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Melaleuca in Florida: A literature review on the taxonomy, distribution, biology, ecology, economic importance and control measures

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Abstract

Melaleuca (*Melaleuca quinquenervia* (Cav.) S.T. Blake) is a large tree species that occurs naturally throughout eastern Australia, New Caledonia, Irian Jaya and southern New Guinea. In North America, melaleuca has primarily infested 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 has been recorded from Louisiana, Texas and California. Additionally, this tree has become moderately invasive in Puerto Rico and Hawaii. Melaleuca rapidly invades moist, open habitats, both disturbed and undisturbed, and forms dense, impenetrable monocultures. In general, invasion is less prominent in 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. Various methods of control (chemical, mechanical, manual, biological and integrated) are evaluated.

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

Taxonomy

Taxonomic position

Melaleuca quinquenervia (Cav.) S.T. Blake goes by numerous common names: melaleuca, bottlebrush tree, broad-leaved paperbark, cajeput, niaouli, paperbark, and punk tree (Craven 1999, Godfrey and Wooten 1981, Holliday 1989, Long and Lakela 1971, Nelson 1994). The scientific epithet *Melaleuca leucadendron* (L.) L. is considered misapplied (Blake 1968). The genus Melaleuca is a member of the Myrtaceae, the myrtle family.

In the family Myrtaceae, about 130 genera and 3,000 species have been recorded (Stebbins 1974, Watson and Dallwitz 1992). Members of this family occur in temperate, sub-tropical, and tropical regions, however, the family is centered in Australia and tropical America (Watson and Dallwitz 1992). The family Myrtaceae is comprised of trees and shrubs with simple leaves, these mostly entire, usually evergreen, commonly opposite, or more rarely alternate (Long and Lakela 1971, Mabberley 1997). Plants in this family are noted for their spicy, aromatic odor caused by ethereal oils and for the presence of numerous stamens in the flowers (Gentry 1993, Tomlinson 1980, Zomlefer 1989). Two subfamilies are traditionally distinguished in Myrtaceae: Leptospermoideae and Myrtoideae (Mabberley 1997). Leptospermoideae has dry, woody fruit (capsules) and opposite or spirally arranged leaves and is found mostly in the Southern or Eastern Hemisphere with the main center of distribution in Australia. Myrtoideae, in contrast, has usually fleshy fruit and always opposite leaves, with main concentrations of this subfamily in tropical America as well as in the South Pacific.

The family Myrtaceae is found naturally in the eastern United States only in subtropical Florida, with eight native species of the Myrtoideae represented in the genera *Calyptranthes* (2 spp.), *Eugenia* (4 spp.), *Mosiera* (1 sp.), and *Myricanthes* (1 sp.) (Tomlinson 1980, Wunderlin

1998). An additional 11 species of the myrtle family have been introduced, in the genera *Callistemon* (1 sp.), *Eucalyptus* (3 spp.), *Eugenia* (1 sp.), *Melaleuca* (1 sp.), *Psidium* (2 spp.), *Rhodomyrtus* (1 sp.), and *Syzigium* (2 spp.) (Wunderlin 1998, Wunderlin and Hansen 2000). These introduced species represent both subfamilies; *Melaleuca* is in the subfamily Leptospermoideae.

Taxonomic features

The genus *Melaleuca* consists of about 230 species. Fifteen species of tropical and subtropical tree species of *Melaleuca* have collectively become known as the *Melaleuca leucadendra* group, or the broad–leaved paperbarks (Craven 1999). *Melaleuca quinquenervia* is distinguished as a separate species within this group through the following key features: the secondary venation on the older leaves are more or less obscure, the young shoots of the plant have at least some spreading-ascending to spreading hairs, the inflorescence is more than 30 mm wide, the inflorescence axis is pubescent, the hypanthium is 1.5 to 2.5 mm long, and the petals are 2.5 to 3.5 mm long (Craven 1999).

Melaleuca is a large, evergreen tree, up to 33 m tall, with drooping, irregular branches. Trees are slender, branched, with somewhat columnar crown. The bark is thick, spongy, whitish at first, exfoliating in pale cinnamon-colored, papery layers that can be easily pulled apart. The bark comprises approximately 15 to 20% of the stem volume. The distinctly aromatic leaves are mostly 4 to 12 cm long, simple, narrowly elliptic to lanceolate-elliptic with the principal veins parallel; they are very short petiolate and arranged in five spiral rows. Leaf blades are at first densely pubescent, becoming glabrous with age; their color is dull green on both surfaces, dotted with reddish punctuate glands. The flowers are crowded in terminal spikes or panicles of spikes on woody axes. Stamens are especially numerous, in five bundles opposite the petals, and conspicuous, giving the inflorescence a “bottle-brush” appearance. Sepals, five, are about 2 mm long, obtuse. Petals, five, are 3 to 4 mm long, white, obovate to orbicular. The 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. The seeds are many, reddish brown and somewhat lustrous, asymmetric, long angular and vary in shape and size within a single capsule, 0.5 to 1 mm long. The physical description of melaleuca presented here is based on Chiang and Wang (1984), Godfrey and Wooten (1981), Langeland and Burks (1998), Long and Lakela (1971) and Woodall (1982).

Biology

Morphology

Melaleuca plants in Florida have an average height from 15 to 21 m (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 the bole (Hofstetter 1991). The root systems are 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, allowing it to readily transport oxygen to the inundated portion of the tree through abundant aerenchyma found in these roots (Gomes and Kozlowski 1980, Meskimen 1962).

Phenology

In Florida, melaleuca is able to produce flowers throughout the year (Hofstetter 1991, Long and Lakela 1971); however, its main flowering periods are in fall and winter (Van et al. 2002). In a recent 2-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 forests during the summer months of May to August (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 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).

Flower and Fruit Production

In Florida, melaleuca trees can become reproductive within a year of germination and may flower profusely within 3 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). Melaleuca trees in Florida are known to be self-compatible and autogamous, but their flowering system also promotes 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.

Seed Production and Dispersion

After flowering, 30 to 70 sessile seed capsules are formed on the twig and each seed capsule contains, on average, 264 seeds (Alexander and Hofstetter 1975, Meskimen 1962). The profuse flowering 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 per cluster are threefold less on trees from Australia (Rayachettry et al. 2002b). Melaleuca seeds are small, averaging about 30,000 seeds per g and vary in size, shape and weight (Meskimen 1962, Woodall 1982). A mean length and diameter of 1.20 mm and 0.26 mm, respectively, have been reported for melaleuca seeds (Rayachhetry et al. 1998).

The rapid colonization by melaleuca is facilitated by its profuse seed production. 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 fire, bole girdling or stem damage, all which interrupt vascular activity, resulting in massive, synchronous seed releases (Rayachhetry 1998). A single tree, when stressed, may release as many as 20 million seeds at one time (Woodall 1981b).

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). Hartman (1999) theorized that the high germination rate of melaleuca seeds that float might be an important dispersal strategy for high water conditions. The majority of melaleuca seeds, however, 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 (Browder and Schroeder 1981). No native small mammals or birds are suspected of dispersing the seeds via frugivory (Hofstetter 1991). Meskimen (1962) suggested transport of seeds on the bodies of birds may be a possible dispersal mechanism.

Seed Banks, Viability and Germinability

Due to the light, continuous seed release of the melaleuca tree, fresh seeds lying on the ground are always present. 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}. Melaleuca's profuse seed production and its ability to hold seed capsules for several years on the tree contribute 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 human-induced control activities kill seed trees or large seed-bearing branches are shed. Rayamajhi et al. (2002b) estimated the above ground seed bank of a 21 m high tree in Florida could contain up to 100 million seeds per tree. In a study of south Florida seeds, 15% of the seeds were found to contain embryos (Rayachhetry et al. 1998); these seeds, 62% were viable, and of the viable seeds, 73% germinated in greenhouse conditions after 10 days. Rayachhetry et al. (1998) theorize that the remaining 27% of the viable seeds that did not germinate after 10 days may be exhibiting dormancy. Based on these studies, a hypothetical 21 m tall tree in Florida with 100 million seeds per tree could have 9 million viable seeds. In Australia, the number of viable seeds per cluster was 7.5 times less than in south Florida (Rayamajhi et al. 2002b).

A saturated soil surface is needed for germination (Woodall 1978) and 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 in inundated conditions can resist wetting and 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 et al. (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).

Melaleuca seeds can remain viable for at least 10 months and up to 2 years in the soil (Rayamajhi et al. 2002b, Wade 1981, Woodall 1983). Germination and viability of seeds decrease significantly with capsule age (Meskimen 1962, Rayachhetry et al. 1998). Results of a seed burial test showed that seed viability was reduced by about 50% after 8 months in soil (Bodle and Van 1999). Seeds can survive submersion in water up to 6 months and still be viable and germinate (Meskimen 1962); however, after 1.0 year, the submersed seeds loose viability (Myers 1975).

The seeds of melaleuca show very little or no 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."

Vegetative reproduction and resprouting

Melaleuca stumps sprout or 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 a destroyed apical bud. A tree that is uprooted and on the ground may develop into a row of 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).

Perennation

Melaleuca exhibits two modes of perennation: seed dormancy and evergreen growth. Year-long leaf retention coupled with south Florida's year-round growing season, allows melaleuca to continue growing throughout the year. 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, which exhibited no signs of senescence. This author has personally observed about a dozen melaleuca trees at Koreshan Park, which are the remnants of the original plantings in 1912. These trees would now be 90 years old and are still fertile. 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 one of the major factors in the persistent spread of melaleuca in Florida.

Intraspecific variation

Hofstetter (1991) suggested possible genetic differences among the melaleuca populations present in Florida. His speculation was based on melaleuca's ability to invade so many different habitats. The genetic differences may have originated from multiple genetic 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 southeast and southwest subregions of Florida (Hofstetter 1991). 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 (1991) assumptions of genetic differences among melaleuca populations in Florida may have been correct. Recent greenhouse and laboratory studies have since demonstrated phenotypic and genetic variations in melaleuca (Center et al. 1999a, Kaufman 1999, Kaufman and Smouse 2001, Wheeler et al. 2002).

Greenhouse experiments conducted by Kaufman (1999) indicated a possible genetic component to differences found among four south Florida melaleuca populations. This author speculated that small genetic differences among populations might enable better performance by individuals under particular environmental conditions. The phenotypic plasticity of the species was thought to be even more important for adaptation under highly variable field conditions, such as varying water levels and pH. Kaufman (1999) also found that certain traits seemed to follow a latitudinal gradient, with increases in leaf width and plant height from south to north distribution of melaleuca in Florida. Kaufman and Smouse's (2001) greenhouse experiments have further supported Hofstetter's (1991) earlier ideas about genetic variation and phenotypic plasticity among melaleuca populations in Florida. The authors compared seedlings grown using seeds collected from three Australian, two east Florida and two west Florida populations of melaleuca. Overall, Australian samples had higher among-population familial variation than those from Florida. This was attributed to a longer time available for evolutionary changes in Australia compared to Florida. However, the Australian populations sampled had less phenotypic plasticity in response to both pH and water effects than the Florida samples. The Florida populations may have experienced founder effects, arrived with greater plasticity abilities, or there may have been "subsequent adaptive evolution of phenotypic plasticity in Florida populations" (Kaufman and Smouse 2001). Other researchers have also found differentiation within Florida melaleuca populations based on isozyme and chemotype analyses (Center et al. 1999a, Wheeler et al. 2002).

These greenhouse and laboratory research indicate phenotypic and genotypic plasticity's important role in adaptability of Florida's melaleuca populations. Reliable scientific information on genotypic and phenotypic differences of melaleuca populations, both in Florida and Australia, is important in developing effective control methods to contain this species.

Ecology and invasion of natural areas

Geographic distribution

Melaleuca quinquenervia 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, this species 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 and Hansen (2000) have 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 biannually from 1993 to 1999 indicate that the general distribution of melaleuca in Florida centers around the areas of original introduction, primarily southwest Broward and northern Dade Counties on the east coast and southern Lee County and northern Collier County on the west coast (Ferriter 1999). In other areas of the continental

United States of America, melaleuca is present as an ornamental and may have naturalized to a small extent in California and Texas (Geary and Woodall 1990, Kaufman 1999, Morton 1966), Louisiana (USDA 2001) and possibly Georgia (Center pers.comm.[2]).

In the eastern United States, melaleuca invasion may have the potential to spread farther north than its current range. The center of melaleuca distribution in Florida is around latitude 26 º N (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 º S and is in areas considered tropical and subtropical with a subtropical humid or tropical humid climate. Both of these regions in Florida and Australia experience wet summers, dry winters and frequent fires (Turner et al. 1998). With the assistance of climatological 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.[2]). Woodall (1978), without the aid of models, came to the 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 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 in Hawaii (Geary and Woodall 1990, HEAR 2000, Kaufman 1999, Sherly 2000, USDA 2001). Melaleuca is also considered moderately invasive in Puerto Rico (Geary and Woodall

1990, Kaufman 1999, 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 and Falanruw 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), and in the U.S. territory of Guam where it has been listed as a moderate invader (PIER 2001, Sherly 2000). More recently, it has been documented as a potential invader in Hong Kong (Hau 2001).

Additional areas where melaleuca occurs outside its native range include Mexico (Sanchez-Silva pers.comm.[3]), Cuba (Thayer pers.comm.[4]), Jamaica (IABIN 2002), and the Bahama Archipelago, which consists of the islands of the Bahamas, and the Turks and Caicos (Correll and Correll 1986). In the Bahamas, melaleuca is reported from Exuma, New Providence, Andros, and Grand Bahama. However, with the exception of the Northwestern Islands, it is considered unlikely for melaleuca to extensively invade many of these areas because of the salinity of the marshes and ponds in the Southern Islands (Hammerton pers.comm.[5]).

History of Florida Introduction

Melaleuca was first offered for sale in Florida in 1887 by Royal Palm Nurseries located in Oneco, Manatee County, and was sold by this nursery from 1887 to1889 and 1913 to 1933 (Dray unpublished[6)]. Within the subsequent forty years, at least ten more introductions occurred in Florida from botanical gardens in France, Italy, and Australia and from plantations in Australia (Pritchard 1976). Henry Nehrling planted seeds in his garden near Orlando around the turn of the 20th century (Meskimen 1962), and John C. Lange also claims to have made an early introduction of melaleuca in Davie in the beginning of the 1900's (Dray unpublished[6]). Even with these previous importations, John C. Gifford, a professor of Tropical Forestry at the University of Miami, is often given credit (and indeed gives himself credit) for being the first to establish the species in south Florida (Gifford 1972). While not the first to introduce melaleuca, he certainly brought much attention to the tree. He received seeds in 1906 from Sydney, Australia, and later planted his seedlings along Biscayne Bay (Gifford 1972). Specimens or seeds were given to Frank Stirling, a local grower, who owned Stirling and Sons Nursery in Davie, Broward County, Florida (Meskimen 1962). In 1912, 25 years after Royal Palm Nursery began selling melaleuca on the west coast and 6 years after Gifford received his seeds, 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, 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 growers who dug up saplings from the west coast populations and propagated them for sale as ornamental landscape plants. The populations south of Lake Okeechobee began to arise in 1941 when trees were planted on levees and spoil islands for erosion control by the US Army Corps of Engineers (Stocker and Sanders 1981). For years, 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).

Habitat requirements

Climate: 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 of melaleuca in Australia, is climatically similar to New Orleans. Both are classified as "Caf” climatic types, characterized by 1) rainy climates and mild winters, 2) coolest month above 0 C but below 18 C, 3) warmest month above 22 C, and 4) constantly moist conditions with rainfall of 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 that have a "Caw" type of climate, which is similar to the “Caf” type of climate except it has a 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 in Florida 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 in Highlands County where temperatures reached –5 C and remained below 0 C for several hours (Center pers.comm.[2]). Following the Highlands County freeze, melaleuca trees throughout the area were severely affected. Many were completely defoliated and appeared dead for several weeks. However, epicormic sprouts developed even on severely damaged trees, most of which recovered over time (Center pers.comm.[2], 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 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 C to -6.6 C, which includes significant portions of the Gulf Coast of Louisiana and Texas. In Hawaii melaleuca occurs in areas with mean annual temperatures from 18 C to 24 C and grows from sea level to 1,400 m (4,500 ft) elevation (Geary and Woodall 1990). Most of southern Florida, where melaleuca readily invades, is less than 8 m (25 ft) above sea level (Geary and Woodall 1990).

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 readily survives on acid sands, organic soils, alkaline marls, and limestone of varied thickness (Hofstetter 1991). In order to establish, 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 has been observed in mangrove zones in Florida (Hofstetter 1991, Woodall 1981b). However, growing conditions for melaleuca in saline zones of Florida are not optimal (Woodall 1981b). Plants can tolerate a pH of 4.4 to 8.0, which encompasses 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 melaleuca's native habitat, Australia, the soil pH is usually 6 or less. Its ability to root deeply allows melaleuca to extract leached nutrients at the water table and therefore thrive in low-nutrient surface soils (Woodall 1981b). Seedlings grow poorly in low-nutrient soil conditions unless recent fires have caused nutrient release from the surface litter (Woodall 1981b, Wade 1981).

Invaded communities: Melaleuca has invaded virtually all types of terrestrial or wetland plant communities and conditions in south Florida, including those where vegetation appears to be healthy and presumed to be comparable to historical vigor (Hofstetter 1991, Woodall 1981b). Melaleuca has been documented from 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). Melaleuca does not typically invade dense tree stands; rather it invades open-canopied forests, sparsely vegetated ecotones, wetland prairies and marshes, and fire-damaged forests (Geary and Woodall 1990). The xeric communities such as scrub land tend to be resistant, but not immune to infestation by melaleuca (Bodle et al. 1994). Only dense hammock-type communities seem to produce enough shade to prevent melaleuca invasion (Woodall 1981b).

Population dynamics

The establishment of melaleuca in Florida has been much more rapid and robust than what is commonly seen in Australia (Rayamajhi et al. 2002b). In its native range, melaleuca is found in low-lying areas that are periodically swept by fire (Laroche 1999a). Low areas and frequent fires are also conditions commonly found in south Florida, making it especially suitable to the establishment of this species. These conditions in conjunction with human interference of natural systems, melaleuca's biological attributes, and the lack of natural enemies are responsible for this tree's explosive invasion of Florida habitats (Hofstetter 1991, Kaufman and Smouse 2001, Turner et al. 1998).

Melaleuca infestation results in a strong shift in the structural and biological attributes of south Florida wetland habitats. As melaleuca invades a wetland marsh, it changes the system from one with low structural diversity into a savannah with temporarily greater structural diversity. Over time, this transitional stage changes into a closed canopy of melaleuca forest with a sparse understory and low structural diversity (O'Hare and Dalrymple 1997). These melaleuca forests are often very dense and monocultural, which greatly influences many attributes of the ecosystem (Schmitz and Hofstetter 1999). The differences in species composition and structure are remarkable, and the pace of invasion of new areas is rapid. Laroche and Ferriter (1992) performed a time series analysis of the invasive capacity of melaleuca. They reported that once an infestation of melaleuca reached 5% in a 259 ha area (1.0 square-mile), it will take approximately 25 years for 95% infestation to occur within that same area.

Because of massive seed release from mother trees, extremely dense, even-aged stands are common, on the order of over 250,000 trees ha^{-1}, each tree 3 to 4 m high (Alexander and Hofstetter 1975). As these dense stands mature, intraspecific competition reduces the stand density to approximately 5,000 trees ha^{-1}, with each tree about 12 m high (Hofstetter 1991). Recently sampled stand densities in dense, pure stands ranged from 11,450 to 36,275 trees ha^{-1} (Van et al. 2002) and from 8,000 to 132,200 trees ha^{-1} (Rayachhetry et al. 2001b) with the range largely depending on site suitability.

Mature melaleuca trees are considered to be intolerant of 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 seedling development will occur in shade. In 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 possible changes in evapotranspiration rates caused by increased leaf area of melaleuca trees relative to typical vegetation found in wet prairies (Allen et al. 1997) and shading effects, dense melaleuca forests may have a long-term impact on soil decomposition rates (Schmitz and Hofstetter 1999) as well as fire regime and fire intensity (Flowers 1991). When melaleuca trees displace the vegetation in a wetland marsh or prairie, the ground-fire fuel load is changed; a result of a continuous rain of litter from melaleuca canopy resulting in a rich layer of undecomposed leaf litter on the forest floor (Flowers 1991), which is quite different from the rapid litter decomposition in a marsh or prairie. Melaleuca's hotter burning 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, Myers 1983). The seed rain from intense fires produces dense, even-aged melaleuca stands estimated to contain from 19,000 to 40,000 saplings ha^{-1} (Meskimen 1962, Hofstetter 1991). Seedlings, on the other hand, are 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 seedlings are more commonly found in low 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 seedlings do have the capacity to withstand typical flooding events in south Florida. Most germinants, however, 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).

Biomass production and litterfall

A study published by Conde et al (1981) estimated standing crop biomass values for melaleuca in south Florida from 122 to 170 dry metric tons ha^{-1} (dry mt ha^{-1}). 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^{-1}. 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 reported that dbh alone is a good allometric predictor for estimating dry above-ground biomass of whole tree as well as of the individual components (trunk, branch, leaf, seed capsule and seed) (Rayachhetry et al. 2001b, Van et al. 2000). The total proportion of wood in the biomass increases with increasing values of dbh (Rayachhetry et al. 2001b), and the proportion of wood in the total 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 melaleuca litterfall in south Florida ranges from 6.5 to 9.9 t dry wt ha^{-1} yr^{-1} (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 ha^{-1} yr^{-1} at two sites of seasonally inundated forests in subtropical southeastern Australia. Greenway found higher productivity at seasonally flooded sites similar to the conclusions reported by Van. et al. (2002) in south Florida. On average litterfall in Florida is composed 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, litterfall in Australia is composed of 67% leaf fall, 17% twigs, 6% bark, 6% flowers and 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 five seedlings (average height of 1 m) on a mixed cypress-pine site in southwest Florida. The growth rates of these seedlings ranged from 33 cm yr^{-1} to 90.5 cm yr^{-1} with an overall average of 55 cm yr^{-1}. Meskimen felt that the difference in the growth rates of the five 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 m (Alexander and Hofstetter 1975). Clearly, additional research on melaleuca productivity across various environmental gradients need further investigation. This is important to determine what, if any, implications this variation may have on effective management of this species.

Economic Importance

Beneficial Effects

In some parts of its native range, melaleuca 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 and proposed that there would be an economic incentive to harvest exotic, invasive plants if an antibiotic or other drug were developed. Cochrane's (1999) study exhibited antibacterial and antifungal activity of melaleuca oil, but 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 1980 and 1981, Timmer and Teague 1991). The reasons for these investigations were to find a way to offset the costs of controlling melaleuca. Melaleuca was found suitable 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 1980 and 1981). However, Geary and Woodall (1990) in their silvicultural review of melaleuca 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 in Florida 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).

Using melaleuca to generate 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. According to Tufts (1991), "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 net value of the wood would be less when compared to the cost of the sensitive methods required when removing melaleuca in the Everglades. In addition, Geary et al. (1981)

pointed out that it is more difficult to use melaleuca biomass as a source of fuel than most other species because of its powdery, low-density bark.

One of the often noted benefits of melaleuca in Florida is to the apiary industry (Balciunas and Center 1991, Morton 1966, Robinson 1981, 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 scarcity (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 product (Balciunas and Center 1991, Morton 1966, Robinson 1981, 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. They also noted that while beekeepers pay rent to place beehives in citrus groves, none pays rent to place hives in melaleuca stands. Robinson (1981) conceded that the dollar value of melaleuca honey is a relatively unimportant share of total production of honey in Florida.

Detrimental Effects

Melaleuca is an aggressive, invasive weed in south Florida (Bodle et al. 1994). Habitat loss due to melaleuca invasion in southern Florida has been estimated to be 0.2 to 0.61 million ha out of a total 3.04 million ha surveyed (Bodle et al. 1994). These authors have also suggested that many remaining natural areas would be overtaken by uncontrolled growth of melaleuca within 30 years. Laroche (1999c) reported that melaleuca control costs for the South Florida Water Management District alone for the time period between 1991 and 1998 was approximately $13 million. An estimate of total expenditures that included biological, mechanical, chemical and mechanical control by participating agencies in south Florida amounted to $25 million for the ten years of reporting time of the Melaleuca Task Force (Laroche 1999a).

The potential economic impact of melaleuca's rampant invasion of south Florida has been reported by many who are concerned with the problem (Balciunas and Center 1991, Diamond et al. 1991, Schmitz and Hofstetter, 1999). In a report by Diamond et al. (1991) 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 negative impact to south Florida's economy would be around $168 million annually. Balciunas and Center (1991) reported that by the year 2010, close to $2 billion would be lost due to various problems related to the expansion of melaleuca in south Florida. The financial losses in this calculation included $1 billion 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. Their claim of financial losses due to fires has been substantiated by Diamond et al. (1991), Flowers (1991), and Wade (1981) who all discussed the difficulty in controlling the intense fires associated with melaleuca and the resultant economic losses to fire departments and property. Other possible economic losses for which no dollar amount was given were related to increased water loss, storm flow and irrigation, and medical expenses incurred due to allergies and other physical injuries. Diamond et al. (1991) estimated that as much as 20% of the population in south Florida is allergic to melaleuca, and Morton (1966) called it "a prime respiratory irritant in south Florida". However, a recent medical study found no significant aeroallergen properties of melaleuca or evidence that odors from the flowers, bark, leaves or oils were respiratory irritants (Stablein et al. 2002). 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.

Additionally, 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). Fewer wetland species such as crayfish, grass shrimp and fishes are found in these dense stands as compared to the wetlands replaced by the stands (O'Hare and Dalrymple 1997). The only wildlife that seem to be able make some use of the stands were found to be upland birds and a mix of wetland and upland mammals. 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. These researchers have suggested that dense melaleuca stands would eventually eliminate adjacent essential wildlife habitats.

Control measures

Legislative

Melaleuca is a regulated plant on the Federal Noxious Weed List, USDA, 7 CR-360 (Plant Protection and Quarantine 2000). A "noxious weed" 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. These plants are prohibited from importation and interstate transport without a special permit.

The Florida Department of Environmental Protection (FDEP) regulates melaleuca as a Class 1, Prohibited Aquatic Plant, pursuant to Chapter 62C-52 (FDEP 1996). These plants are prohibited for possession, collection, transportation, cultivation and importation except with a special permit issued by FDEP. 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 (FDACS 1996), which defines a noxious weed 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. According to this rule, it is unlawful to introduce, possess, move, or release any noxious weed except under permit issued by FDACS.

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 that regulate invasive plants was included for the 16 counties within the boundaries of the South Florida Water Management District (Doren et al. 2000). According to this account of local regulations in south Florida ten counties and municipalities regulate melaleuca.

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 (NCDA 1996). A Class A noxious weed in North Carolina 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. The South Carolina Department of Agriculture also regulates melaleuca as a noxious weed under Title 46, Agriculture, Chapter 23, Noxious Weeds, which defines a noxious weed 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).

Chemicals

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 release from treated trees (Molnar et al. 1991). Woodall's (1981a) methodology incorporated retreatment using either prescribed burning or manual removal of 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 stands as funding allows (Laroche et al. 1992, Laroche 1998a, Maffei 1991, Molnar et al. 1991).

Use of herbicides remains the primary, practical and cost-effective control method for managing melaleuca. A variety of herbicide treatments have been tried on melaleuca with varying success. In general, herbicide treatments are more effective on melaleuca seedlings than on mature trees. "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" (Langeland 1990a). Individual treatments of target trees, using girdling or cut-stump methods, results in the most effective kill rate with the least non-target damage (Laroche 1998a). Laroche (1993), in an attempt to find an effective delivery system for sensitive natural areas, used a plug injection system to inject herbicide directly at the cambial region of the tree, which allowed use of 3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione (hexazinone) in areas with standing water. All these individual-tree efforts were labor-intensive, costly and time consuming, and are not widely used to treat dense stands of mature melaleuca. Pure melaleuca stands are treated using aerial application method, which is more cost-effective (Langeland 1990a, Laroche 1998b, Turner et al. 1998). This method has the disadvantage of causing some non-target damage; however, it has the advantage of quickly treating large areas of infestations and multiple trees with each application (Laroche 1998a, Turner et al. 1998). Laroche (1998a), based on personal observations, suggested 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 effective time for herbicide treatment in melaleuca control is during late winter and early spring when the plants are most actively growing.

Historically, hexazinone and *N*-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]-*N,N'*-dimethylurea (tebuthiuron) have been used successfully for controlling melaleuca (Burkhead 1991, Cofrancesco et al. 1995, Laroche et al. 1992, Maffei 1991, Molnar et al. 1991) and indeed these herbicides are considered to be the most effective in melaleuca control (Laroche 1999b). Aerial application of both tebuthiuron and hexazinone on melaleuca stands resulted in up to 100% seedling and over 80% mature tree mortality (Stocker and Sanders 1981, 1997). However, tebuthiuron and hexazinone are no longer allowed to be applied directly to water in Florida (Laroche 1998a). Tebuthiuron was taken off of the Florida market altogether in 1993. 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 manufacturer for this herbicide requested that the state cancel the SLN Label (Laroche 1999b).

Isopropylamine salt of 2-[4,5-dihydro-4-methyl-4-(1-methylethyl)-5-oxo-1H-imidazol-2-yl]-3-pyridinecarboxylic acid (imazapyr), isopropylamineamine salt of *N*-(phos-phonomethyl) glycine (glyphosate) and triethylamine salt of 3,5,6-trichloro-2-pyridinyloxyacetic acid (triclopyr) have also been found to be effective on melaleuca (Laroche 1999b). Imazapyr has a SLN 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 1999b). A full aquatic label for imazapyr is expected within the next couple of years. Imazapyr herbicide in a 50% solution with water, has proven to be consistently effective and can be used in flooded areas (with SLN Label); it is now used widely both in ground and aerial control of melaleuca (Bodle et al. 1994, Laroche 1999b). Imazapyr is very effective on a fresh wound created by girdling to cambium layer (Timmer and Teague 1991) and on freshly cut stumps (Stafford 1999). Other field studies by Laroche et al.

(1992), Laroche (1998b), Maffei (1991), Pernas et al. (1994), and Pernas and Snyder (1999) supports imazapyr's effectiveness in melaleuca control. Laroche et al. (1992) have also shown imazapyr to be moderately effective when mixed with glyphosate in aerial applications (63% mortality after 18 months with no follow-up). In light of the unavailability of hexazinone as an aerial application technique, Laroche (1998a) recommends a combination of imazapyr at 1.68 kg ha^{-1} ai and glyphosate at 3 kg ha^{-1} ai applied with a methylated seed-oil surfactant in a total volume of 144 to 188 l ha^{-1}. Glyphosate, when applied undiluted, has shown good control in both cut-stump (ca 85%) and girdling techniques (ca 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).

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 (Belle et al. 1999, Coladonato 1992). According to Belle et al. (1999), the most successful timing for prescribed burning is late wet season when the water table is at or near the surface to induce seed germination so that the majority of seedlings die during the ensuing dry season, or immediately after the onset of consistent summer rains to allow seed germination and consequent submergence of seedlings for an extended period to lessen their chances of survival. Both of these optimal burning conditions are possible during normal seasons. Normal seasons are not always present so a resource manager must be prepared to follow-up these burn scenarios with herbicide treatment of post-emergent seedlings. In addition, a certain percentage of seeds and seedlings will survive prolonged exposure to droughts and flooding. A better strategy is to get seeds on the ground while ground cover is still intact providing a fuel load. This could be achieved through herbicide treatment or felling trees first to get the mature trees to release seeds and then monitor for seedling emergence. Controlled burning while the seedlings are still small would most likely kill all seedlings (Belle et al. 1999). Seedlings that are less than 3 to 6 months old or only 10 to 20 cm high 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 melaleuca seeds, seedlings and mature trees have the ability to withstand prolonged periods of inundation. An increasing water level would have little effect on reducing the establishment success of melaleuca (Hartman 1999). The maintenance of extremely long periods of high water level may reduce seed germination and the number of seedling densities, but this alteration of water levels in natural areas may also have adverse affects on native plants and animals (Lockhart et al. 1999).

Mechanical and manual

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, Thayer 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). Manual removal of melaleuca is restricted to seedlings less than 2 m tall (Thayer 1999).

Biological Control

Mammals and 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.

Insects: In Florida, until relatively recently, melaleuca has been free of any insect enemies. This lack of insect herbivory has been postulated as one of the primary causes for its rampant expansion in Florida compared to its growth in its native 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 (Rayamajhi et al. 2002a). Surveys were conducted along the eastern shore of Australia, searching for biological control agents for melaleuca. Over 450 herbivorous insect species that feed on melaleuca have been collected in Queensland and northern New South Wales (Rayamajhi et al. 2002a). Studies conducted in the early 1990's showed that even low levels of insect herbivores would rapidly suppress growth of saplings (Balciunas and Burrows 1993). As a large number of insect herbivores are reported to damage melaleuca plants, many studies have ensued to look for host specific insects for biological control of melaleuca in Florida (Balciunas 1990, Balciunas and Burrows 1993, Balciunas and Center 1991, Balciunas et al. 1994). Two insect herbivores have been released in south Florida for biological control of melaleuca. The first insect, the melaleuca leaf weevil (*Oxyops vitiosa* Pascoe), was released in south Florida in 1997 (Center et al. 1999b), and the melaleuca psyllid (*Boreioglycaspis melaleucae* Moore) was released in spring 2002 (Pratt et al. 2002c). These two insects, as well as the defoliating sawfly (*Lophyrotoma zonalis* Rohwer), 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, Rayamajhi et al. 2002a). Other insects, which are being screened in Australia and Florida, are a bud gall fly (*Fergusonina* spp.) and its obligate association with the *Furgusobia* nematode (*Fergusobia* spp.) (Davies et al. 2001, Goolsby et al. 2000, Rayamajhi et al. 2002a), a tube dwelling moth (*Poliopaschia lithochlora* Lower) (Rayamajhi et al. 2002a) and a leaf-blotching mirid bug, (*Eucerocoris suspectus* Distant) (Burrows and Balciunas 1999, Rayamajhi et al. 2002a). Additional insects that are being researched in Australia include *Pomponatius typicus* Distant, *Lophyodiplosis indentata* Gagne (Turner et al. 1998), and *Gelechioidea* moths (Burrows et al. 1994).

The melaleuca leaf weevil has now been established in south Florida for close to 5 years. Results from the 1st year of establishment at 13 different release sites in south Florida led Center et al. (1999b) 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 the melaleuca leaf weevil is capable of increasing population densities at a rate comparable to that of other successful weed biological control agents (Pratt et al. 2002a). Pratt et al. (2002b) have now developed models that describe larval densities of the melaleuca leaf weevil that will fully exploit melaleuca foliar resources and this information may be useful to land managers when redistributing this biological control agent. The melaleuca leaf weevil larvae has the advantage of a defensive terpenoid secretion on the surface, which protects them against generalist predators such as the introduced fire ant (*Solenopsis invicta* Buren) and have contributed to its success in the field (Montgomery and Wheeler 2000, Wheeler et al. 2002). However, there are two disadvantages of the melaleuca leaf weevil as a control agent. The first is that its larvae are restricted to feeding on flush foliage with low toughness (Wheeler 2001) and the second is that the larvae pupates in the soil, which may restrict 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 the melaleuca leaf weevil was reduced by more than 90% (Center et al. 2000). Studies are now underway to find ways to mass-produce the melaleuca leaf weevil for wider distribution in the field (Wheeler and Zahniser 2001) and to collect additional populations of this insect in Australia (Madeira et al. 2001). The melaleuca psyllid is a good compliment to the melaleuca leaf weevil because its nymphs induce defoliation of older leaves and encourage sooty mold growth on their excreted honeydew, which may help reduce photosynthetic activity of the leaves (Rayamajhi 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).

Many resource managers have encouraged and supported research related to biological control agents and have hoped to incorporate this type of control into a integrated plan for management of melaleuca (Jones 1999, Timmer and Teague 1991, Pernas and Snyder 1999, Langeland 1990a and 1990b, Laroche 1998a, Woodall 1981a, Tufts 1991, Maffei 1991, Molnar et al. 1991). According to Balciunas and Center (1991), woody plant species such as melaleuca require a diversity of biocontrol agents, at least five 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 through biological control would enhance the overall efficacy of melaleuca control in Florida (Wineriter and Buckingham 1999).

Diseases: Fungal species on melaleuca and its close allies have been reported from Florida, Australia and other parts of the world (Rayachhetry et al. 1996d and 1996b, Rayamajhi 2002a). Six fungal species, *Fusicoccum* anamorph of *Botryosphaeria ribis* Gross & Duggar, *Puccinia psidii* G. Wint., *Fusarium sp*., *Pestalotiopsis sp*., *Phyllosticta sp*., and *Guignardia sp*. were found to be associated with melaleuca diseases (Rayachhetry et al. 1996d, 1997b and 1997a, 2001a, Rayamajhi et al. 2002a). *B. ribis,* a native canker fungus discovered from melaleuca, appears to be a wound and stress related pathogen that requires exposed sapwood or injury stresses in order to establish and cause disease on the stem (Rayachhetry et al. 1996d and 1996b). Once established, *B. ribis* can perpetuate in stem tissues and proliferate rapidly under stress conditions (Rayachhetry et al. 1996a and 1996c). Affected vascular tissue of plants usually appear brown to black and infected plants may manifest die back syptoms, show vascular wilt or crown thinning (Rayachhetry et al. 1996c). The use of *B. ribis* alone and in association with herbicides has been studied (Rayachhetry et al. 1997a and 1999). Preliminary research shows that *B. ribis* alone was less effective than the herbicide alone and that mixtures of this fungus with a low rate of imazapyr was comparable to the higher rate of the herbicide alone (Rayachhetry et al. 1999). *P. psidii,* an exotic pathogen originally from South and Central America, has also been studied and has been shown to vigorously attack growing melaleuca branch tips (Rayachhetry et al. 1997b and 1997a). The relationship between *P. psidii* and melaleuca appears to be new and may contribute to future control of melaleuca (Rayachhetry et al. 2001a). 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 useful when applied in conjunction with other control measures. Additional research will be needed to develop these 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 useful in integrated management of melaleuca.

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Footnotes

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