings have the ability to form heterophyllic aquatic leaves in submersed conditions, which can increase the survival of these seedlings in prolonged periods of flooding. Both studies demonstrate that a seedling does have the capacity to withstand typical flooding events in south Florida. Most germinants will die during flooding (Woodall 1983). Mature melaleuca trees are tolerant of droughts but a severe drought will kill seedlings (Woodall 1981b). In less severe droughts, root elongation in seedlings can keep up with a water table that recedes at 1 cm a day for up to 3 months (Woodall 1981b).

12. Response to Herbicides and other Chemicals

Use of herbicides is currently the most practical and cost-effective control method for managing melaleuca (Bodle et al 1994). A variety of different herbicidal treatments, both different herbicides and different methods of herbicide applications, have been applied to melaleuca and success has varied. In General, herbicide treatments have been found to be more effective on melaleuca seedlings than on mature trees. Langeland, (1990a) states, "Selection of herbicides for melaleuca control is difficult because the trees are often in aquatic habitats, saturated soils, or sensitive natural areas where damage to non-target vegetation is a concern." Individual treatments of target trees, using girdling or cut/stump methods, results in the most effective kill rate and in the least amount of non-target damage (Laroche 1998a). Laroche (1993), in an attempt to find another method sensitive to natural areas, evaluated the use of a plug injection system, which injected a herbicide directly into the cambium layer of the tree and allowed him to use hexazinone over standing water. All of these efforts have proven to be labor-intensive, costly and time consuming and are not widely used in areas of dense stands of mature melaleuca. For treating pure stands of melaleuca, aerial application is commonly employed as a more cost-effective control (Langeland 1990a, Laroche 1998b, Turner et al. 1998). This method has the disadvantage of non-target damage, however has the advantage of being able to quickly treat large areas of infestations and multiple trees with each application (Laroche 1998a, Turner et al. 1998). When foliarly applying herbicide, dilution rate (with water) guidelines are 20:1 for aerial, and 50 to 400:1 for ground application (Bodle et al. 1994). Laroche (1998a) based on personal observations, speculated that a herbicide application during January and February when melaleuca exhibits new growth would be most effective. This observation has been confirmed by Van et al. (2002), who, based on phenological studies, have suggested that the most efficacious time for melaleuca control is during its annual growth cycle during later winter and early spring (when the plant is most active).

Historically, hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] and tebuthiuron {*N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea} have been used successfully for controlling melaleuca (Burkhead 1991, Cofrancesco et al. 1995, Laroche et al. 1992, Maffei 1991, Molnar et al. 1991) and are indeed the two herbicides considered to be most effective for control (Laroche 1999). Using aerial application, both tebuthiuron and hexazinone, resulted in up to 100% control on melaleuca seedlings and better than 80% control on mature trees (Stocker and Sanders 1981, 1997). However, neither tebuthiuron nor hexazinone can be applied directly to water in Florida (Laroche 1998a). Tebuthiuron was taken off of the Florida market altogether in 1993. Up until 1995, hexazinone had a Special Local Need (SLN) Label, which allowed it to be used in wetland areas during the dry season, but in 1995 the herbicide manufacturer for this chemical requested that the state pull this use and cancel the SLN Label (Laroche 1999). The current label for hexazinone allows its use on melaleuca in certain situations such as dry wetlands and individual trees in dry areas.

Imazapyr (isopropylamine salt of 2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid), glyphosate [isopropylamineamine salt of *N*-(phos-phonomethyl) glycine] and triclopyr (triethylamine salt of 3,5,6-trichloro-2-pyridinyloxyacetic acid) have also been found to be effective on melaleuca (Laroche 1999). Imazapyr has a Special Local Need Label, which allows it to be used in flooded areas for frill and girdle and cut-stump methods and an Experimental Use Permit (EUP), which allows imazapyr to be sprayed aerially over water (Bodle et al. 1994, Laroche 1999). A full aquatic label for imazapyr is expected within the next couple of years. Imazapyr herbicide in a 50% solution with water, is proven to be consistently effective, can be used in flooded areas (with Special Local Need Label), and, as such is used widely both in ground and aerial control of melaleuca (Bodle et al. 1994, Laroche 1999). Imazapyr has been shown to be very effective both using a girdling technique (bark removed around entire circumference of the tree and herbicide applied directly to the cambium) (Timmer and Teague 1991) and using a cut/stump method (Stafford 1999). Other supporting field studies of the effectiveness of imazapyr include: Laroche et al. (1992), Laroche (1998b), Maffei (1991), Pernas et al. (1994), and, Pernas and Snyder (1999). Laroche et al. (1992) have also shown imazapyr to be moderately effective (63% mortality after 18 months, no retreatment) when mixed with glyphosate in aerial applications. Glyphosate, when applied undiluted, has shown good control in both cut/stump (~85%) and girdling techniques (~70%) (Laroche et al. 1992). Only certain glyphosate products are federally registered for applications over standing water (Stocker and Sanders 1997). Glyphosate alone does not appear to provide the same level of control as imazapyr (Pernas et al. 1994). When mixed with imazapyr, glyphosate has shown increased control in cut/stump treatments (Pernas et al. 1994). Undiluted applications of triclopyr provide good control (85%) using the cut/stump technique (Laroche et al. 1992) as well as with girdling (Timmer and Teague 1991).

A number of herbicides have been tested for aerial application success and results have been mixed. As stated above, only hexazinone (4.5 kg/ha ai) and tebuthiuron (11.2 kg/ha ai) produced greater than 80% control. In light of the unavailability of hexazinone as an aerial application technique, Laroche (1998a) recommends a combination of imazapyr at 1.68 kg/ha ai and glyphosate at 3kg/ha ai applied with a methylated seed-oil surfactant in a total volume of 144 to 188 L/ha.

Table 1 provides a quick checklist of herbicide studies reviewed for this document. Check citations for rates, surfactants and efficacy. Good overall summaries of melaleuca herbicidal control include Laroche (1998a, 1999) and Bodle et al. (1994).

Herbicide control is most effective when used in conjunction with a sound management strategy. Woodall (1981a) proposed a quarantine strategy for ultimate control of melaleuca, which consisted of focusing on killing single trees and small outlier stands distant from primary stands. His hypothetical model of a melaleuca "population cell" showed that the biggest payoff is from controlling the most isolated, most distant seed trees and as one proceeds toward the central denser portion of the population the relative benefits from killing individual trees decline. Woodall felt that this would help keep larger populations in a 'holding pattern' giving time for research and better solutions, also giving time for developing effective biological controls. Retreatment of melaleuca populations is imperative (Burkhead 1991) as one-time treatments may only accelerate the tree's spread through enhanced seed-out from treated trees (Molnar et al. 1991). Woodall's (1981a) methodology incorporated retreatment using either prescribed burning or manual control (pulling out seedlings) for a follow-up or retreatment with herbicide. Many resource managers in Florida have adopted Woodall's approach, modifying it only by incorporating large aerial herbicide treatments of dense monotypic stands as funding allows (Laroche et al 1992, Laroche 1998, Maffei 1991, Molnar et al. 1991).

13. Response to Other Human Manipulations

(a) Cultural

As melaleuca is a fire-adapted species, and the spread of the tree is encouraged by fire (Hofstetter 1991, Myers 1983), prescribed burning, as a control tactic must be used cautiously.

Burning can be an important tool in the management of melaleuca if timed correctly (Laroche 1999, Coladonato 1992). The most successful timing for prescribed burns is thought to be during times of unfavorable conditions for seeds (Laroche 1999). These conditions include: 1) burning in late wet season when the water table is at or near the surface in order to release seeds onto a wet to moist seedbed. Seedling would appear within a week, most of the seeds would germinate then, during the ensuing dry season many if not all of the seedling would die from drought response. 2) burning immediately after the onset of consistent summer rains. In this scenario water levels would be rising, soils would be wet, germination would occur, and as water levels continue to rise, seedlings would be submerged for an extended period lessening their chance of survival (Laroche 1999). Both of these optimal burning conditions rely heavily on 'normal' seasons. Because normal seasons are not always present, a resource manager must be prepared to follow-up these burn scenarios with herbicide treatment of post-emergent seedlings. In addition, as discussed earlier in this review, a certain percentage of seeds and seedlings will survive prolonged exposure to droughts and flooding. A better strategy suggested is to get seeds on the ground while ground cover is still intact and therefore provides a fuel load. This could be done using a herbicide treatment first to get the mature trees to release seeds, then monitor for germination. A fire after germination, while the seedlings are still small would most likely kill all seedlings (Laroche 1999). Seedlings that are less than 3 to 6 months old or only 4 to 8 inches are often killed by hot surface fires (Coladonato 1992). Resource managers commonly employ this last method of prescribed burning as part of an integrated management approach for the control of melaleuca (Maffei 1991, Pernas and Snyder 1999).

Flooding alone has not been shown to be an effective tool for control of melaleuca. As discussed previously in this review, melaleuca seeds, seedlings and mature trees all have the ability to withstand prolonged periods of inundation. It is generally felt that increasing water levels would have little effect on reducing the establishment success of melaleuca (Hartman 1999). In addition, while the maintenance of extremely long periods of high water may reduce the numbers of seeds germinating and the number of seedlings, this alteration of water levels in a natural area would also have adverse affects on native plants and animals (Lockhart 1999). Utilizing other methods of control such as prescribed burning (discussed above) or felling trees in conjunction with the onset of a normal wet season has been recommended as successful method of integrating flooding (Laroche 1999).

(b) Mechanical/Manual Removal

The most noted threat of melaleuca is to the sensitive natural areas of south Florida. The very nature of these native lands precludes the use of heavy equipment to mechanically remove melaleuca trees due to disturbance of soils and native vegetation (Bodle et al. 1994, Laroche 1999). Mechanical removal is appropriate in areas such as canal and utility rights-of-way and other similar areas adjacent to infested wetlands (Bodle et al. 1994). Stumps left after mechanical control must be treated with herbicide to avoid the production of root sprouts and coppicing from the stump (Bodle et al. 1994). Currently, felling trees in place and manual removal of seedlings less than 2 meters tall are the only forms of mechanical/manual control being used in the natural areas of south Florida (Laroche 1999).

14. **Response to Herbivory, Disease and Higher Plant Parasites**

Herbivory

(a) *Mammals/Birds* – There is no significant herbivory of melaleuca by mammals or birds (Hofstetter 1991). Pritchard (1976) speculated that cattle might graze melaleuca seedlings, and thereby control infestations, in improved pasturelands.

(b) *Insects* – In Florida, until relatively recently, melaleuca has been free of any insect enemies. This lack of insect herbivory has been speculated to be the one of the primary causes for its rampant expansion in Florida as compared to its host range (Turner et al. 1998). The United States Department of Agriculture, Australian Biological Control Laboratory (USDA-ABCL) started a long-term exploration program in 1986 (Rayachhetry et al. 2002a). Surveys were conducted along the eastern shore of Australia, searching for biological control agents for melaleuca. Over 450 plant feeding insect species, which feed on melaleuca, have been collected in Queensland and northern New South Wales (Rayachhetry et al. 2002a). Studies conducted in the early 1990's in melaleuca's host range showed that even low levels of insect herbivores would rapidly suppress growth of saplings (Balciunas and Burrows 1993). Because of the large numbers of insect herbivores found and the documented plant damaging herbivory, many studies have ensued to look for insect biological control agents to introduce for management of melaleuca in Florida (Balciunas 1990, Balciunas and Burrows 1993, Balciunas and Center 1991, Balciunas et al. 1994). To date, two insect herbivores have been released in south Florida, the leaf weevil, *Oxyops vitiosa*, and the melaleuca psyllid, *Boreioglycaspis melaleucae*. The first insect biological control agent, *Oxyops vitiosa*, was released in south Florida in 1997 (Center et al. 1999) and *Boreioglycaspis melaleucae* was recently released in spring 2002 (Pratt et al.

2002c). These two insects, as well as the defoliating sawfly, *Lophyrotoma zonalis*, have been subjected to extensive host specificity testing and all three have been shown to be specific to melaleuca (Balciunas and Buckingham 1996, Buckingham 2001, Burrows and Balciunas 1997, Purcell et al 1997, Rayachhetry et al. 2002a). Other insects, which are being screened in Australia and Florida, are a leaf-blotching mirid bug, *Eucerocoris suspectus*, a bud gall fly and worm, *Fergusonina/Fergusobia sp*., and a tube dwelling moth *Poliopaschia lithochlora* (Rayachhetry et al. 2002a). Additional insects that are being researched in Australia include *Pomponatius typicus and Lophyodiplosis indentata* (Turner et al. 1998) and *Gelechioidea* moths (Burrows et al. 1994).

The melaleuca leaf weevil, *Oxyops vitiosa*, has now been established in south Florida for close to 5 years. Results from the first year of establishment at 13 different release sites in south Florida led Center et al. (1999) to conclude, "..populations seem firmly entrenched and, barring any unforeseen catastrophes, should persist indefinitely." As of winter 2000, more than 47,000 adults and 7,000 larvae have been released at over 97 location in south Florida (Center et al. 2000). Populations now occur in Dade, Broward, Lee, Collier, Palm Beach, Martin, Monroe, Sarasota and Glades Counties. Recent Florida field data on this insect show that *Oxyops* is capable of increasing population densities at a rate comparable to that of other successful weed biological control agents (Pratt et al. 2002b). Pratt et al. (2002a) have now developed model based data that describes those larval densities of *Oxyops* that will fully exploit melaleuca foliar resource and may be used as target levels for land managers when redistributing this biological control agent. *Oxyops* has the advantage of a defensive terpenoid secretion on the surface of larvae, which is thought to protect the larvae against generalist predators such as the introduced fire ant (*Solenopsis invicta)* and to have contributed to its success in the field (Montgomery and

Wheeler 2000, Wheeler et al. 2002). However, there are two disadvantages of *Oxyops* as a control agent. The first is that it is restricted to feeding on flush foliage with low toughness (Wheeler 2001). Thus, it is not a good biological control agent to attack older trees. The second is that it pupates in the soil, which restricts it from establishing in permanently flooded sites (Purcell and Balciunas 1994). Even with these two drawbacks, preliminary studies have shown that flowering on trees severely damaged by *Oxyops* was reduced by more than 90% (Center et al. 2000). Studies are now underway to find ways to mass-produce *Oxyops* for wider distribution in the field (Wheeler and Zahniser 2001) and to find additional, genetically identical populations in Australia (Madeira et al. 2001). The melaleuca psyllid, *Boreioglycaspis melaleucae*, released in spring 2002, is a good compliment to *Oxyops* because its nymphs induce defoliation of older leaves and encourage sooty mold growth on their excreted honeydew (Rayachhetry et al. 2002a). It is too soon to know if the pysllid has become established and is effective in the field, but field-reared adults have been recovered (Pratt et al. 2002c).

According to Balciunas and Center (1991), woody plant species such as melaleuca require a diversity of biocontrol agents, at least 5 species, to achieve control. With two insect herbivores released and more in quarantine, this goal may soon be realized. It is generally believed that while removal of existing stands of melaleuca may be best accomplished by other means (herbicides and mechanical), a reduction in flowering and seed set, lower reproduction rates, and reduced plant vigor though biological control, would enhance the overall efficacy melaleuca control in Florida (Laroche 1999, Wineriter and Buckingham 1999). Many resource managers throughout the years have encouraged research of insect biological control agents and have hoped to incorporate this type of control into a integrated plan for management of melaleuca

(Laroche 1999, Timmer and Teague 1991, Pernas and Snyder 1999, Langeland 1990ab, Laroche 1998, Woodall 1981a, Tufts 1991, Maffei 1991, Molnar et al. 1991).

Diseases

Fungal species on *Melaleuca* and its close allies have been assessed in Florida, Australia and other parts of the world (Rayachhetry et al. 1996a, 1996b, 2002a). Six fungal species found to be associated with melaleuca include a *Fusicoccum* anamorph of *Botryosphaeria ribis*, *Puccinia psidii*, *Fusarium sp*., *Pestalotiopsis sp*., *Phyllosticta sp*., and *Guignardia sp*. (Rayachhetry et al. 1996a, 1997a, 1997b, 2001, 2002a).

Testing of of *B. ribis,* a native Florida canker fungus, in melaleuca has shown that this fungal species requires a wound exposing the sapwood or injury stresses such as loss or damage of leaves or branches in order to establish (Rayachhetry et al. 1996a, 1996b). Once established, *B. ribis* in stems of melaleuca can perpetuate in the tissues and proliferate rapidly under stress conditions (Rayachhetry 1996c, 1996d). Affected vascular tissue of plants usually appear brown to black in color and infected plants may die back, show vascular wilt or crown thinning (Rayachhetry et al. 1996d). The use of *B. Ribis* alone and in association with herbicides has been studied (Rayachhetry et al. 1997b, 1999). Preliminary research shows that *B. ribis* alone was less effective than the herbicide alone and that mixtures of this fungus with imazapyr are comparable to the herbicide alone (Rayachhetry et al. 1999). *Puccinia psidii,* another native Florida pathogen, has also been studied and has been shown to vigorously attack growing melaleuca branch tips (Rayachhetry et al. 1997a, 1997b). The relationship between this rust fungus, *P. psidii*, and melaleuca appears to be a new association for this fungus and may contribute to future control of melaleuca (Rayachhetry et al. 2001). While these pathogens alone will not control melaleuca, which is apparent in their current coexistence with melaleuca in natural areas of south Florida, they may be used in conjunction with other types of control or the detrimental effects of these pathogens on melaleuca may be able to be optimized.

Further research is warranted on the use of pathogens for control of melaleuca in south Florida. Although these biological control agents have not received much attention, in the future, pathogens may also be used in integrated management of melaleuca.

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Table 1

Active ingredient	Herbicide name	Method	Location	Citation*
imazapyr	**Arsenal**	girdle	south Florida	Timmer and Teague, 1991
imazapyr		foliar	south Florida	Timmer and Teague, 1991
imazapyr		cut/stump	south Florida	Timmer and Teague, 1991
imazapyr		drilling holes	south Florida	Timmer and Teague, 1991
imazapyr		girdle	south Florida	Bodle et. al., 1994
imazapyr		aerial	M.E. Thompson Park	Laroche et al., 1992
imazapyr		cut/stump	M.E. Thompson Park	Laroche et al., 1992
imazapyr		frill and girdle	M.E. Thompson Park	Laroche et al., 1992
imazapyr		aerial	Lake Okee. & WCAs	Laroche, 1998b
imazapyr		cut/stump	Estero Bay State	Stafford, 1999
imazapyr		cut/stump	Big Cypress NP	Pernas et al., 1994
imazapyr		frill and girdle	Big Cypress NP	Pernas et al., 1994
imazapyr		cut/stump	Big Cypress NP	Pernas and Snyder, 1999
imazapyr		frill and girdle	A.R.M Loxahatchee	Maffei, 1991
imazapyr + triclopyr	**Arsenal + Garlon 3A**	aerial	M.E. Thompson Park	Laroche et al., 1992
imazapyr + glyphosate	**Arsenal + Rodeo**	aerial	M.E. Thompson Park	Laroche et al., 1992
dicamba + 2,4-D	**Banvel 720**	cut/stump	Lake Okeechobee	Stocker and Sander, 1981, 1997
dicamba + 2,4-D		foliar	south Florida	Timmer and Teague, 1991
glyphosate + 2,4-D	**Campaign**	cut/stump	Big Cypress NP	Pernas et al., 1994
triclopyr	**Garlon 3A**	girdle	south Florida	Timmer and Teague, 1991
triclopyr		foliar	south Florida	Timmer and Teague, 1991
triclopyr		aerial	M.E. Thompson Park	Laroche et al., 1992

Active ingredient	Herbicide name	Method	Location	Citation*
triclopyr		cut/stump	M.E. Thompson Park	Laroche et al., 1992
triclopyr		frill and girdle	M.E. Thompson Park	Laroche et al., 1992
triclopyr		girdle	East Everglades	Molnar et al., 1991
triclopyr		cut/stump	East Everglades	Molnar et al., 1991
triclopyr		aerial	A.R.M. Loxahatchee	Maffei, 1991
triclopyr	**Garlon 4**	aerial	M.E. Thompson Park	Laroche et al., 1992
triclopyr	**not reported**	frill and girdle	Big Cypress NP	Burkhead, 1991
bromacil	**Hyvar X**	cut/stump	Lake Okeechobee	Stocker and Sander, 1981, 1997
glyphosate	**Rodeo**	girdle	south Florida	Timmer and Teague, 1991
glyphosate		foliar	south Florida	Timmer and Teague, 1991
glyphosate		aerial	M.E. Thompson Park	Laroche et al., 1992
glyphosate		cut/stump	M.E. Thompson Park	Laroche et al., 1992
glyphosate		frill and girdle	M.E. Thompson Park	Laroche et al., 1992
glyphosate		aerial	Lake Okee. & WCAs	Laroche, 1998
glyphosate		disked + broadcast	Lake Okeechobee	Cofrancesco et al., 1995
glyphosate		cut/stump	Big Cypress NP	Pernas et al., 1994
glyphosate		cut/stump	Big Cypress NP	Pernas and Snyder, 1999
glyphosate + triclopyr	**Rodeo + Garlon 3A**	aerial	M.E. Thompson Park	Laroche et al., 1992
glyphosate	**Roundup**	cut/stump	Big Cypress NP	Pernas et al., 1994
tebuthiuron	**Spike**	cut/stump	Lake Okeechobee	Stocker and Sander, 1981, 1997
tebuthiuron		pellet applications	Lake Okeechobee	Stocker and Sander, 1981, 1997
tebuthiuron		pellet applications	A.R.M. Loxahatchee	Maffei, 1991
hexazinone	**Velpar**	injection	south Florida	Laroche, 1993
hexazinone		strip	M.E. Thompson Park	Laroche et al., 1992
hexazinone		foliar	Lake Okeechobee	Stocker and Sander, 1981, 1997
hexazinone		pellet applications	Lake Okeechobee	Stocker and Sander, 1981, 1997
hexazinone		cut/stump	Lake Okeechobee	Stocker and Sander, 1981, 1997

Active ingredient	Herbicide name	Method	Location	Citation*
hexazinone		disked + broadcast	Lake Okeechobee	Cofrancesco et al., 1995
hexazinone	**Velpar L**	girdle	south Florida	Timmer and Teague, 1991
hexazinone		foliar	south Florida	Timmer and Teague, 1991
hexazinone		cut/stump	south Florida	Timmer and Teague, 1991
hexazinone		drilling holes	south Florida	Timmer and Teague, 1991
hexazinone		soil	south Florida	Timmer and Teague, 1991
hexazinone		aerial	M.E. Thompson Park	Laroche et al., 1992
hexazinone		cut/stump	M.E. Thompson Park	Laroche et al., 1992
hexazinone		frill and girdle	M.E. Thompson Park	Laroche et al., 1992
hexazinone		basil soil	M.E. Thompson Park	Laroche et al., 1992
hexazinone		girdle	East Everglades	Molnar et al., 1991
hexazinone		cut/stump	East Everglades	Molnar et al., 1991
hexazinone	**Velpar ULW**	broadcast	M.E. Thompson Park	Laroche et al., 1992
hexazinone	**not reported**	frill and girdle	Big Cypress NP	Burkhead, 1991
2,4-D	**2,4-D**	girdle	south Florida	Timmer and Teague, 1991
fluridone	**Sonar**	girdle	south Florida	Timmer and Teague, 1991