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Source: Castanea, 71(3) : 210-225

Published By: Southern Appalachian Botanical Society

URL: https://doi.org/10.2179/05-27.1

CASTANEA 71(3): 210–225. SEPTEMBER 2006

Invasion History of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida

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ABSTRACT

The Australian punk tree *Melaleuca quinquenervia* is a notorious invasive weed that threatens the biological integrity of Florida's Everglades ecosystems. A comprehensive plan initiated to manage *M. quinquenervia* includes an ambitious biological control program, and as part of this program we investigated the origins and invasion history of *M. quinquenervia* in Florida. Scrutiny of public and private records showed that extant populations derive from more than a dozen introductions, with the earliest occurring during 1886 in Sarasota County. Six sources, some Australian and some extra-Australian, have contributed to Florida's populations. The tree became naturalized in southern Florida during the 1920s, but a paucity of records makes it difficult to determine when naturalized populations began to proliferate via an exponential growth phase. Human distribution of seeds and seedlings is a confounding factor in attempting to decipher rates of *M. quinquenervia* invasion.

> *"A few seeds in a letter from far-off Australia, a few trees started, and finally there is a changed landscape. No one can predict what will happen when he drops a seed from foreign parts in a new environment. If it happens to be a weed, he may regret it . . ."*
>
> —John Gifford (1945)

The invasion of natural areas by exotic plants presents a critical impediment to the preservation of native biodiversity and to ecosystem restoration efforts (Braithwaite et al. 1989, D'Antonio and Vitousek 1992, Zedler and Rea 1998). While eradication of harmful alien species (*sensu* Kowarik 1995) is desirable it is oftentimes impractical, especially when the invader has become widespread. In such instances, a comprehensive regional strategy employing an integrated pest management (IPM) approach to regulating populations of a nuisance plant can aid managers in allocating resources and coordinating efforts to optimize results. Recent examples from Florida target the notorious Everglades invader *Melaleuca quinquenervia* (Cav.) S.T. Blake, and the equally pestiferous *Schinus terebenthifolius* Raddi (Laroche 1994, 1999; Ferriter 1997).

A cornerstone of these regional strategies is the call for intensive efforts to develop biological control agents of the weed (*sensu* Harley and Forno 1992) and to integrate them into management practices (Laroche 1994, 1999; Ferriter 1997). Biocontrol projects can be enhanced by understanding the introduction history of the invasive species. For example, ecological studies of a target weed in its native range help to identify stages in the plant's life history when biocontrol stresses can be most effective (Julien and White 1997). Weeds often have a broad geographic distribution, however, and many aspects of a species' biology can vary across its range. Also, individual populations in a plant's adventive range (a region where the plant is not native, but has become naturalized) are likely to be most susceptible to biocontrol agents from genetically similar populations in its native range (Harley and Forno 1992, Van Driesche and Bellows 1996). Thus, knowledge of the sources of introduced plants allows researchers to focus

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attention on populations in the plant's native range that are closely related to adventive populations targeted for control, thereby improving prospects for success. Unfortunately, information regarding the invasion history of pest plants is often lacking (Kowarik 1995), thereby impeding management efforts.

Melaleuca quinquenervia (traditionally known in Florida as the punk tree: Small 1933, Little 1953, Long and Lakela 1971, Wunderlin 1982; see Starr and Starr 2003 for photos) is an alien species that occupies at least 200,000 ha of wetlands in southern Florida (Bodle et al. 1994, Laroche 1998). It encroaches upon a variety of habitats: freshwater marshes (including sawgrass prairies), cypress swamps, pine flatwoods, hardwood hammocks, salt marshes, mangrove forests (occasionally), and is particularly prominent along ecotones (Myers and Ewel 1990). During early stages of invasion, the presence of *M. quinquenervia* fosters increased structural diversity in herbaceous marsh communities which results in a concomitant increase in wildlife diversity (O'Hare and Dalrymple 1997). The ultimate outcome of invasions, however, is replacement of native habitat by dense *M. quinquenervia* forests with drastically reduced biodiversity (Austin 1978, O'Hare and Dalrymple 1997). Such transformations threaten the biological integrity of Florida's Everglades ecosystem (Mazzotti et al. 1997), which has been designated an International Biosphere Reserve (in 1976), a World Heritage Reserve (in 1979), and a Wetland of International Importance (in 1987) (Maltby and Dugan 1994).

Herein, we describe the origins and invasion history of *Melaleuca* populations in Florida. This research provides the background for an investigation studying the ecological genetics of *M. quinquenervia* (Dray 2003), part of an ambitious biological control program aimed at regulating populations in its adventive range (Laroche 1994, 1999; Turner et al. 1998).

METHODS

Taxonomy

Melaleuca nomenclature has been very confused until recently, so deciphering the invasion history of *M. quinquenervia* required careful review of its taxonomic history. Blake (1968) conducted an in-depth review of herbarium specimens available to him, and his treatise provided the basis on which we parsed early importation records. Close scrutiny of public and private records facilitated the unambiguous association of some extant Florida populations with original plantings. Specimens from these and other populations representing the putative distribution of *M. quinquenervia* in Florida were reviewed by local taxonomic experts. Vouchers from these populations were deposited at the Fairchild Tropical Botanical Garden herbarium, and at the Australian National Herbarium where identifications were confirmed by Dr. Lyn Craven.

Introduction history

Historical records were obtained for *M. quinquenervia* importations into Florida by searches of the published literature (books, scientific journals, reports, news articles, sales catalogs), unpublished literature (horticultural records, personal diaries, private correspondence), and personal interviews. Surveys were conducted at all putative introduction sites for evidence of previous or extant *M. quinquenervia* populations. Several introductions originated from private or public gardens, so curators at the Royal Botanic Gardens—Sydney (Australia), Giardini Botanici Hanbury (formerly La Mortala Gardens, Ventimiglia, Italy), Le Jardin Botanique (formerly Les Tropiques, Nice, France), and Parc Zoologique d'Ivoloina (formerly Ivoloina Agricultural Station, Tamatave, Madagascar) were queried regarding past and present holdings in the genus *Melaleuca*. Specimens were obtained from gardens where *M. quinquenervia* was present at putative source sites, and the identities of these specimens were confirmed by Dr. Craven. Also, herbaria at the Royal Botanic Gardens—Kew (K), the New York Botanical Garden (NY), and Fairchild Tropical Botanic Garden (FTG) were searched for specimens of *M. quinquenervia* collected in Florida.

Table 1. *Melaleuca* **species, other than** *M. quinquenervia*, **imported into Florida during 1900–1960**

Species[1]	Earliest Importation	USDA Accession	Original Source [total no. importations from discrete sources]
M. acacioides F. Muell. [as *M. graminea* S. Moore]	16-Jan-1959	255099	Albany, Western Australia [1]
M. acuminata F. Muell.	25-Apr-1929	81174	La Mortola Gardens, Ventimiglia, Italy [3]
M. argentea W. Fitzg.[2]	03-Apr-1959	256463	Brisbane Botanic Gardens, Mt. Coot-tha, Queensland [1]
M. armillaris Smith	18-Dec-1930	90712	Royal Botanic Gardens, Sydney, New South Wales [3]
M. bracteata F. Muell. [as *M. genestifolia* J.E. Smith]	1927	none	unknown—imported by Royal Palm Nurseries, Oneco, Florida [2]
M. brevifolia Turcz. [as *M. neglecta* Ewart & B. Wood]	23-Jul-1956	234107	Adelaide Botanic Gardens, Adelaide, South Australia [2]
M. cajeputi Powell[2] [as *M. angustifolia* Gaertn.]	10-Apr-1959	256704	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. cheelii C. White	30-Mar-1959	256303	Brisbane Botanic Gardens, Mt. Coot-tha, Queensland [2]
M. cordata Turcz.	28-Apr-1926	67077	private garden of Edwin Ashby, Blackwood, South Australia [2]
M. cuticularis Labill. [as *Cajeputi cuticularis* (Labill.) Skeels]	02-Mar-1912	32924	La Mortola Gardens, Ventimiglia, Italy [1]
M. deanei F. Muell.	06-Dec-1955	230416	Adelaide Botanic Gardens, Adelaide, South Australia [2]
M. decussata R. Br. in Ait.	23-Jul-1956	234104	unspecified location in Australia [1]
M. diosmifolia Andr. [as *M. doesmaefolia* Andrews]	27-Apr-1932	99436	La Mortola Gardens, Ventimiglia, Italy [1]
M. eleuterostachya F. Muell. [as *M. adnata* Turcz.]	06-Dec-1955	230414	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. elliptica Labill.	18-Dec-1930	90713	Royal Botanic Gardens, Sydney, New South Wales [3]
M. ericifolia Smith [as *Cajeputi ericifolia* (Smith) Lyons]	1911	30793	La Mortola Gardens, Ventimiglia, Italy [4]
M. fulgens R. Br.	28-Apr-1926	67079	private garden of Edwin Ashby, Blackwood, South Australia [5]
M. gibbosa Labill.	23-Jul-1956	234106	unspecified location in Australia [1]
M. glomerata F. Muell.	30-Mar-1959	256304	unspecified location in the Northern Territory [1]
M. holosericea Schauer in Lehm.	28-Apr-1926	67080	private garden of Edwin Ashby, Blackwood, South Australia [1]
M. huegelii Endl.	01-Jan-1956	230909	unspecified location in Australia [2]
M. hypericifolia Smith [as *Cajeputi hypericifolia* (Salisb.) Skeels]	1911	30761	La Mortola Gardens, Ventimiglia, Italy [5]
M. incana R. Br.	14-May-1968	330382	Parks and Gardens Section, Canberra, A.C.T. [1]
M. lanceolata Otto [as *Cajeputi pubescens* (Schauer) Skeels]	1911	30795	La Mortola Gardens, Ventimiglia, Italy [6]
M. lateritia A. Dietr.	28-Apr-1926	67081	private garden of Edwin Ashby, Blackwood, South Australia [4]
M. *laxiflora* Turcz. [as *M. crassifolia* Benth.]	28-Apr-1926	67078	private garden of Edwin Ashby, Blackwood, South Australia [4]
M. leucadendra (L.) L.[2] [as *M. leucadendron* (L.) L.]	19-Nov-1953	210753	unspecified location in Australia [1]
M. linariifolia Smith	27-Apr-1932	99437	La Mortola Gardens, Ventimiglia, Italy [4]

Table 1. Continued

Species[1]	Earliest Importation	USDA Accession	Original Source [total no. importations from discrete sources]
M. macronychia Turcz.	06-Apr-1959	256529	private garden, Blackwood, South Australia [1]
M. megacephala F. Muell.	06-Dec-1955	230420	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. micromera Schauer in Lehm.	06-Dec-1955	230421	Adelaide Botanic Gardens, Adelaide, South Australia [2]
M. microphylla Smith in Rees	10-Apr-1959	256707	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. minutifolia F. Muell.	10-Apr-1959	256708	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. nesophila F. Muell.	27-Apr-1932	99438	La Mortola Gardens, Ventimiglia, Italy [2]
M. nodosa (Gaertn.) Smith	03-Nov-1927	75565	Royal Botanic Gardens, Melbourne, Victoria [1]
M. pauciflora Turcz.	06-Dec-1955	230423	Adelaide Botanic Gardens, Adelaide, South Australia [1]
M. pauperiflora F. Muell.	16-Jul-1952	202095	Dept. of Works, Adelaide, South Australia [2]
M. pentagona Labill.	06-Apr-1959	256530	private garden of Edwin Ashby, Blackwood, South Australia [1]
M. preissiana Schauer in Lehm. [as *M. pubescens* Schauer]	18-Dec-1930	90716	Royal Botanic Gardens, Sydney, New South Wales [1]
M. puchella R. Br. in Ait. [as *Cajeputi pulchella* (R. Br.) Skeels]	02-Mar-1912	32928	La Mortola Gardens, Ventimiglia, Italy [1]
M. pungens Schauer in Lehm.	16-Jan-1959	255100	Popanginning, Western Australia [1]
M. pustulata J.D. Hook	01-Mar-1904	10510	Royal Botanic Gardens, Sydney, New South Wales [1]
M. radula Lindl.	28-Apr-1926	67082	private garden of Edwin Ashby, Blackwood, South Australia [4]
M. scabra R. Br. in Ait.	16-Jan-1959	255101	Geraldton, Western Australia [1]
M. squamea Labill.	08-Apr-1927	73443	Aldenham House Gardens, Elstree, Herts, England [1]
M. squarrosa Donn ex Smith	23-Jul-1956	234109	unspecified location in Australia [2]
M. steedmanii C. Gardner	06-Dec-1955	230425	Adelaide Botanic Gardens, Adelaide, South Australia [6]
M. styphelioides Smith	03-Nov-1927	75567	Royal Botanic Gardens, Melbourne, Victoria [2]
M. subtrigona Schauer in Lehm.	09-Apr-1959	256584	Dripstone, New South Wales [1]
M. teretifolia Endl. in Endl.	09-Apr-1959	256585	Dripstone, New South Wales [1]
M. thymoides Labill.	28-Apr-1926	67083	private garden of Edwin Ashby, Blackwood, South Australia [1]
M. thyoides Turcz.	16-Jan-1959	255103	Murchison, Western Australia [1]
M. uncinata R. Br. in Ait.	28-Apr-1926	67084	private garden of Edwin Ashby, Blackwood, South Australia [2]
M. violacea Schauer in Lehm.	28-Apr-1926	67085	private garden of Edwin Ashby, Blackwood, South Australia [1]
M. websteri S. Moore.	28-Apr-1926	67086	private garden of Edwin Ashby, Blackwood, South Australia [2]
M. wilsonii F. Mueller [as *Cajeputi wilsoni* (Mueller) Skeels]	02-Mar-1912	32929	La Mortola Gardens, Ventimiglia, Italy [3]

[1] Currently accepted names according to Blake (1968), Bailey and Bailey (1976), and Holliday (1989). Names under which these species were originally imported, if different from currently accepted names, are in braces.

[2] Species closely related to *Melaleuca quinquenervia* as members of the *M. leucadendra* complex.

RESULTS AND DISCUSSION

Taxonomy

Melaleuca is a member of the Myrtaceae, a widespread family in the tropics and southern temperate zones comprising about 3,000 species (Watson and Dallwitz 1992). There are two subfamilies: the Myrtoideae, which have fleshy fruits and opposite leaves; and the Leptospermoideae, which have dry fruits and alternate or opposite leaves (Cronquist 1981). *Melaleuca*, along with *Eucalyptus*, *Leptospermum*, *Metrosideros*, and *Callistemon*, belongs to the largely Australasian Leptospermoideae, a paraphyletic taxon (Judd et al. 1999). The genus *Melaleuca* comprises about 275 taxa, including several species recently transferred from *Callistemon* (Dawson 1978, Barlow 1988, Holliday 1989, Craven and Dawson 1998, Craven 1999). Linnaeus established the genus in 1767, based on an Amboinan (in present day Indonesia) specimen collected by Rumphius (Blake 1968). Table 1 records 56 species of *Melaleuca* imported into Florida during the first half of the 20th century.

Melaleuca quinquenervia is one of the broad-leaved paperbarks, which includes *M. leucadendra* (L.) L. and closely allied species. It was first described as *Metrosideros quinquenervia* by Cavanilles from specimens collected in April 1793 near Port Jackson, New South Wales (Blake 1968, Craven 1999). Distinguishing among the broad-leaved paperbacks is difficult. Thus, most early botanists followed Bentham's 1867 treatise and simply classified *Metrosideros quinquenervia* and other broad-leaved paperbacks as varieties of *Melaleuca leucadendra*, a taxon first described by Rumphius as *Arbor alba* in 1750 (Blake 1968, Craven 1999). The taxonomy remained confused until Blake's (1968) revision, based on floral morphology and indumentum (hair) type, in which he established the new combination *Melaleuca quinquenervia*. This history means that the binomial *M. leucadendra* was misapplied to most broad-leaved paperbarks imported into Florida, which should properly be ascribed to *M. quinquenervia* (Blake 1968, Wunderlin 1998). Other authors have clarified relationships and recognized new taxa, so that the broad-leaved paperbark complex now includes 15 species (Barlow 1988, Craven 1999).

Melaleuca quinquenervia occurs naturally throughout Queensland, New South Wales, New Caledonia, and southern New Guinea (Blake 1968, Craven 1999). Blake (1968) records cultivated specimens from South America (Guyana, French Guiana), Africa (Uganda, Senegal, Madagascar), and Asia (Hong Kong, Taiwan). It also is cultivated in Benin, Egypt, and the Bahamas (Gifford 1945, Correll and Correll 1982, Aboutabl et al. 1991, Moudachirou et al. 1996). Confirmed United States collections include specimens from California, Florida, Hawaii, Louisiana, Texas, and Puerto Rico (Morton 1966, Blake 1968, Little et al. 1974). Scientific names under which *M. quinquenervia* was imported into the United States include: *Metrosideros quinquenervia* Cav., *Melaleuca leucadendron* (L.) L., *Melaleuca viridiflora* (L.f.) Byrnes, and *Cajeputi leucadendra* (Stickm.) Rusby. Common names for *M. quinquenervia* include niaouli, paperbark, broad-leaved paperbark, five-veined paperbark, broad-leaved tea tree, Belbowrie, punk tree, and cajeput (Meskimen 1962, Morton 1966, Blake 1968, Boland et al. 1984, Craven 1999). This latter name more properly applies to the related species *M. cajeputi* Powell.

Introduction history

Species of *Melaleuca* have long been under cultivation. Blake (1968) cites herbarium specimens of *M. cajeputi* collected in 1777 from a garden in Djakarta, Java (Indonesia). Directors of private and public gardens throughout the world added a myriad of *Melaleuca* species to their collections, especially in the late 19th and early 20th centuries when interest seems to have been particularly strong. During this period, both the Hope Gardens in Jamaica (1904: *M. leucadendra*) and the Missouri Botanic Gardens (1906: *M. cajeputi*) obtained *Melaleuca* specimens for display (Blake 1968). Les Tropiques (owner: Dr. A. Robertson-Proschowsky) in Nice, France, and the nearby La Mortala Gardens (owner: Sir Thomas Hanbury) in Ventimiglia, Itlay, also featured multiple *Melaleuca* species (U.S. Department of Agriculture 1902, 1905, 1913). Bailey (1916) lists 14 species of *Melaleuca* grown as ornamental trees in the United States at this time.

The earliest records of cultivated plants now known to be *M. quinquenervia* come from Uganda, where J.D. Snowden collected specimens in 1815 (Blake 1968). This species became coveted for its showy, creamy-white flowers, shaggy bark, ease of cultivation, rapid growth, and vigor in a variety of habitats (Maiden 1889, Bailey 1916, Andrews 1930, Nehrling 1933, Gifford 1945). Additionally, *M. quinquenervia* was thought to be useful for "subduing malarial vapors" (von Mueller 1888, Gifford 1945, Morton 1966). The thick, spongy bark was used for packing fruit prior to shipping (von Mueller 1888), and as bedding material and insulation (Morton 1966). The heartwood was used for lumber (von Mueller 1888, Gifford 1945). Essential oils distilled from leaves have for centuries been used medicinally (von Mueller 1888, Fairchild 1943, Gifford 1945, Morton 1966), and constitute a principle component in some commercial disinfectants. The identity of the trees producing commonly marketed *Melaleuca* oils is often confused, and many uses ascribed to *M. quinquenervia* should actually be referred to *M. alternifolia* or *M. cajeputi* (Blake 1968).

Credit, or blame, for successfully importing *M. quinquenervia* into Florida's east coast has generally been ascribed to Dr. John Gifford (Fairchild 1943, Schory 1958, Morton 1966, Troop 1979, Gordon and Thomas 1997, Laroche 1998) although earlier introductions were known (Meskimen 1962, Morton 1966, Turner et al. 1998). Populations along Florida's west coast have been attributed to plantings made by A.H. Andrews of the Koreshan Unity sect (Rahn 1936, Schory 1958, Meskimen 1962). However, careful scrutiny of personal correspondence by the principals involved, early horticultural catalogs, and United States Department of Agriculture (USDA) plant introduction records suggests that other importations contributed to the species' invasion of Florida as well. Table 2 presents known introductions of *M. quinquenervia* into Florida (see also Figure 1). The species was introduced into California (as *Metrosideros quinquenervia* by Coronado Nurseries, San Diego) at about the same time as it was introduced in Florida, and was sold in the California landscaping trade early in the 20th century (Hall 1910). The following narrative details the earliest known introductions of *M. quinquenervia* into Florida.

ROYAL PALM NURSERY. The first *M. quinquenervia* recorded in Florida were seedlings offered for sale as *M. leucadendra* by the Royal Palm Nurseries in Oneco, Manatee County (Reasoner and Reasoner 1887). Pliny Reasoner moved to Florida and started breaking ground for a nursery in 1881. His earliest plantings were fruits (mostly citrus) and palms (Pinardi 1980), but as the acreage under cultivation increased so did the variety of plants being grown at the Royal Palm Nurseries. Pliny and his brother Egbert searched the world for plants that would thrive in Florida, while 'accentuating its tropical beauty'. Their nursery thus became a portal through which many non-native species were first introduced into Florida (Stoutamire 1926). A state historical marker in Oneco ascribes priority for the introduction of *Melaleuca* (as well as Brazilian pepper, Australian pine, and other notable genera—several of which are now invasive) to the Reasoner brothers.

Sales catalogs were published annually by Royal Palm Nurseries beginning in 1885, and are the most comprehensive source of information regarding plants imported by the Reasoner brothers. *Melaleuca quinquenervia* first appeared in the catalog in 1887 (Reasoner and Reasoner 1887). Unfortunately, nursery records do not indicate when the Reasoners first acquired *Melaleuca* seeds, but for seedlings and saplings to be available for sale in 1887 the importation most likely occurred sometime during 1886. A few trees from the earliest *Melaleuca* plantings have survived at the original nursery site allowing us to confirm their identity as *M. quinquenervia*. The source of these early plants is unknown, though it is probable that they were acquired from a botanic garden ("Commencing in 1885, . . ., exchange arrangements were soon completed with all the then known gardens and nurseries in the tropics and subtropics around the world.", note, p. ii, Reasoner 1927), perhaps even the Sydney Botanic Garden with whom the Reasoners had frequent correspondence. *Melaleuca quinquenervia* was sold at the Royal Palm Nursery from 1887–89 and again from 1919 until 1933 (Dray 2003). The tree's popularity is attested to by its prominent use by landscape architects involved in developing Palm Beach and other towns during the 1920s and 1930s (Pinardi 1980).

HENRY NEHRLING. The second known introduction was in 1898 by teacher and amateur horticulturist Henry Nehrling (Nehrling 1944, Meskimen 1962). Nehrling obtained *Melaleuca*

Table 2. Introductions of *Melaleuca quinquenervia* (as *M. leucadendra* or *M. viridiflora*) in Florida

Date	USDA Accession	Source			Reference
		Contact	Locale	Imported by	
1886	none	unknown	unknown	Pliny Reasoner, Royal Palm Nurseries	Reasoner and Reasoner 1887
1898	none	Sir Thomas Hanbury	La Mortala Gardens, Ventimiglia, Italy	Henry Nehrling	Nerhling 1944, Meskimen 1962
30-Apr-1900	5065	A. Robertson-Proschowsky	Les Tropiques, Nice, France	USDA	USDA 1902
13-Jun-1902	8871	A. Robertson-Proschowsky	Les Tropiques, Nice, France	USDA	USDA 1905
24-Oct-1902	9111	A. Robertson-Proschowsky	Les Tropiques, Nice, France	USDA	USDA 1905
1906	none	Dr. J.H. Maiden, Director	Royal Botanical Gardens, Sydney, New South Wales, Australia	John Gifford	Gifford 1972
17-Nov-1908	24166	Dr. J.H. Maiden, Director	Royal Botanical Gardens, Sydney, New South Wales, Australia	John Gifford	USDA 1909
29-Aug-1911	31736	Dr. J.H. Maiden, Director	Royal Botanical Gardens, Sydney, New South Wales, Australia	USDA	USDA 1912
1912	none	B. Harrison, Tweed River, New South Wales	Law, Somner, & Co., Melbourne, Victoria, Australia	A.H. Andrews Koreshan Unity	Andrews 1930
31-Mar-1916	42357	Eugene Jaegle	Agricultural Station, Ivoloina, Madagascar	USDA	USDA 1919
31-Mar-1917	45510	Eugene Jaegle	Agricultural Station, Ivoloina, Madagascar	USDA	USDA 1922
21-Apr-1930	4104	A.H. Andrews	Estero, FL	A.H. Andrews, Koreshan Unity	unpubl. USDA records
18-Dec-1930	90715	G.P Darnell-Smith, Director	Royal Botanical Gardens, Sydney, New South Wales, Australia	USDA	USDA 1932
30-Oct-1943	147097	T.A. Semple, USDA Soil Conservation Service	Nahampaoma, Madagascar	USDA	USDA 1951
30-Mar-1959	256305	G.H. Spalding, USDA Agricultural Explorer	Northern Territory, Australia	G.H. Spalding, USDA Agricultural Explorer	USDA 1966
30-Mar-1959	256306	G.H. Spalding, USDA Agricultural Explorer	Maryborough, Queensland, Australia	G.H. Spalding, USDA Agricultural Explorer	USDA 1966
10-Apr-1959	256706	G.H. Spalding, USDA Agricultural Explorer	Adelaide Botanic Garden, Adelaide, South Australia	G.H. Spalding, USDA Agricultural Explorer	USDA 1966

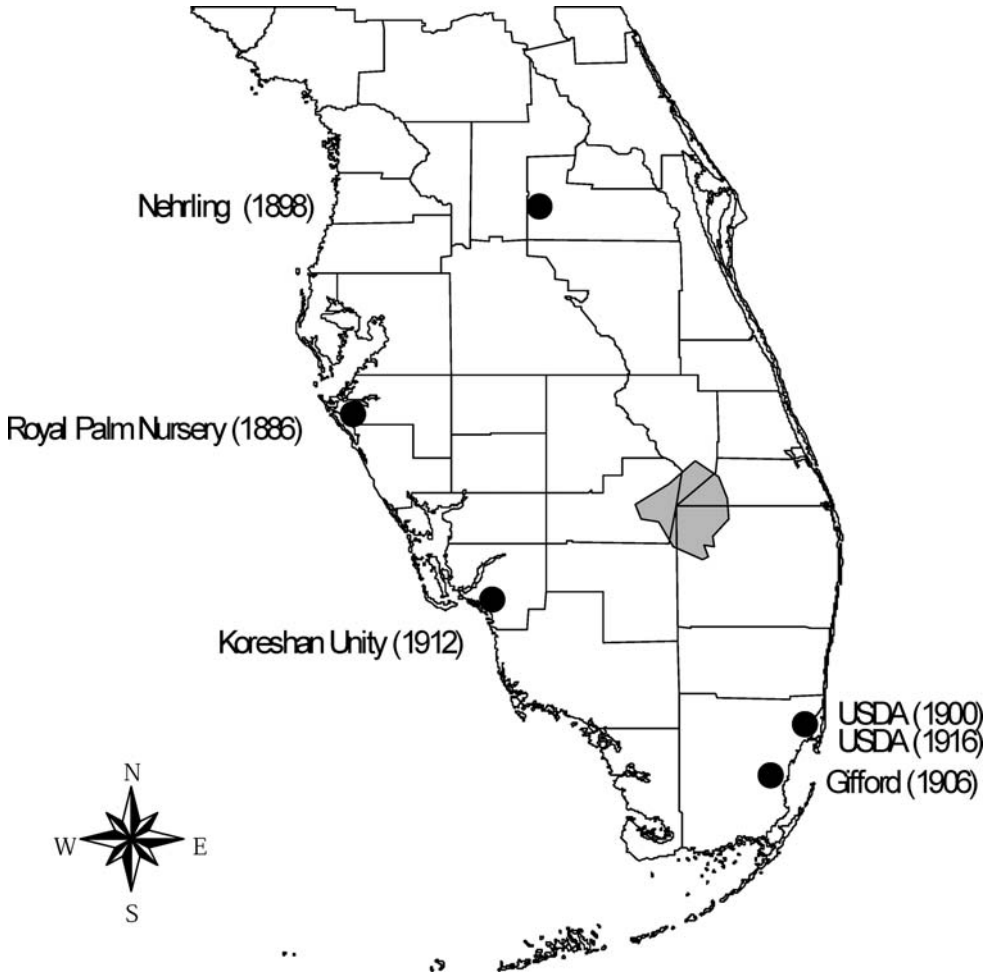

Figure 1. Locations, dates, and recipients of original *Melaleuca quinquenervia* introductions into Florida.

seeds from La Mortala Gardens and cultivated them at his nursery (Palm Cottage Gardens) in Gotha, Orange County, Florida. The site was designated a USDA experimental station for a short period in the early 1900s because of Nehrling's penchant for importing exotic plants, but none of Nehrling's *Melaleuca* (and few of his other imports) have survived at the Gotha site. However, a severe frost in 1917 prompted Nehrling to establish in 1919 a second nursery (Tropical Gardens and Arboretum) near Naples, Lee County, Florida, at which he transplanted *M. quinquenervia* as well as many other cold-sensitive species. This site is currently a privately owned theme park called Caribbean Gardens where a few of the trees planted by Nehrling survive, allowing us to confirm their identity.

Nehrling corresponded and traded plants with the most prominent horticulturists in southern Florida, but there are no records to indicate that he ever distributed *M. quinquenervia* seeds or seedlings among his friends and acquaintances. Examination of the Caribbean Gardens property indicates, however, that *M. quinquenervia* escaped cultivation at this site to invade surrounding marshes. Strangely, despite his associations with the Reasoners, David Fairchild, and A.H. Andrews (see below), Nehrling was apparently unaware of others having imported *Melaleuca* and believed himself to be its primary proponent (Nehrling 1933, Nehrling 1944).

The broad-leaved paperbarks at La Mortala Gardens are of unknown origin. In addition to *M. quinquenervia*, La Mortala Gardens harbored at least six other species of *Melaleuca* during this period (U.S. Department of Agriculture 1913). Today the gardens contain ten species of *Melaleuca*, but neither *M. quinquenervia* nor *M. leucadendra* is present (Dray 2003).

U.S. Department of Agriculture. Three of the earliest introductions originated from Les Tropiques. USDA records indicate that seeds from the first shipment (imported as *Melaleuca viridiflora*; U.S. Department of Agriculture 1902), received during 1900, were successfully cultivated and seedlings distributed to individuals in southeastern Florida. Some of the distributed seedlings must have been planted in Coconut Grove, Miami-Dade County, Florida, because David Fairchild observed a 5 m-tall *M. quinquenervia* growing in the Grove during 1906 before John Gifford made his well-documented plantings (see below; Gifford 1972).

U.S. Department Agriculture (1905) records indicate that additional seeds were imported from Les Tropiques twice during 1902, but none of the seedlings germinated from this material survived. Records concerning the origins of the plants at Les Tropiques have been lost as the property changed hands over the years. Le Jardin Botanique now occupies a portion of Dr. Robertson-Proschowsky's former gardens, but only two species of *Melaleuca* have survived (*M. styphelioides* Smith and *M. preissiana* Schauer in Lehm.; Dray 2003).

In 1916 the USDA received seeds from the Ivoloina Agricultural Station near Tamatave, Madagascar (U.S. Department of Agriculture 1919). This 400-hectare forestry station still harbors a thriving *M. quinquenervia* population (Ramanoelina et al. 1994). Both major Australian chemotypes (Boland 1989) are represented in Madagascar (Ramanoelina et al. 1994), so the latter trees likely derive from multiple sources in Australia. Unfortunately, records of plant introductions into Ivoloina have been lost (Dray 2003). Seedlings grown from the Madagascar material were distributed throughout southeastern Florida (USDA, unpubl. records). Later importations by the USDA, including a second seed shipment from Madagascar, are listed in Table 2.

John Gifford. Probably the best known introductions are those of John Gifford. He was apparently unfamiliar with earlier importers of *M. quinquenervia*, as he believed himself to be the first to import this Australian tree (Gifford 1910, 1945, 1946, 1972). Gifford received *M. quinquenervia* seeds (as *M. leucadendron*) in November 1906 from Dr. John Maiden, Director of the Royal Botanical Gardens at Sydney, New South Wales, Australia. It is unclear whether these seeds came from trees in the garden (there are at least two 100+ year old *M. quinquenervia* growing in the garden today; Kaufman 1999) or from the surrounding forests. Gifford first planted his seeds at the USDA Plant Introduction Station on Brickell Avenue in Miami, Miami-Dade County, Florida, in 1907 with the help of USDA botanist Ed Simmonds (Gifford 1972). He later transplanted some of the resulting seedlings at his home along Biscayne Bay in nearby Coconut Grove (Gifford 1972). Additional shipments of seeds were received from Dr. Maiden in 1908 and 1911 (Table 2).

Seedlings grown from these three shipments attained heights of 3.5–6.0 m, flowered, and produced seed within 12–36 months (U.S. Department of Agriculture 1912, Gifford 1945). Therefore, Gifford and the USDA quickly possessed an abundance of seeds and seedlings to distribute to others. Simmonds frequently gave *M. quinquenervia* seedlings to local visitors at the USDA station (Gifford 1945). One of the earliest recipients was the Davie Experimental Farm, near Fort Lauderdale, which was eventually abandoned although the *M. quinquenervia* survived to serve as seed sources (Fairchild 1938). Somewhat later, Frank Sterling established a *M. quinquenervia* nursery in Davie with seed given to him by Gifford (Meskimen 1962, Gifford 1972), and from which he reportedly sold thousands of saplings (Fairchild 1947). Seeds from Gifford's trees were also exported to Louisiana and the Bahamas (Gifford 1946). When the USDA Plant Introduction Station moved to its present location in 1923, Gifford's trees were among the first seedlings planted.

John Lange. An early south Florida pioneer, John C. Lange, claimed to have planted the first *M. quinquenervia* in Davie, Broward County, Florida, around 1900 (Pritchard 1976), an event that is commemorated by a historical marker at what is now Lange Park. The park and surrounding neighborhood in Davie contain several very large trees that reputedly have

survived from these plantings. Lange claimed to have obtained his seeds from local sources. So if, as reported, these trees were planted around 1900 then they would most likely represent material derived from the first introduction from Les Tropiques. However, immigration of settlers into western Broward County did not begin until 1909 (Wagner 1982). The Lange family didn't arrive in Zona (the original name for Davie) until about a decade later (Wagner 1982, Dray 2003). Thus, Mr. Lange's trees are most likely derived not from the French seeds in 1900, but instead likely represent the previously mentioned plantings of Gifford's material at the Davie Experimental Farm. *Melaleuca* species do not form annual growth rings by which these trees might be aged, but molecular or other techniques may eventually help resolve this issue. For now, it seems unlikely that Lange's trees represent an additional introduction event.

KORESHAN UNITY. In 1894, Dr. Cyrus Teed moved to Estero, Lee County, Florida, to establish a permanent home for the utopian communal society known as Koreshan Unity (Anonymous 1994). His followers sought to replace the native pines and cypress they had felled around Estero with one or more tropical forest species that would grow rapidly, be long-lived, and provide useful timber and other products for their community (Gifford 1946, Meskimen 1962). They tried more than 20 species of *Eucalyptus*, none of which proved suitable (but many of which survive today), before finally being directed to *M. quinquenervia* (as *M. leucadendron*) by a nurseryman (Mr. B. Harrison) in Burringbar, Tweed River, New South Wales (Meskimen 1962). During 1912, Koreshan horticulturist Allen Andrews received a packet of *M. quinquenervia* seeds from a Melbourne, Australia, seed house (Gifford 1946). Since *M. quinquenervia* does not naturally occur near Melbourne, it is likely that the seeds derived from Mr. Harrison who had arranged the shipment. Analysis of leaf essential oils from trees in Estero and Burringbar support this hypothesis (Dray 2003). The trees flourished in the Koreshan Unity nurseries, and seed was soon being spread along the edges of the surrounding swamps (Gifford 1946, Anonymous 1966). Later, small saplings were harvested from the swamps and sold to pioneers in the local area (Dray 2003).

W. P. HAZARD. Another early pioneer in southwestern Florida, Mrs. W.P. Hazard, claimed that her husband made a separate introduction into the Estero area sometime during 1913–14 (Meskimen 1962). The putative source for these seeds was the USDA (Meskimen 1962), which would suggest the Hazard plants derived from either the Gifford material or the French material. Andrews (Meskimen 1962) disputed this claim, however, asserting that he had queried the USDA which had no record of shipping material to the Hazards. Our searches of USDA records confirm this assertion. Andrews (Meskimen 1962) later argued that the Hazard material had been purchased from the nursery at Koreshan Unity. Meskimen (1962) reports that a former Hazard employee believed the seeds originally came from Malaya (present day Malaysia), but the only paperbark found there is *M. cajeputi* (Blake 1968, Craven 1999). The trees in and around Estero are *M. quinquenervia*, so it seems likely that the Hazard's plants originated from the Koreshan Unity. While not entirely conclusive, these data suggest that trees on the Hazard property most likely do not derive from a distinct introduction event.

U.S. ARMY CORPS OF ENGINEERS. In an effort to stabilize levees constructed to prevent Lake Okeechobee from flooding nearby agricultural communities and croplands, the United States Army Corps of Engineers made extensive *M. quinquenervia* plantings (as *M. leucadendra*) during 1938–41 (U.S. Army Corps of Engineers 1959). The proximate source of trees for these plantings was a nursery established by the USACE in Clewiston, Florida. We were unable to locate USACE records detailing the seed source for this nursery. However, Norman Reasoner was hired as an Agronomic Consultant by the USACE at about this same time (Pinardi 1980). So it seems likely that the USACE plantings derive from Reasoner's Tropical Nursery (as it was then called) rather than representing some new importation from overseas.

Invasion of natural areas

Only a small number of alien species escape cultivation to establish self-sustaining populations in their adventive ranges, and even fewer become successful invaders of natural areas (Kowarik 1995, Williamson and Fitter 1996). Determining when in their invasion histories such plants became naturalized is an inexact science. These species are often imported

many times and planted in many different locations. Further, the expansion of populations of alien plant species is often interrupted by two discrete lag phases (Kowarik 1995). During the first lag phase, the plant is being cultivated, but there is no clear evidence that it has begun spreading on its own. During the second lag phase, the population has begun spreading on its own, but has not yet achieved an exponential growth phase. Thus, searches of the literature and other historical sources may indicate when a species has been imported and cultivated, and then offer little information about the plant until it 'suddenly' appears as a serious weed. This gap in information corresponds to the two lag phases in Kowarik's (1995) model, and is identifiable in the invasion history of *M. quinquenervia* in Florida.

The earliest flora focused specifically on Florida (Small 1903) was published nearly two decades after *M. quinquenervia* was first imported, but is drawn primarily from surveys in the southeastern part of the state. Importations preceding this date occurred in the central part of the state, thus it is unsurprising that the genus *Melaleuca* is not mentioned by Small (1903). Prior to publication of the second edition of this flora (Small 1913) *Melaleuca* seeds had been imported by both the USDA and Gifford, and Small had collected specimens from the USDA station at Brickell Avenue in Miami (NY: *Small s.n.*, 1912). Thus, his omission of this species (Small 1913) suggests that *M. quinquenervia* had not yet escaped cultivation and begun to spread in southeastern Florida. This conclusion is supported by Harshberger (1914), who crossed the Everglades in 1911 but did not record *M. quinquenervia* among the plants encountered during his trip.

The earliest evidence that *M. quinquenervia* was becoming naturalized in Florida appeared in newspaper articles written by Henry Nehrling. A posthumously published compilation of these articles (Nehrling 1933) shows that by the mid-1920s the species was spreading from the Koreshan plantings to become naturalized in the cypress swamps near Estero (southwestern Florida). Observations by Simpson (1926) and Small (1933) suggest that *M. quinquenervia* was also becoming naturalized in southeastern Florida during this period. Collections of *M. quinquenervia* (as *M. leucadendra*) by Buswell in the Big Cypress (NY: *Buswell s.n.*, 1930) and by Moldenke at an undisclosed south Florida location (NY: *Moldenke 3591*, 1927) offer further evidence that *M. quinquenervia* escaped cultivation and spread into natural areas during the 1920s. These data show that the duration of the first lag phase in Kowarik's (1995) model was relatively short for *M. quinquenervia*: about a decade in southwestern Florida, and perhaps two decades in southeastern Florida.

No records relating to naturalization of the trees planted at the Royal Palm Nursery or at Nerhling's Palm Cottage Gardens were discovered. There is a small *M. quinquenervia* forest along a stream on the old Nursery property, but the absence of other large stands in the area suggests that these trees generally failed to escape cultivation. This may perhaps be attributable to the paucity of wetland habitat nearby. *M. quinquenervia* occurs most commonly in the wetlands and swamps of eastern Australia, a habitat more similar to the southern Florida introduction points than to either the Reasoners' nursery in Oneco or Nehrling's garden in Gotha—both of which are located in well-drained habitat. In any event, trees from these introductions do not appear to have contributed to naturalized stands at least until after the Reasoners shipped large numbers of the trees to Palm Beach from whence they may have escaped.

Nehrling apparently was the first to report *M. quinquenervia*'s aggressive nature, and to sound an alarm about potential harm to the native environs (Hedwig 1984). Andrews (quoted in Gifford 1946) likewise observed *M. quinquenervia*'s invasive nature during the 1920s, and opined that the tree was more aggressive in Lee County than in Dade (now Miami-Dade) County. A couple of decades later, Fairchild (1943) remarked that early plantings at the Davie Experimental Station had gone wild and engulfed a nearby abandoned orange grove. Like Gifford, though, Fairchild apparently did not foresee the damage this sort of behavior could cause in the Everglades.

Observations by Gifford (1940, 1944) and Fairchild (1943) show that *M. quinquenervia* continued its spread into the eastern Everglades during the 1930s, but it is difficult to determine how much of the species' present geographical distribution in Florida is attributable to natural

dispersal and how much to human efforts. Clearly, dispersal of *M. quinquenervia* was greatly enhanced by its proponents (Gifford 1940, Pritchard 1976). As noted above, workers at the Koreshan Unity spread seeds along the western edge of the Everglades soon after receiving material from Australia. Meskimen (1962) reports that Hully Sterling scattered seed from an airplane over the eastern edge of the Everglades (in what is now Broward and Miami-Dade counties) during 1936 (see also Gifford 1946, 1972). Further, the Reasoner Brothers landscape architects exported thousands of seedlings to Palm Beach County and other areas (Pinardi 1980).

Human-aided dispersal is a common contributor to success of alien invaders (Pyšek et al. 1995), both by speeding the arrival of alien plants at so-called safe sites (Kowarik 1995, Wiens 1997) and by providing sources for reinvasion when local extinctions occur (i.e., the rescue effect; Gotelli 1995). These factors assist species in overcoming barriers to population establishment such as Allee effects (reduced population growth at low densities), demographic stochasticity (random fluctuations in birth and death rates), minimum viable population size (the critical density below which a population is doomed to extinction), and environmental stochasticity (random environmental changes that drastically alter the suitability of a particular habitat, e.g., prolonged droughts).

Kowarik (1995) observed that 95% of woody invaders in Germany endured a time lag of more than 50 years before beginning a period of rapid population growth. A study by Laroche and Ferriter (1992) shows that *M. quinquenervia* has been in such a growth phase since at least 1965 (see also Pritchard 1976). Determining when this exponential growth began is problematic, however, as Laroche and Ferriter (1992) represents the only quantitative data available on the subject. The Central Florida Beekeeper's Association issued an alarm in 1955 about the rapid spread of *M. quinquenervia* (Pritchard 1976). Unfortunately, they did not provide any quantitative data in support of their claims. Their concern was principally that *Melaleuca* honey is considered undesirable and could spoil the quality of their product. Ironically, the Florida State Beekeepers Association protested control measures aimed at curbing the spread of *M. quinquenervia* two decades later (Pritchard 1976).

Summary

The invasion history of *Melaleuca quinquenervia* in Florida presents an intriguing irony in that an alien species so vilified today was so esteemed in the past that its earliest importers argued about who deserved credit for its introduction. Our research suggests that extant populations derive from more than a dozen introduction events, the first of which occurred about 1886, and represent at least six distinct sources. Contrary to popular perception, John Gifford was not responsible for first introducing this plant into Florida. This distinction belongs to Pliny and Egbert Reasoner of the Royal Palm Nurseries. Nor was Gifford the species' primary proponent in southern Florida; he is just the best known. The Reasoner Brothers Landscape Architecture department planted thousands of *M. quinquenervia* seedlings from their nursery during landscaping work in Tampa and Palm Beach, and probably imported trees into Miami-Dade County as well (Pinardi 1980). Also, Koreshan historians recall bundles of saplings being handed out to settlers from southwestern Florida, and the USDA distributed *M. quinquenervia* seedlings for decades (Dray 2003).

Melaleuca quinquenervia was imported into this country for a variety of reasons. Henry Nehrling was merely interested in obtaining an attractive exotic tree to add to his personal gardens. The Reasoners and the USDA imported *M. quinquenervia* as an exotic landscape plant that was well suited to the tropics and that could be readily propagated and sold. Gifford (1945, 1972) originally sought these trees (1) as a landscape species, (2) as a method of combating malaria and yellow fever (a use also advocated by von Mueller, 1888), and (3) to provide a useful forestry crop that could grow successfully on the edges of the Everglades. Likewise, the Koreshan Unity sought a useful fast-growing forestry crop to replace the pines and cypress they were harvesting from their lands.

For many years, Gifford advocated using this tree in drainage projects (Gifford 1935). He believed that draining the land naturally (i.e., via trees) was infinitely superior to the man-made drainage systems (i.e., canals and earthworks) then being initiated (Gifford 1935, 1945, 1972). A

natural system comprised of a tropical forest would be limited in scope, permit native species time to adapt to the changing environs, and help conserve water and wildlife. In contrast, man-made systems would drain the land quickly and thereby destroy native species. Despite his advocacy of natural drainage projects, Gifford was an ardent and tireless supporter of the establishment of Everglades National Park (Gifford 1972). It is thus ironic that the tree Gifford was so proud of having introduced poses such a serious threat to the biodiversity of the Everglades ecosystem which he dearly loved (Austin 1978, Mazzotti et al. 1997, O'Hare and Dalrymple 1997).

Some of the early introduction events can be traced to discrete Australian sources. Others derive from extra-Australian material. These facts suggest that *M. quinquenervia* in Florida may harbor several distinct ecotypes, perhaps as many as six. The relatively close proximity of many original Florida populations (Figure 1) has likely led to intermingling of these ecotypes. Historical distribution records support this hypothesis. Still, the composition of naturalized populations may generally be biased towards the ecotype from the closest introduction point. This is currently being investigated, as is the influence that the presence of multiple ecotypes may have on biological control agent performance.

The species began pioneering within two decades of introduction, and was naturalized no later than 1930 (Nerhling 1933, Gifford 1940). A related species, *Callistemon viminalis* (Gaertner) G. Don f., started spreading into natural areas in a similarly short period of time (Small 1933), but has thus far failed to rival the menace *M. quinquenervia* presents to the Everglades. Purposeful seeding of natural areas by the tree's proponents may partially explain this discrepancy. Even so, *M. quinquenervia*'s ability to spread unaided, clearly demonstrated by Laroche and Ferriter (1992), has strongly influenced the geographic distribution we see today.

ACKNOWLEDGMENTS

Dr. Lyn Craven (Australian National Herbarium) verified the identities of *Melaleuca* specimens collected as part of this study. Dr. Bob Pemberton (U.S. Department of Agriculture, Agricultural Research Service, Invasive Plant Research Laboratory) introduced us to materials on the Reasoner brothers, and made available copies of the Royal Palm Nursery catalogs. Dr. Ray Schnell (USDA, ARS Subtropical Horticulture Research Station) provided access to early USDA publications and unpublished horticultural records from the USDA Plant Introduction Station in Miami. Their kind assistance is gratefully acknowledged.

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Received July 11, 2005; Accepted December 29, 2005.