Lantana camara: Its Introduction, Dispersal and Impact on Islands of the Tropical Pacific Ocean

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Abstract

There are numerous examples of either deliberate or accidental plant introductions into the characteristically delicate Pacific Island ecosystems. In many cases, these introductions have led to significant modification of the floras of the respective island groups. The purpose of this study is to use the case of one exotic plant species, Lantana camara, to show how its introduction, in conjunction with other modifications of the environment by man, has led to the alteration of the floras of many of the major island groups throughout the tropical Pacific Ocean. Lantana seems to have been introduced into the Pacific Islands as an ornamental in "European" gardens. Subsequent to its original introduction, it has escaped from cultivation and become naturalized on almost all of the major island groups in a relatively short period of time. Moreover, it is generally a dominant member of the secondary flora wherever it has become naturalized. In this paper an attempt has been made to determine: 1) when lantana was introduced into the different island groups; 2) its present distribution; 3) the factors which have led to this distribution; 4) the factors which have allowed it to become naturalized; and, 5) the impact it has had upon the vegetation of the different island groups.

Introduction

To the careful observer, one of the most salient characteristics of the vegetation in the tropical Pacific Islands is the presence of exotic species which dominate many secondary vegetation associations on almost all of the major island groups. The purpose of this study is to use the case of one exotic plant species, *Lantana camara*, to show how its introduction, in conjunction with other direct or indirect modifications of the environment by man, has contributed to the irreversible alteration of Pacific Island floras.

Island ecosystems, such as those of the tropical Pacific Ocean, tend to be in a very delicate state of equilibrium and are particularly sensitive to external influences. The native floras of these ecosystems are generally impoverished and characterized by a high degree of endemism with only limited competition for available ecological niches. Consequently, there is a high susceptibility to displacement or disturbance of these native floras, and, despite their long evolutionary history, they have been significantly modified in a relatively brief period

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of human occupancy. Factors which seem to have been most responsible for producing this situation are: the introduction of animals, the removal of the primary vegetation by man, and the introduction of competitive exotic plant species.

There are numerous examples of either deliberate or accidental plant introductions into the Pacific Islands which have modified the various Pacific Island floras. Some of the most interesting cases are the introductions of species which have displaced native species as dominants in secondary vegetation associations. Whereas a great majority of the plant species represented in the Pacific Islands have an affinity to the flora of Southeast Asia, many of the introduced weedy species are part of the flora of tropical America. Noteworthy examples of American species, almost all of which have been introduced after European contact and which have subsequently become noxious weeds in the Pacific Islands, are Schinus terebinthifolius, Synedrella nodiflora, Elephantopus mollis, Psidium guajava, Leucaena leucocephala (=L. glauca), and Lantana camara. The case of Lantana camara is of particular interest, owing to the comparative recency of its introduction, its subsequent rapid naturalization, and the considerable effect it has had on many Pacific Island environments.

General Background

Lantana camara, a member of the family Verbenaceae, is a perennial erect shrub which, although native to the West Indies, now has a pantropic distribution. There are several varieties, many of which are commonly grown as ornamentals in gardens throughout the United States as well as in other temperate areas. The most common form found in the Pacific Islands is *Lantana camara* L. var. aculeata (L.) Moldenke. It is a spreading shrub with long weak branches and numerous recurved prickles. The flower head is generally about one inch across consisting of numerous small, brightly colored (pink, orange and yellow) flowers. It develops into an aromatic, ovoid-shaped, blackberry-like fruit about one-half inch across consisting of numerous tiny, juicy two-seeded drupes. As an ornamental in temperate regions, it rarely attains a height greater than one or two feet (some horticultural varieties are taller). In the tropics, however, it ranges from about two to six feet in height, and under favorable conditions, has been known to reach a height of twenty feet (Neal, 1965: 772).

Habitat

Lantana is a very tenacious shrub which is capable of establishing itself in a variety of different habitats, although it is more often than not found in disturbed sites. It grows well in the poorest of soils, in the full sun, and even in the shade of semi-open forests. It seems to thrive on neglect and will grow where many other weedy species can not survive, as well as in the more favorable sites.

Where lantana has become naturalized, it is found near sea level only a few yards from the beach as well as at elevations over 1000 feet, as is the

case in Tahiti, New Caledonia (Virot, 1951: 264), and Hawaii where it extends up to 3000 feet in some localities (W. Bryan, 1915: 209). It also grows well on both the moist windward sides as well as the more arid leeward sides of most of the major island groups (Heckel, 1911; Greenwood, 1943; Egler, 1942). It is sometimes found in undisturbed sites along river banks, but this is an exception rather than a rule. More commonly, it has invaided disturbed sites (such as abandoned fields, roadsides, pastures, waste places and areas disturbed by forest exploitation) where it has become a dominant member of the secondary growth.

The major factors which seem to limit its range are: 1) its apparent inability to compete with the taller native forest species, although it is commonly found under the canopies or even climbing up the branches of taller vegetation; 2) its need for temperatures above 40°F (Neal, 1929: 269) and its associated susceptibility to frost which causes the leaves and stems to die (Anon, 1964: 178); 3) its low tolerance of saline soils or brackish water, which induce chlorosis and make the plant sterile (Fosberg, 1949a: 196); and, 4) its tendency to rot in boggy or hydromorphic soils (Hamilton, 1919: 495).

Present Pacific Island Distribution

The presence of *Lantana camara* has been reported in almost all of the major "high" volcanic island groups, including the Hawaiian Islands, Society Islands, Cook Islands, Samoa, Fiji Islands, New Caledonia, New Hebrides, New Britain, New Guinea, and Ponape and some of the islands of the Truk group in the Caroline Islands (see following map). It is also reportedly present in Guam and on some of the upraised coral limestone islands, such as Tongatapu (Tonga), Niue, and Makatea as well as in "continental" Australia and New Zealand (for citations see Appendix).

Lantana is noticeably lacking, however, in the flora of most of the islands in the great groups of low lying coral atolls: the Marshall Islands, Caroline Islands, Tuamotu Archipelago, Gilbert Islands, Line Islands, Phoenix Islands, Tokelau Islands, and the westernmost Hawaiian Islands. It is also absent in the Galapagos Islands and in mountain areas at elevations above 2000 to 3000 feet. The appendix lists those areas where it has been possible to document the presence or absence of lantana. The list, based on first-hand observations by the author and an extensive literature review (primary sources included: Sachet and Fosberg, 1955, 1971; Merrill, 1937, 1947; Walker, 1947; Blake and Atwood, 1942), gives an indication of the present distributional pattern of lantana in the Pacific. However, owing to the scarcity of data for parts of Melanesia and Polynesia and the outdated nature of some of the references, the distribution of lantana is no doubt wider than is indicated here. The balance of this paper will deal with the history of its introduction into the Pacific Islands, the factors responsible for its rapid spread and present distribution, and the impact it has had on island environments.

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Introduction of Lantana camara

At the time of the early European explorations and scientific expeditions in the Pacific, lantana was not reported among the flora of any of the major island groups (Merrill, 1954: 220; Fosberg and Sachet, 1957: 436–437). The West Indies are considered to be its native habitat and, as early as 1789, it was known to grow naturally in Jamaica and most of the other islands of the West Indies where it is called "wild sage" (Curtiss, 1789: plate 96). During the eighteenth century, it was cultivated as an ornamental in temperate regions (such as England) where it required artificial conditions. In India, where it had been established for such a long time that Linnaeus used India as the type locality for the species (Birindelli, 1969: 3), it was likewise planted by Europeans in gardens and as hedges (Anon, 1958: 1). Owing to lantana's considerable ornamental value and the fact that it does not seem to be capable of long-range dispersal by natural agencies (at least in the Pacific), it is reasonable to assume that it was probably from European gardens that lantana was introduced into the Pacific Islands.

The first known case of the introduction of lantana into the islands was its introduction into Tahiti in 1843 by a Captain Chappe of the French Navy (Setchell, 1926a: 204). It was introduced into Hawaii in 1858 by the botanist William Hillebrand, who imported it to plant in his garden (Birindelli, 1969: 7-10). It was similarly introduced into a military doctor's garden in New Caledonia around 1861 (Heckel, 1911: 511) where it had become naturalized by 1868 (Guillaumin, 1933: 477).

There are no exact dates for its introduction into other island groups, but approximations have been made for some areas. It was not mentioned in Seemann's *Flora Vitiensis* in 1865 (Seemann, 1865), in Gibb's account (1909) of the montane flora of Fiji, nor in the *Fiji Department* of *Agriculture Annual Report* of 1914; but it was frequently mentioned after this time (Parham, 1958: 181-184). By 1921 it was recorded as being common on Viti Levu, Vanua Levu, Taveuni, Kandavu and Ovalau of the Fiji group (Parham, 1958: 135).

In other parts of Melanesia, it was first cited as being present in the New Hebrides in the early 1930's (Aubert de la Rue, 1937: 61; Guillaumin, 1935: 1-2) and in the Loyalty Islands by the late 1920's (Daniker, 1931: 209-210). It was not mentioned in early accounts of the New Guinea and New Britain floras (Schumann and Hollerung, 1889; Schumann, 1898; Lam, 1925a, 1934; Kanehira and Hatusima, 1939), although it is now present in both areas.

In addition to Tahiti and Hawaii, in Polynesia, lantana was recorded for Samoa as early as 1898 (Christophersen, 1935: 191) and is thought to have been introduced from Hawaii (Lloyd and Aiken, 1934: 97). In the Tongan Archipelago, it was absent from early accounts of the floras of the islands of Vava'u in 1901 (Burkill, 1901) and 'Eua in 1890 (Hemsley, 1894: 58), but by 1917 was legally declared a noxious weed throughout the island group (Wylie, 1967: 697). On Rarotonga in the Cook Islands, although it was not mentioned in Cheeseman's Flora of Rarotonga of 1903, it was reported as "seldom seen" in 1929, and is now considered a noxious weed (Wilder, 1931: 93) as well as being naturalized on a number of small reef islands off Rarotonga (Fosberg, 1972: 13). On Pitcairn Island, it was reported as being a "troublesome weed" by 1929 (Brown, 1935: 246).

In Micronesia, lantana was mentioned as having been introduced into the Marshall Islands from Samoa by 1899 (Volkens, 1903: 90), although subsequent accounts cite it as being absent (Lam, 1925b; Kanehira, 1931; Fosberg, 1955). On Ponape in the Eastern Carolines, lantana was naturalized and formed dense thickets by 1936 (Glassman, 1952: 27, 103), and although not reported in Merrill's "Enumeration of the Plants of Guam (1914) nor in Glassman's "Survey of the Plants of Guam" (1948), it was reported by Stone to be widespread in cultivation and naturalized there by 1970 (Stone, 1970: 506). It was also reported as present on Jaluit Atoll in the Marshalls by 1941, but apparently did not survive the effects of typhoon Ophelia I in 1958 (Blumenstock, 1961: 67, 103; Fosberg and Sachet, 1962: 1, 33).

Lantana had also become naturalized on Norfolk Island by 1902 (Maiden, 1903: 776); in North Auckland, New Zealand, by 1913 (Cockayne, 1928: 381); and was present in parts of Queensland and New South Wales, Australia, by 1870 (Bentham, 1870: 34; Diels, 1929: 139) where it was reported as being naturalized by 1884 (Woolls, 1884: 202).

In almost all of the above cases, lantana appears to have been introduced as an ornamental because of its colorful flower clusters, only to subsequently escape and become naturalized very rapidly. This assumption is documented for Tahiti (Setchell, 1926a: 204); New Caledonia (Heckel, 1911: 512; Guillaumin, 1933: 477; Barrau and Devambez, 1957: 332); Hawaii (Hillebrand, 1888: 342); and Australia (Hamilton, 1919: 495; Whittet, 1968: 444) and can be extrapolated to other island groups. Degener reports that "lantana usually escapes from the garden and shortly overuns the country to become an extremely costly and troublesome weed" (Degener, 1945: 251). In Hawaii, by 1871 (only 13 years after its introduction), it has escaped from cultivation and had become naturalized on all of the main islands (Birindelli, 1969: 7–10). The rapid naturalization of *Lantana camara* becomes even more remarkable when compared to another form of lantana, *Lantana trifoliata* L., a smaller shrub with pink flowers which has been present in Hawaiian gardens for about the same period of time as *L. camara*, but has never escaped from cultivation (Hillebrand, 1888: 342).

Factors Responsible for the Present Distribution

The rapid spread and naturalization of lantana within a given island group, subsequent to its original introduction, seems to be closely correlated with the following factors: 1) a favorable physical environment in the islands; 2) an abundance of open habitats; 3) the adaptability of lantana as a pioneer species in ruderal sites; 4) lantana's dispersal mechanisms, which are well adapted for short or intermediate range dispersal; and, 5) the relative absence of com-

petitive plant species, plant diseases, and predators (which were probably factors in keeping it from becoming a troublesome pest in its native habitat). However, in order to better understand the present distribution of lantana and the factors leading to this distribution, the impact of man on the island environment, both directly and indirectly, must also be taken into consideration.

The spread of lantana has definitely been accelerated by man's modification of the island environment for agricultural, pastoral, forestry, and urban purposes. For centuries, even before the first European contact, the native peoples of the islands have cleared the land by burning, ring-barking, and other means. Subsequently, much of the land has been abandoned or eroded, thus creating favorable environments for colonization by pioneer species like lantana.

The use of fire for clearing land, both by native Pacific Islanders and Europeans has had a particularly important role in destroying the native vegetation and opening up areas to colonization by lantana and other introduced plants. The case of the fire encouraging the spread of lantana is well documented for New Caledonia where extensive areas were opened up by repeated burning (Heckel, 1911: 512; Virot, 1956: 58, 1951: 264). In the New Hebrides as well as in Tonga and other island groups, the traditional shifting agricultural system has opened up extensive areas to colonization by lantana, *Leucaena* and other pioneer plant species (Sachet, 1957: 41). Not only do the dried leaves and branches of lantana constitute an excellent fuel, but its trunks, which are rich in sap, remain unattackable (Guillaumin, 1933: 477).

The overriding factor in opening up areas to weed infestations, however, seems to have been the introduction of large mammals (primarily grazing animals) into the island environment. Pigs, which were raised before European contact, have been known to disturb the natural vegetation by rooting for food, both in forested and unforested areas. However, the introduction of cattle, sheep, horses, goats and even deer by Europeans seems to have had a more important role in disturbing the native vegetation. On many islands these animals were able to roam unchecked, owing to the absence of natural predators which are found on the major continents. In Hawaii, for example, between 1918 and 1923, at least 13,000 goats were killed on the island of Kahoolawe and, at the present time, owing to its devegetated state, the island is used only as a military artillery target. The same pattern exists for the grazing of cattle, sheep and horses. In 1851, on the island of Hawaii alone, there were an estimated 12,000 cattle roaming unrestriced, another 8,000 or more on ranches, besides 10,000 sheep and 11,700 horses (Birindelli, 1969: 27–29).

In the case of New Caledonia, the effect of introduced livestock was equally severe. Cattle were first introduced between 1845 and 1850 (Barrau, 1958: 573) and in addition to horses and goats, deer were also introduced between 1860 and 1870, originally to give a rural atmosphere to the government park. From a nucleus of 12 deer (*Cervus hippelaphus*) imported from Java in 1870, seventy years later, there were an estimated 200,000 feral deer in New Caledonia. The effect

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of these 200,000 deer, plus an estimated 100,000 cattle, 10,000 horses and 30,000 goats, was devastating on the estimated 700,000 hectares of low capacity natural "pasture" (Barrau and Devambez, 1957: 325–327; Virot, 1956: 59). Although most of the other islands in the Pacific do not have the large areas of gradually sloping land found on Hawaii and New Caledonia, the effect of grazing animals has been much the same, and extensive areas of Fiji and Tonga have also been opened up to infestation by lantana and other weeds.

The exploitation of forest species for subsistence and commercial purposes has also been a major factor in the elimination of the natural vegetation. Before European contact, timber was used in the construction of houses, canoes, temples, etc. After European contact, further exploitation occurred as a number of tropical hardwoods native to the islands, such as sandalwood, *Santalum* spp., became economically exploitable. These practices again contributed to the diversity of open habitats suitable for colonization by introduced exotic vegetation. It has been in these open habitats, including roadsides, vacant lots, trails, refuse dumps and other ruderal sites created by man, that lantana invades as a pioneer species.

Although lantana seems incapable of long range dispersal, it is well adapted for short-range or intra-island dispersal once it has been introduced into an area. The branches and rootstocks of lantana are quite brittle and are easily broken; this, together with its ability to reproduce vegetatively, has possibly been a factor in its rapid spread. The branches also have small prickles which could conceivably attach themselves to passing animals or humans. The major means of dispersal, however, seems to have been the spread of the seeds by birds.

Although grazing animals have created disturbed habitats into which lantana can move, it is unlikely that they were instrumental in the physical dispersal of the seeds owing to a toxic effect of lantana that causes photosensitization in various animals. The plants contain a photodynamic substance which, when ingested by domestic animals, sensitizes them to light so that they may develop serious symptoms often resulting in death after exposure to strong sunlight (Muenscher, 1961: 10, 11, 202; Morton, 1967: 62). Cases of cattle dying as a result of the toxic effect of lantana have been recorded in Hawaii (Turbet, 1929: 35), Fiji (Turbet, 1931: 25–26), and Australia (Neal, 1965: 724). Birds, however, do not seem to be susceptible to photosensitization, and the small aromatic, drupe-like fruit of the lantana seem to be a favorite food of a number of introduced birds (Bryan, W., 1908: 57; Heckel, 1911: 511; Birindelli, 1969: 15).

Careful studies carried out in Hawaii have indicated that at least six bird species, all introduced after lantana, feed on the berries and that the seeds often pass through the digestive tracts in a viable state. At one time, it was thought that, of these six species, the Chinese or lace-necked dove, (*Streptopelia chinensis*), was responsible for initiating the spread of lantana (Birindelli, 1969: 16). However, it now seems that the Chinese dove may have contributed little to the spread of lantana (Schwartz and Schwartz, 1951: 102), and that the false mynah

or Indian starling (Acridotheres tristis) has been the bird most responsible in Hawaii (Bryan, W., 1915: 306; Yuncker, 1934: 34). The mynah was introduced from India in 1865 by William Hillebrand (the very same person who introduced lantana) to control insects and army worms then plaquing Hawaiian pastures, which it did very successfully (Bryan, W., 1915: 306; Munro, 1960: 170; Birindelli, 1969: 15-22; Bryan, E., 1958: 20). Degener stated that "as soon as the mynah was brought to the islands, lantana spread rapidly" (Degener, 1945: 253).

The mynah was likewise introduced into New Caledonia in 1871 (Barrau and Devambez, 1957: 329) as well as into Fiji (Derrick, 1965: 156), Tahiti, Samoa, (Thaman, 1965–73, personal observations), the New Hebrides, the Solomons, the Russells (Mayr, 1945: 145, 171, 196, 265), New Zealand (Falla *et al.*, 1967: 231) and Australia (Bell, 1969: 113). As in Hawaii, the mynah has increased in number and, in many cases, has, along with other birds, been cited as the main dispersal agent for the seeds of lantana (Heckel, 1911: 511; Hamilton, 1919: 495; Greenwood, 1943: 102; Virot, 1956: 57–60). In Fiji, it was found that even with constant grubbing, lantana could not be controlled because "birds caused reinfestation very quickly after clearing" (Barnes, 1930: 114).

Although the favorable climate, an abundance of open habitats, favorable dispersal mechanisms, and a relative absence of natural competition have enabled lantana to become naturalized shortly after its original introduction in most of the major island groups, it is noticeably absent on most islands in the groups of low lying coral atolls; in some of the more isolated high island groups such as the Austral Islands and Wallis and Futuna; and in the Solomon Islands. The absence of lantana in these areas is most likely a result of at least one or more of the following factors: 1) the fact that lantana was never introduced, either deliberately or accidentally; 2) insufficient available water owing to the comparatively low rainfall which percolates rapidly into the coralline soils; 3) excessive hardness and salinity of the ground water; 4) the impoverished nature and excessive salinity of the soil; or, 5) the high incidence of tropical hurricanes.

Whereas most of the plant species commonly present among the flora of low lying coral islands are well adapted to conditions of high salinity and the low mineral content of the coralline soils, lantana, which is not native to the littoral environment, often exhibits severe localized chorosis under such conditions. Fosberg remarks that, "*Lantana camara*, ordinarily a most aggressive weed, is yellow and sterile where planted in the Marshall Islands" (Fosberg, 1949a: 91). This example can be extrapolated to the other groups of low-lying coral islands where excessively saline soils and ground water may also be the factor preventing the naturalization of lantana. Even where lantana has been cited as present on low-lying coral islands (Midway, Tarawa, Bikajli, Canton, Hull and Rangiroa), it usually persists only as an ornamental and only in the case of Rangiroa, where "a few plants (were) seen in (the) scrub," has it become naturalized (Sachet, 1969: 42).

The possible effects of tropical hurricanes as a factor in preventing lantana from becoming naturalized on low-lying coral atolls is documented for Jaluit Atoll in the Marshalls, where, it was reported present prior to Hurricane Ophelia I in 1958 but non-existent afterwards (Blumenstock, 1961: 67, 103; Fosberg and Sachet, 1962: 1, 32).

Lantana's absence in the Solomon Islands, Wallis and Futuna, as well as some of the other high island groups, where suitable environments exist, is probably either a result of its never having been introduced or merely due to the lack of published comprehensive botanical surveys conducted in these groups to document its presence. Lantana is also generally absent throughout the Pacific at elevations over 2,000 to 3,000 feet, and in the Galapagos Islands. At higher elevations, the growth of lantana is probably inhibited by the cooler nighttime temperatures and the frequent occurrence of frosts. In the case of the Galapagos, which is affected by the cold waters of the Humboldt Current, the mean annual temperature is only 70°F, and the mean annual precipitation along the coasts of the 14 islands of the group is only three to four inches (Von Hagen, 1969: 231; Bowman, 1966: 1077). The resultant vegetation is extremely xerophytic, thus helping to explain the absence of lantana. [Other more xerophytic species of *Lantana* are found among the Galapagos flora (Stewart, 1911)].

Impact on the Environment

In almost every island group where lantana has become established, it has also become a serious pest and a dominant member of most secondary vegetation associations, usually displacing native species. It has become such a serious pest in some islands that drastic steps have become necessary in order to eradicate it, or at least impede its rapid spread. In cultivated areas, it can be controlled by plowing under and constant grubbing or clipping. However, in pastures, abandoned fields, and other disturbed areas it is almost impossible to clear.

The following cases are illustrative of this situation in various island groups in the Pacific. In Tahiti, Setchell reports that: "Lantana and guava each form thickets on the coastal plains and valleys, and even extending in some places a little way up the slopes. These are by far the most troublesome weeds of Tahiti" (Setchell, 1926b: 252). The same pattern is evident throughout the Tongan archipelago where lantana, along with other weedy species such as indigo (*Indigofera suffruticosa*), guava (*Psidium guajava*), *Leucaena leucocephala* and Guinea grass (*Panicum maximum*), has invaded thousands of acres cleared for traditional "bush fallow" cropping and grazing. It was considered such a terrible pest in Tonga that in 1917 a law was passed stating that: "Any person who shall plant or carry from one place to another any portion of the plant known as *Talatala Hina* (*Lantana camara*) shall be guilty of an offence and shall be liable to a period of imprisonment for three years or, at the discretion of the court, a fine not exceeding one hundred (100) pounds" (Wylie, 1967: 697).

Lantana is considered a noxious weed in the Cook Islands (Wilder, 1931: 93) and on Pitcairn Island it has been described as "a troublesome weed, forming almost impenetrable thickets smothering out seedlings of desirable trees, shrubs, and herbs" (Brown, 1935: 246). On the island of Ponape in the Carolines, it has replaced the native vegetation in many areas and forms closed communities (Glassman, 1952: 27; 1957: 206).

In Fiji, lantana is the major weed found in coconut plantations, pastures, and waste places (Parham, 1958: 135); it is found not only on the moist windward sides of the islands but also on the drier leeward sides (Greenwood, 1943: 102) as well as growing wild within the city limits of Suva. It has similarly been mentioned as an uncontrollable pest in the New Hebrides where, among other escaped weeds, it has been cited as the "worst of all" and, "even in the absence of fire, might succeed the native *niaouli* (*Melaleuca leucadendron*) vegetation" Sachet, 1957: 41, 44; Guillaumin, 1935: 351; Aubert de la Rue, 1937: 61). It has also spread rapidly in the Loyalty Islands where it forms monotonous thickets and likewise has modified the *niaouli* vegetation (Däniker, 1931: 190, 209, 210).

Lantana has also taken over considerable areas of Norfolk Island (Maiden, 1903); has become an important member of the secondary vegetation on the North Island of New Zealand (Cockayne, 1928: 381; Allen, 1936: 190); and "grows profusely", forming impenetrable thickets over considerable areas in the coastal districts of Queensland and New South Wales in Australia (Whittet, 1968: 444; Diels, 1929: 139).

It is in the Hawaiian Islands and New Caledonia, however, where lantana has had the greatest impact. In the Hawaiian Islands, for example, Pope has called it "the most serious pest that has ever gotten into the Hawaiian Islands" (Pope, 1929: 191). Egler quotes one of his students as stating that the invasion of exotics, including lantana has:

"... taken over the lowlands and now, with new lands to conquer, is marching up the hillsides (apparently in complete disregard of environmental differences), destroying the native vegetation in its path. Indigenous plants are helpless before the onslaught; the native forest doomed, disintegrates and retreats, sometimes even before the invaders have arrived. An ultimate and complete ascendency of the alien vegetation is but a matter of time alone (sic)" (Egler, 1942: 15–16).

By 1902, it had become such a terrible pest in both the arid and humid districts of the islands, rendering thousands of acres of agricultural and grazing land unusable, that the Board of Agriculture and Forestry (in what was the first concerted effort to use introduced insects to control weeds) sent personnel to Mexico to study insects that feed on lantana (W. Bryan, 1915: 385; King, 1966: 413). As a result of this study, twenty-three species of parasitic and predatory insects were introduced into Hawaii. This attempt was somewhat successful in controlling the lantana in the more arid areas but unsuccessful in humid areas (Egler, 1942: 18, 20). It was later observed that these insects were all from the dry areas of Mexico, and consequently, in 1953, the Board of Agriculture and Forestry in Hawaii collected insects from Cuba and other humid areas of Central America, as well as from Africa (Birindelli, 1969: 34–35; Bennet, 1970: 662). By the early 1960's these insects, along with the lantana scale insect (*Orthezea insignis*), which was accidentally introduced between 1895 and 1900, have subsequently helped check the spread of lantana in Hawaii (Davis and Krauss, 1961: 205; Pope, 1929: 193; Degener, 1945: 253).

Biological control of lantana was similarly attempted with varying degrees of success in Fiji in the 1920's (Veitch and Greenwood, 1924; Simmonds, 1928; Kermack, 1928) and in Tonga in 1937 (Cottrell-Dormer, 1937).

In New Caledonia, the impact seems to have been at least as great as in Hawaii. Here, lantana replaced the natural vegetation and infested the coastal districts on both the windward and leeward coasts and penetrated into the mountain passes of the central range. It transformed the native *niaouli* (*Melaleuca leucadendron*) savannas into impenetrable thickets; colonized both pasture and cultivated land; and transformed previously traversible native forests into impenetrable thickets as well as suffocating both mature trees and seedlings which served to support it (Schlecter, 1905: 13-14; Heckel, 1911: 511-514; Guillaumin, 1933: 476-477; Virot, 1951: 264 and 1956: 58; Barrau and Devambez, 1957: 332-334).

The establishment of more aggressive pasture has proven to be the most effective and economic means of control in New Caledonia. In certain areas, lantana has been effectively controlled by the establishment of *Chloris gayana*. Other plants that can also be used for the same purpose are *Melinis minutiflora*, or climbing legumes such as *Centrosoma pubescens* or *Calopogonium mucunoides* (Barrau, 1958: 575). Effective competition of other exotic species such as *Schinus terebinthifolium*, *Prosopis pallida*, *Leucaena leucocephala*, *Miscanthus floridulus* have also been a factor in limiting the areas occupied by lantana in some instances (Fosberg, 1973). In Tonga, for example, considerable areas, once occupied by lantana are now covered by more aggressive exotics such as *Leucaena leucocephala*, *Panicum maximum*, and *Psidium guajava*. Similarly, in Fiji, lantana has been replaced in some areas by *Acacia farnesiana* and *Psidium guajava* (Simmonds, 1928: 18).

Although in most areas lantana is considered a terrible pest, having displaced the native flora and rendering considerable areas of pasture and cropland virtually unusable, in some areas, it has been considered useful as a producer of humus and for loosening soil through the action of its long, deep roots (Hamilton, 1919: 495; W. Bryan, 1915: 383). Furthermore, with the introduction of both insect parasites and other competitive exotics, the degree of damage caused by lantana has been minimized in some cases. It must be stressed, however, that regardless of present or future means of control, the impact that lantana has had on the environments of many of the Pacific Islands has been considerable, and, in most cases, has contributed to irreversable changes in Pacific Island vegetation.

Summary

The study of the introduction, naturalization, and subsequent modification of the vegetation of various Pacific Islands by Lantana camara var. aculeata seems to be an excellent example of primary long-range dispersal by man, coupled with the subsequent invasion of habitats opened by human agencies. Although the natural environments of most of the tropical Pacific Islands are well-suited to exotic species such as lantana (in terms of climate, soils, and the relative paucity of biotic competition), the actions of man represent the overriding factor in lantana's rapid colonization of the Pacific Islands in less than a century. *Lantana camara*, however, is only one of many exotic plants (and animals) species that have been introduced with good intentions into the Pacific Islands, only to become uncontrollable noxious weeds or pests.

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APPENDIX

Islands, island groups and locations in Melanesia, Micronesia, Polynesia and other areas of the tropical Pacific Ocean where it has been possible to document the presence or absence of *Lantana camara* (L.) Moldenke. The date indicates either a) the assumed date of introduction; b) the date when it was first reported to have been observed as being present or absent; c) the date of the publication where it was reported as being present or absent; or d) the date of observation by the author. The conditions of growth which are included in the table include: I) naturalized and invasive, generally constituting a noxious weed; II) naturalized and possibly invasive; III) present as an ornamental and probably not invasive. The source or sources documenting each citation are listed in the righthand column. (The grouping of islands is based on geographic rather than ethnic affinities and the asterisk *denotes locations where lantana was observed as being present by the author).

| Melanesia | | | | | | |
|---|----------------|------------------------|--|---|-------|---|
| | sent | Absent | | | | |
| Location | Date | Condition of growth | Source(s) | Location | Date | Source(s) |
| Aneitym (New Hebrides) | 1934b | I | Aubert de la Rue, 1937 | Bismarck Archipelago | 1971c | Moldenke, 1971 |
| Efate (New Hebrides) | 1934b | 1 I | Aubert de la Rue, 1937 | (Territory of N.G.) | 10/51 | Charle 1071 |
| Espiritu Santo (New Hebrides) Kandavu (Fiji Islands) | 1934b 1958c | 1 T | Guilaumin, 1935 Parham, 1958 | Bismarck Mountains (Territory of N.G.) | 1965b | Clark, 1971 |
| Mare (Loyalty Islands) | 1931c | Ť | Däniker, 1931 | Chesterfield Islands | 1957b | Cohic, 1959 |
| Misool (West Irian) | 1971c | ÎI ÎI | Moldenke, 1971 | (New Caledonia) | 19970 | come, 1959 |
| New Britain (Territory of N.G.) | 1971c | îî | Moldenke, 1971 | Louisiade Archipelago (Territory of Papua) | 1971c | Moldenke, 1971 |
| New Caledonia | 1861a | I | Guillaumin, 1933; Däniker, 1929; Heckel, 1911; Moldenke, 1971 | Solomon Islands | 1969c | Whitmore, 1966, 1969; Moldenke, 1971, Fosberg, 1940 |
| New Guinea, Territory of | 1971c | 11 | Moldenke, 1971 | | | |
| Ovalau (Fiji Islands) | 1958c | 1 | Parham, 1958; Moldenke, 1971 | | | |
| Tanna (New Hebrides) | 1934b | I | Aubert de la Rue, 1937 | | | |
| Taveuni (Fiji Islands) | 1921b | I | Parham, 1958; Simmonds, 1928; Lever, 1931 | | | |
| Vanua Levu (Fiji Islands) | 1921b | I | Parham, 1958; Moldenke, 1971 | | | |
| *Viti Levu (Fiji Islands) | 1931b | I | Turbet, 1931; Parham, 1958; Moldenke, 1971 | | | * |
| Yule Island (Territory of Papua) | 1971c | п | Moldenke, 1971 | | | |

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| | | | Micronesia | | | |
|---|----------------|------------------------|-----------------------------------|--|----------------|--|
| | ent | Absent | | | | |
| Location | Date | Condition of growth | Source(s) | Location | Date | Source(s) |
| Bikajli (Marshall Islands) | 1971c | m | Moldenke, 1971 | Arno Atoll (Marshall Islands) | 1950b | Hatheway, 1953; Anderson, 1951 |
| Guam (Marianas Islands) Moen (Caroline Islands) | 1970c 1971c | II II | Stone, 1970 Modenke, 1971 | Bikini Atoll (Marshall Islands) | 1953c | St. John and Mason, 1953; Taylor, 1950 |
| Ponape (Caroline Islands) | 1936b | Ĩ | Glassman, 1952; Moldenke, 1971 | Eniwetok (Marshall Islands) | 1960c | St. John, 1960 |
| Tarawa (Gilbert Islands) Truk (Caroline Islands) | 1951b 1971c | | Catala, 1957 Moldenke, 1971 | Fais (Caroline Islands) Gaferut (Caroline | 1965b 1954b | Fosberg and Evans, 1969 Niering, 1961 |
| Udot (Caroline Islands) | 1971c | п | Moldenke, 1971 | Islands) Hall Island (Caroline Islands) | 1959c | Stone, 1959 |
| | | | | Jaluit Atoll (Marshall Islands) | 1958b | Blumestock, 1961; Fosberg and Sachet, 1962 |
| | | | | Kapingamarangi (Carolin Islands) | 1954b | Niering, 1956 |
| | | | | Kayangel Atoll (Caroline Islands) | 1952b | Gressitt, 1953 |
| | | | | Namonuito (Caroline Islands) | 1959c | Stone, 1959 |
| | | | | Northern Marshalls Pagan Island | 1952b 1958c | Fosberg, 1955 Fosberg, 1958 |
| | | | | (Marianas Islands) | | |
| | | | | Palau (Caroline Islands) Pingelap Atoll (Caroline Islands) | 1930b 1948c | Kanehira, 1931 St. John, 1948 |
| | | | | Puluwat Atoll (Caroline Islands) | 1954b | Niering, 1961 |
| | | | | Romonum Island (Caroline Islands) | 1965b | Stone, 1967 |
| | | | | Saipan (Marianas Islands) | 1930b | Kanehira, 1931 |
| | - | - | | Satawal Island (Caroline Islands) | 1965b | Fosberg, 1969 |
| | | - | Consideration of some lasts | Tabiteuea (Gilbert Islands) | 1948b | Luomala, 1953 |
| | - | - | all and statements | Tinian (Marianas Islands) | 1930Ь | Kanehira, 1931 |
| | | 1.4.2 | | Wake Island Yap (Caroline Islands) | 1963Ь 1930Ь | Fosberg and Sachet, 1969; Fosberg, 1959 Kanehira, 1931 |

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| Polynesia | | | | | | |
|--|----------------|---------------------|---|---|----------------|--|
| | Present | | | | Absent | 1 |
| Location | Date | Condition of growth | Source(s) | Location | Date | Source(s) |
| *Bora Bora (Society Islands) | 1965d | I | Thaman, 1965* | 'Alofi (Wallis and Futuna Islands) | 1969b | St. John and Smith, 1971* |
| Canton Island (Phoenix Islands) | 1973b | III | Fosberg, 1973 | Atafu (Tokelau Islands) Austral Islands | 1937c 1971c | Macgregor, 1937 Moldenke, 1971 |
| *'Eua (Tonga Islands) | 1917c | I | Wylie, 1967; Yuncker, 1959; Thaman, 1969* | Baker Island (Phoenix Islands) | 1924b | Christophersen, 1927 |
| *Ha'apai (Tonga Islands) | 1917c | I | Wylie, 1967; Thaman, 1971* | Caroline Atoll (Line Islands) | 1965b | Clapp and Sibley, 1971a |
| *Hawaii (Hawaiian Islands) | 1871b | I | Hillebrand, 1888; Moldenke, 1971; Thaman, 1967* | Christmas Island (Line Islands) | 1962b | Chock and Hamilton, 1962; Christophersen, 1927 |
| Hull Island (Phoenix Islands) | 1973b | I | Fosberg, 1973 | Easter Island | 1971c | Moldenke, 1971; Guillaumin, Camus, |
| Kahoolawe (Hawaiian Islands) | 1913b | I | Forbes, 1913b | Ellice Islands | 1971c | Tardieu-Blot, 1936 Moldenke, 1971 |
| Kauai (Hawaiian Islads) | 1871b | I | Hillebrand, 1888 | Fakaofo (Tokelau Islands) | 1937c | Macgregor, 1937 |
| Koromiri (Cook Islands) | 1969b | I | Fosberg, 1972 | Fanning Ísland (Line Islands) | 1924b | Christophersen, 1927 |
| Lanai (Hawaiian Islands) | 1871b | I | Hillebrand, 1888 | | | |
| Makatea (Tuamotu Archiepelago) | 1932b | п | Wilder, 1934; Moldenke, 1971 | Flint Island (Line Islands) | 1937c | Fosberg and St. John. 1937 |
| Mangareva (Gambier Archipelago) | 1971c | п | Moldenke, 1971 | French Frigate Shoals (Hawaiian Islands) | 1967b | Amerson, 1971; |
| *Manono (Western Samoa) Maui (Hawaiian Islands) | 1969d 1871b | I | Thaman, 1969* Hillebrand, 1888; | | | Lamoureux, 1961; Christophersen and |
| , | | | Moldenke, 1971 | Funafuti (Ellice Islands) | 1898b | Caum, 1931 Maiden, 1904 |
| Midway (Hawaiian Islands) | 1954b | ш | Neff and DuMont, 1955; Moldenke, 1971 | Futuna (Wallis and Futuna Islands) | 1969b | St. John and Smith, 1971 |
| *Molokai (Hawaiian Islands) | 1871b | I | Hillebrand, 1888; Moldenke, 1971; Thaman, 1967 | Henderson Island (Tuamotu Archieplago) | 1957b | St. John and Philipson, 1962 |
| Molokini (Hawaiian | 1913b | I | Forbes, 1913b; | Howland Island (Phoenix Islands) | 1924b | Christophersen, 1927 |
| Islands) | | | Moldenke, 1971 | Jarvis Island | 1924b | Christophersen, 1927 |
| *Moorea (Society Islands) Motutapu (Cook Islands) | 1965d 1969b | I | Thaman, 1965, 1972* Fosberg, 1972 | (Line Islands) Johnston Island (Line Islands) | 1946b | Fosberg, 1949b |

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Polynesia: Continued

| | | | Polynesia | | | |
|----------------------------|--|-----------------------|--|-------------------------------------|-------|--|
| | it | Absent | | | | |
| Location | Date | Condition of growth | Source(s) | Location | Date | Source(s) |
| *Niue | 1971c | п | Moldenke, 1971; Thaman, 1973 | Kure Atoll (Hawaiian Islands) | 1968b | Woodward, 1972; Lamoureux, 1961 |
| *Oahu (Hawaiian Islands) | 1858a | I | Hillebrand, 1888; Birindelli, 1969; Moldenke, 1971; | Laysan Island (Hawaiian Islands) | 1961b | Lamoureux, 1963; Christophersen and Caum, 1931 |
| 0 (C 1 II 1) | 10/01 | | Thaman 1967, 1972 | Lisianky Island | 1924b | Christophersen and |
| Oneroa (Cook Islands) | 1969b | I | Fosberg, 1972 | Hawaiian Islands) | 10201 | Caum, 1931 |
| Pitcairn Island | 1928b | I | Brown, 1935; Moldenke, 1971 | Manu'a Islands (American Samoa) | 1939b | Yuncker, 1945 |
| *Raiatea (Society Islands) | 1965d | I | Thaman, 1965* | Maria Atoll | 1934b | Fosberg and St. John, |
| Rangiroa (Tuamotu | 1963b | III | Sachet, 1969 | (Austral Islands) | 0.000 | 1952 |
| Archiepelago) | | 10000 | | Marquesas Islands | 1971c | Moldenke, 1971 |
| Rarotonga (Cook Islands) | 1929b | 1 | Wilder, 1931; | Necker (Hawaiian | 1924b | Christophersen and |
| | 11050000000 | | Moldenke, 1971 | Islands) | | Caum, 1931 |
| *Savai'i (Western Samoa) | 1969d | I | Thaman, 1969* | Nihoa (Hawaiian | 1924b | Christophersen and |
| Taakoka (Cook Islands) | 1969b | 1 | Fosberg, 1972 | Islands) | | Caum, 1931 |
| *Tahiti (Society Islands) | 1843a | I | Setchell, 1926a; Thaman, 1965, 1972* | Niihau (Hawaiian Islands) | 1931b | Forbes, 1913a |
| *Tongatapu (Tonga Islands) | 1917c | 1 | Wylie, 1967; Yuncker, 1959; Thaman, 1968, | Nukunono (Tokelau Islands) | 1937c | Macgregor, 1937 |
| | | | 1969, 1973* | Oeno Atoll (Tuamotu Archipelago) | 1960c | Philipson and St. John, 1960 |
| *Tutu'ila (American Samoa) | 1969d | I | Thaman, 1969, 1973* | Palmyra Atoll | 1924b | Christophersen, 1927 |
| *'Upolu (Western Samoa) | 1898b | Î | Christophersen, 1935; | (Line Islands) | 19240 | Christophersen, 1927 |
| opola (Western Samoa) | 10,00 | ÷ . | Lloyd and Aiken, | Rapa (Austral Islands) | 1926b | Riley, 1926 |
| | | | 1934; Thaman, 1969* | Raroia Atoll | 1954b | Doty, 1954 |
| *Vava'u (Tongan Islands) | 1917c | I | Wylie, 1967; | (Tuamotu | 17540 | 200, 1994 |
| futu a (Tongan Islands) | 10110 | | Thaman, 1971* | Archiepelago) | | |
| | | | | Rose Atoll | 1954c | Sachet, 1954 |
| | | | 20 | (American Samoa) | | |
| | | | | Uvea (Wallis and | 1969b | St. John and Smith, |
| | - | and The second in | | Futuna Islands) | 1 | 1971 |
| | 1 | CONTRACTOR N | | Vostok Island | 1965b | Clapp and Sibley, |
| | 1 | | | (Line Islands) | 1 | 19716 |
| | - | and the second second | the second s | Washington Island | 1924b | Christophersen, 1927 |
| | and the second s | | and have a superior | (Line Islands) | | A DATE OF THE OWNER OF THE OWNER |

| Other Pacific Locations | | | | | | | |
|--------------------------------|-------|------------------------|---|---------------------------------|-------|--|--|
| Present | | | | Absent | | | |
| Location | Date | Condition of growth | Source(s) | Location | Date | Source(s) | |
| New South Wales (Australia) | 1870c | I | Bentham, 1870; Diels, 1929 | Clipperton Island (France) | 1958b | Sachet, 1962a and b | |
| Norfolk Island (Australia) | 1902b | I | Maiden, 1903 | Galapagos Islands (Chile) | 1971c | Wiggens and Porter, 1971; Stewart, 1911 | |
| *North Island (New Zealand) | 1913b | I | Cockayne, 1928; Cheeseman, 1925; Thaman, 1971* | Lord Howe Island (Australia) | 1897b | Maiden, 1898 | |
| Queensland (Australia) | 1870c | I | Bentham, 1870; Woolls, 1884; Bailey, 1900; Diels, 1929 | | | | |