EPIDEMIOLOGY OF THE INVASION BY *MICONIA CALVESCENS* AND REASONS FOR A SPECTACULAR SUCCESS

ÉPIDÉMIOLOGIE DE L'INVASION PAR MICONIA CALVESCENS *ET RAISONS D'UN SUCCÈS SPECTACULAIRE*

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Miconia calvescens is a small tree native to rainforests of tropical America where it is uncommon. First described around 1850, it was introduced to European tropical greenhouses then distributed to tropical botanical gardens all over the world because of its horticultural success. *M.c.* was introduced as an ornamental plant in the Society Islands and the Hawaiian Islands and in 25-35 years became a dominant invasive plant in both archipelagoes. Small populations were recently discovered in the Marquesas Islands (Nuku Hiva and Fatu Iva) in 1997. *M.c.* is also naturalized in private gardens of New Caledonia and Grenada (West Indies), in tropical forests of Sri Lanka, and in the Queensland region in Australia. The survey of the epidemiology of invasion in Tahiti shows that *M.c.*'s extension was slow but continuous since its introduction in 1937. Hurricanes of 1982-83 played more a role of "revealer" rather than of "detonator" of the invasion. The lag phase observed between the introduction date and the observation of dense populations may be explained by the generation time of *M.c.*. Several hypothesis may explain the spectacular success of *M.c.*: (1) the characteristics of the invaded area; (2) the plant's bio-ecological characteristics; (3) the "facilitation phenomenon" and the "opportunities". *M.c.* provides an interesting study-case for understanding of biological invasions in islands, and a catastrophic example of an alien invasive species that threatens the biodiversity of islands.

Miconia calvescens *est un petit arbre originaire des forêts humides d'Amérique tropicale où il est peu commun. Décrit vers 1850, il a été introduit dans les serres tropicales d'Europe puis distribué dans les jardins botaniques tropicaux du monde entier en raison d'un grand succès horticole. Introduit comme plante ornementale dans les îles de la Société et dans les îles Hawai'i, M.c. est devenu en 25-35 ans une plante envahissante majeure dans ces 2 archipels. De petites populations ont été récemment découvertes aux îles Marquises (Nuku Hiva et Fatu Iva) en 1997. M.c. s'est également naturalisé dans des jardins privés en Nouvelle-Calédonie et à la Grenade (Antilles), dans les forêts tropicales du Sri Lanka et de la région du Queensland en Australie. Le suivi de l'épidémiologie de l'invasion à Tahiti montre que l'extension de M.c. a été lente mais continue depuis sa première introduction en 1937 ; les cyclones de 1982-83 ont joué un rôle de "révélateur" plutôt qu'un "détonateur" de l'invasion ; la phase de latence observée entre la date d'introduction et l'observation de couverts denses peut être expliquée par le temps de génération de M.c. Plusieurs hypothèses peuvent expliquer le succès spectaculaire de M.c. : (1) les caractéristiques de la zone envahie ; (2) les caractéristiques bio-écologiques de la plante ; (3) le "phénomène de facilitation" et les "opportunités". M.c. constitue à la fois un modèle d'étude intéressant pour comprendre les processus d'invasion biologique dans les îles et un exemple catastrophique d'une espèce étrangère envahissante menaçant la biodiversité des îles.*

Epidemiology is commonly defined as "a branch of medical science that deals with incidence, distribution and control of a disease in a population" (Woolf, 1977). By analogy, biological invasions by alien animals or plants might be compared to infectious diseases caused by pathogens. First of all, invaders like epidemic agents show three main stages during the invasion process (Di Castri, 1989; Shigesada and Kawasaki, 1997):

(1) initial establishment, or colonization, in a non-infected region usually by small number of individuals or even a single propagule.
(2) persistence, or naturalization: the species become established in the wild with the ability to reproduce by sexual or vegetative means without assistance of man.
(3) spatial spread, or extension: the species expands its range, altering the structure, composition and processes of ecosystems with significant damage to native biotas.

Secondly, knowledge of the origin of an infectious agent (the native range of an invader), its nature (the biology and ecology of an invader), its spatial spread (the population dynamics of an invader) and the symptoms of the disease (the conservation impacts of an invader), as well as the reasons of success, is important to fully understand the epidemic (the process of biological invasion) and to elaborate efficient curative means (control methods). Finally, prevention of invasion, as for diseases, is often the only defense (McDonald, 1997).

M.c., sometimes called “the green cancer” in French Polynesia or “the purple plague” in the Hawaiian Islands in public information literature, is considered by scientists to be the worst plant pest in these two Polynesian archipelagoes and potentially the most damaging weed of rainforests of Pacific islands (Meyer, 1996; Medeiros *et al.*, 1997). The biological invasion by *M.c.* is perhaps one of “the most incredible and spectacular cases of a noxious plant invasion” in island terrestrial ecosystems (R. Petocz, Environmental Consultant for SREP, in a letter dated November 1993 to Jeffrey A. McNeely, Biodiversity Officer at IUCN, after his visit to Tahiti). For conservation biologists and natural areas managers, *M.c.* also represents a dramatic example of the need for active management of long-term threats that cause massive losses in biological diversity (Loope and Medeiros, 1995).

In this paper, I have compiled the available information on *M.c.* in its native range, its discovery and cultivation as an ornamental plant, its current status and distribution worldwide, and its expansion in French Polynesia, especially the dynamics of its extension in Tahiti. This review enables the examination of different hypotheses explaining the striking success of this invasive species. Information already published in previous comprehensive studies (Meyer 1994; 1996) is discussed and supplemented with many unpublished documents and updated data.

ORIGIN

As with many alien plants that subsequently became serious plant pests in new areas where they have been introduced accidentally or intentionally by man, very little information is known about the natural life-history characteristics of *M.c.* in its native range. As far as we know, there is no biological or ecological study conducted on this species in any country where it is native. This may be explained by the fact that there are about 1000 species of *Miconia* throughout tropical America (Wurdack, 1980) and because *M.c.* has evoked no real ecological or economical interest to date. Other *Miconia* species are well-known in their native range by local people for their traditional uses (such as *M. longistyla* for timber in Panama, *M. macrophylla* for its edible fruits, *M. cinnamomifolia* for its fruits used to make a yellow dye in the West Indies, *M. agrestis* in Peru and Guyana whose fruits might contain an anti-biliary substance, or *M. fothergilla* whose sap is applied to stings to relieve pain (Baillon, 1880)) or by scientists for their bio-ecological particularities (such as *M. argentea*, a dominant pioneer in large gaps on Barro Colorado Island in Panama (Brokaw 1985) or the seedling establishment of *M. albicans* after fire in pine savanna of Belize (Miyanishi and Kellman, 1986)).

Most information concerning *M.c.* in its native range comes from taxonomic descriptions of the family Melastomataceae published in early monographies (mostly written during the

19th century) or in relatively recent floras of the American tropics, when the Melastome family, one of the largest families in the world with about 4000 species and 200 genera (Cronquist, 1981), is included. Melastomataceae, however, have not been treated in the "Flora Neotropica" yet. De Candolle (1828), Triana (1871), Grisebach (1879), von Martius (1887) and Cogniaux (1891) made the first descriptions of *M.c.* and gave some locations of this species in its native range without giving any information on the life-history traits of the species itself (see ref. in Meyer,1994). A few comments on *M.c.* can be found in studies dealing with the family Melastomataceae or with the genus *Miconia* in selected regions of tropical America, such as the Yucatan Peninsula in Mexico (Gleason, 1940) or the region of Rio de Janeiro, Brazil (Baumgratz, 1980). Herbarium specimens are certainly one of the best source of information, apart from their fundamental interest in taxonomy and systematic, especially when the label written by the plant collector describes the exact location, the forest type, the surrounding plant community and some characteristics of the habit of the plant.

A compilation of all the documents on *M.c.* in its native range (**Table 1**) demonstrate that:

(1) the species has a wide distribution from southern Mexico to northern of Argentina;
(2) the discolorous form, with purple-blue leaves underneath (also found in cultivation), appears to be restricted to Central America (Meyer, 1994; 1996). However, in Costa Rica, it is observed that the leaves are "purple on the underside of young plant but as the plant matures, the undersides of the leave turn green" (R. Burkhart, pers. comm., 1993);
(3) it is a small tree up to 15 m high;
(4) it is found in tropical rainforests or wet forests (where the mean annual rainfall and temperature are respectively > 2000 mm and > 22º C (Budowski, 1965));
(5) it is found in lowland to montane forests, up to 1800 m elevation;
(6) it grows in disturbed or second-growth forests, in semi-open areas (such as small gaps, forest edges, stream banks, trail sides) and more rarely in the understory of dense primary forest. The exploratory entomologist R. Burkhart (formerly at the Hawaii Department of Agriculture) observed *M.c.* growing in Costa Rico at about 700 m elevation, mainly "along streams in forested areas" or "at edge of forest" (Burkhart, 1993-1994). *M.c.* seems to behave as "an early successional tree species of wet thickets and dense mixed forest, colonizing small light gaps" (R. Burkhart in Medeiros *et al.*, 1997).

According to botanists who have done extensive field work and/or have collected the species in the American tropics, *M.c.* "is not a particularly common species" (F. Almeda, pers. comm., 1992) and "never [...] occurs in monospecific formations" (F. Almeda, in a letter dated November 1988 to P. Birnbaum). P. Morat, the current director of the Laboratoire de Phanérogamie of the Natural History Museum of Paris emphasized that, with only some 40 herbarium specimens present in Paris, this species has been little collected and concluded that "in its native countries, it is obviously a very banal species" (letter dated September 1988 to J. Florence).

Table. 1. Location, habitat and habit of *M.c.* in its native range in tropical America (from North to South)

Native country	Habitat	Elevation range	Max. height	Source
MEXICO	tropical rainforest, montane rainforest	250-1170 m	12 m	Herbarium specimens
GUATEMALA	tropical rainforest, dense forest, mixed and secondary forest, exposed site	150-1400 m	10 m	Herbarium specimens
	moist or wet thickets, dense mixed forest	< 1800 m	12 m	Flora of Guatemala (Stanley and Williams, 1963)
BRITISH HONDURAS	primary forest, old second growth woods	45-620 m	10 m	Herbarium specimens
	wet forests at low elevation			Melastomataceae of the Yucatan Peninsula (Gleason, 1940)
NICARAGUA	rainforest	-	-	Herbarium specimens
COSTA RICA	rainforest, premontane rainforest, wet second growth forest	635-900 m	15 m	Herbarium specimens
PANAMA		-	10 m	Flora of Panama (Woodson and Schery, 1958)
		<1000-2000 m	-	Flora of Panama (d'Arcy, 1987)
COLOMBIA	secondary forest	1200 m	4 m	Herbarium specimens
		-	-	Cogniaux (1891)
EQUADOR	dense forest, trail side	400	4 m	Herbarium specimens
		300-1800 m	16 m	Flora of Equator (Harling and Sparre, 1980)
PERU	dense lowland rainforest, montane rainforest, cloudforest, disturbed rainforest, inundated forest, river bank, along trail, in moderate or dense shade	100-1500 m	15 m	Herbarium specimens
		-	10 m	Flora of Peru (McBride, 1941)
BOLIVIA	wet thickets	1500 m	8 m	Herbarium specimens
		-	-	Cogniaux (1891), Woodson (1958), d'Arcy (1987)
BRAZIL	cut-over woods, galery-forest, forest edge, river bank	300 m	8 m	Herbarium specimens
	sciaphile or semi-heliophile	-	6 m	Triana (1971), Cogniaux (1891), Baumgratz (1980)
PARAGUAY		-	6 m	Herbarium specimens
		-	-	Cogniaux (1891)
ARGENTINA		-	-	Herbarium specimens
		-	-	Grisebach (1879), Cogniaux (1891)

DISCOVERY AND CULTIVATION

M.c. was first discovered by Auguste Ghiesbrecht, a Belgian botanical explorer (or "naturaliste-voyageur") who lived in Mexico for 10 years. The discovery occured probably between 1850-1855, during A. Ghiesbrecht's second expedition to the Chiapas district, S. Mexico (Morren, 1849). He found the species in "the wet and shady forests that surrounded the mysterious ruins of Palenque" (Linden, 1858) and sent it to his botanist collegue and friend Jules, J. Linden, a famous plant dealer at Luxemburg between 1845 and 1852 and the director of the Jardin Royal de Zoologie et d'Horticulture in Brussels between 1852 and 1861 (Staflew and Cowan, 1981). They had explored together, collecting many plants, in Brazil in 1835 and in Mexico (especially the districts of Tabasco, Xalapa, Chiapas) between 1838 and 1840, along with the Belgian botanist Nicholas Funck (Linden and Planchon, 1867).

Linden (1858) first named the species *Cyanophyllum magnificum* because of its large magnificent leaves with purple-blue undersides and exhibited it in 1857 in London, the Paris Society of Horticulture exposition, and the Horticultural Festival of Berlin. The first morphological description of *Cyanophyllum magnificum* was written in August 1857 by Koch, the editor of the German horticultural bulletin "Berliner Allgemeine Gartenzeitung". The first picture of this plant (drawn by Riocreux) was published in 1859 in the "Revue Horticole" (**Fig. 1**), a French journal of practical horticulture (Groenland, 1859). The species is described as "a jewel of the plant kingdom" (Linden, 1858) that "aroused the admiration of all lovers of plant wonders" (Groenland, 1859). It was mentioned later on as "one of the best and most striking of all conservatory foliage subject" in the authoritative "Cyclopedia of American Horticulture" (Bailey, 1930) and as one of the most magnificent hothouse plants in the German horticultural journal "Pareys Blümengartnerei (1932)" (B. E. Leuenberger, pers. comm., 1993). Since its discovery, this very attractive ornamental plant has been propagated in the greenhouses of many botanical gardens in Europe and distributed to many tropical gardens worldwide where it was cultivated (**Table 2**) under the name *Miconia magnifica* Triana (Wurdack, 1971) or under the common name "velvet tree" (Graf, 1986) because of the small stellate hairs found on young stems and leaves (Wurdack, 1986). A form with more bronzy foliage and flat leaves rather than arched, and known in garden as *Miconia velutina* Linden & Rodigas does not differ sufficiently to warrant botanical separation (Wurdack, *op. cit.*) but may be worth distinguishing horticulturally as *M.c. velutina* (Everett, 1981).

Fig. 1. First drawing of *M.c.* in cultivation (syn. *Cyanophyllum magnificum* Lind. or *Miconia magnifica* Triana in horticulture) published in 1859 (*in* Groenland, 1959).

Information on the cultural practices of this species found in horticultural literature are noteworthy. According to the "Gardener's Chronicle" (Anonymous, 1930), "*Miconia magnifica* delights in a high temperature [...], it cannot be grown too near the glass, its leaves are thin in texture, and if not shaded when the sun comes directly upon them with any force, they are liable to be scorched [...], plenty of water should be given at the roots". In "Tropical and Subtropical Gardening", the author advised to "water copiously while in active growth [...], watch for leaf-eater, scale and mealy bugs" (Oakman, 1975).

Horticultural recommendations teach us some important biological characteristics of *M.c.*: (1) the species needs a lot of humidity and a warm temperature; (2) direct sunlight must be avoided (3) it reproduces vegetatively from cuttings ("strikes easily from hardwood or soft tip cutting", Oakman, *op. cit.)* (4) it is often attacked by insects in greenhouses. It is ironic in light of its now well-documented invasive tendencies that horticulturists consider this species to be very difficult to grow ("unfortunately, it is not very often met in these days, possible owing to the fact that it is not the easiest of plants to grow successfully" (Anonymous,1930) "contrarily to other Melastomataceae, the species of *Miconia* have difficulties to implant outside their native range. When cultivated in hot-houses, they required a lot of care" (De Wit, 1965)). Nowadays, *M.c.* is still cited and recommended for planting in the main horticultural plants books such as "Exotica" (Graf, 1974), "Hortus Third" (Bailey and Bailey, 1976), "Tropica" (Graf, 1986) or "Tropical Planting and Gardening" (McMillan *et al.*, 1991).

Table 2. Cultivation sites of *M.c.* as an ornamental plant (outside tropical America)

Country of Introduction	Site of introduction	Dates of cultivation	Source
ALGERIA	Jardin d'Essai du Hamma	1952	Carra and Gueit (1952)
BELGIUM	Jardin Royal de Zoologie et d'Horticulture de Bruxelles	1857-1907	F. Billiet, pers. comm. 1993
GERMANY	Botanisher Garten München	until 1943	A. Kress, pers. comm., 1993
INDONESIA	Bogor Botanical Garden	1950-1960	O. Dharmaputra and I. Suhirman, pers. comm., 1992
THE NETHERLANDS	Rijksuniversiteit, Utrecht	1978	B. J. Ter Welle, pers. comm., 1992
THE PHILIPPINES	Los Banos, near Manilla	still in cultivation	R. Petocz, pers. comm., 1993
UNITED KINGDOM	Royal Botanic Garden, Edinburgh	until 1969	J. D. Main, pers comm., 1993
	Liverpool Botanic Garden, Calderstones Park	no longer	*id.*
USA	Fairchild Tropical Botanical Garden, Miami	no longer (from seeds collected in Mexico in 1967)	C. Hubbush, pers. comm., 1993
	United States National Arboretum, Washington DC	1971	*id.*
ZAIRE	Jardin Botanique de Kisantu	1972	Pauwels (1972)

SITES OF NATURALIZATION

Although *M.c.* has not succeeded in naturalizing in some tropical countries where it has been planted and cultivated as a garden ornamental, such as in the Bogor Botanical Garden (O. Dharmaputra and I. Suhirman, pers. comm., 1992), it has become established in the surrounding vegetation in others. Indeed, *M.c.* is able to self-reproduce and to form viable populations from a single individual (Meyer, 1994; Meyer, in press). The tropical regions where *M.c.* is naturalized show a pronounced climatic similarity with the native country of tropical America, with an annual rainfall above 2000 mm (**Table 3**). However, in new areas of introduction where naturalization occurs, *M.c.* is not consistent in its tendency to invade.

Table 3. Sites of naturalization of *M.c.*

Country of introduction	Site of introduction	Date of introduction	Elevation range (m)	Rainfall (mm/yr)	Source
AUSTRALIA	Flecker Botanical Garden, Cairns	1968			M. Bryannah, pers. comm., 1996
	Townsville Botanic Gardens	1963			S. Csurhes, pers. comm., 1997
	Melbourne Botanical Garden	before 1980			*id.*
GRENADA	St George	around 1970	300	1520-2540	P. Cazin, pers. comm., 1995
JAMAICA	Castleton Garden, St Mary	before 1970	244	2030	Wurdack 1971
NEW CALEDONIA	Yahoué valley, Nouméa	1970's	500-600	1700-2000	R. Lavoix, pers. comm., 1993, 1994; J.-C. Pintaud, pers. comm., 1995, 1996
SRI LANKA	Botanical Gardens of Peradeniya	1888	480	3020	A. H. M. Jayasuryia, pers. comm., 1993
	Kandy district		700-900	5400	*id.*

New Caledonia--The only known population of *M.c.* in New Caledonia is found in a private botanical garden located above the town of Nouméa above the Yaouhé Valley on the slopes of the Mount Koghi (summit at 1061 m elevation). This botanical garden was created in 1957 by Lucien Lavoix, "an excellent horticulturist as well as a botanist" (Barrau, 1966) who introduced many alien species as ornamental or cultivated plants. According to his son Raymond Lavoix who now owns the garden, *M.c.* was introduced 20 years ago probably from Tahiti (R. Lavoix, pers. comm., 1993) and "the population is not very abundant and propagates very slowly" (R. Lavoix, per. comm., 1994). He estimated several years ago the *M.c.* population to be 100 individuals, the biggest one being 4-5 m tall and fruiting (R. Lavoix, pers. comm., 1993). The current population was checked in 1996 by J.-C. Pintaud, a botanist of ORSTOM-Nouméa: he found a single mature tree and several saplings between 1-2 m tall, located around the mother tree. However, the 800 ha of the botanical garden have not been carefully prospected by J.-C. Pintaud, and R. Lavoix recognized having sold plants in his nursery before being aware that the species is a pest plant. The habitat where *M.c.* is naturalized is a disturbed forest with bamboos and palms at about 500-600 m elevation (J.-C. Pintaud, pers. comm., 1996). Soil is composed of schistose or ultrabasic rocks and climate is wet, with mean annual rainfall between 1700 and 2000 mm (Sautter, 1981). The particular nature of the soil (ultrabasic rocks are very poor in mineral elements such as N and K, and a high concentration of Mg and toxic heavy metals such as Ni, Co and

Cr) may constitute a major obstacle to the establishment of *M.c.* and other alien plant species in this southern part of New Caledonia.

Jamaica--Although *M.c.* is not cited among the 24 species of *Miconia* present in Jamaica (Adams, 1972), the species is naturalized and common at Castleton Garden and flowering specimens were collected in 1970 (Wurdack, 1971). The botanical garden is located at 244 m elevation (Heywood *et al.*, 1990) in the region of St. Mary on the North side of the island where the surrounding vegetation is mainly cultivated pastures and second-growth scrub (Asprey and Robbins, 1953). Soil consists of limestone and annual precipitation in the garden is about 2030 mm (Heywood, *op. cit.*). In a letter addressed to A. Chonin of the Service de l'Économie Rurale (French Polynesian Department of Agriculture) and dated August 1979, J. J. Wurdack stated that *M.c.* requires "high humidity and more-or-less acid soil". This may explain why the species is "naturalized only to a limited extent in Jamaica where areas of acid soils are limited". Unfortunately, my attempts since 1992 to contact botanists in Jamaica who could provide some information on *M.c.* were not successful and the degree of naturalization is currently not known.

Grenada--The only known population of *M.c.* in the island of Grenada (Lesser Antilles) is above the town of St. George at about 300 m elevation below the Grand Étang Forest Reserve (P. Cazin, pers. comm., 1995). Rainfall ranges from 1520 and 2540 mm and soils are "lithosols and red earths" according to the characteristics of major agro-ecological zones of Grenada (unpub. data). The plant was introduced by John Griswick, an artist and ornamental plants enthusiast living in the island for 20 years; he received a specimen of *M.c.* from Sri Lanka 15 years ago and cultivated a single plant in his private property. The plant mature and reproduced profusely, then died in 1980-90 (P. Cazin, pers. comm., 1995). According to P. Cazin, an agricultural engineer, there was a single new reproductive tree growing in 1995 about 4 m tall and 15 cm basal diameter, originating from a seedling of the first tree. Many seedlings have been removed by the owner and the few seedlings left were found on the ground near the parent tree. Most of them were heavily attacked by unidentified leaf-eaters (P. Cazin, pers. comm., 1995). The Lesser Antilles has about 20 native species of *Miconia* (Howard, 1989). None of them are invasive probably the result of natural enemies that keep their populations in check.

Sri Lanka--*M.c.* was introduced to the Royal Botanical Garden, Peradeniya, from Mexico in 1888 (A.H.M. Jayasuriya, pers. comm., 1993). Despite a century of cultivation, naturalization has not taken place within the garden proper whose elevation is about 480 m and annual precipitation 3020 mm (Heywood *et al.*, 1990). The species has become naturalized 40 km south of the garden, however, in a wetter area in higher elevation wastelands near Nawalapitiya and Ginigathena, Kandy district, Central Province, where mean annual rainfall and temperature are respectively 5400 mm and 21º C. (A.H.M. Jayasuriya, pers. comm., 1993). *M.c.* is found in disturbed natural vegetation between 700-900 m elevation along rivers and trails. According to A.H.M. Jayasuriya, a botanist and curator of the National Herbarium of Sri Lanka, the plant "is still grown in botanical gardens and occasionally in some home gardens [...] but is not a perturber of vegetation communities in Sri Lanka" (letter dated January 1989 to P. Birnbaum), "there are small scale naturalizations in one or two areas but the species has not established as a weed" (A.H.M. Jayasuriya, pers. comm., 1993). *M.c.* populations are small and seem not to be extensive. The forest structure in Sri-Lanka, with a canopy reaching 30-40 m tall whereas it doesn't exceed 10-20 meters in Pacific tropical oceanic islands, could explain the difference in the invasion success of *M.c.* (Meyer, 1994; Meyer, in press).

Australia--The introduction of *M.c.* as a garden ornamental was first reported in the Flecker Botanical Garden in Cairns (North Queensland) and a few other gardens (Humphries and Stanton, 1992). The species is known to have been introduced in the Flecker Botanical Garden in 1968, the original source of the specimen was a plant supplier, Limberlost Nursery, also located in Cairns (M. Bryannah, pers. comm., 1996). In 1996, "a small number of specimens" were observed in the Botanical Garden, some of them were fruiting. According to S. Csurhes, Exotic Species Officer at the Land Protection Branch, *M.c.* was also introduced in 1963 in Townsville Botanical Gardens, in Melbourne Botanical Garden before 1980 and in private nurseries (S. Csurhes, pers. comm., 1997). It has escaped and is now naturalized in the tropical region of North Queensland (Cairns, El Arish and Mossman) where it is considered to have a great invasive potential (Csurhes, this volume).

SITES OF INVASION

Since its introduction as an ornamental plant in the Society Islands (Moorea, Raiatea, Tahaa, Tahiti) and in the Hawaiian Islands (Hawai`i, Kaua`i, Maui, O`ahu), *M.c.* has become a dominant invasive species in these two Polynesian archipelagoes. The species thrives from nearly sea level up to 1300 m elevation in disturbed and native wet forests where the mean annual rainfall is usually above 2000 mm (**Table 4, Fig. 2**). Islands where *M.c.* has been introduced earlier show more extensive invasion except in the island of O`ahu where a few seedlings have been discovered despite an old introduction, such as in the Wahiawa Botanical Garden (Conant and Nagai, this volume). The low rainfall (about 1500 mm/yr) may explain the relative failure of this species that might be considered growing in suboptimal ecological conditions.

The Society Islands--*M.c.* was first introduced to Tahiti (Windward Group) in 1937 by Harrison W. Smith in his private botanical garden (nowadays called the "Harrison Smith Botanical Garden") located in the Papeari district; its introduction in the neighboring island of Moorea, about 20 km N-W of Tahiti, is not precisely known but the plant was already noticed in the early 1970's on mountain trails (Meyer 1994; 1996). A single tree was noted by J. Florence in the Opunohu valley in 1983 (letter dated April 1983 to the Chief of the Forestry Section, Service de l'Économie Rurale).

M.c. was introduced in the island Raiatea (Leeward Group) between 1955-1958, by Jacques Rentier, former chief of the Service de l'Économie Rurale at that time, in the private garden owned by Mme Lenormand and located in the low valley of Uturaerae (R. Amiot, pers. comm. to the journalist J.-P. Besse in June 1997). In the 1970's and the 1980's, seeds were accidentally introduced to the Tetooroa and the Faaroa valleys respectively with soil in plant pots from Tahiti (Meyer 1996; Meyer and Malet 1997).

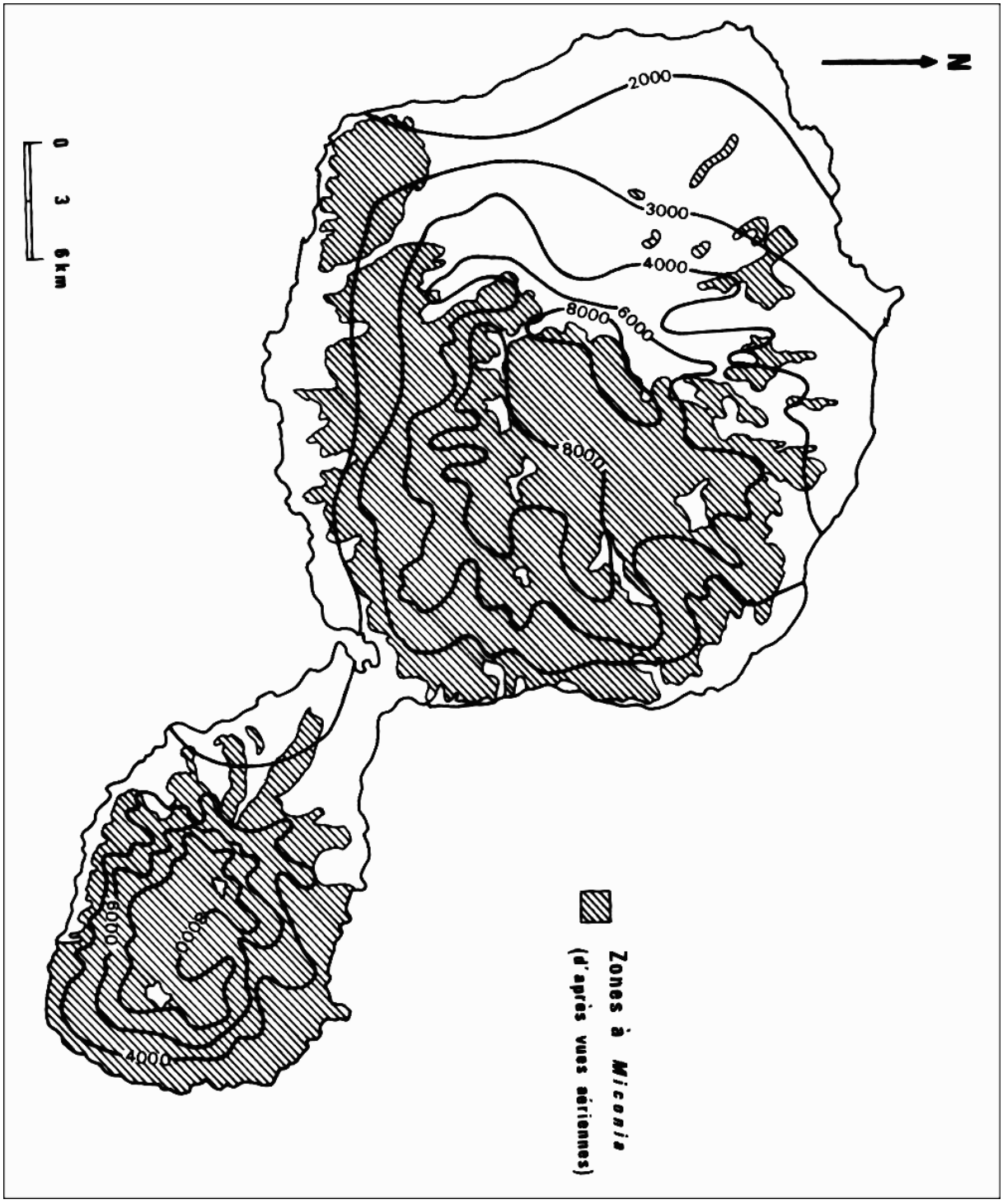
M.c. was introduced in Tahaa in the early 1980's, probably with infected soil stuck on the wheels of bulldozers used for road-construction and is now naturalized in a single valley. On the island of Huahine, seedlings of *M.c.* were observed in 1995 in the village of Fare, growing on a soil dump originating from Tahiti, and quickly eliminated (Meyer and Malet, 1997).

Finally, a few seedlings were found on the uninhabited island of Mehetia, on a pile of soil and rock brought by Tahitians for the building of a small house (M. Wong, pers. comm., 1997).

Table 4. Sites of invasion by *M.c.*

ISLAND	Site of introduction	Date of introduction	Elevation (m)	Rainfall (mm/yr)	Source
FRENCH POLYNESIA					
Society Islands					
TAHITI	Harrison Smith Botanical Garden, Papeari	1937	10	> 2000	H. W. Smith, personal notes
	65-70% of the island (70 000-80 000 ha)		10-1300	> 2000	Birnbaum, 1991 ; Meyer, 1994 ; 1996
MOOREA	Mont Mouaputa ?	1960's ?			Meyer, 1994 ; 1996
	> 10 % of the island (> 1200 ha)		10-1200	> 2000	Krantz and Schwartz, 1994 ; Meyer, unpub. data.
RAIATEA	Uturaerae valley	1955	50-400	2700-5300	Meyer, 1994 ; 1996
	2% of the island (240 ha)				*id.*
TAHAA	Pueheru valley (2 ha)	early 1980's	150	2800	Meyer and Malet, 1997
HUAHINE	Fare village (few seedlings)	mid 1990's	0	-	Meyer and Malet, 1997
MEHETIA	(few seedlings)	mid 1990's	-	-	M. Wong, pers. comm., 1997
Marquesas Islands					
NUKU HIVA	pass between Terre Deserte and Tovii plateau (7 seedlings)	1996	1100	> 3000	J.-Y. Meyer, unpub. data
	Road from Taiohae to Tovii (1 sapling)		550	-	A. Bonno, pers. comm., 1997
	Hatiheu pass (few seedlings)				W. Tetuanui, pers. comm., 1997
FATU IVA	between Omoa and Hanavave (1 tree)	early 1990's	-	-	B. Tehevini, pers. comm., 1997
HAWAIIAN ISLANDS					
O'AHU	Wahiawa Botanical Garden	1961	290	1500	Medeiros *et al.*, 1997
	Lyon Arboretum ca. 80 ha	1964	120-400	> 2000	*id.*
MAUI	Helani Gardens	early 1970's	20-490	> 2000	Medeiros *et al.*, 1997
	ca. 280 ha				Hobdy, 1997
KAUA'I		early 1980's	40-150	-	Medeiros *et al.*, 1997
HAWAI'I	Onomea	1959			K.Onuma, pers. comm., 1997
	100 000 ha		10-760	> 2000	K.Tavares, pers. comm., 1997

Fig. 2. Distribution of *M.c.* in the island of Tahiti (hatched area) in relation with the mean annual rainfall (solid line) in mm/yr



The Marquesas Islands--The recent discovery of a small population of *M.c.* in Nuku Hiva (Marquesas, Northern group) in June 1997 during a botanical expedition with botanists Steve Perlman and Ken Wood (National Tropical Botanical Garden, Kaua'i) was alarming. A total of 7 seedlings (between 20-70 cm tall) were found near the pass between Terre Déserte and Tovii plateau at 1050 m elevation. They were immediately uprooted. The plants were growing on an embankment just below the road, near the edge of pristine cloudforest. As no mature tree was found, it is likely that the seedlings originated from soil infected by *M.c.* seeds. The approximative age of the plants (according to their size) coincide with roadworks made in 1996 by bulldozers from Tahiti (Meyer, unpub. data). According to the Service du Développement Rural based in Taiohae (Nuku-Hiva), other small seedlings have been found and destroyed since the beginning of 1997 on the road from Taiohae to Tovii (A. Bonno, pers. comm., 1997) and below the pass of Hatiheu (W. Tetuanui, pers. comm., 1997).

A single plant, 4.5 m tall with a basal diameter of 15 cm., was discovered in September 1997 on the island of Fatu Iva (Marquesas, Southern group) by a young pig hunter. According to the Service du Développement Rural, the plant was located near the road between Omoa and Hanavave and was not flowering at the time of discovery (B. Tehevini, pers. comm., 1997). No seedlings have been found around the tree and a survey is currently being done by S.D.R.(J.-P. Malet, pers. comm. 1997).

SPREAD IN THE ISLAND OF TAHITI

I have reconstructed the invasion of Tahiti by *M.c.* since its first introduction through a compilation of the sightings of this species (published in scientific papers, technical reports, local magazines and other documents), and the testimony of local people who witnessed the progression of the plant in Tahiti since the 1970's (**Fig. 3**).

1937 - 1970

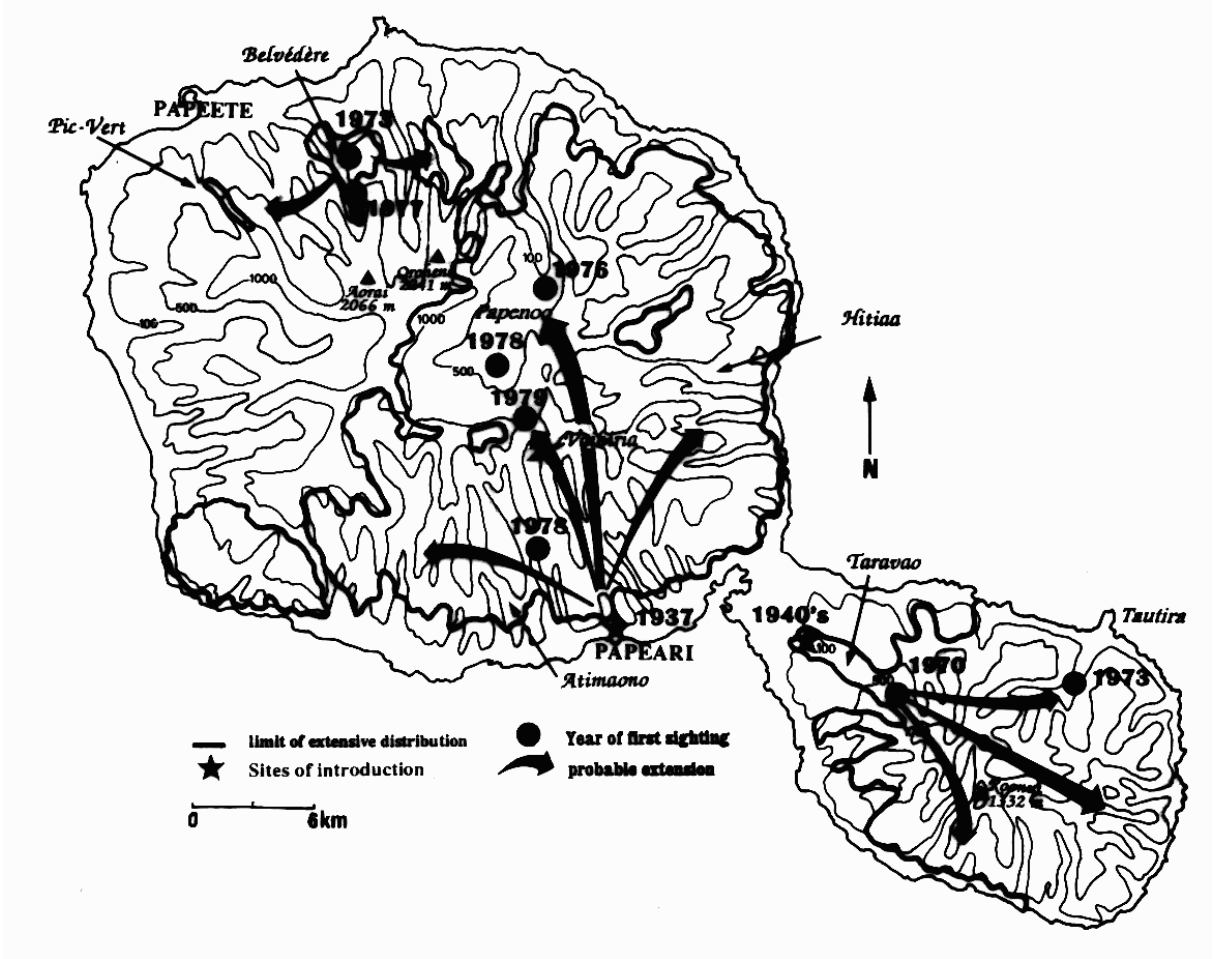
~ the species was first introduced in April 1937 in the Motu Ovini private garden owned by Harrison W. Smith and located in the district of Papeari (S-W coast of Tahiti); the plant was "potted and set out in October 1937" (Harrison W. Smith, personal unpublished notes);
~ the species was planted a few years later on the ground of the Agricultural Station on the plateau de Taravao by Jean-Marie Boubée (Raynal, 1979), an agricultural engineer who arrived in Tahiti in 1934, and a collaborator and close friend of Smith. According to Michel Guérin of the Délégation à l'Environment (pers. comm., 1997), Boubée acquired a piece of land on the Taravao plateau where he introduced many of the exotic plants cultivated by Smith. After the death of Smith in 1947, Boubée inherited the botanical garden (Barrau and O'Reilly, 1972).
~ the plant was noticed in the botanical garden of Papeari by L. G. M. Baas Becking under the name *Miconia flammea* (Becking, 1950), a taxonomic confusion that could be explained by the red-colored undersides of the leaves of this other *Miconia* species;
~ René Papy (1951-54) cited *Miconia magnifica* in the appendix, entitled "List of the alien species in the Motu Ovini private park of Papeari", of his work on the vegetation of the Society Islands;
~ the name *Miconia magnifica* is surprisingly included in 1963 in the list of the cultivated plant of French Polynesia that are attacked by parasites, expecially by *Icerya seychellarum* Westw. (Cohic, 1963). However it is not found in Jean-Noël Maclet's "List of the plants of economical interests and the main adventices plants existing in French Polynesia" (Maclet, 1958) whereas *Acacia farnesiana, Mimosa invisa, Psidium cattleyanum* and *Rubus rosifolius* are cited as noxious plants. Maclet was the director of the Harrison Smith Botanical Garden between 1962 and 1967 (M. Guérin, pers. comm., 1997);
~ the species was not noticed in a study of the organization of the district of Papeari made between 1967-68 by F. Ravault, a geographer, whereas *Cecropia peltata* is noticed to form

pure stands, and the author observed "the invasion of some coconut groves by *Psidium guajava, Lantana camara, Mimosa pudica*" (Ravault, 1980).
~ Robert Millaud, a former chief of the Service de l'Économie Rurale, showed Michel Guérin, a horticultural engineer who arrived in Tahiti for his national service, the species growing on the Taravao plateau in 1968. Guérin immediately recognized it as *Miconia magnifica*, because the plant was cultivated as a tropical ornamental in the greenhouse of the "École National Supérieure d'Horticulture" of Versailles (France) where he earned his horticultural degree.
~ in August 1969, the pharmacist and botanist Paul Pétard, visiting the *Cinchona succirubra* and *C. ledgeriana* plantations on the Taravao plateau at about 400 m elevation observed that these species were growing well "despite the colonization of purau (*Hibiscus tiliaceus*), *Aleurites*, acacias (*Leucaena leucocephala*) and miconias" (Pétard, 1986).

1970 - 1982
~ the first published record of its invasiveness was observations of dense stands on the plateau de Taravao dated in the early 1970's. Henry Whittier, in his book on the mosses of the Society Islands published in 1976 (this manuscript was accepted for publication in 1972), noticed that "there is a forest of *Metrosideros, Aleurites, Cyathea* and *Miconia* at about 800 m elevation on Taravao" (Whittier, 1976). Although Whittier cited *Lantana camara* and *Eugenia sp.* as common introduced species, nothing is said about the invasiveness of *M.c.*;
~ during one of his botanical trip to Tahiti in 1971, the botanist Raymond Fosberg of the Smithsonian Institution of Washington observed *M.c.* rapidly naturalizing on the Taravao plateau (pers. comm., 1991 *in* Loope, 1992);
~ the plant is considered to be "the number one enemy of the Tahitian vegetation" according to the botanist J. Raynal of the Natural History Museum of Paris, who noticed in September 1973 dense covers "on the top of the Taravao plateau [...], in the vicinity of the botanical garden in Papeari", "the species is said to exist around the Belvédère", and that they were "many young plants in the Vaitepiha valley at Tautira" (Raynal, unpubl. report). *M.c.* was not noticed in this valley in 1963-64 by local people working on archeological excavations for the Musée de Tahiti et des îles (V. Mu-Liepman, pers. comm., 1996);
~ Michel Guérin, who was the director of the Harrison Smith Botanical Garden between 1974 and 1988, cut down in 1974 the big *M.c.* tree (8-10 m tall) that grew in the garden and that flowers and fruits profusively, after being awarded by F.R. Fosberg and J. Raynal of the potential danger of this species (M. Guérin, pers. comm., 1997);
~ the botanists F.R. Fosberg and M.-H. Sachet observed the plant growing in wet valleys: "by 1974 it has spread to an alarming extent. Today it has supplanted all other vegetation on certain slopes on the south side of the island [...] it appears to be the major threat to the already endangered flora of Tahiti" (Fosberg and Sachet, 1981);
~ a dense stand of *M.c.* is illustrated on the cover page of the journal "Te Natura O Polynesia" (a quarterly bulletin edited by the Tahitian association for nature protection "Ia Ora Te Natura") dated of the first quarter of the year 1975, with the legend "proliferation of Miconia on the plateau of Taravao" (photo taken by J. Drollet, pers. comm., 1997);
~ the species was observed in the valley of Papenoo in 1976 during an ethnobotanical study. It presents a "particularly invasive behavior, especially in the peninsula of Taravao [...] but only a few individuals were found in the prospected area but it is said to be common higher in the valley" (Martin, 1976);
~ Steve Montgomery, Wayne Gagné and Betsy Gagné were "saddened to see the firm advances that *M.c.* has made into the native forest of the Taiarapu Peninsula above Vaiufaufa, and also to see it established below Mr. Aorai" during their trip to the Society Islands in June-July 1977 (Montgomery *et al*., 1980);
~ in November 1978, *M.c.* was observed by Gérard Mondon, a botanist of the Service de l'Économie Rurale "on complete slopes above cultivated areas" in the Teamatea Valley near Vaite river (Papeari district) and in the Vaihiria valley (G. Mondon, unpub. data). He noticed it again in October 1978 in Papenoo valley where the species "is common" up to the pass of Anuhe where "it forms dense stands";

~ in 1979 *M.c.* is located in all of the southern part of the island of Tahiti Nui, especially the Vaihiria district where it is "predominant from the coastal zone up to the Urufaau pass (at 884 m elevation between Vaihiria and Papenoo) and enters in the center of the island" (Le Vot, 1979). J. Raynal wrote in a later paper published in 1979 that "there are monospecific stands from Taravao to Vaitepiha, the main valley of Tahiti Iti" (Raynal, 1979);
~ finally, *M.c.* was found abundant around lake Vaihiria in May 1982: "the extension of *Miconia* is particularly striking on the edges of the lake where it has invaded the forests of *Cyathea-Pandanus*" (Florence, 1982).

Fig. 3. Historical spread of *M.c.* in Tahiti according to published records



The Role Of The 1982 - 1983 Hurricanes--P. Birnbaum made the statement that the hurricanes that hit Tahiti severely between December 1982 and April 1983 have caused the sudden and explosive spread of *M.c.* in the island. According to this author, the hurricanes represent "an exceptional abiotic factor" that "can explain the demographic explosion of *Miconia*" (Birnbaum, 1991); "the speed of invasion then became astonishing" (Birnbaum, 1993); "the 1983 cyclones multiplied the ecological niches favourable for this species and constitute the detonator of the demographic explosion" (Birnbaum,1994). His statement is based on (1) pre-cyclone aerial photos taken in 1978 and showing that the cover of *M.c.* in forest canopy is only 1% to 2% (100-200 ha) on the Taravao plateau; (2) an aerial photomap made in 1989 showing that *M.c.* was present on over 75% of the island and dominated a large part of the canopy (Birnbaum,1991).

However, according to the botanist J. Florence (ORSTOM/Museum of Natural History of Paris), the Taravao plateau was the only place in Tahiti where it was possible to have a good correlation between the aerial photographs of 1978 and a vegetation cover (observed on the field), mainly because it has a relatively flat terrain, and that *M.c.* may have been "elsewhere in the canopy" on Taravao plateau and "in other localities of Tahiti Iti where it was still present" (J. Florence, pers. comm. 1994). Birbaum's statement has been unfortunately found its way into several scientifical papers: "the hurricanes [...] detonated a demographic explosion of *M.c.* " (Loope, 1992); "the massive invasion of [...] forests in the Society Islands by *M.c.* following hurricanes Reva and Veena in 1983" (Medeiros *et al.*, 1995); "in the wake of two successive devastating hurricanes in 1983, a fast-growing South American melastome *M.c.*, rapidly invaded montane cloud forest habitat" (Merlin and Juvik, 1995). Although no direct evidence exists, *M.c.* is cited as a typical example of the interaction of periodic natural disturbance and forest recovery in the presence of an alien species and support of the disturbance hypothesis as an explanation of biological invasions.

What was the role of the hurricanes of 1982-83 in the extension of *M.c.*? The 6 hurricanes that hit the Society Islands between December 1982 and April 1983, with strong winds reaching 180-200 km/hr and a rainfall reaching 4 m per day (Doumenge, 1984) certainly had an enormous impact on the native vegetation. It is likely that they suppressed the canopy by breaking the top of the trees and by defoliating the emergent trees. The increased light in the understory enabled faster growth of *M.c.* seedlings already present in the shade of the native forest (as shown by the study and control of *M.c.* in the island of Raiatea (Meyer and Malet, 1997) but these were preceded by an earlier and massive establishment. An earlier and more prolific reproduction rate may have occured in this wind-disturbed canopy. Indeed, it seems that *M.c.* flowers only where the branches reach the canopy or when it attains the full light (Birnbaum 1991; Meyer, in press). Colonization of *M.c.* in open spaces such as treefall gaps or landslides created by hurricanes is less probable because the species can not establish in open sunlight and does not colonize large gaps (Meyer, 1994).

In my opinion, the hurricanes acted more as a "revealer" of the invasion of *M.c.* in 1983 than as a "detonator". According to J. Florence (pers. comm., 1994), the hurricanes "put in light, in the strict sense of the term, the invisible presence of *M.c.* " in Tahiti. *M.c.* was undoubtedly present in the understory of the secondary and native forests in the main part of the island of Tahiti before the 1982-83 hurricanes (see above, and pers. comm. of L. Stein, former chief of the Forestry Section of the Service de l'Économie Rurale). The spread of *M.c.* was not explosive, but slow and continuous, or in other words an insidious invasion ("a slow undermining establishment in the lower strata of vegetation" according to J. Florence, pers. comm., 1994).

The Lag Phase Period--Some alien species remain uncommon or very localized for long periods of time before they exhibit a rapid expansion. A genetic change (a more adapted

genetic combination), local environment changing (e.g. fire, wind, flood) or the arrival of another alien species which can act as a pollinator or a dispersal agent can explain the time-lag or lag phase (Ewel, 1986). The duration of this lag phase can reach up to 75-100 years (e.g., *Mimosa pigra* in Australia, *Schinus terebinthifolius* in Florida, *Pittosporum undulatum* in Jamaica). Longer durations of the lag time are usually explained as a consequences of major disturbance events which create conditions favoring regeneration (Bingelli, 1995).

There seems to have been a relatively short lag phase for *M.c.* of about 25-35 years between its date of first introduction and the observations of dense stands both in the Society Islands and in the Hawaiian Islands (**Table 5**). This delay might be explained by the autoecology (reproductive biology and regeneration requirements) of *M.c.* rather than by any exceptional disturbance. Studies in the island of Raiatea have demonstrated that the optimal vegetative growth of a seedling is 1.5 meter per year and that the first age of reproduction in reached after 4 to 5 years from seeds in the best ecological conditions (Meyer and Malet, 1997).

Table 5. Delay in the spread of *M.c.* in French Polynesia and in the Hawaiian Islands

ISLAND	Approximate date of introduction	First observation of dense stands	"lag phase" (yr)
FRENCH POLYNESIA			
TAHITI	1937	early 1970's	33
MOOREA	1960's	1990's	30
RAIATEA	1955	1988	33
TAHAA	early 1980's	NO (1-10 mature trees)	-
NUKU HIVA	1995-96	NO (NO mature tree)	-
FATU IVA	1990's ?	NO (NO mature tree)	-
HAWAIIAN ISLANDS			
O'AHU	1961	NO (5-10 mature trees)	-
KAUA'I	early 1980's	NO (3 mature trees)	-
MAUI	early 1970's	1993	23
HAWAI'I	1959	1985	26

If one assumes that 5-10 years is an average time to form a reproductive tree from seed, 10-20 years will be necessary to build the second generation of approximatively 10-100 reproductive trees. After a period of time between 15-30 years, the third generation will be formed by a dense cover of about 100-1000 trees (as observed on the plateau of Taravao in the early 1970's, about 30 years after its introduction). The generation times needed to form a monospecific stand from a single individual of *M.c.* may explain the lag phase we observed in the Polynesian archipelagoes. The lag between the time *M.c.* was introduced and its invasiveness could also be explained by a unnoticed expansion until the hurricane events after which the plants were quite obvious.

DISCUSSION

The Reasons Of Success--The spectacular success of *M.c.* in the Polynesian archipelagoes (Society and Hawaiian Islands) and its failure in other sites of introduction may be explained by a combination of the following reasons:

(1) The plant was introduced without its natural enemies.
In its native range of tropical America, there are numerous insects and pathogens that are present that keep *M.c.* in check and limit the spread of its natural populations. In 1993, the exploratory entomologist R. Burkhart (formerly of the Hawaii Department of Agriculture) visited the native range of *M.c.* in Costa Rica and Brazil. He noticed that the species had heavily damaged leaves. He collected several fungi including a leaf-spot fungus *Coccostroma myconae*, and a number of insects: weevils (Curculionidae); leaf beetles (Chrysomelidae); and, Lepidoptera (Limacodidae, Riodinidae and Lycaenidae) (Burkhart, 1993-94). Butterflies with colonial processional larvae *Euselasia spp.* (Lepidoptera: Riodinidae) that are voracious foliage feeders appear to be the most common and damaging of the insects occuring on the leaves of *M .c.*.

Horticulturists and gardeners have noticed the considerable susceptibility of *M.c.* leaves to phytophagous insects. Moreover, it is not uncommon to find leaves of *M.c.* in the Society or Hawaiian Islands extensively destroyed by the Chinese rose-beetle (*Adoretus sinicus*), a generalist leaf-eater that is abundant near cultivated of inhabited areas. The impact of this non host-specific insect has not been evaluated.

(2) The characteristics of the invaded zone.
Alien species find themselves in an environment different from that in which they evolved. According to Mack (1996) biotic factors are not as important barriers to naturalization and invasion as physical factors are. The similarity of an alien's home range to a potential new range is considered to be a good predictor for invasiveness (Reichard, 1997).

On the island of Tahiti there is an extremely good match between the annual rainfall and the distribution of *M.c.* The low amount of annual precipitation can also explain the failure of *M.c.* in Wahiawa Botanic Garden, O`ahu, Hawai`i. Soil nature or toxicity may explain why *M.c.* which prefers acids soils has not expanded in Jamaica and New Caledonia. *M.c.* has not invaded the Tamanu Plateau, Tahiti, (600m elev., and average annual rainfall > 3000 mm) where soils are of a clay texture and are less acid to neutral (Jamet, 1985). The structure of the vegetation (a smaller stature and a more open canopy in Polynesian forest compared to Neotropical and Sri-Lankan rainforests) may play a major role in the reproductive success of *M.c.* (Meyer, 1994; Meyer, in press).

(3) The intrinsic characteristics of the plant.
Invader species have diverse sets of ecological, physiological, genetic and morphological characteristics that make them suitable for wide dispersion, colonization and competition. With the rapid germination of seeds on a wide range of substrates and under various light conditions, a fast vegetative growth (a maximum annual growth rate of 1.5 m), an early age of reproduction (first flowering season after 4-5 years), a large and persistent seed bank (up to 50,000 seeds/sq m), the ability to self-reproduce and at least three seasons of flowering and fruiting each year (Gaubert, 1992; Meyer, 1994; Meyer and Malet, 1997; Meyer, in press), *M.c.* can be considered an "ideal weed" *sensu* Baker (1965).

Unlike many other alien species, seedlings of *M.c.* can establish in moderate or dense shade and the species does not need natural or man disturbances to become established in native forests.
(4) The "facilitation phenomenon", the opportunities and the role of chance.
Man has played a paramount role in the success of *M.c.* Its attractive purple and green foliage resulted in its introduction as an ornamental in many tropical countries, including the Polynesian Islands. Harrison Smith was in close contact with the Royal Botanic Garden,

Peradeniya, (Barrau and O'Reilly, 1972) and imported *M.c.* directly from Sri Lanka. *M.c.* was then dispersed to other islands either voluntarily as an ornamental or accidentally with infected soil or on vehicles that had not been cleaned. The tiny seeds are readily transported on boots or clothes of hikers, hunters, or anyone who has been in an infested area.

Other effective dispersal agents are frugivores attracted to the fleshy berries of *M.c.* The seeds are dispersed by alien birds (*Zosterops lateralis* and *Pycnonotus cafer*) introduced respectively in 1937 and 1979 to Tahiti, and by *Z. japonicus* in the Hawaiian Islands (and maybe *Leiothrix lutea*, widely naturalized in the native forests and a disperser of *Clidemia hirta*, A.C. Medeiros, pers. comm. 1997). Other non-native mammals such as rodents (especially the Polynesian rat *Rattus exulans* (Meyer, 1994)), cattle or wild pigs are potential dispersers. The "facilitation phenomenon" between invasive plants and alien animals as dispersal agents is well documented in other cases of biological invasion in islands.

The role of natural and anthropogenic perturbations (especially hurricanes, see above) has favored the expansion of *M.c.*. Roads are known corridors for weeds and ruderal species but also facilitate the penetration on invasive species in native forests (see the case of *M.c.* in Tahaa and Nuku Hiva discussed previously).

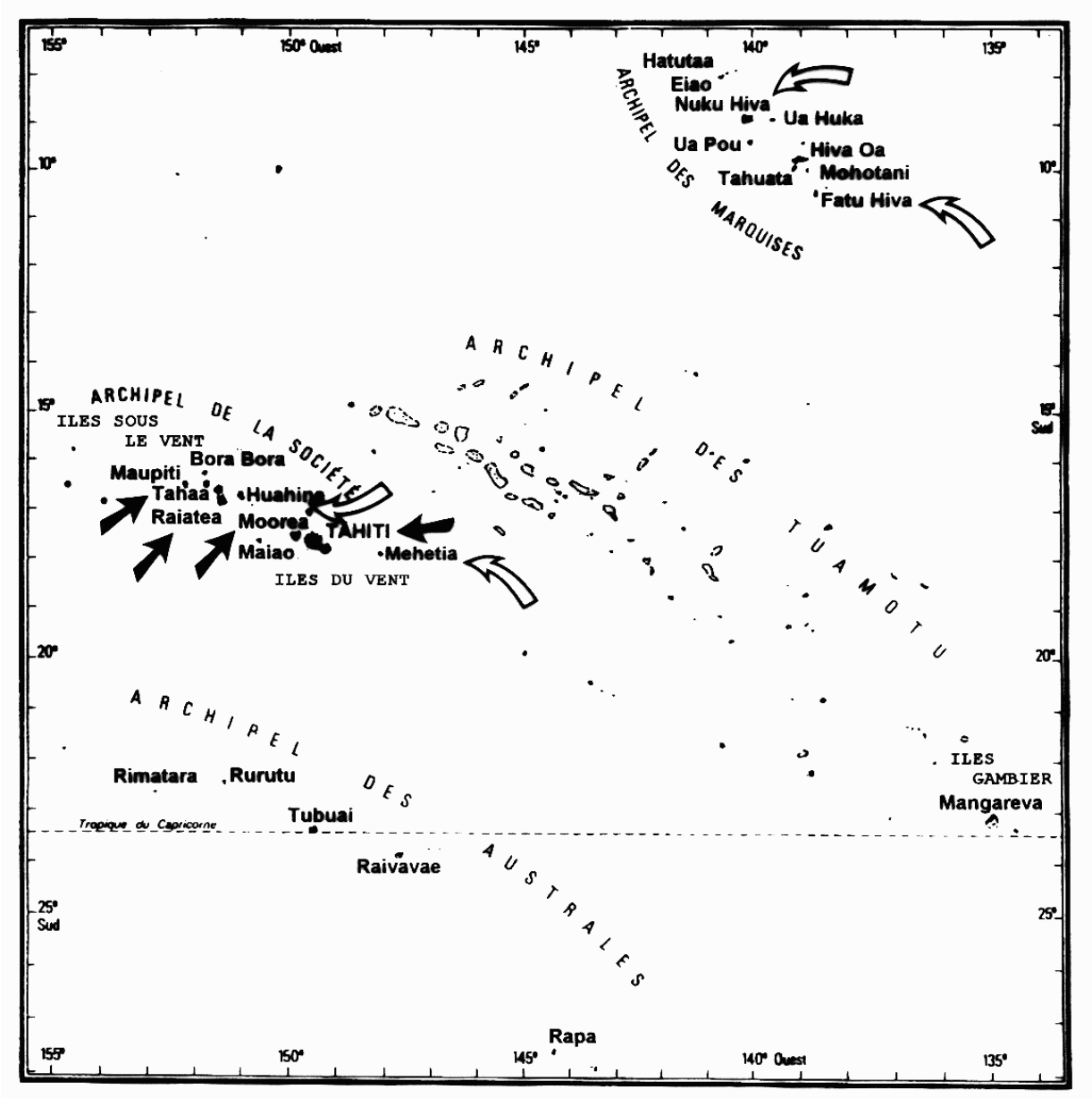
"Invasion biology is the interplay of historical chance and biological necessity" (Di Castri, 1990). *M.c.* was first introduced to Tahiti in the district of Papeari, on the wet side of the island. The Harrison Smith Botanical Garden is located close to the native wet forest into which *M.c.* could easily escape and establish itself. *M.c.* has been first used as fence posts on the Taravao plateau (as in Costa Rica, Burkhart, 1993-1994). These posts may have sprouted, as cuttings of *M.c.* are very easily propagated.

Last but not least, the lack of political decision in the 1970's to control *M.c.* in its early stage of invasion. Even though the alarm was raised by scientists and naturalists, and the potential threat of the species recognized, the lack of response enabled the expansion of the infestation, contributing to its current success. *M.c.* continued to spread until the local authorities decided, in 1988, to start a Miconia Research Program in collaboration with ORSTOM.

CONCLUSIONS

For scientists, *M.c.* represents a spectacular case of biological invasion by an introduced species in island ecosystems. In less than 50 years, this alien species succeeded to invade two-thirds of the island of Tahiti. It is now found on at least 7 high islands of French Polynesia (**Fig. 4**) and is well-established on 3 of them (Tahiti, Moorea, Raiatea). For managers of natural areas, *M.c.* is a direct threat to the native flora. The effects on the native forest are devastating, particularly on the native understory plants. Half of the endemic plants to Tahiti are considered to be directly endangered (Meyer and Florence, 1996) and 60% of the endemic flora of the Society Islands is threatened in the long term (Florence, this volume).

Fig. 4. Current distribution of *M.c.* in French Polynesia: high islands where *M.c.* was known to be present before 1997 (black arrow); high islands were *M.c.* has been recently discovered in 1997 (white arrow)



M.c. also has a great invasive potential in the Hawaiian Islands (Medeiros, Loope and Hobdy, this volume ; Conant and Nagai, this volume; Tavares, this volume), in tropical regions of Australia (Csurhes, this volume), and maybe in other new areas of introduction where it is naturalized but not yet invasive. The recent discovery of *M.c.* in Nuku Hiva and Fatu Iva in the Marquesas Islands is alarming, as well as the presence of seedlings in Huahine and Mehetia in the Society Islands. In most cases, soil movements between islands are responsible for the new introductions. These examples show that this pest can still extend its range in French Polynesia despite all the control and education efforts conducted since 1988. In all the new areas where the plant has been recently discovered, however, populations were small (usually formed by seedlings) and rapid eradication possible.

This review of the invasion by *M.c.* shows that knowledge of the bio-ecology of an introduced species both in its native country and in the new areas of introduction, and the epidemiology of its invasion, are essential elements in understanding the dynamics of invasion and the potential invasiveness of introduced species. As "the major sources of exotics will be ornamental plants" (Pickard, 1984), a special concern (early detection and control) should be given to tropical plants introduced in botanical gardens or private gardens that "escape" cultivation.

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