SPECIES: Melaleuca quinquenervia

INTRODUCTORY

SPECIES: Melaleuca quinquenervia

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Munger, Gregory T. 2005. Melaleuca quinquenervia. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: http://www.fs.fed.us/database/feis/ [2007, September 24].

FEIS ABBREVIATION:
MELQUI

SYNONYMS:
None

NRCS PLANT CODE [98]:
MEQU

COMMON NAMES:
melaleuca
cajeput
paperbark tree
punktree

TAXONOMY:
The currently accepted scientific name for melaleuca is *Melaleuca quinquenervia* (Cav.) S. T. Blake (Mytraceae) [9,30,31,37,41,42,94,115,116].

Turner and others [96] provide a brief review of the *Melaleuca* genus in Australia, indicating that all known *Melaleuca* spp. (up to 250) are native, and all but 9 are endemic. Boland and others [9] suggest there are about

150 described species of *Melaleuca.*

The name melaleuca is of Greek origin, meaning "black and white", presumably referring to the white bark that is often charred black by fire (Debenham 1962 as cited in [96].

LIFE FORM:
Tree
Tree-shrub

FEDERAL LEGAL STATUS:
Noxious weed [97]

OTHER STATUS:
Florida Department of Environmental Quality lists melaleuca as a Class I Prohibited aquatic plant ("under no circumstances...permitted for possession, collection, transportation, cultivation, and importation...") [27].

DISTRIBUTION AND OCCURRENCE

SPECIES: Melaleuca quinquenervia

- GENERAL DISTRIBUTION
- ECOSYSTEMS
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- BLM PHYSIOGRAPHIC REGIONS
- KUCHLER PLANT ASSOCIATIONS
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- SRM (RANGELAND) COVER TYPES
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GENERAL DISTRIBUTION:
Melaleuca is native to eastern Australia, New Caledonia, southern New Guinea, and adjacent Indonesia [9,41,42]. In Australia it occurs from Sydney to Cape York, usually within 25 miles (40 km) of the coast [9]. Melaleuca forests in the coastal lowlands of southeastern Queensland, Australia, have been severely reduced in recent decades due to development and are now being conserved [33].

In the continental United States, melaleuca is apparently only invasive in southern Florida [30]. It has been planted on the island of Oahu in Hawaii [114], but its spread is minimal (Skolmen 1981 as cited in [30]). Several sources indicate that it may be grown as an ornamental in southern Louisiana, Texas, and California [41,42,107], and perhaps less commonly in Puerto Rico (Little and others 1974 as cited in [30]). As of this writing (2005), there are no published accounts of melaleuca escaping cultivation in the United States outside of Florida. Atlas of Florida Vascular Plants provides a county distribution map of melaleuca in Florida.

Melaleuca was probably first introduced to southern Florida during the late 1800s to early 1900s, at several different locations (review by [48]). Meskimen [48] provided a thorough review of its introduction and subsequent spread in southern Florida. Melaleuca can now be found in both central and southern peninsular Florida [115,116]. In southern Florida extensive stands generally occur along the coasts, inland from the large metropolitan areas of Palm Beach, Broward, and Dade counties in the east and Lee County in the west. The most extensive melaleuca stands are located near the sites of original introduction. These are also the areas that have been most severely altered by human activities and where melaleuca has been most widely planted for landscape purposes (see Other Uses) [23].

In central Florida melaleuca apparently spreads little, if at all. It is found mainly in and around urban areas [30].

Protected ornamentals have been noted in Alachua County (lat 29°30'N). Stands of escaped melaleuca are generally uncommon in inland areas farther north than Lake Okeechobee, although established melaleuca stands have been observed along lakeshores as far north as Orange County (lat 28°30'N) [52]. Northward migration of melaleuca in peninsular Florida is thought to be limited mainly by frost (see Site Characteristics) [24].

Because nearly all of the scientific literature and management concern is centered around melaleuca in peninsular Florida, the following biogeographic classification systems illustrate only where melaleuca might be found in peninsular Florida. A paucity of information about melaleuca distribution outside peninsular Florida precludes use of these lists for wider distribution information. Even within peninsular Florida, comprehensive distribution information is unavailable. Therefore, these lists are somewhat speculative and may be imprecise.

ECOSYSTEMS [29]:
FRES12 Longleaf-slash pine
FRES41 Wet grasslands

STATES/PROVINCES: (key to state/province abbreviations)
UNITED STATES

CA	FL	HI	IA	TX	PR

BLM PHYSIOGRAPHIC REGIONS [8]:
None

KUCHLER [39] PLANT ASSOCIATIONS:
K079 Palmetto prairie
K080 Marl everglades
K090 Live oak-sea oats
K091 Cypress savanna
K092 Everglades
K105 Mangrove
K112 Southern mixed forest
K113 Southern floodplain forest
K116 Subtropical pine forest

SAF COVER TYPES [26]:
70 Longleaf pine
71 Longleaf pine-scrub oak
73 Southern redcedar
74 Cabbage palmetto
83 Longleaf pine-slash pine
84 Slash pine
85 Slash pine-hardwood
89 Live oak
100 Pondcypress
101 Baldcypress
102 Baldcypress-tupelo
103 Water tupelo-swamp tupelo
104 Sweetbay-swamp tupelo-redbay
105 Tropical hardwoods
106 Mangrove
111 South Florida slash pine

SRM (RANGELAND) COVER TYPES [81]:

805 Riparian
806 Gulf Coast salt marsh
807 Gulf Coast fresh marsh
810 Longleaf pine-turkey oak hills
811 South Florida flatwoods
813 Cutthroat seeps
814 Cabbage palm flatwoods
816 Cabbage palm hammocks
817 Oak hammocks
818 Florida salt marsh
819 Freshwater marsh and ponds
820 Everglades flatwoods
822 Slough

HABITAT TYPES AND PLANT COMMUNITIES:
As of this writing (2005), there are no published accounts listing melaleuca as a climax dominant or indicator species in any habitat type classifications in North America. As Meskimen [48] emphasized, any descriptions of associations between melaleuca and other plant species in southern Florida should not necessarily be viewed as stable or well-defined communities. Nevertheless, such descriptions are valuable to illustrate native plant taxa and communities that may be at risk of melaleuca invasion (see Impacts).

Melaleuca is frequently mentioned in association with a variety of forested and nonforested native plant species and communities in southern Florida. Forested habitats include wet pine (*Pinus* spp.) flatwoods, depressions in drier pine flatwoods, disturbed cypress (*Taxodium* spp.) swamps, the ecotone between "dwarf" pondcypress (*T. ascendens*) and pines, and Miami rock ridge pinelands [25,30,51,53,84,104]. According to Geary and Woodall [30], melaleuca frequently occurs in southern Florida within the forest cover types [26] pond cypress, south Florida slash pine (*P. elliottii* var. *densa*), and to a lesser extent, baldcypress (*T. distichum*).

Nonforested communities in southern Florida are also subject to melaleuca colonization. Melaleuca invades sawgrass (*Cladium mariscus* ssp. *jamaicense*), freshwater marsh, wet prairie or marl prairie, and the herbaceous perimeter frequently found around pondcypress swamps [3,51,104]. According to Richardson [75], wet prairie St. Johnswort/pipewort (*Hypericum*/*Eriocaulon* spp.) communities where hydrology is altered by drought and/or human-caused drainage are particularly vulnerable. Geary and Woodall [30] suggested that "most shrub, herb, and graminoid species in southern Florida are likely to be found in association with" melaleuca. Common associates include saw-palmetto (*Serenoa repens*), pineland threeawn (*Aristida stricta*), wax-myrtle (*Myrica cerifera*), sawgrass, buttonbush (*Cephalanthus occidentalis*), and toothed midsorus fern (*Blechnum serrulatum*) [30].

John M. Randall/The Nature Conservancy

There are some accounts suggesting certain habitats are more susceptible to melaleuca invasion than are others. According to Myers and others [50,51,52], melaleuca is most likely to "displace native vegetation" in the ecotone between south Florida slash pine flatwoods and pond cypress forest (for further discussion about invasibility of the pine-cypress ecotone see Impacts), and around the edges of cypress (*Taxodium* spp.) domes and strands. Moist pine flatwoods in some areas of southern Florida have been "extensively" invaded by melaleuca, while more northern or drier flatwoods appear less vulnerable to invasion [1].

Melaleuca may establish extremely dense, even-aged, monospecific stands. Di Stefano [20] described melaleuca stands in southwestern Florida with >4,500 stems/ha of melaleuca, where the understory was quite sparse and consisted of occasional toothed midsorus ferns and cabbage palmettos (*Sabal palmetto*). Van and others [100] described the understory of dense, mature melaleuca forests as sparse, consisting of shade-adapted shrubs such as wax-myrtle and Guianese colicwood (*Myrsine guianensis*), ferns such as maiden fern (*Thalypteris* spp.) and osmunda (*Osmunda* spp.), sedges such as sawgrass, and various grasses.

There is some indication that melaleuca can colonize mangrove (*Rhizophora*, *Avicennia*, and/or *Laguncularia* spp.) and mangrove-associated communities. Richardson [75] indicated that melaleuca is salt tolerant and has "intermingled" with mangroves in some areas of southern Florida, and Hoffstetter [35] cited a personal communication (Taylor Alexander) indicating melaleuca tolerates "brackish sites" and will "grow in mangroves." Wade and others [104] pointed out that in its native habitats (see General Distribution and Site Characteristics), melaleuca sometimes forms a band of vegetation in the brackish areas just to the landward side of mangroves (unidentified taxa) (Coaldrake 1961, Coulter 1952, Williams 1967, as cited in [104]). In Florida this habitat is often occupied by buttonbush. Although Myers [50] was unable to experimentally induce melaleuca establishment in a mixed stand of white mangrove (*L. racemosa*) and red mangrove (*R. mangle*) in southern Florida, Wade and others [104] suggested that the buttonbush zone is susceptible to invasion.

Perhaps due to its prolific and ubiquitous nature in southern Florida, melaleuca-invaded habitat may increasingly garner unique status in various biogeographic classification schemes. For instance, Ewel [25] lists melaleuca swamp as 1 of 13 major types of Florida swamps. Characteristics of the melaleuca swamp-type include moderate hydroperiod
(6- to 9-month), high fire frequency (1/decade), low organic matter accumulation (<3.3 feet (1 m)), and shallow groundwater source.

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Melaleuca quinquenervia

GENERAL BOTANICAL CHARACTERISTICS:
Melaleuca is an evergreen tree of variable form and size. Crown form ranges from open to relatively slender with few branches, depending on stand density [9,31]. Plants may be multistemmed [54] or with a single, moderately straight trunk [9,31]. In its native range melaleuca commonly appears as a 26- to 33-foot (8-10 m) "tall shrub" on dry sites exposed to fires and prevailing winds. In wet plains it grows to a 66- to 98-foot-tall (20-30 m) tree with a well-developed trunk. At "higher altitude" it takes the form of a small shrub <3 feet (1 m) tall [94]. Geary and Woodall [30] indicate average height of trees in "mature" stands in Florida "swamps" ranges from 49 to 69 feet (15-21 m), with a maximum height of 98 feet (30 m). Branches are ascending on young trees, commonly somewhat drooping on older trees [31]. Twigs are long and slender, often drooping [9].

Leathery leaves are mostly 2 to 5 inches (4-12 cm) long and 0.4 to 2 inches (1-6 cm) wide, arranged in 5 spiral rows [9,31,42,94]. Van and others [100] estimated that leaf longevity was about 2 to 4 years, depending on overall growth rates.

Inflorescences are densely flowered spikes 1 to 4 inches (3-10 cm) long. After flowering, twigs continue to elongate from the ends of spikes, producing either foliage or more flowers [9,30,42,48]. Borne terminally, growth flushes typically alternate between inflorescences and foliage [48].

Fruits are woody capsules, 0.2 inch (0.4 cm) in length and width, persistent up to a year [9,31]. Twigs and branches may contain 12 or more infructescences, each containing 30 to 70 aggregated capsules, separated by a series of leaves or bud scales [48,74].

Ken Langeland/University of Florida

Seeds are tiny (0.02-0.04 in. (0.5-1 mm) long or a little more; up to 850,000 or more/oz. (30,000/g)) and numerous (see Seed Production). Their shape is generally asymmetric and long angular. Seed shape and size vary considerably within a capsule [30,31,42,48,112].

Further attributes of seeds and fruits, as observed by Rayamajhi and others [74] in southern Florida, are provided in the following table. Data are means and 1 standard deviation.

Infructescence length	2.4 ± 0.5 inches (6.0 ± 1.3 cm)
Number of capsules/infructescence	49.0 ± 17.0
Number of capsules/cm within infructescences	8.0 ± 0.3
Number of seeds/capsule	264.0 ± 39.0
Dry weight of seeds/capsule	0.00023 ± 0.000067 ounce (6.6 ± 1.9 mg)

Values are means ± standard deviations.

Bark is thick (sometimes >0.8 inch (2 cm)), corky or spongy, and composed of many thin layers [9,31,42,48,94]. On the lower trunk the outer bark layers are looser and usually become torn, ragged, and partly unrolled [9,31].

Melaleuca exhibits several morphological and physiological responses to flooding. Flooding induces rapid production of abundant adventitious aerenchymous roots along the lateral roots, upper section of the taproot, and submerged portion of the stem, elongating upward until the tips just protrude above the water's surface [48,51,80,92]. At least some of these roots are persistent, becoming dormant and dried once floodwaters recede, then producing new adventitious roots in subsequent floods [48]. Flooding may also trigger a decline in aboveground biomass production
and alter stomatal performance, at least in seedlings. In a greenhouse study, Sena Gomes and Kozlowski [80] found melaleuca seedling leaf, stem and whole plant dry weight was significantly ($p \leq 0.01$) reduced following 60 days of flooding (0.4 inch (1 cm) above soil surface), but there was no effect on root dry weight. Reduced stem biomass was associated with reduced stem branching and extensive leaf abscission. Complete submersion of seedlings induces production of morphologically distinct leaves, characterized by a more lanceolate shape, reduced area per leaf, and fewer stomata. Submersion also results in shorter leaf internode length, giving submersed seedlings a "rosette-like appearance." It has been suggested that this "adaptive aquatic behavior" may increase melaleuca seedling survival during seasonal floods [43] (see Seedling establishment/growth).

RAUNKIAER [65] LIFE FORM:
Phanerophyte

REGENERATION PROCESSES:
Melaleuca regenerates both continuously and episodically from seed [112], and by sprouting from branches and stems in response to tissue damage [48,54].

Woodall [112] summarized melaleuca sexual reproductive strategies as follows: "Because seed retention extends beyond seed ripening, melaleuca has 2 distinct reproduction possibilities. First, a virtually continuous, although low-level, seed release ensures that some of the seed lying on the ground near the tree will be fresh, which allows the species to exploit all reproduction opportunities—no matter how short in duration. Second, the retention of several years' seed production allows for a particularly heavy seedfall if some natural catastrophe kills advance reproduction along with seed trees."

Meskimen [48] noted three characteristics of melaleuca that contribute to its propensity to saturate an area with seeds:

- Heavy flower crops normally produced 2-5 times a year
- Many seeds produced per flower
- Canopy-stored seeds viable through many flowering cycles

Asexual regeneration:

Melaleuca sprouts from branches and stems in response to frost, fire, mechanical, and herbicide damage [48,54]. When branches or stems are cut or broken, multiple sprouts are produced from buds located beneath the bark and within inches of the injury [48]. Entire crowns of saplings and large trees that are defoliated by frost or fire can recover in just a few months by epicormic sprouting. The extent of damage and sprouting response appear similar for both frost and fire damage, in that they are proportional to the intensity of heat or cold exposure. With increasing intensity of heat or cold, smaller diameter branches are killed and epicormic sprouting becomes limited to larger branches or stems. Melaleuca can also recover from windthrow, partial breakage, or other types of incomplete felling in two ways. First, existing branch tips may reorient vertically. Second, sprouts may be produced from latent buds on the upper-facing portions of stems. The result may be a "vigorous," if multistemmed, survivor [48]. Wade [102] suggested that seedlings 4 to 5 inches (10-13 cm) in height may have the ability to sprout.

There is some indication that melaleuca can sprout from the root crown, although details describing the biology of this habit are sparse. Meskimen [48] noted that melaleuca seedlings sprout "very close to ground level" and "from the bases of stems in the spring," in response to fire and frost, respectively. Woodall [110] indicated that melaleuca saplings will sprout "from the root collars" in response to freeze damage, and Myers [52] suggested that seedlings can sprout "at the root collar" in response to damage from fire. Wade [102] indicated that "basal sprouts will develop whenever a tree is completely topkilled" by fire. Multiple shoots may be produced from basal sprouting, likely the origin of multistemmed individuals [48]. According to Woodall [110] the "tendency to sprout" decreases with age in mature trees.

Melaleuca's ability to root sprout is unclear. According to Meskimen [48] melaleuca does not root sucker. Turner and others [96] indicated that melaleuca "has the capability of root sprouting," but as of this writing (2005) there are no other published accounts of root sprouting in melaleuca.

Breeding system: Melaleuca flowers are perfect [101]. Vardaman [101] concluded that melaleuca has a mixed breeding system that "promotes outcrossing but allows inbreeding if sufficient outcrossing does not occur."

Pollination:

Field studies in southern Florida showed that pollination within the same flower resulted in significantly ($p<0.05$) reduced fruit set compared with pollination between flowers on different trees or pollination between flowers on the same tree. These studies also indicated that male and female flower parts often develop at different rates, which tends to promote pollination between flowers [101].

Melaleuca is pollinated by a variety of insects, especially honeybees (see Other Uses). Vardaman [101] suggested that melaleuca could be pollinator-limited in some areas of southern Florida, particularly where honeybee hives are remote, but found no supporting evidence from a lone study site.

Seed production: Melaleuca is a prolific seed producer. According to Geary and Woodall [30] each flower spike produces an average of 30 capsules. Each capsule contains 200 to 350 seeds, and a single branch may bear 8 to 12 capsules. A review by Hofstetter [35] estimated that a 33-foot (10 m), open-grown tree may bear 20 million or more canopy-stored seeds. Rayachhetry and others (unpublished data, as cited in [73]) estimated that a melaleuca tree 69 feet (21 m) tall and 15 inches (38 cm) dbh in a "dry" habitat in southern Florida may bear as much as 75 pounds (34.2 kg) of fresh (19 lbs. (8.7 kg)) capsules containing 3.7 pounds (1.7 kg) of dry seeds, or about 51 million seeds. Assuming 9% of seeds produced are viable and capable of producing seedlings (see Seed banking and Germination), this tree may bear approximately 5.6 million viable seeds in its canopy [73].

It appears that melaleuca is reproductively precocious for a tree. According to Gifford (1912, as cited in [48]), 3-year-old saplings were observed to "bloom profusely," and even seedlings less than a year old may bear seed. Meskimen [48] observed flowering and seed production in numerous wild melaleuca seedlings estimated at less than 2 years old.

Flowering and seed production are apparently much reduced on shaded branches [48]. Extremely dense stands appear to produce very few flowers. Flowering in these stands is mostly limited to exposed branches, usually in the very top of the canopy. However, such stands may also contain large canopy-emergent individuals, presumably founders of the dense, main-canopy cohort, which can continue to produce substantial numbers of seeds in their upper crowns [54].

Seed dispersal:

Seeds are contained within capsules and are retained in the canopy upon maturity. Capsule dehiscence and seed release are thought to be triggered by capsule desiccation. Natural seed release is triggered by mechanical injury, radial growth, fire, frost, shade dominance, and possibly age [30,48,93,112]. Herbicide application may also induce seed release [112].

Melaleuca seed release occurs both episodically and continuously. Depending upon severity, injury to part or the entire tree can cause a relatively rapid purge of substantial numbers of canopy-held seeds. According to Woodall [112], "a hot crown fire causes complete capsule dehiscence in a matter of days" (see Plant Response to Fire).

Light seedfall occurs more or less continuously in the absence of substantial damage. Woodall [112] observed continuous seed rain from undamaged trees from July to January in southern Florida. Weekly seedfall during this period was approximately 2,260/m^2 in a mature closed stand (4600 trees/ha). Seed release from undamaged trees is primarily the result of self-pruning due to shade. Because self-pruning is a result of competition for light among branches, and because this competition is most intense during periods of rapid growth, seedfall from undamaged trees is probably greatest during periods of rapid growth [112].

The importance of wind dispersal is unclear. Woodall [112] suggested that melaleuca seeds do not appear strongly adapted to wind dispersal. It was estimated that, under "average conditions," most seeds fall no farther than 8.5 times the height of the seed source, usually <560 feet (170 m) [112]. Meskimen [48] observed that "even light breezes" may cause seeds to fall "at least 1.5 times the vertical distance" from which they are released. It was speculated that seeds released from high in the crowns of mature melaleuca trees may travel "considerable distances in normal breezes," and even greater distances when released during high winds. In support of this assertion, it was observed that scattered melaleuca reproduction could sometimes be found hundreds of yards or more from the nearest seed trees [48]. A simulation model developed by Browder and Schroeder [11] suggested the maximum distance that viable seed might be carried by 100-knot winds, such as might occur during a hurricane, is 4.4 miles (7.1 km). Duever and others [23] suggested that hurricanes are "probably not a significant environmental factor as far as the growth and spread of melaleuca is concerned. Hurricane damaged branches and fallen trees will not release their seed until long after winds have subsided. Fallen branches release their seed so close to the ground that the advantage of height is lost. Hurricanes could, however, transport seed-bearing branches some distance from the original tree."

Fresh melaleuca seeds apparently resist wetting and may remain on the surface of water for days, indicating that dispersal by water currents over greater distances than provided by freefall is possible [112]. Dispersal of floating seeds may be enhanced by wind, particularly where seeds have fallen on floating litter or debris [48]. Thoroughly wetted seeds will not float [113]. Meskimen [48] suggested that viable seeds sink if surface tension is broken, while nonviable seeds may float indefinitely.

Meskimen [48] suggested that animals or humans may disperse seeds considerable distances if seeds are lodged in fur, feathers, clothing, etc.

Seed banking:

Melaleuca stores its seed in the canopy from which it is released upon injury to the tree. Woodall [112] suggested that ripe seeds are held indefinitely. According to Meskimen [48], capsules may remain indefinitely on small branches but are eventually sloughed off larger branches as their diameter increases.

Although potentially vast numbers of seed may be stored in the canopy, it appears that viability of canopy-stored melaleuca seed diminishes with age. In an unreplicated laboratory experiment, Meskimen [48] observed germination of melaleuca seeds from 8 distinct clusters of capsules located along a single branch. No age estimate was made of seeds from the 8 different branch positions, but germination was greatest (% germinable) and most rapid among middle-aged groups and became somewhat slower and diminished for the older groups. Ultimately, perhaps only a small portion of canopy-held seeds become germinants. Rayachhetry and others [73] sampled canopy-held melaleuca seeds in southern Florida. They found an average of more than 85% of canopy-stored seeds contained no embryo. Of the <15% of canopy-held seeds that contained embryos, an average of 62% (0% to 98%) were viable. Overall, an average of 9% (0% to 41%) of canopy-held seed was viable [73].

Seed-bearing melaleuca trees can rapidly replenish canopy-held seed stores following disturbance-induced seed rain. Myers and Belles [54] sampled capsule clusters from 3 mature trees that had been subjected to 100% crown scorch. Sample trees were harvested at postfire year 2, and seed capsules were separated into 3 categories: 1) burned and presumably open (seeds dispersed) after the fire, 2) mature capsules with viable seed presumably produced since the fire, and 3) immature. Numbers of burned clusters per tree ranged from 2,663 to 3,971. Numbers of mature clusters per tree ranged from 1,850 to 2,402, and numbers of immature clusters per tree that would have been mature within a few months of sampling ranged from 1,320 to 3,905.

The propensity for melaleuca to accumulate soil seed banks is unclear. It appears that some seeds may remain viable but ungerminated for some time following dispersal. Woodall (unpublished observations cited in [113]) observed that some melaleuca seeds remained germinable following 10 months of "shallow burial in a swamp soil that fluctuated between saturated and unsaturated conditions." Approximately 63% of seeds that were buried in a "well-drained saw-palmetto prairie soil" lost their germinability within 10 months. In both cases it was suggested that burial prevented germination. It was also suggested that "rain plowing," or burial by rain splash, possibly delayed germination by continually bringing some seeds to the surface while burying others [113]. Whether "rain plowing" on sandy soils can bury seeds deep enough to inhibit germination is unknown. Differences in germination may also have been due to different moisture conditions in the different soils. According to Van and Rayamajhi (unpublished data cited in [74]), "a small fraction of seeds remain viable in dry sites even after 2 years in the soil."

It appears unlikely that soil seed banks accumulate where soils receive periodic moisture. In a greenhouse experiment in which all treatments involved subjecting seeds to some type of moisture, Myers [51] found that no further germination occurred after 10 days following treatment initiation. Germination may proceed over a longer period under field conditions, but with adequate soil moisture, nearly all dispersed germinable seeds germinate relatively quickly [51,54]. Rayachhetry and others [73] estimated that an average of 27% of canopy-held seeds judged viable did not germinate within 10 days of soaking. They suggested that these seeds demonstrated some type of dormancy and may contribute to a transitory soil seed bank.

Germination:

Several field studies in southern Florida indicate that melaleuca seeds germinate best when soils are moist, but not when inundated or dry [51,54,55]. Seeds that are dispersed when soil conditions are dry apparently will germinate only once rains provide adequate moisture. Apparently germination is also initially constrained when dispersal occurs over standing water [54]. While seeds can germinate while submerged [34,43,51], Myers [50] suggested that it is rare under "normal" field conditions, and that germination may be inhibited by low levels of dissolved oxygen common in stagnant floodwaters. Ungerminated seeds that are submerged will often germinate once floodwaters recede [50,54]. In field observations, postfire germination was recorded for more than 2 months, until sites became flooded during summer rains. Data recording ceased during the flooded period and was resumed once floodwaters receded. Following flooding, only 3 new seedlings appeared among all fifteen 1.1-foot^2 (0.1 m^2) plots. It was not clear if any germination had occurred while the sites were flooded, but if so, no germinants survived the nearly 4 months of inundation [54].

There are conflicting reports regarding floating vs. sinking melaleuca seeds as a measure of viability. While

Meskimen [48] suggested that when seeds land on substrate that is subsequently flooded, viable seeds remain submerged while nonviable seeds float indefinitely, Hartman [34] found the opposite to be true.

Woodall [111] suggested that southern Florida soil types can influence melaleuca germination depending upon how well the substrate provides moisture to the surface. Organic soils such as peat hold large amounts of water at very low tensions and therefore provide water to the surface more reliably than marl (calcium carbonate clay) or sand [111].

Melaleuca seed germination may be affected by light availability. There is some evidence that germination is inhibited by burial (see Seed banking). Results from field studies in Big Cypress National Preserve indicate melaleuca germination is greater on recently burned sites compared with similar unburned sites where intact vegetation, litter, and periphyton (postflood detritus from algae/other aquatic plants) may increase shade [51,54,55]. In a laboratory experiment, Hartman [34] found that while at least some seeds germinated under conditions ranging from full light to total darkness, germination was significantly ($p<0.003$) lower in darkness (5% germination after 40 days) compared with "high" light (17% germination) or low (27% of "high") light (12% germination) treatments.

Seedling establishment/growth:

Seedling establishment is probably the stage in the life history of melaleuca that most influences its distribution in southern Florida. "Once past the early seedling stage, melaleuca rarely succumbs to natural forces in southern Florida" [35]. Newly germinated seedlings are small, lacking in energy reserves, and susceptible to fire, frost, flooding, and drought [44,48]. Woodall [111] indicated that, depending on site conditions, 1st-year seedling growth is often slow.

Melaleuca seedling establishment can be prodigious, especially following fire (see Plant Response to Fire). Myers and Belles [54] reported an average of 1,609 seedlings/m^2 at one site in southern Florida. Although establishment of such dense thickets may represent an extreme scenario, it does demonstrate the contribution of seedling establishment to melaleuca's invasive potential [48]. But seedling mortality can drastically limit melaleuca recruitment. Melaleuca seedling establishment is often hindered by extreme or prolonged drought or flooding [54,111]. Younger seedlings appear most vulnerable, with tolerance increasing as seedlings mature [54].

The most important factor affecting melaleuca seedling establishment in southern Florida is probably hydroperiod [51]. Ideal sites remain moist to saturated during the 4- to 6-month wet season (summer), providing conditions that promote initial growth and development sufficient to survive the dry season [51,111]. Greatest amounts of germination, establishment, and initial height growth generally occur during wet periods [113]. Seedlings that germinate at the beginning of the wet season, prior to flooding, may survive if flooding is of short duration. Seed that falls during flooding may germinate immediately after the flooding recedes, probably the most favorable situation for survival. Seedlings that establish after surface inundation has receded must develop sufficiently to survive the ensuing dry season. Seedlings that germinate outside the wet season are unlikely to survive. While germination may be triggered by a brief rain, or even fog or heavy dew, these situations usually provide insufficient moisture for continued development [51]. Because surface flooding tends to inhibit germination and establishment, the beginning and end of the wet season are most favorable for establishment in areas where extensive flooding occurs [111,113].

Laboratory research that examines the effects of flood depth and duration may be instructive for understanding melaleuca seedling survival. Laboratory experiments demonstrated that seedlings under partially flooded and soil-saturated conditions grew significantly ($p<0.01$) taller than seedlings grown in moist, well-drained medium [48] and that seedling height growth over 6 months was greater under saturated soil conditions compared to moist, well-drained soil [50,51]. However, plants grown under saturated conditions "produced weaker stems that were unable to support the aerial portions in an upright position" [51].

Complete submersion under flood waters can severely reduce melaleuca seedling survival. Myers and Belles

[54] studied melaleuca seedling establishment following wildfire in Big Cypress National Preserve. At one site, postfire seed rain and maximum seedling numbers occurred just prior to the onset of summer rains and submersion. Although preflood seedlings were numerous (mean of 1,609/m^2 at one site), comparatively few seedlings survived wet season floods (mean of 30/m^2 at the previously mentioned site). Survivors were typically found "on hummocks or rises associated with the bases of larger trees" where flood duration was shortest. It was not clear from this study what caused such high levels of seedling mortality. Submerged seedlings may be killed if they are smothered by algae [44,50]. In a greenhouse experiment, Myers [50] showed that melaleuca seedling survival was minimal following ≥4 months of submersion.

Short of immediate mortality, seedling submersion typically results in drastically reduced growth, growth stagnation, or even reduced biomass. Nevertheless, at least some melaleuca seedlings may survive extended periods of submersion. In a greenhouse experiment, Myers [51] demonstrated that melaleuca seedlings can survive complete submersion for up to 6 months, although submersion for extended periods increases mortality. All treatments involving submersion resulted in reduced biomass accumulation [51]. In laboratory experiments, Meskimen [48] found that submerged melaleuca seedlings exhibited little height growth. Preflood leaves on submerged seedlings rapidly abscised, and were replaced only on the lower portion of the stem by "extremely short, thick leaves." Once the submerged plants were drained they resumed what appeared to be "normal" growth [48]. In a greenhouse experiment, Hartman [34] studied the effects of inundation on potted seedlings. Inundated seedlings grew more slowly than seedlings potted in moist soil, but mortality (~10% after 165 days) was not substantially different between treatments.

Seedlings may be more tolerant of fluctuating floodwaters. In greenhouse experiments, Myers [50] found that seedlings subjected to an alternating regime of submergence and drainage every 3 days seemed less affected by submergence than seedlings in a 2-week cycle. It was noted that rapidly fluctuating water levels are characteristic of artificially drained habitats, which are common in southern Florida. Seedlings are much less tolerant of submersion for longer periods [50]. In a laboratory experiment, Lockhart and others [44] studied the responses of 7-week-old melaleuca seedlings to hydroperiod lengths and patterns (1st flooded then drained, and vice versa). Seedling height growth was greatest when soil was wet to slightly drained for 12 weeks immediately after germination, followed by variably flooded conditions during which plants were both partially and fully submerged. Height growth was generally greater under longer hydroperiods than with shorter hydroperiods. Under initially flooded conditions submerged seedlings grew less rapidly in height compared with emergent seedlings. Branching was significantly ($p<0.02$) greater with shorter hydroperiods, regardless of timing of flooding [44].

Prolonged drought can substantially reduce postdisturbance seedling establishment [44,111,113]. Young melaleuca seedlings are particularly susceptible to drought [44,54]. Woodall [113] demonstrated that when favorable germination conditions are soon followed by a prolonged dry period, extant seeds germinate and the germinants then die. In the absence of further seed dispersal onto the site, this leaves little germination potential once rains resume (but see Seed production). Yet melaleuca seedlings can apparently tolerate some short-term drought. Woodall [111] described how "root elongation" of melaleuca seedlings can "keep up" with a water table that recedes gradually (1-3 cm/day). Seedlings would probably die if recession continued into depths lower than -3.3 feet (-1 m) for more than short periods [111].

The presence and character of a litter layer may affect melaleuca seedling establishment. Postfire seedling establishment is thought to be enhanced, at least in part, by lack of litter [112] (see Fire Adaptations and Discussion and Qualification of Plant Response to Fire). Woodall [111] discussed observations of both the prevention and encouragement of establishment by a litter layer. Fully erect 1-week-old seedlings are typically only 0.08 to 0.16 inch (2-4 mm) tall and their roots little longer. Germinants are often prohibited from rooting by a dense mat of overlapping leaves (typical of melaleuca's own litter) prior to either becoming flooded or desiccated. Desiccation can occur if the leaf litter dries, curls somewhat, and thereby breaks the pathways by which moisture can migrate to the litter. Yet a fresh covering of pine or cypress needles (as might fall after a fire) is structured in a way that provides germinants access to a favorable rooting medium, while simultaneously protecting both seedlings and the soil surface from drying [111].

Melaleuca seedlings grow well on organic soils or rotting stumps, but on these substrates a relatively stable water source is imperative [111]. In a laboratory experiment, 100% of germinating seeds rooted in a peat substrate, while approximately 45% of germinating seeds rooted in clay loam [34]. Meskimen [48] observed melaleuca seedlings established on logs, butts of cypress trees, root masses, etc. This phenomenon occurred on structures lying above the water line in permanently or semipermanently flooded habitat where melaleuca establishment might otherwise have been unlikely, such as deep-water marshes or the interiors of baldcypress stands. Apparently melaleuca establishment under such conditions can lead to growth of mature trees, as it was noted that many large mature trees appeared to be "growing right out of the sides of the butts of old fire-killed cypress trees" [48].

Sandy soils get hotter than most other soils. Because the upper layers of a sandy soil dry rapidly, there is less evaporative cooling, and melaleuca seedlings on such sites are subject to desiccation and heat damage [111].

A number of observations have illustrated how site conditions can affect seedling establishment. Meskimen [48] noted that newly established melaleuca stands are typically localized and aggregated rather than continuous over extensive areas in southwestern Florida where pine flatwoods are interspersed with ponds, sloughs, and cypress stands. The following explanations were offered. First, seeds may be concentrated in natural depressions, ponds, or sloughs by receding floodwaters. Second, most seeds typically fall only a short distance from the parent tree. Third, the small size and limited resources of melaleuca seeds probably preclude establishment over all but the most conducive site conditions [48]. Yet at least some seedling establishment is possible even when environmental conditions are poor [113]. "Prolonged favorable conditions required for successful establishment are restricted to areas that are neither too wet nor too dry and times of the year when moisture availability is most predictable. The most favorable sites for melaleuca include depressions in pine flatwoods, the broad ecotonal region where pine and pond cypress intermix, and the less flooded edges of cypress strands and domes" (Myers 1983; cited in [52]).

To demonstrate how timing of fire, drought, and hydroperiod can favor or limit seedling establishment, it may be instructive to examine 3 prescribed fires conducted by Myers and Belles [54] during 3 different seasons in Big Cypress National Preserve. 1) A mid-January burn coincided with moist soil conditions. Germination began within a week of the fire, and by week 4 there was an average of 2,137 seedlings/m^2 at this site. Substantial seedling mortality ensued during the 20 week dry season, until average seedling density was reduced to 30/m^2. However, nearly all these survivors established and survived ensuing rainy season floods and another dry season. 2) A mid-March burn was followed by April rains, resulting in a mean of 103 seedlings/m^2 at postfire week 6. An ensuing 7-week drought reduced average seedling density to 7/m^2. Onset of summer rains in June prompted another episode of germination. Prior to flooding of the site (postfire weeks 16-34) average seedling density reached a maximum of 645/m^2. Seedling density was subsequently reduced by prolonged submersion and the next spring drought. Virtually all surviving seedlings (mean seedling density 135/m^2) also survived their second wet season. 3) An early July burn was conducted over shallow standing water. Initial postfire germination was limited (mean seedling density 42/m^2), probably due to standing water. Seed rain may also have been lower at this site due to the moderating effect of flood waters on fire behavior. Water levels rose between postfire weeks 3 to 5, and the site remained flooded until postfire week 17, at which time average seedling density was 18/m^2. Germination commenced following the receding of floodwaters, with average seedling density reaching a maximum of 126/m^2. Mortality was 96% during the ensuing dry season, but most of those that survived the drought had grown enough to also survive the next season's flooding (~ 5/m^2).

SITE CHARACTERISTICS:
The following information concerning site characteristics is intended in reference to melaleuca growing in peninsular Florida, except where otherwise noted.

General biogeography:

The most favorable sites for melaleuca establishment, with regard to moisture conditions, include depressions in pine flatwoods, the broad ecotonal region where pine and cypress mix, and drained organic soils [23]. Other sites where melaleuca has been mentioned as occurring include disturbed wet prairie [2], wet pine flatwoods [115,116], cypress swamps, "low areas" [30], and generally "disturbed sites" [115,116]. Melaleuca invades the littoral zone of Lake Okeechobee, where it was originally planted along the shoreline in the 1940s to stabilize the newly constructed levee [44]. According to Greenway [33] melaleuca forests in southeastern Queensland, Australia, are associated with coastal floodplains, where it forms open, relatively monospecific stands that burn regularly [24].

Disturbance:

Melaleuca's invasiveness may be enabled by natural disturbance, especially fire. Massive seed rain typically follows disturbance such as fire, frost, and breakage from wind events (see Seed dispersal). Once established, melaleuca is likely to attain and retain dominance on sites visited by frequent fire (see Fire Regimes). March to June is typically considered wildfire season in southern Florida [76].

Aside from invading natural communities in southern Florida, disturbance associated with human activities can also promote melaleuca invasion. Areas where the native plant community has been compromised, combined with favorable moisture conditions, present opportunities for melaleuca colonization. Examples include drained fields with ridges and furrows on abandoned farmlands, depressions in stump-harvested pinelands, and road and canal construction through wetlands that create road embankments, ditches, levees, and borrow pits [23,51,52]. In their review, Geary and Woodall [30] point out that lowering of water tables through drainage and excessive groundwater withdrawals has increased the area easily invaded by melaleuca in Florida. The effect of these changes is to shorten the annual hydroperiod, leading to increases in size and severity of wildfires (see Wade and others [104]). Because melaleuca tolerates fire, seasonal drought, and seasonal flooding, it may invade to the detriment of native plants on these sites [30].

Soils: Most reviews (e.g. Ewel [24], Hofstetter [35]) indicate that while melaleuca establishes best on sandy soils, it can survive on nearly any soil in southern Florida. It is also commonly found in "typical 'glades' ecosystems," characterized by "high organic soils" [63]. Many soils in southern Florida that support melaleuca are shallow and underlain by limestone [30]. Rayachhetry and others [69] studied melaleuca in and around the freshwater marshes of the Everglades in southern Florida. Populations occurred naturally on poorly drained organic soils in "dry, seasonally flooded, and permanently flooded" habitats. In general, soils supporting melaleuca are in the orders Entisol, Spodosol, and Histosol (USDA 1975 as cited in [30]).

There is some disagreement about the influence of pH on melaleuca success on different soils in southern Florida. Although melaleuca is often found growing in soils with pH >7 "in the eastern Everglades," a laboratory experiment by Kaufman [38] indicated that plants may perform better in more acidic soils. Biomass and height at 150 days, and growth rate from 0 to 150 days were all significantly ($p<0.0001$) greater for seedlings grown at pH 6.9 than at pH 7.3 [38]. Although melaleuca can be found growing, and sometimes reproducing, on alkaline marl soils in southwestern Florida, laboratory research [48] indicated poor germination and poor seedling growth on these soils. Acid sandy soils, which support many well-developed melaleuca stands in southwestern Florida, were generally more conducive to germination in these experiments than other soils. Myers [51] also noted from experimental evidence that melaleuca seedlings establish best on acid-sandy soils. Seedlings planted on alkaline-marl soils were stunted and chlorotic. Myers and Belles [54] found that seedlings grown in pots using pineland sand soils (pH 5.6; low nutrients) collected from Big Cypress National Preserve established and grew substantially better than seedlings grown using commercial potting mix (pH 7.0; high nutrients). Native melaleuca sites in eastern Australia commonly have soil pH ≤6 (Kaufman personal observation cited in [38]).

But Woodall [111] was skeptical of the influence of soil pH on melaleuca success and reported the following field observations: (1) A 1.2-m-deep soil pit was dug in a vigorous melaleuca stand in Lee County. The soil pH was 4.4 at -7.9 inches (-20 cm) and 8.0 at -20 inches (-50 cm). Roots proliferated all the way to the bottom of the pit. These pH values encompass virtually the entire range of pH to be expected in surface soils in southern Florida. (2) Sandy surface soils of pine flatwoods in Lee County that have been heavily infested with melaleuca can have a pH as high as 8.1. (3) Even marl soils, which in Meskimen's lab test [48] showed no germination, today support melaleuca reproduction. Therefore, according to Woodall [111], "the hypothesis cannot be supported that melaleuca reproduces poorly where pH is above 7, and furthermore, we cannot expect a map of soil pH to tell us where melaleuca is incapable of invasion."

Woodall [111] also offered the following insights on melaleuca and soil nutrient competition: "Sites that are generally considered nutrient-poor (such as pine savannas or wet prairies) support a reasonably vigorous growth of melaleuca. How can the species accomplish this? Its ability to root deeply in periodically flooded soils is one explanation. When pines and melaleuca grow together on the same site, melaleuca's lateral roots are deeper than those of pine. Furthermore, melaleuca can send vertical roots straight down to the water table. The downward movement of leached nutrients stops at the water table, so a species (like melaleuca) that can physiologically tolerate the conditions near the water table has an obvious nutritional advantage over plants that are restricted to the more leached surface soils."

Melaleuca may tolerate some soil salinity [24,111], although these conditions are probably less than optimal [111].

Climate: Wade and others [104] provided the following review of climate in southern Florida: "The climate is subtropical with alternating wet and dry seasons. Average annual precipitation is between 45 and 65 inches (114-165 cm), depending upon location, and is characterized by wide annual fluctuations- from less than 30 to over 105 inches (76-267 cm). Between 70 and 80 percent of the rain generally falls during the May-to-October wet season. Average annual temperature is 71° to 75 °F (22-24 °C), but below-freezing temperatures can be expected several times a year in the low-elevation interior glades. Frost can be expected in all South Florida counties about once every other year, but severe cold snaps...are very unusual and have an immediate and profound effect on the composition of plant and animal communities" [104].

Where frequent and/or prolonged periods of freezing temperatures become increasingly common , melaleuca becomes less invasive. Melaleuca occurs "abundantly" within USDA plant hardiness zones 9a to 10b [96], where average annual minimum temperature is 20° to 40 °F (-6.7° to 4.4 °C). Frost occurs in most years in coastal southern Queensland, Australia (Coaldrake 1961, as cited in [111]), where melaleuca is native. Freezing temperatures damage mature trees, resulting in branches dying back to varying degrees depending on severity of the freeze [78,96]. Mature trees generally recover by epicormic sprouting [96]. Seedlings and small saplings are occasionally killed during freezes, but are usually only top-killed [78]. Freezing weather may retard growth of individual trees and thin melaleuca stands, but elimination of affected populations is not likely [111]. Woodall [111] observed that the record freeze of January 1977 in southern Florida did not kill many, if any, mature trees. Many trees lost all their foliage and fine branches but subsequently recovered by sprouting from dormant epicormic buds. Senescent leaves and immature growth flushes were typically damaged, while mature leaves were sometimes unharmed. A few saplings were killed to the ground but responded by sprouting from the "root collar" (see Asexual regeneration) [111]. Geary and Woodall [30] suggested that periodic cold temperatures probably limit melaleuca natural regeneration north of Lake Okeechobee. But noting others' observations of recovery following complete freeze-induced defoliation, Turner and others [96] suggested that melaleuca may not be freeze-limited in its current southern U.S. distribution.

Hydroperiod: Once established, melaleuca tolerates extended flooding and moderate drought [24,54]. In a laboratory experiment, Lockhart and others [44] studied responses of melaleuca saplings (~1.6 feet (0.5 m) tall and 1-2 years old) to various hydroperiods. Over the 53-week study period saplings exposed to a longer hydroperiod grew significantly ($p<0.004$) taller, with significantly ($p<0.04$) more branching, compared with saplings under a shorter hydroperiod. Hydroperiod had no effect on final root or shoot biomass or final stem diameter. Complete submersion for 8.5 weeks consistently resulted in ≈ 20% mortality [44]. Although melaleuca is often found growing under saturated to inundated conditions, growth is best when soil is moist but not saturated. A laboratory experiment by Kaufman [38] demonstrated that biomass and height at 150 days, and growth rate from 0 to 150 days, were all significantly ($p<0.0001$) greater for seedlings grown in a moist medium compared with saturated soil.

The seedling stage is where melaleuca is most susceptible to flooding and drought (see Seedling establishment/growth). Even in the presence of a seed source melaleuca does not successfully establish in every year or invade every community equally. Wetter sites are more susceptible in drier years, while drier sites may see greater establishment during wetter than average years [35,54].

Hawaii:

In Hawaii, neither fire nor widespread hydrologic alteration are common. Therefore, melaleuca does not benefit from these kinds of site conditions in Hawaii as it does in Florida. Melaleuca 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 [30]. It is found from sea level to 4,500 feet (1,400 m) elevation. Trees grow well in rainfall of 40 inches (1,020 mm) at lower elevations (Skolmen 1980 as cited in [30]), and 200 inches (5,080 mm) at higher elevations. "Good growth" occurs where mean annual temperatures are between 65° to 75 °F (18-25 °C), and apparently trees grow in even cooler temperatures at higher elevations [30].

Australia: In eastern coastal Australia where melaleuca is native, its distribution is centered around 26° latitude, in areas characterized by humid tropical/subtropical climate, wet summers and dry winters, frequent fire, elevations from sea level to 330 feet (100 m), occasionally to 540 feet (165 m), and that are relatively frost free (reviewed by [9,96]). Typical sites are along stream and estuary banks and in marshes and seasonal swamps [9]. In southeastern Queensland, melaleuca forests are seasonally inundated (up to 20 inches (50 cm) deep for 2-6 months) during the wet season [33].
The following climate data were compiled from 88 locations across eastern coastal Australia [10]:

	Minimum	Maximum
Annual mean temperature	62.8 °F (17.1 °C)	79.7 °F (26.5 °C)
Coldest month minimum temperature	40 °F (4.3 °C)	68.7 °F (20.4 °C)
Hottest month maximum temperature	79 °F (26.1 °C)	92.7 °F (33.7 °C)
Annual temperature range	53.4 °F (11.9 °C)	77.7 °F (25.4 °C)
Wettest quarter mean temperature	59.4 °F (15.2 °C)	81.5 °F (27.5 °C)
Driest quarter mean temperature	56.8 °F (13.8 °C)	78.1 °F (25.6 °C)
Annual mean precipitation	33.0 inches (837 mm)	135 inches (3,438 mm)
Wettest month mean precipitation	4.6 inches (117 mm)	26.5 inches (672 mm)
Driest month mean precipitation	0.08 inch (2 mm)	3.4 inches (86 mm)
Annual precipitation range	2.1 inches (54 mm)	23 inches (586 mm)
Wettest quarter mean precipitation	13.2 inches (336 mm)	75 inches (1,900 mm)
Driest quarter mean precipitation	0.35 inch (9 mm)	10 inches (260 mm)

SUCCESSIONAL STATUS:
As of this writing (2005), there is very little information on succession and community/stand dynamics in native plant communities where melaleuca is present in southern Florida. Given melaleuca's propensity for rapid and profuse regeneration following disturbance, particularly after fire (see Fire Ecology and Fire Effects), it is likely that invasion will have the greatest impact on successional trajectories where disturbance is frequent and/or severe.

Melaleuca commonly invades herbaceous communities in southern Florida (see Habitat Types and Plant Communities) and is likely to alter succession on these sites. Richardson [75] indicates melaleuca invasion in wet prairies (St. Johnswort/pipewort spp.) may interact with drought or human-caused drainage to inhibit succession to marsh (sawgrass/arrowhead (*Cladium*/*Sagittaria* spp.)) communities. Apparently dense melaleuca reproduction in these areas "has retarded normal succession." The canopy cover of dense stands of melaleuca saplings shades the herbaceous layer, severely reducing cover of native species [75].

Melaleuca also invades a variety of forest, woodland, and savanna habitats in southern Florida. It is classified as shade intolerant [30], although Woodall [111] asserts that "the only native tree stands that may have shade deep enough to inhibit melaleuca are dense hardwood swamps and hammocks. The canopies of virtually all pine stands and most cypress stands are too open to seriously inhibit melaleuca establishment."

See Cultural control for a discussion of "forced succession" as a control method.

SEASONAL DEVELOPMENT:
In Florida, flowering may occur throughout the year, with heaviest blooming during the wet season (June-November), and sporadic flowering during the dry season (December-May) [50]. Meskimen [48] suggested that heavy rainfall may trigger flowering. Individual trees may bloom from 2 to 5 times per year and individual twigs 3+ times per year [30,48]. Pronounced region-wide flowering occurs at least twice per year [30]. Over 2 seasons at 6 sites in southern Florida, Van and others [100] observed that flowering began in October and November, with peak flower production from November to January, and was mostly completed by February and March. Flowering phenology may vary across a landscape or even within a stand (reviewed by [48]), and may be influenced by soil type [30]. Individual trees may be in flower while the surrounding stand is not [48].

In Hawaii, melaleuca flowers all year (Skolmen, as cited in [30]).

There is some evidence for a seasonal pattern in melaleuca growth. Meskimen [48] suggested minimum growth occurs in the summer and peak growth is in fall. Over 2 seasons at 6 sites in southern Florida, Van and others [100] observed new shoot growth beginning in midwinter, immediately after peak flowering, and peaking in spring. New shoots were produced from the apical buds of both flowering and nonflowering branches, but not all apical buds were active in the same season. Very little new growth was observed from May to August [100].

Continuous, light seedfall (see Seed dispersal) may occur seasonally. Woodall [112] observed light seedfall from undamaged trees from July to January, perhaps associated with seasonal growth.

FIRE ECOLOGY

SPECIES: Melaleuca quinquenervia

- FIRE ECOLOGY OR ADAPTATIONS
- POSTFIRE REGENERATION STRATEGY

FIRE ECOLOGY OR ADAPTATIONS:
Fire plays an important role in regulating the structure and function of plant communities in southern Florida [56,104]. According to Meskimen [48], "the ability of melaleuca to withstand fire cannot be questioned, and it is probable that its existence and perpetuation are actually favored by fire." Myers and Belles [54] also suggested "melaleuca's spread is facilitated by fire."

Fire adaptations:

Melaleuca possesses several traits that permit its survival following fire, and perhaps even aid in its perpetuation and spread.

Bark characteristics: Two distinct characteristics of melaleuca bark are considered important fire adaptations. First, the thick, spongy, multilayered bark can hold considerable moisture, particular within the innermost layers. This protects the cambium from heat damage during a fire [24,51,94,96,102], allowing the plant to recover via epicormic sprouting along sections of undamaged stem (see Plant Response to Fire). The thickest, most moisture-laden bark is found around the bole and large branches of mature trees, and cambium underlying such bark is well protected. Younger, thinner branches on mature trees and most bark-covered surfaces on younger plants are more susceptible to heat-damaged cambium [52]. Only tissues within "a few millimeters" of the bark surface are susceptible [48]. According to Van and others (unpublished data, as cited in [99]), "large" variations in melaleuca bark thickness have been observed "at different sites" in southern Florida.

Paradoxically, in addition to providing protection from fire, the dry, shaggy outer layers of bark are highly flammable and provide a ladder fuel that can quickly carry fire into the canopy, destroying leaves and branches [51,94,102]. It is suggested that where melaleuca invades forested habitats in southern Florida, this structure is likely to increase probability of lethal crown fires that are uncommon in native southern Florida forest communities [104] (see Fire regimes).

Photo courtesy the South Florida Sun-Sentinel 2005

Serotiny:
Melaleuca stores mature seed in closed capsules that remain attached to the branches until they are desiccated [96,102]. Although natural twig mortality causes continual release of some seeds, fire triggers release of millions of seeds [102]. Postfire seed release is apparently triggered by vascular injury to the capsule [48]. Capsules are unlikely to ignite due to their dense, woody structure and the short residence time of most crown fires. Seeds are held in the capsule until several days after the fire, so few seeds are exposed and consumed in the fire [102]. Capsules begin opening within a few days postfire [51]. Most canopy-held seeds are released during the first several weeks following fire [54,55]. As of this writing (2005) no direct evidence exists linking fire severity with the proportion of canopy-held melaleuca seed released following fire. Nevertheless, assuming that seed release is triggered by an injury-induced break in the vascular connection between the capsule and the plant, it is logical to assume that the degree of injury, which itself is proportional to intensity and duration of heating, is closely related to the proportion of canopy-held seed released. For more information see Seed dispersal.

Postfire germination and seedling establishment: Melaleuca can yield a rapid and prodigious postfire seed rain that, coupled with postfire site conditions that are conducive to germination and seedling establishment, can subsequently establish sizable populations of melaleuca seedlings. Melaleuca is one of the 1st postfire species to colonize in many southern Florida habitats [52]. Postfire conditions of reduced competition and ash-enriched soil are likely to promote establishment and rapid growth of seedlings [96]. Results from field studies in Big Cypress National Preserve suggest melaleuca germination is greater on recently burned sites compared with similar unburned sites where vegetation, litter, and periphyton are intact

[51,54,55]. Meskimen [48] observed that "densest pockets of melaleuca seedlings occur around seed trees which bear the scars of recent grass fires." In a field study located in wet prairie-dwarf cypress habitats in Big Cypress National Preserve, Myers and others [55] observed substantially greater melaleuca germination where seeds were hand-dispersed within 30 days following prescribed fire, compared with adjacent unburned plots. Recruitment beyond seedling stage was extremely low in both treatments due to subsequent dry or flooded conditions. Hartman [34] examined seedling establishment following a fire in a stand of 6 melaleuca trees approximately 20 feet (6 m) tall, 3 of which survived fire. By 9 postfire months, seedling density ranged from 0.5 to 4.7/m² in a 10 m²
area around the surviving trees. At 21 postfire months, an average of 58% of seedlings initially surveyed (at 9 postfire months) had survived. Myers [51] described how seed dispersed following a late-dry season fire is most likely to yield a successfully established stand of new melaleuca seedlings: "Rapid germination after initial moisture application would be an advantage to seed released at the beginning of the wet season, especially if the soil remains moist to wet but not flooded for any extended period. Massive amounts of melaleuca seeds are most commonly released following a late dry season fire. This puts the seed on the ground at the most opportune time" [51]. For more information see Regeneration Processes and Plant Response To Fire.

Postfire sprouting:

While foliage, twigs, and smaller branches may be consumed or severely damaged by fire, they are rapidly replaced by new growth originating from epicormic buds on the main stem and larger branches [24,30,48,51,52,53,102]. Even seedlings may have some ability to recover from fire-caused injury by sprouting from the base [48]. Any melaleuca plant that survives fire is well positioned to exploit the postfire nutrient pulse through its existing root system [102]. For more information see Asexual regeneration and Plant Response To Fire.

Fuel:

Melaleuca invasion may alter fire regimes (see below) in southern Florida by changing fuel conditions. In doing so, site conditions may be influenced in ways that favor melaleuca at the expense of native species.

One way melaleuca invasion can alter fuels is by increasing surface litter. Flowers [28] indicates replacement of sawgrass by melaleuca in southern Florida substantially increases surface fuel loads. These changes in surface fuels may increase ignition of organic soils, "a condition that is much less common in the cooler burning sawgrass fires" [28] and often lethal to sawgrass [53]. A review by Greenway [33] suggested that litterfall in some melaleuca forests in eastern Australia is among the highest recorded for Australian temperate/subtropical sclerophyll forests. Van and others [100] monitored litterfall at 6 melaleuca-dominated wetland forest sites in southern Florida. Total litterfall averaged 8.3 tonnes dry weight/ha/yr (range 6.5-9.9 t/ha/yr in 3 different habitats) from July 1997 to June 1999. Average proportions of litter components over 2 years were: leaves 70%, small wood (<0.4 inch (1 cm) in diameter) 16%, capsules 8%, bracts (both floral and foliar) 4%, and flowers 3%. Litterfall biomass was significantly ($p<0.001$) greater in seasonally flooded (9.9 t/ha/yr) habitats than in either nonflooded (7.5 t/ha/yr) or permanently flooded (8.0 t/ha/yr) habitats [99]. Litterfall occurs year round, but generally increases during dry and windy periods [33,99].

Changes in aerial fuels resulting from melaleuca invasion, coupled with flammable bark that serves as ladder fuel, may also alter fire severity in ways that favor melaleuca. Wade [102] suggested that the combination of loose flammable bark and volatile foliage result in a high propensity for torching of melaleuca trees during fire. In addition, melaleuca frequently establishes extremely dense stands (several thousand stems/acre), making them highly susceptible to running crown fires [102,104]. Extensive areas of southern Florida contain major vegetation types that are primarily adapted to surface fire (see Myers [53]). However, as discussed above and below, melaleuca is well adapted to survive most fires regardless of severity.

In addition to litterfall data [100] (see above), information on melaleuca allometry is available for estimating melaleuca live fuels. Van and others [99] measured stand characteristics and biomass at 6 sites in southern Florida. These sites were blocked in pairs according to hydrologic conditions (dry, seasonally wet, and permanently wet habitats). Stand characteristics varied substantially between sites. Basal area ranged from 78.4

to 190.9 m^2/ha, plant density ranged from 8,000 to 132,200 individuals/ha, and aboveground biomass ranged from 129 to 263 t/ha. Regression equations for estimating aboveground biomass, based on stem diameter, height, and dry weight, did not differ significantly ($p=0.2017$) by site. For regression equations and site-specific data see [99]. Rayachhetry and others [69] also provide detailed information on melaleuca allometry in southern Florida habitats.

Fire regimes:

Melaleuca invasion in southern Florida is of major concern, in part because the presence of melaleuca may alter native fire regimes. For example, melaleuca invasion in pine flatwoods can alter the major native fire regime of frequent (1- to 5-year return interval), low-severity surface fires, instead becoming a mixed regime with less frequent (<35 to 200-year return interval) fires and greater incidence of crown fires. Crown fires are typically nonlethal to melaleuca trees but usually result in pine mortality [53]. As Myers [53] explained, "fire in stands of melaleuca containing any mature capsule-laden individuals leads to the spread of the melaleuca forest into susceptible habitats nearby, resulting in a shift from a fire regime controlled by surface fuels to one dominated by aerial fuels. This is a fire regime heretofore unknown in the Florida environment and is likely to result in significant changes to wetland habitats, especially the species composition. Once melaleuca gets a foothold in a pine- or cypress-dominated habitat, the shift from low-intensity to high-intensity fire regime results in the mortality of the native pine and cypress and subsequent conversion to melaleuca" [53].

The melaleuca fire regime is difficult to categorize. Myers [53] classified the fire regime in southern Florida melaleuca forests as mixed-severity to capture the variation in fire severity among these habitats: "The fire regime mediating Florida's melaleuca forests varies from one characterized by low-intensity surface fires in savannas, with some torching of individual trees, to high-intensity crowning fires in denser stands." "Understory burns occur in melaleuca savannas. In mixed stands of melaleuca and cypress or pine, the fires are lethal to cypress or pine but not to melaleuca. In pure melaleuca forest, high-intensity crowning fires are not lethal to the main stem of the trees. The combination of limited stem mortality and high-intensity fire is unusual in North American ecosystems. Placing melaleuca forest in the mixed fire regime is a compromise between low mortality and high intensity" [53].

Research is needed to ascertain the impacts of melaleuca-mediated changes in fire regime on biotic and abiotic components of southern Florida's ecosystems. For example, does melaleuca invasion result in significant levels of organic soil consumption resulting from severe ground fires, compared with areas of intact native flora? If so, what ecosystem changes are wrought by such reductions in organic soils?

Although melaleuca has evolved several adaptations that permit its exploitation of fire within the plant communities and ecosystems of southern Florida, the relationship between melaleuca and fire in its native habitats is unclear. Seasonal swamp forests and woodlands in northern Australia that are dominated by *Melaleuca* spp. are "adapted to regular fire" [89], although the occurrence of *Melaleuca quinquenervia* appears limited mostly to eastern Australia (see General Distribution). A review by Meskimen [48] indicates that melaleuca is a fire-seral species in at least parts of its native range. However, Balciunas and Burrows [4] suggested that in eastern Australia it "is considered fire intolerant, and natural stands are confined to wetlands." It was further asserted that melaleuca fire tolerance in Australia is reduced by stress associated with insect herbivory, and that perhaps a classical biological control program using Australian insect herbivores could reduce melaleuca's fire tolerance in southern Florida [4].

The following table provides fire return intervals for important plant communities and ecosystems where melaleuca might be found in peninsular Florida.

Community or Ecosystem	Dominant Species	Fire Return Interval Range (years)
mangrove	*Avicennia nitida-Rhizophora mangle*	35-200

Everglades	*Cladium mariscus* ssp. *jamaicense*	<10
melaleuca	*Melaleuca quinquenervia*	< 35 to 200 [53]
slash pine	*Pinus elliottii*	3-8
slash pine-hardwood	*P. elliottii*-variable	< 35 [103]
South Florida slash pine	*P. elliottii* var. *densa*	1-5 [53,103]
longleaf-slash pine	*P. palustris-P. elliottii*	1-4 [53,103]
longleaf pine-scrub oak	*P. palustris-Quercus* spp.	6-10 [103]
oak-gum-cypress	*Quercus-Nyssa*-spp.-*Taxodium distichum*	35 to > 200 [53]
southeastern oak-pine	*Quercus-Pinus* spp.	< 10
live oak	*Q. virginiana*	10 to< 100 [103]
cabbage palmetto-slash pine	*Sabal palmetto-Pinus elliottii*	< 10 [53,103]
baldcypress	*Taxodium distichum* var. *distichum*	100 to > 300
pondcypress	*T. distichum* var. *nutans*	< 35 [53]

POSTFIRE REGENERATION STRATEGY [88]:
Tree with adventitious bud/root crown/soboliferous species root sucker
Tall shrub, adventitious bud/root crown
Crown residual colonizer (on-site, initial community)

FIRE EFFECTS

SPECIES: Melaleuca quinquenervia

- IMMEDIATE FIRE EFFECT ON PLANT
- DISCUSSION AND QUALIFICATION OF FIRE EFFECT
- PLANT RESPONSE TO FIRE
- DISCUSSION AND QUALIFICATION OF PLANT RESPONSE
- FIRE MANAGEMENT CONSIDERATIONS

IMMEDIATE FIRE EFFECT ON PLANT:
Fire usually kills many, if not most, melaleuca seedlings [54,93]. According to Timmer and Teague [93] fire kills most seedlings less than about 12 inches (30 cm) tall. Based on results from field experiments, Myers and Belles [54] predicted that most fires will kill more than 90% of seedlings under 8 inches (20 cm) tall. Survival generally increases with plant size [54]. Fire effects on saplings are variable and depend on individual fire behavior and season of burn (see Plant Response to Fire) [54,55]. Myers and Belles [54] predicted that fire will generally not kill saplings larger than 6.6 feet (2-3 m) tall, but may cause >50% mortality of saplings smaller than about 20 inches (≤50 cm) tall.

A single fire results in little to no mortality in mature melaleuca stands [30,54] despite a high occurrence of torching and crown fire in melaleuca-invaded communities (see Fire Ecology or Adaptation).

Fire apparently results in little, if any damage to canopy-held seeds. According to Woodall [112], even a hot crown fire is unlikely to kill more than a "minor percentage" of these seeds.

DISCUSSION AND QUALIFICATION OF FIRE EFFECT:

As of this writing (2005), no published reports describe the effects of a long-term repeated pattern of frequent burning on melaleuca. Myers and Belles [54] noted speculation that frequent burning may gradually remove the outer layers of protective bark and eventually lead to greater mortality. There is also speculation that persistent, incremental damage from herbivory may weaken melaleuca plants and leave them more vulnerable to fire damage [4] (see Biological control). For further discussion about fire as a method for controlling melaleuca see Fire Management Considerations.

PLANT RESPONSE TO FIRE:

While foliage, twigs, and smaller branches may be consumed or severely damaged by fire, these are readily and rapidly replaced by new growth originating from epicormic buds that produce postfire sprouts on the main stem and larger branches [24,30,51,52,53,102]. Postfire sprouting along branch sections terminal to emptied capsules (see below) is uncommon [48]. Following a particularly severe fire, sprouting can occur below any point on the bole not killed by fire [52]. Basal sprouts develop if the tree is completely top-killed [102]. In some cases, even seedlings less than a year old may sprout at the "root collar" [52]. Meskimen [48] suggested that seedlings <0.5 inch (1.3 cm) in diameter can sprout "very close to ground level" following fire.

Melaleuca reproduction may be most abundant following fire. This is in large part due to the synchronous release of potentially millions of canopy-stored seeds per mature seed tree from serotinous capsules (see Regeneration Processes) onto a fire-exposed seedbed [30,48,53]. The rate at which canopy-held seed is released after fire may be closely related to fire severity. Meskimen [48] observed that on branches where foliage is consumed seeds may be released within 1 day. Where foliage is only scorched seed release takes "somewhat longer." Myers and Belles [54] measured postfire seed rain following an "extremely intense" wildfire in Big Cypress National Preserve that consumed most of the crowns but left mature, seed-bearing melaleuca trees standing. At 3 different sites, more than 95% of stored seed was released during the first 5 postfire weeks, with light seedfall continuing for several months. Melaleuca is likely the first among species present to disperse postfire seed [51]. Despite the sometimes rapid and near-complete purge of the canopy seed bank following fire, melaleuca produces a new seed crop within a short time [52]. Flowering can occur "within weeks after fire" [24]. According to Ewel [24], prolific postfire epicormic sprouting greatly increases the surface area of small branches, and presumably also flowering, thereby enhancing reproductive potential.

Myers [52] indicated that when seed trees are present, melaleuca is one of the first postfire species to colonize.

DISCUSSION AND QUALIFICATION OF PLANT RESPONSE:

Postfire recovery in melaleuca saplings is probably influenced by fire severity and interactions with additional environmental stressors [54,55]. For example, field experiments [55] showed that greater fire intensity seemed to produce comparatively greater sapling mortality. Yet a stand subjected to a "very mild July burn" that led to less mortality in melaleuca <3.3 feet (1 m) tall, compared with a more intense March burn, nevertheless had comparatively greater mortality in the 3.3- to 9.8-foot (1-3 m) sapling class. The difference was attributed to flooding immediately following the July burn [54,55].

Postfire melaleuca seedling establishment and recruitment are variable, depending upon conditions (see Seedling establishment/growth). Prolonged drought or flooding can substantially reduce, but rarely eliminates, postfire seedling establishment [54].

As of this writing (2005) there are no published studies establishing a firm causal relationship between burned sites (compared with an undisturbed ground layer) and increased seedling establishment. There is some observational field evidence that melaleuca germination is greater on recently burned sites compared with similar unburned sites where vegetation, litter, and periphyton are intact, but subsequent seedling mortality across all treatments precluded drawing conclusions about establishment [51,54,55]. Nevertheless, Myers and Belles [54] suggested that, on comparable sites, establishment from seed released after nonfire disturbance (i.e. herbicide, frost, or other damage to crowns that leaves the ground layer intact) is likely to be low compared with establishment from fire-induced seed release.

Frequent mention is made (e.g. [110]) of the significance of postfire nutrient availability for seedling establishment and growth (see also information on soil nutrient competition in Site Characteristics), but as of this writing (2005) there are no published studies documenting a postfire fertilization effect impacting melaleuca invasion in southern Florida.

FIRE MANAGEMENT CONSIDERATIONS:
Melaleuca invasion may result in changes in fuels and fire behavior relative to what might be expected in native communities. Melaleuca invasion presents novel challenges for fire suppression in southern Florida, mostly related to increased incidence of crown fire, spotting, and ground fire in organic soils [28,102]. Flowers [28] provides a review of fire suppression problems and tactics for melaleuca-invaded sites in southern Florida.

In communities where melaleuca is replacing sawgrass, development of dense melaleuca stands often provides substantial increases in both aerial and surface fuel loads. When fires occur in invaded areas, these changes in fuel conditions may increase incidences of fire spotting. Melaleuca invasion in sawgrass habitats is also implicated in the increased incidence and severity of ground fire in organic soils (see Fuel). Increased burning of organic soils may have serious implications for smoke management due to the volume and intensity of smoke that these ground fires can produce [28].

Fire spread rates may be greater in melaleuca invaded areas, compared with "pine/palmetto/gallberry type fires." This is attributed to a combination of lighter, more easily ignitable ground fuels, peeling melaleuca bark that acts as a ladder fuel, and the increased incidence of spotting [28].

In general, melaleuca management is made difficult by the fact that disturbance resulting in canopy damage in trees of seed-bearing age leads to a rapid purge of canopy-held seed [55]. Of particular difficulty are occasions where understory or ground layer vegetation is also disturbed, such as following fire. Ensuing seedling establishment may initiate a new, often denser melaleuca stand. However, excluding fire (or other disturbance) from established melaleuca stands is probably not a desirable alternative. Although fire exclusion may limit the spread of melaleuca, subsequent successional changes may be undesirable. Further, even with active suppression fire is probably inevitable in the long term [55].

Melaleuca-infested sites that experience wildfire should be given high priority for control, since the postfire environment is probably the most susceptible to melaleuca population increases. The quantity of seedlings established after fire is likely to be huge, and initial growth may be rapid relative to what would occur on an equivalent unburned site. In the event of a wildfire releasing vast quantities of seed, seed trees should be treated with herbicide within 1 postfire year to prevent replenishment of seed stores, then establishing seedlings should be controlled [54]. Saplings that survive the fires may also be treated with herbicides [55].

It is unclear what time interval between fires is feasible or most effective for controlling postfire seedlings. Myers and Belles [54] found a 2-year interval between fires to be effective, although they acknowledged results may differ depending on site productivity. Fuel loads may be too low to carry a 2nd fire for 2 to 3 years, perhaps limiting the effective use of fire as a means to control seedlings (see below). However, field studies did show that gulfhairawn muhly (*Muhlenbergia capillaris* var. *filipes*) prairie can be reburned within 2 years and that nearly all seedlings established after the initial seed release event could still be killed (see Immediate Fire Effect on Plant). Follow-up inspections and treatments are likely to be needed [54].

On sites where a prescribed fire is planned, but that contain scattered seed-bearing melaleuca, these "outliers" should be dealt with prior to burning. If outliers cannot first be controlled, burning should be conducted while the soil is still wet enough to stimulate germination, but close enough to the onset of dry season to limit seedling establishment and survival. In addition to surveying for and controlling seedlings that establish after fire, seed trees should be controlled before they replenish seed stocks [54].

Stand structure and age class structure can also be important considerations for mitigating postfire seed release. Mature and emergent melaleuca trees release tremendous amounts of seed after burning, while fires in even-aged "dog hair" stands may burn without releasing many seeds because they produce less seed (see Seed production). "In control efforts where complete stand eradication is not possible in the short term, it may be useful to target mature outliers as well as emergents in dense stands. In other words, remove the trees producing the most seed first. A wildfire in the remaining stand may release relatively few seeds" [54,55].

A study by Myers and others [55] demonstrated the influence of timing, both of burn season and weather/hydroperiod, on melaleuca germination, seedling establishment, and recruitment to sapling status, in the postfire environment. Where seed-bearing trees are present, fire often results in rapid (within 5 weeks after fire) release of most (>95%) canopy-stored seed. Most germination occurs when seeds encounter moist soil. When seeds fall on dry substrate, germination is delayed until the next significant rain event. Because vast quantities of seed are released, large numbers of seedlings may result under optimum germination conditions. However, it appears that substantial seedling mortality is common when the site becomes either flooded or dries. The seasonal weather pattern in southern Florida is relatively predictable. Melaleuca seedling survival is greatest when seedlings establish during the wet season as flood waters wane. Seedling mortality is greatest for cohorts established during the transition from wet season to dry season. But more punctuated weather episodes such as brief droughts or short-lived rainy periods are common as well, and can lead to correlative periods of germination, establishment and mortality. The predictive power of weather forecasting over periods of weeks to months has obvious limits. Nevertheless, planning prescribed fires for times that put seed on the ground when it is least likely to result in newly established melaleuca cohorts is desirable [55].

Melaleuca seedling establishment can be largely controlled using prescribed fire [54]. However, determining the appropriate timing of burn treatments for seedling control can be difficult. Burns must be conducted after seed rain is complete and most germinable seeds have germinated, but before establishing seedlings are large enough to sprout following fire. A general rule governing this timing probably does not exist. Intervals between seed release and seedling establishment, and between establishment and the ability to survive fire, varies among sites, between years, and within a year depending on moisture conditions following seed rain, prefire fuels, seed rain volume and duration, and seedling growth rates [54]. Results of a study by Myers and Belles [54] suggest that seedlings <3 months old almost never sprout in response to top-killing. Also, at any given age, larger seedlings (height or diameter) were significantly ($p<0.01$) more likely to survive top-kill by fire or clipping, compared with smaller seedlings. Mean height at which seedlings first demonstrated sprouting following burn treatments ranged from 1.9 to 6 inches (4.7-15.2 cm), and mean basal diameter ranged from 0.07 to 0.12 inch (0.17-0.31 cm). For treatment descriptions and detailed results, see [54]. Seedling size may be a more critical metric than seedling age in predicting control effectiveness using fire. Therefore, on sites that support rapid and robust melaleuca seedling establishment and growth, the window of opportunity for controlling seedlings with prescribed fire is likely to be shorter than on less productive sites. Myers and Belles [54] "cautiously" recommended conducting fire treatments within 6 months of seedling establishment on "high quality" melaleuca sites, while suggesting that a 24-month postestablishment window is possible on sites where seedling growth is slowest. In their field studies in Big Cypress National Preserve, they found >90% of seedlings ≤2 years old were killed by fire.

Unfortunately, any seed trees that survive fire may have replenished their store of canopy-held seed by the time enough fuel has accumulated to carry a second fire. Research in Big Cypress National Preserve demonstrated that surviving melaleuca seed trees replenished stores of seed capsules within 2 years after the initial fire, and a 2nd prescribed burn resulted in an additional cohort of establishing seedlings. Depending on the site and the plant community, successive burns may largely stave off establishment of new seedlings, even though mature seed trees remain on site and producing seed [54,55].

Most evidence indicates that a single fire, and perhaps several periodic fires, are unlikely to cause any substantial mortality in mature melaleuca stands (see Fire Effects discussion above). Meskimen [48] related an anecdote about a stand of melaleuca planted as a windbreak around sugarcane (*Saccharum officinarum*) fields, which were burned each year. While details of fire behavior and effects were not described, he stated that trees were "exposed to extreme heat and sometimes direct fire which causes complete defoliation." These trees displayed no signs of damage other than fire scarred bark, and seemed to exhibit normal growth. Nevertheless, Myers and Belles [54] suggested that the ramifications of a prolonged program of repeated burning in melaleuca stands are unknown.

Disturbances that release the canopy seed bank but leave intact fuel beds offer the best opportunities for seedling and sapling control with fire. Unlike postfire seedling establishment, in which fuels sufficient to kill newly established seedlings are consumed in the original fire, an episode of mass seed dispersal and germination associated with a nonfire disturbance would be accompanied by retention of predisturbance fuels and potential for burning many vulnerable young melaleuca seedlings. On most sites, for instance, regeneration established from seed released due to herbicide-kill or frost-damage could easily be killed by burning [54,104]. Again, burning should be implemented after most seeds have dispersed and germinated but before seedlings have reached a size where many are likely to survive the fire. In some instances germination may be delayed for months due to either flooding or drought, and growth after germination will vary greatly from site to site. Sites where seeds have been released must be monitored to verify that germination has occurred and that seedlings do not exceed a meter in height [54].

Timmer and Teague [93] indicate controlled burning can be used to eliminate seedlings or sprouts that occur following control of adult seed-bearing trees (see the discussion on Control and subsequent information on various nonfire control methods). Tuck and Myers [95] have advocated use of properly timed prescribed fire for melaleuca management. Objectives can include reducing seed crops, preventing flowering, eliminating seedlings, and thinning young stands. They also suggest that herbicides may be more effective on fire-weakened melaleuca than on unburned plants. A melaleuca control program on the Arthur R. Marshall Loxahatchee National Wildlife Refuge in southern Florida has utilized prescribed fire following herbicide application to control seedlings and to further weaken surviving mature trees [46]. Myers and others [55] recommended prescribed burning as a follow-up 2 to12 months after pulling small plants and cutting and herbicide treatments for larger plants. For dense stands, Myers and Belles [54] speculated that burning followed by ground-based foliar herbicide application to sprouts at 3 to 9 months postfire, is more effective than spraying untreated or unburned stands from aircraft.

MANAGEMENT CONSIDERATIONS

SPECIES: Melaleuca quinquenervia

- IMPORTANCE TO LIVESTOCK AND WILDLIFE
- OTHER USES
- IMPACTS AND CONTROL

IMPORTANCE TO LIVESTOCK AND WILDLIFE:
The importance of melaleuca-invaded habitat for wildlife in southern Florida is unclear. According to Geary and Woodall [30] melaleuca stands "are of dubious value to wildlife." Melaleuca-invaded habitats in southern Florida may support some populations of native rodents, but the value of melaleuca-invaded habitats relative to native habitats for native rodents and their predators remains unclear [47,58].

Schortemeyer and others [79] recorded 30 species of birds from November through April in or near melaleuca study sites in southern Florida. They suggest that melaleuca may provide nesting and roosting sites for anhingas, egrets, and herons, and resting and feeding perches for Everglade kites, in areas where altered hydroperiods have damaged or eliminated natural sites such as willow (*Salix* spp.) strands.

O'Hare and Dalrymple [57] conducted a comprehensive survey of wildlife in southeastern Florida marshlands across a gradient of melaleuca coverage. Overall species richness was highest in areas with moderate melaleuca coverage (or melaleuca savanna), perhaps due to high levels of structural diversity of vegetation. Much of the observed difference in overall species richness was associated with high numbers of migratory upland birds.

Although migratory upland birds apparently favored melaleuca savanna habitat over dense melaleuca stands or relatively uninvaded marsh habitats, species abundance generally remained below that for the same bird species in native forested habitats such as cypress swamps, hardwood hammocks, and south Florida slash pine rocklands. There were no significant ($p<0.05$) differences between melaleuca cover types in average number of individuals or average number of species of captured macroinvertebrates or herpetofauna. For fishes, there were no significant ($p<0.05$) differences between melaleuca cover types in average number of species, but average number of captured individuals was significantly ($p=0.03$) lower in the densest (75%-100% coverage) melaleuca habitats. A shift in species mix of both birds and mammals with melaleuca cover was noted, with more typical marsh species found in the lowest melaleuca cover types and more upland or forest-dwelling species found in the densest melaleuca habitats [57].

According to O'Hare and Dalrymple [57], moderate levels of melaleuca invasion in southeastern Florida native marsh habitats may not necessarily diminish typical native faunal species composition and productivity. As native graminoid/herbaceous wetlands are converted to closed-canopy melaleuca forest, presence of upland, arboreal, and/or forest species increases, but not necessarily at the immediate expense of wetland species diversity. They recommend that efforts to control melaleuca and restore native plant communities be made in ways that recognize the persistence of native fauna in invaded habitats and allow for retention of the extant wildlife community. Nevertheless, Schortemeyer and others [79] suggested that melaleuca wildlife value should not be overstated, since melaleuca's continued spread across the landscape is likely to diminish overall native habitat [79].

As of this writing (2005) there is no published information describing importance of melaleuca for livestock.

Palatability/nutritional value:

Relatively low moisture (56%) and high crude fiber contents indicate melaleuca has a low digestibility coefficient and is probably not a desirable deer food [79]. Young foliage is highest in nitrogen content and lowest in percent dry mass, compared with mature foliage [105].

The following table provides chemical analysis, on a percent oven-dry basis, of melaleuca browse material. Samples were collected in spring from the Everglades Wildlife Management Area [79].

Protein	Crude Fat	Crude Fiber	Ash	N-free Extract	Ca	P	K	Mg	Na
4.95	8.18	25.34	6.51	54.97	1.93	0.06	0.42	0.20	0.31

Cover value: No information is available on this topic.

OTHER USES:

Although melaleuca was previously planted in Florida as an ornamental landscape tree, retail trade in melaleuca has largely ceased [7]. It was planted as early as 1941 on levees and dredged materials islands at Lake Okeechobee, Florida to prevent storm waves from eroding the levees [91]. Melaleuca was introduced in Hawaii for ornamental uses, windbreaks, and as "watershed cover" [42]. It is apparently also cultivated as an ornamental in southern Louisiana, Texas, and California, and perhaps Puerto Rico (see General Distribution).

Melaleuca is an important honeybee plant in southern Florida [30,36,48,77].

Melaleuca chips may be useful as a component of commercial potting medium [12,17,18].

Essential oil is distilled from leaves, twigs, and seeds. The oil has both traditional and modern uses, mainly associated with its antiseptic properties [94]. It has been used for medicinal purposes and as food flavorings [22]. Commercial production of essential oil from melaleuca apparently ceased in 1955 when a Swiss company began producing a synthetic form [9].

Wood Products:

Globally, melaleuca has been used for structural lumber, fuel, pulpwood, and insulation/stuffing [22]. It has been used for traditional dwelling construction in New Caledonia. Melaleuca wood has been used extensively for carpentry and joinery work. It is workable mainly while it is still green, becoming extremely hard after drying and ageing. The wood is also resistant to common wood-eating insects [94]. No "significant" industries in Florida utilize melaleuca for any these products [22]. According to Geary and Woodall [30], melaleuca wood products value is diminished by the "quality of its corky bark."

IMPACTS AND CONTROL:

Impacts:

Melaleuca has been called "the greatest exotic weed threat" to wetlands in southern Florida. Its impacts threaten natural areas such as Big Cypress National Preserve and the Everglades. Systematic reconnaissance flights indicated that by 1992 there were 119,000 acres (48,160 ha) of melaleuca-infested habitat in Big Cypress National Preserve [59]. Everglades National Park is 1 of only 3 sites internationally listed by The International Biosphere Reserve, World Heritage, and Ramsar as critical reserves. The native flora of southern Florida represents a unique assemblage of communities. Southern Florida encompasses the only region of the continental United States where temperate, subtropical and tropical floral elements coexist. This unique area has produced approximately 65 endemic plant taxa, many of which are threatened due to habitat diminishment (reviewed by [96]).

Melaleuca's negative impacts in southern Florida largely stem from the species's interference with and displacement of native species [21]. A review by Hofstetter [35] indicates that in the Everglades and southeastern Florida melaleuca may invade "essentially all types of communities, including those where vegetative components appear to be healthy and presumed" to be "comparable to historical vigor." Intact native communities may be more resistant to invasion in southwestern Florida but are still susceptible, particularly following unnatural disturbance or other human-caused environmental degradation.

Presence of melaleuca in fire-maintained sawgrass communities can promote conversion of these habitats to melaleuca forest. Everglades marshlands are comprised of fire-maintained communities of mostly sawgrass prairies. Natural fires periodically eliminate the native, fire-intolerant hardwoods that would otherwise colonize this habitat. However, because melaleuca is so well-adapted to fire it is able to persist and even thrive in this environment, eventually shading out the herbaceous community and transforming the site into a melaleuca forest [96]. See Habitat Types and Plant Communities for more information about specific taxa and communities that are potentially impacted.

Conversion of native forest types to melaleuca forest may or may not impact understory species composition and density, depending on the community invaded. Where invaded and uninvaded forest overstory structure is similar, casual observation indicates that the understory may be relatively unchanged, such as in cypress swamps and pine flatwoods where melaleuca establishment is typically "not dense enough" to alter stand structure. Understory vegetation may be most severely impacted where melaleuca invasion increases forest overstory density or leads to conversion of prairie or savanna to melaleuca-dominated forest, such as in pine flatwoods depressions, sloughs, wet prairies, and the seasonally flooded ecotone surrounding cypress swamps [48].

Conversion of the dominant overstory species as a result of melaleuca invasion in forested habitats may be a more obvious impact. Geary and Woodall [30] indicate "mature" melaleuca stands in Florida "swamps" range from 7,000 to 20,000 stems/ha, and up to 133 m^2/ha of basal area. Stands growing on shallow or better-drained soils produce similar stem densities, although volume is "substantially" reduced. Myers [51] described how melaleuca "invades portions of fire-maintained pine and cypress forests in southern Florida, and in some cases appears to pre-empt sites where the native vegetation would normally regenerate following fire. Melaleuca accomplishes this by being the first woody species to get its seed on the ground following a late dry season fire. Once established it forms a dense canopy, shading out or preventing seedling establishment of other species. Melaleuca's shaggy bark and flammable leaves may facilitate burning at a greater frequency than normally took place. The result is the development of a new melaleuca-dominated community maintained by fire" [51].

Strong melaleuca competition in invaded communities may result from greater exploitation of soil resources. Results from Di Stefano and others [20,21] revealed that melaleuca-dominated stands (8-10 years old) contained significantly ($p<0.05$) more woody species root biomass in the upper 8 inches (20 cm) of soil than nearby grand eucalyptus (*Eucalyptus grandis*) (9 years old) or slash pine (20 years old) plantation stands, or palmetto prairie. The 3 forested sites contained similar levels of aboveground biomass.

One of the most important factors in the success of melaleuca in southern Florida may be its relationship to fire. Melaleuca is well-adapted to perpetuation in a fire-prone environment, perhaps more so than any dominant native plant species in southern Florida. As a result, Wade and others [104] suggested that if melaleuca is present in a burned stand, and postfire hydrologic conditions are conducive to germination and establishment of substantial numbers of melaleuca seedlings, native species in the new stand may be substantially reduced. Because of its many adaptations to fire, melaleuca may have an advantage over many native species in response to dry season fire, to which many native species are apparently not well adapted (reviewed by [35]). Melaleuca invasion may pose particular risk to fire-dependent communities in southern Florida. Myers and others [55] pointed out that marshes, wet prairies, cypress swamps, and pinelands, all habitats that are susceptible to melaleuca invasion, also are all common habitats in southern Florida that require fire for survival. For more information about melaleuca and fire, see Fire Ecology and Fire Effects.

Geary and Woodall [30] attributed the success of invasive melaleuca in Florida to altered hydrology, as well as altered fire regime. Lowered water tables as a result of drainage and excessive groundwater withdrawals in some areas of southern and central Florida have led to changes in the natural hydroperiod. In many areas shortening of flood duration may have led to increased size and severity of wildfires [104]. In addition, sites experiencing stand-replacing fire are frequently subject to seed rain from established melaleuca trees that were planted as ornamentals. The combination of altered hydrology, altered fire regime, and available seed sources can lead to postfire sites that become fully-stocked melaleuca stands with much reduced native plant presence [30]. Melaleuca invasion may itself alter fire regimes, as well as fuels [28].

South Florida Water Management District and the U.S. Army Corps of Engineers consider impacts of invasive melaleuca in the littoral zone of Lake Okeechobee when adjusting lake water levels. Lower lake levels may stimulate melaleuca growth and establishment, and prolonged periods of reduced water levels may lead to the expansion of established melaleuca populations (reviewed in [44]).

Ewel [24] has argued that southern Florida may be especially susceptible to invasion by nonnative plants because it is geologically young and not all ecological niches are fully occupied by its indigenous flora. In particular, pondcypress growing on sites that are too wet to support south Florida slash pine, but are drier than is optimal for pondcypress, may be unable to effectively compete with invading melaleuca [24,52]. Pondcypress stands in these ecotones are short, open-canopied, and subject to frequent fires [24]. Myers [52] and Ewel [24] suggest pondcypress in southern Florida occupies sites for which it is not well adapted. Melaleuca invasion in "dwarf cypress" habitats, which are typically a mix of wet prairie and stunted south Florida slash pine and pondcypress, may represent displacement of native species that had occupied "suboptimal sites due to an absence of competition" (see Myers [52] for details). The ecotone between pondcypress and south Florida slash pine forest communities seems particularly susceptible to melaleuca invasion [52].

It is commonly asserted that one reason nonnative invasive plants are so successful is that they are largely unconstrained by the impacts of herbivory from coevolved pests in their native habitat (e.g. a review by Mack and others [45]). Balciunas and Burrows [4] demonstrated how ambient, nonoutbreak levels of insect herbivory significantly ($p<0.05$) suppressed height and diameter growth of melaleuca saplings in northern Queensland, Australia. They also suggested that reduced levels of herbivory on southern Florida melaleuca, compared with herbivory in Australia where the species is native, might explain part of melaleuca's strong competitiveness in southern Florida's plant communities [4]. Comparative data from melaleuca populations in eastern Australia and southern Florida suggest that seed production is substantially greater in Florida melaleuca trees than those in

Australia [74].

Indirect impacts may also result
from presence of melaleuca in peninsular Florida. Melaleuca is a host to lobate lac scale (*Paratachardina lobata*), a nonnative invasive insect pest in southern Florida. Lobate lac scale has a broad host range, attacking well over 100 different woody plants including native species, ornamentals, and crop plants. Damage to melaleuca from lobate lac scale is apparently minimal, but melaleuca can serve as a reservoir for lobate lac scale's infestations of more desirable plants [82].

Although melaleuca has been blamed for human respiratory and allergic reactions [49], a study by Stablein and others [86] concluded that melaleuca is not a significant source of aeroallergen, and melaleuca odor is not a respiratory irritant.

As of this writing (2005), there is very little information indicating whether melaleuca is invasive in areas of North America outside Florida. Woodcock and others [114] described a melaleuca plantation established in the early 1930s on a mid-elevation (869-951 feet (265-290 m)) site on the island of Oahu, Hawaii. The relatively open character of the stand permitted native woody plants to establish in the understory, while excluding more light-demanding nonnative species. It was hypothesized that the melaleuca plantation may be fostering the regeneration of a native successional forest. According to Little and Skolmen [42], in Hawaii melaleuca is "naturalized, but not a pest as in Florida."

Control:

The challenge of melaleuca control is influenced by an ever-changing, frequently ephemeral arrangement of environmental conditions, stand structures, seed sources, regeneration status, and fuel loads. Anticipating and identifying windows of opportunity in target susceptibility can enhance success. For instance, treatments for controlling seed-bearing melaleuca may be timed to minimize opportunities for successful seedling establishment resulting from the inevitable postdisturbance seed rain. Treatments that put seed on the ground in late fall or early winter, typically when the soil is still moist from seasonal rains, stimulate germination. Yet many, if not all of the delicate young seedlings are likely to die during the predictably dry months of March, April, and May [54]. Van and others [100] suggested the best time for melaleuca control in southern Florida might be spring, when plants are most actively growing (see Seasonal Development).

Because treating seed-bearing adults inevitably leads to substantial seed release, follow-up treatment or multiple treatments of establishing seedlings will be required to prevent immediate reinvasion. Control activities minimizing disturbance to soil and surrounding desirable plants may help mitigate subsequent melaleuca seedling establishment [93,110] (see Site Characteristics). Myers and Belles [54] point out the importance of field monitoring for knowing a) when germination begins following major seed release, b) whether germination is complete, c) whether additional germination episodes occur following receding flood waters or cessation of drought, and d) size of the largest seedlings in a cohort relative to cohort age. This last point may be important for determining whether the largest seedlings are capable of sprouting in response to top-kill.

Woodall [110] recommended focusing control efforts first on outlying individuals that serve as seed sources for new infestations. Dense, well-established melaleuca stands are more difficult, time consuming, and expensive to eradicate, especially over large areas. Once outliers are eliminated and dense, well-established stands are contained, strategies for complete eradication can be implemented [110].

For areas with scattered, mature melaleuca seed trees that have not recently burned, Woodall [113] recommended killing trees and releasing seed from late October to late December. Moisture provided by occasional winter showers will stimulate germination. Lack of fire will promote plant "competition," resulting in slow-growing melaleuca seedlings. Typical spring drought conditions will kill most germinants. The ensuing summer wet season should stimulate germination of any ungerminated seeds left on the site. These and any remnant seedlings can be removed with prescribed fire during the following dry season [113].

In extremely dense melaleuca stands seed production may be substantially reduced within the dominant age cohort due to shading. However, these stands may also contain larger, older, canopy-emergent individuals that bear large numbers of capsules. It may be prudent to first focus control efforts in these stands on the emergents. Without these, extremely dense stands may pose a comparatively lessened threat of massive seed release [54].

A strategy utilized by resource managers at Big Cypress National Preserve is to delay follow-up treatments in melaleuca control units for 3 years, allowing seedlings an opportunity to reach a height that facilitates detection with a minimal chance of seed production [59]; however, some plants may produce seed at <3 years of age [48].

Prevention:

Because melaleuca seed dispersal is typically distance-limited, treatment of outlier trees that occur far from established melaleuca populations may prevent establishment of new, invasive populations. If the outlier is eliminated in such a way that seeds are not released, then the probability of colonization in that habitat is substantially reduced [11]. Woodall [110] describes how, "as one proceeds toward the central denser portion of a melaleuca population, the relative benefits from killing individual trees decline. The biggest payoff is from controlling the most isolated, most distant trees." Biennial inspections of uninvaded areas will help identify melaleuca outliers [110].

Integrated management:

A combination of stressors, both natural and human-caused, might be integrated for more effective management and control of melaleuca: "A judiciously timed, integrated approach using chemicals, mechanical means, and fire can be effective. Present control efforts use mechanical cutting followed by a dose of herbicide. Little attention, on the other hand, has been given to the site susceptibility and timing of treatment. Sites should be treated when the seeds would be most unlikely to encounter favorable conditions for establishment. Full advantage should be taken of both fire and frost. Both occur naturally every few years. Fire can be prescribed at practically any time as long as fuel is available. Both destroy melaleuca biomass in leaves, branches, and small diameter stems, all of which are replaced by sprouts. To accomplish this, the tree uses and depletes stored food reserves. If the tree is cut and treated with herbicide while these reserves are low, the energy for sprouting would be lacking and follow-up treatment would be minimal. Due to the time of year, frost-released seed is likely to encounter unfavorable site conditions, and fuel for burning still remains. Treatment of seed trees following frost and prescribed burning should greatly reduce sprouting. A late wet or early dry season prescribed burn would put the seed on the ground at an unfavorable time" [51].

Biological control agents may further reduce melaleuca populations that have been damaged by other means, such as mechanical, chemical, or fire. Center and others [16] described a release site for melaleuca snout beetle where an estimated 51,360 cut stumps "had coppiced profusely." Snout beetles had fed upon an estimated 25% of coppices. Of those plants that were fed upon, damage on 53% was low (generally consisting of nibbling on one or a few tips), damage on 31% was moderate (extensive damage to several stem tips), and damage on the remaining 16% was high (almost all foliage destroyed) [16].

Physical/mechanical:

Mechanical clearing or felling of mature melaleuca trees can be an effective means of control. However, to be most effective desirable vegetation should be subsequently established and maintained, and posttreatment seedling control undertaken. Follow-up treatment(s) are required to control stump sprouts [93]. In a field experiment, 98% of melaleuca plants 2.3 to 3.9 feet (0.7-1.2 m) tall sprouted after a single cutting. The month in which stems were cut had no effect on biomass recovery after a single cutting. Following a 2nd cutting (2 years after the 1st cut), melaleuca mortality rates were still ≤27% for all but 3 months of the year. Mortality rates in June, July, and August were 72%, 55%, and 42%, respectively. High mortality in August may have been influenced by flooding during that month [83]. Plants <3.3 feet (1 m) tall may be hand-pulled and should be stacked to prevent sprouting. Plants > 3.3 feet (1 m) tall are best cut with a machete or chainsaw and the cut surface treated with herbicide [55].

According to Timmer and Teague [93], mature trees that are mechanically cleared should be removed from the site and destroyed to reduce seed dispersal and sprouting. However, Myers and Belles [54] cut >5,000 melaleuca trees in the course of field research, and observed sprouting in "only a few" downed stems, all of which were lying on extremely wet soils or floating. In all cases, sprouts died during subsequent drought.

Fire: See Fire Management Considerations.

Biological:

One reason frequently offered for the success of nonnative invasive plants is that in their new environment they are freed from the negative impacts of pests and parasites with which they coexisted in their native habitats (e.g. see the review by Mack and others [45]). Balciunas and Burrows [4] demonstrated how ambient, nonoutbreak levels of insect herbivory significantly ($p<0.05$) suppressed height and diameter growth of melaleuca saplings in northern Queensland, Australia. They speculated that a classical biological control program using Australian insect herbivores should also suppress melaleuca sapling growth in southern Florida, as well as reduce flowering and seed production, and perhaps lower fire tolerance. Several sources suggest that an integrated biological control program will reduce melaleuca's impact on native species [4,70,107].

Preliminary investigation indicates melaleuca has not acquired indigenous herbivores (or other pathogens) at sufficient densities to cause appreciable damage to trees in southern Florida [19]. Yet several organisms, indigenous and introduced, have shown some potential for reducing melaleuca in southern Florida.

Botryosphaeria ribis
is an indigenous fungus in southern Florida. It is pathenogenic to melaleuca but is not known to cause "large-scale epiphytotics" on melaleuca in the field. However, *B. ribis* canker development and tree mortality may be enhanced by stresses associated with drought, low temperatures, or complete defoliation, so *B. ribis* may enhance the efficacy of other control activities [70]. Although compatibility between the herbicide chemical imazapyr and *B. ribis* has been demonstrated in-vitro [71], field studies demonstrated that stump regrowth following treatment with imazapyr and *B. ribis* mixtures were not significantly ($p=0.05$) different from regrowth of stumps treated with imazapyr alone [72]. It is logical, though speculative, that defoliation by fire may enhance the pathogenic effect of *B. ribis*
infection, suggesting inoculation prior to prescribed fire in melaleuca-infested areas may reduce postfire melaleuca survival. Further research is needed to establish the efficacy of purposeful *B. ribis* inoculation in concert with other control methods or natural melaleuca stressors.

Puccinia psidii
is a rust fungus that occurs on a variety of Myrtaceae throughout the Caribbean islands and North (Florida), Central, and South America (reviewed in [68]). In 1997, *P. psidii* was discovered on new growth of about 70% of melaleuca trees and saplings over a 1.2-mile (2 km) strip in southern Florida. Trees were 10 to 16 feet (3-5 m) tall, top-killed, and bushy in appearance, with many new shoots [67]. *P. psidii* can cause defoliation and twig dieback in infected melaleuca [66,67,68]. The *P. psidii*-melaleuca "pathosystem" may contribute to melaleuca control in southern Florida, especially if integrated into current control programs [68]. Again, research is needed to establish if purposeful use of *P. psidii* could be useful for melaleuca control.

Lobate lac scale, an invasive exotic insect in southern Florida, is reported to feed on melaleuca, but as of this writing (2005) melaleuca damage has seemed inconsequential [82] (see Indirect impacts).

Balciunas [5] speculated that melaleuca snout beetle may reduce melaleuca's fire tolerance in Florida, especially of saplings, presumably by depleting energy reserves needed for postfire sprouting. The melaleuca snout beetle (*Oxyops vitiosa*), an Australian weevil, was released as a biological control agent at 13 sites throughout the range of established melaleuca in southern Florida in 1997 [15,16]. Melaleuca snout beetle establishment (as of May 1999) occurred at 10 of these sites [16] (for a comprehensive description of these sites, introduction methods, and establishment results, see [15,16]). Because of slow dispersal rates (≈ 0.6 mile/year (1 km/yr)), melaleuca snout beetle has been collected and redistributed to >150 locations in southern Florida [60]. Both the adults and larvae prefer to feed on young melaleuca foliage. Although larvae develop best on new leaves, the long-lived (>1 year) adults can subsist on less nutritious, mature foliage and stems during quiescent periods of foliage production [60,106]. Eggs and larvae are most abundant in late fall and early winter when susceptible young foliage is most abundant, and are absent or uncommon in spring and summer unless regrowth from damaged trees is present. Females usually oviposit on the surface of young leaves and expanding buds during the flush of young foliage produced after flowering. The resulting larvae pass through 4 instars, each lasting about 5 days (in eastern Australia). Fourth instars crawl or drop from the host plant, burrow into the ground, and pupate for about 11 days (in eastern Australia) [60,64]. Establishment of beetle populations appears hindered on permanently flooded sites due to drowning of larvae when they drop to search for pupation sites [16,60]. Dispersal of newly released populations may be most rapid on sites with scattered melaleuca in open "savanna-like" areas. Open-grown trees with an abundance of new foliage support healthier snout beetle populations, compared to dense stands with a paucity of young foliage [16]. Based on observations in its native range in eastern Australia, Balciunas and others [6] predicted that melaleuca snout beetle would have the greatest impact on sapling size trees in southern Florida. Feeding by larvae on new foliage causes tip dieback, and persistent damage causes loss of apical dominance. Subsequent branching and new growth provides a feedback of additional resources to sustain continual adult and larval populations. Tissue loss and diversion of photosynthetic resources associated with snout beetle feeding appears to limit flowering in mature melaleuca trees [60,62] and may delay reproductive maturity of saplings [62].

The melaleuca psyllid (*Boreioglycaspis melaleucae*), an Australian native, was released in southern Florida as a biocontrol agent in February 2002 [61,107]. It has established across a variety of melaleuca-invaded habitats in southern Florida, from permanently flooded wetlands to upland pine flatwood sites. Both adults and larvae feed on melaleuca sap, usually feeding at the tips of new twigs [108]. Most damage is attributed to nymphs [61]. "Tender, expanding buds and leaves as well as mature older leaves are destroyed by nymphs. When populations are large, damage may extend to somewhat woody stems" [61].

Eucerocoris suspectus, a Hemipteran native to Australia, was approved for quarantine testing in the U.S. in 1995. Adults and nymphs feed on young melaleuca leaves and shoots [14].

Chemical:

Herbicides are among the most effective and widely used tools for controlling melaleuca in peninsular Florida [40]. Herbicides are most effective when integrated within a suite of control measures and strategies. Cost and logistics can make chemical control difficult to implement over large areas of infestation. As Myers and Belles [54] explained, "for small administrative units, like Corkscrew Swamp Sanctuary, portions of Sanibel Island, and some state parks, existing control technologies focusing on herbicides have worked well. For larger units, like Loxahatchee National Wildlife Refuge, the Conservation Area, and Big Cypress Preserve, the sheer scale of the problem has limited control success" [54].

Damage to melaleuca trees from herbicide may induce the release of substantial numbers of canopy-held seeds. Aside from the cut-stump application method, herbicide treatments presumably result in longer periods of seed release, compared with postfire seed rain, because the herbicides act more slowly than fire [55]. Burkhead [13] indicated melaleuca capsules opened within 6 months after stem injection treatment with either hexazinone or triclopyr. Woodall [112] observed differences in the rate of seed dispersal with different herbicides. Seedfall from trees injected with either picloram or dicamba accelerated rapidly following treatment, corresponding to the rapid effect these chemicals had on the health of treated trees, peaking at 2 weeks posttreatment and remaining above baseline level for 10 weeks to 3 months. In contrast, herbicides that cause gradual damage to trees may not affect seedfall as strongly or as rapidly [112]. Although melaleuca capsules are retained in the tree canopy, mature seeds are not connected to the plant's vascular system so herbicide treatment will not impact seed viability [46]. In some cases, control efforts may actually lead to greater spread due to posttreatment seedling establishment [54].

Herbicide treatments are also complicated by the necessity of retreating the trees that sprout [54,93]. While at least some fraction of mature melaleuca trees that are treated with herbicides can survive initial treatment, detailed information about subsequent sprouting is lacking. Herbicide treatments that leave trees standing (i.e. foliar spray, stem injection or soil-applied herbicide) may result in regrowth of canopy foliage and other aerial tissues [13]. Initial application of chemicals to cut stumps (see below) may also be insufficient to prevent stump sprouting, requiring retreatment.

Timing of herbicide application may also be important. Stocker and Sanders [90] suggested that stem injection treatments administered near the beginning of the growing season only affected tissues above the cut line, since transport in the plant was primarily toward the growing shoots at that time of year. Myers and Belles [54] compared effectiveness of 3 foliar-applied herbicides, applied in January, March, May, June, or November, for controlling melaleuca stump sprouts. Imazapyr was generally more effective than hexazinone, and glyphosate was least effective. Imazapyr killed significantly ($p<0.05$) more trees when sprayed in November (83.1%) or January (79.3%), compared with March (47.8%), June (32.5%), and May (25.0%). Overall, control effectiveness was significantly ($p<0.004$) greater for larger (greater crown volume) trees. Reasons for variation in treatment effectiveness by month were unclear. Rather than considerations of seasonal effectiveness of herbicides at killing trees, Myers and Belles [54] recommended timing herbicide treatments to minimize the chances for successful post-treatment seedling establishment (see Control and Fire Management Considerations).

Foliar application of herbicides yields inconsistent results and may be ineffective compared with other methods. Foliar-applied herbicides are probably most effective for controlling stump sprouts, or aerial sprouts in dense and/or low-statured stands following disturbance (such as fire) [54]. For dense stands, Myers and Belles [54] speculated that burning, followed by ground-based foliar herbicide application to sprouts at 3 to 9 postfire months, is more effective than spraying untreated or unburned stands from aircraft. They tested 3 foliar-applied herbicides for controlling postfire sprouting on melaleuca trees (1.3 to 8.5 feet (0.4-2.6 m) tall). Trees were sprayed either 3 months after fire (mortality sampled at postfire month 20) or 9 months after fire (mortality sampled at postfire month15). Sites were burned under prescription in March and January. Considering all treatment and burn periods, foliar-applied triclopyr produced significantly ($p<0.01$) greater mortality (81%) than imazapyr (55%), which in turn produced significantly ($p<0.01$) greater mortality than glyphosate (19%).

Use of soil-applied pelleted herbicide can control melaleuca and has less site impact than felling and stump treatment. Pelleted herbicide is best for nonseedbearing trees since subsequent seed release is protracted and slow to initiate [110]. Stocker and Sanders [90] found that soil applied pellets of hexazinone and tebuthiuron resulted in 100% mortality of mature trees in periodically flooded habitat.

Stem injection of chemicals is an effective, relatively low-impact melaleuca control method. Injected seed trees purge their canopy-held seedbank relatively quickly. Ideally, most seeds are released within 1 month of injection [110]. Burkhead [13] found injection had little adverse impact on nontarget plant species in experimental plots in Big Cypress National Preserve. Grasses within 1.6 feet (0.5 m) of hexazinone-treated trees were killed but reestablished within 1 year of treatment. Imazapyr, picloram + 2,4-D, triclopyr, and hexazinone have all shown good results when used in stem injection [13,54,90]. Myers and Belles [54] also successfully used stem injection (with Hexazinone) to treat postfire sprouting. Mortality was 96% at 5 months after fire and 98% at 9 months after fire, but this treatment was significantly ($p<0.05$) less effective when applied at 2 months after fire. See Fire Management Considerations for more information about fire and melaleuca control.

Felling melaleuca trees and applying herbicide to cut stumps is also an effective chemical control method. Woodall [110] recommended picloram + 2,4-D for cut-stump treatment. Laroche and others [40] tested several herbicides for effectiveness when applied to cut stumps. Imazapyr yielded 100% control, while application of triclopyr, glyphosate, or hexazinone resulted in >85% melaleuca mortality. Myers and Belles [54] and Stafford [87] also successfully used imazapyr applied to cut stumps. Stafford described moderate but temporary damage to nearby herbaceous plants. It was speculated that this damage was caused by herbicide uptake from soil or root grafts associated with treated melaleuca stumps, rather than from sloppy spraying. Myers and Belles [54] found that applying herbicide to cut stumps of melaleuca trees that had recently burned was also effective.

Regardless of the herbicide used, Myers and Belles [54] suggested the cut-stump method was "slightly more effective" in killing the target tree than stem injection. Also, standing trees are more likely to disperse seeds over a greater area compared with downed trees. Further, while downed trees can release their seed within 2 weeks after cutting, stem-injected trees may take substantially longer (up to 1 year was suggested) for all branches to die and release seed. Inducing rapid seed release by felling trees results in more rapid germination and establishment of closer (both temporally and spatially) cohorts of seedlings, permitting effective seedling control using a follow-up prescribed fire. With stem injection, seedling establishment may occur over a more extended time period, rendering seedling control using prescribed fire problematic. "If burning is conducted when the earliest established seedlings are still small enough to be killed, all seeds may not have been released from dying (or surviving) trees. Such a burn may also stimulate remaining seeds to be released. These seeds will encounter bare mineral soil, reduced competition, and fuel loads too low for a repeat burn. On the other hand, if the burn is conducted after all seeds are released, some early establishing seedlings may already be large enough to survive the burn.". Stump treatments may also be timed to take advantage of seasonal flooding and the suppressive effects of inundation on stump sprouting [54] (see Cultural control below).

However, Woodall [110] recommended against cut stump treatments for general purposes: "Large amounts of the chemical are needed because the circulation of fluids within the tree stops when the tree is cut. Any herbicide that can prevent stump sprouting can do a much more efficient job when injected into the stem of an otherwise undamaged tree. Stump treatment is advisable when: (1) the stem is too small for injection and the rooting medium is unsuitable for soil application, or (2) the need to remove all seeds is so critical as to require felling. A good example of (1) is a small sapling rooted on a cypress knee; an example of (2) is a large seed tree immediately adjacent to a prepared seed bed, such as the right-of-way of a powerline being constructed" [110].

Melaleuca seedlings can also be controlled with herbicides. According to Timmer and Teague [93] "herbicide treatments using either broadcast foliar sprays or soil treatment may prevent germination and/or establishment" of seedlings. In a greenhouse study, Woodall [109] attained complete kill of 45-day-old seedlings with bromacil, diuron, picloram + 2,4-D, and hexazinone, complete kill of 106-day-old seedlings with bromacil, diuron, and picloram + 2,4-D, and complete or near-complete kill of 106-day-old seedlings with hexazinone. Stocker and Sanders [90] achieved 100% mortality of seedlings between 8 and 24 inches (20-60 cm) tall after 6 weeks following broadcast applications of bromacil, tebuthiuron, and hexazinone, and after 44 weeks using glyphosate.

For more information, a review of specific control methods using herbicides is provided by Timmer and Teague [93].

Cultural: Timmer and Teague [93] indicated that, where water levels can be manipulated, seedlings can be controlled by flooding the treatment area. However, they did not indicate the optimum depth or duration of flooding for effective control. In addition, several studies have shown that melaleuca seedlings can survive complete submersion for several months, indicating that this approach may only be marginally effective unless conducted over a long time.

On the other hand, stump sprouting following felling of mature melaleuca trees may be reduced or even eliminated if stumps are subsequently submerged. Mechanical treatments conducted just prior to seasonal flooding may be particularly useful in dense melaleuca stands with access for large mechanized cutters. For best results, stumps should be submerged within at least 2 weeks of cutting and should be submerged for at least 40 days. If seasonal flooding is insufficient, stump sprouts can be treated with foliar-applied herbicides [54].

Woodall [110] described "forced succession," in which conditions are created that will induce the development of a shade tolerant native plant community, while gradually reducing melaleuca overstory and discouraging melaleuca regeneration. Gradually thinning melaleuca, perhaps over a 10-year period, increases light levels sufficiently to maintain a favorable microclimate, resulting in improved vigor of native seedlings that are likely already present in the understory of melaleuca-dominated stands. Simultaneously, care is taken to maintain a thick, undisturbed litter layer that inhibits establishment of melaleuca seedlings. Thinning may be carried out by felling or chemical stem injection, although felled trees should remain where they fall to prevent undue disturbance. Thinning should remove the largest, oldest trees first to minimize sprouting, since sprouting decreases with age of trees [110].

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