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MYNDUS CRUDUS (HOMOPTERA: CIXIIDAE), A VECTOR OF LETHAL YELLOWING OF PALMS [1]

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ABSTRACT

Myndus crudus Van Duzee has been implicated as a vector of lethal yellowing (LY) disease of palms by field evidence and transmission experiments. LY has been reported from countries of the Caribbean, Florida, Texas, and parts of Africa. M. crudus is known from most of the countries affected by LY in the Americas but is not known from Africa. The life cycle of M. crudus is typical of known cixiids, with nymphal development and adult activity on different hosts. Management of LY through insecticidal control or utilization of natural enemies of M. crudus does not appear promising. Since grasses serve as hosts of the nymphs, the relationships between various species of grasses and M. crudus are being investigated with the objective of developing a management tool to be integrated with the use of LY-resistant palms and possibly other integrated pest managment techniques.

INTRODUCTION

Myndus crudus Van Duzee is a cixiid planthopper known from many localities of the American tropics and subtropics. It is of interest to economic entomologists because of its role in the disease cycle of lethal yellowing (LY) of palms (Fig. 1), a fast-spreading, highly destructive disease which affects coconut and other palm species. Research on lethal yellowing was reviewed by McCoy et al. (1983).

Fig. 1. A coconut planting in Florida devastated by lethal yellowing disease.

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At least 30 species of palms are susceptible to LY (Parthasarathy 1974, McCoy and Gwin 1977, Howard et al. 1979, Thomas & Norris 1980). Two of the susceptible species are important crop trees, viz., the coconut palm, Cocos nucifera L., and the date palm, Phoenix dactylifera L. The coconut palm is one of 20 crop plants that dominate the world's food supply (Mangelsdorf 1966, Vietmeyer 1986). The date palm is an indispensable food source in the Middle East and an important crop in arid regions elsewhere. Both of these species of palms provide products that are important for domestic consumption as well as for export. Various species of palms are important as ornamental plants, and at least 15 of these are susceptible to LY.

Electron micrography of tissue samples from palms with LY symptoms has consistently revealed the presence of mycoplasmalike organisms (MLO) in sieve tubes (Beakbane et al. 1972, Heinze et al. 1972a, Plavsic-Banjac et al. 1972, Thomas 1979, Thomas & Norris 1981). In one experiment (Howard et al. 1983), MLO's were observed in tissue samples from palms with LY symptoms, but not in symptomless palms of the same species and age growing under similar conditions.

Mycoplasmas and MLO's are sensitive to tetracycline antibiotics, but not to penicillin. The fact that oxytetracycline, but not penicillin, remisses LY symptoms is evidence that the disease is caused by MLO's (McCoy 1972, 1973, 1974a, 1974b, 1974c, 1975, McCoy & Gwin 1977, Hunt et al. 1974, Steiner 1976).

The geographical distribution of LY has recently been reviewed (Howard 1983). The disease has been reported in the following localities in the Americas: Cuba, Hispaniola (Haiti and the Dominican Republic), Jamaica, Cayman Islands, Florida, New Providence (Bahamas), Yucatan Penninsula (Mexico) and the Rio Grande Valley of Texas. The disease has apparently been present in countries of the Caribbean for more than 100 years. A disease believed to be identical to LY has been known in West Africa since the early decades of the present century, and was recently reported in Tanzania.

EVIDENCE THAT M. CRUDUS SPREADS LY

On the basis of the pattern of spread of a coconut disease in Cuba presumed to have been LY, Johnston (1912) hypothesized that the disease was spread by flying insects. Additional observations (Bruner & Boucle 1943, Carter & Suah 1964, Johnson and Eden-Green 1978, McCoy 1976, Nutman & Roberts 1955) and evidence from field experiments (Heinze et al. 1972b, Howard & McCoy 1980) supported this hypothesis. By the early 1940's it was suspected that LY was caused by a virus and probably transmitted by members of the Homoptera (Bruner & Boucle 1943). M. crudus was suspected as a possible vector as early as 1958 (Farr 1985) but other homopterans as well as insect species outside of this order were investigated as possible vectors during the 1960's and 1970's. The discovery of the association of MLO's with LY in 1972 concentrated the search on species of the suborder Auchenorrhyncha of the order Homoptera, since most known vectors of MLO-associated plant diseases belong to this taxonomic group (D'Arcy & Nault 1982). Based on surveys of auchenorrhynchous insects associated with coconut palms in Jamaica (Schuiling 1976) and Florida (Woodiel 1976), M. crudus was the only insect of this suborder found consistently on coconut palms in both areas (Woodiel et al. 1975). Further evidence was obtained in Florida, where M. crudus was collected on all but the rarest LY-susceptible palm species (Howard & Mead 1980); the geographical distribution of LY coincided with relatively high populations of M. crudus (Howard 1980); and insecticidal suppression of M. crudus populations reduced the apparent rate of spread of LY (Howard & McCoy 1980)

In light of the above evidence, a transmission experiment was conducted at the Fort Lauderdale Research and Education Centre in which thousands of M. crudus captured in LY-affected areas were introduced into a large cage containing palms of several species. One coconut palm and a Manila palm, Veitchia merrillii (Becc.) H.E.Moore, developed symptoms of LY after 15 months in this cage, and MLO's were observed in sieve tubes in tissue samples collected from these palms. The results of this pilot experiment (Author, unpublished) encouraged us to design a replicated transmission experiment to test M. crudus as a vector. A coconut palm and 1 or 2 Manila palms were planted in each of 10 large cages (Fig. 2). Six of the cages also contained a Thurston palm, Pritchardia thurstonii F. Muel. & Drude. All palms were obtained from LY-free areas. Five cages into which M. crudus were introduced (treatment cages) alternated with 5 cages used as controls. Each treatment cage received about 850 M. crudus per month from LY-affected areas. This number of planthoppers per unit time is probably similar to the numbers that visit palms outdoors in LY-affected areas. To increase the chances of transmission, an attempt was made to duplicate conditions under which LY had been observed to spread in nature. Grasses were planted in the cages, and a screen that would permit maximum light penetration without allowing passage of M. crudus was chosen for the cage walls, since LY researchers since the 1940's (Bruner & Boucle 1943) had observed that shaded palms tended to escape LY infection. It was anticipated that the experiment would be conducted over a period of many months because the incubation period of LY may last up to 15 months (Dabek 1975, Romney 1972). The cages and maintenance procedures were designed to reduce the chances of contamination by insects larger than M. crudus (Howard & Thomas 1980) and the experimental design, with treatments alternating with controls, virtually precluded the possibility of contamination being limited to the treatment cages.

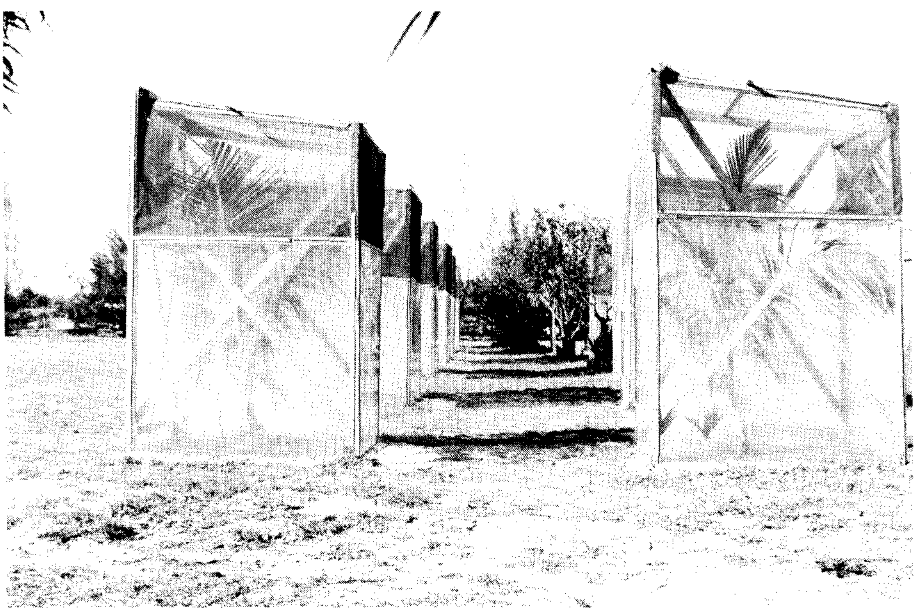

Fig. 2. Lethal yellowing transmission experiment, Fort Lauderdale, Florida, 1978.

The first symptoms in a palm appeared 7 months into the experiment and the experiment was terminated after 34 months, at which time the coconut palms had grown too large for the cages. Palms with symptoms of LY were removed at late stages in the disease and diagnoses were confirmed by electron microscopic examination of tissue sections for the presence of MLO's. At least 1 palm in every treatment cage contracted LY. Three of 5 coconut palms, 5 of 7 Manila palms, and 2 of 3 Thurston palms in the treatment cages contracted LY. Diagnoses of symptomatic palms were confirmed in all cases by the presence of MLO's in sieve tubes. Healthy palms, except for Thurston palms saved for another experiment, were also removed from cages and sections made of bud tissue. MLO's were not present in the samples from symptomless palms. Throughout the experiment the cages were inspected frequently and insects other than M. crudus which contaminated cages were collected and identified. Most were small gnats (Diptera). Phytophagous insects consisted of species that were discounted as potential vectors because their biology and life histories would preclude such a role, and/or they occurred only in controls or in both control and treatment cages.

These results provided strong evidence for M. crudus as a vector of LY, served as evidence that the diseases of these 3 palm species are caused by the same pathogen and, because symptomatic and symptomless palms were examined for MLO's, strengthened the theory that MLO's are associated with the disease.

Transmission experiments with M. crudus undertaken independently of us are to be encouraged, since positive results would further strengthen the evidence for M. crudus as the vector of LY. Negative or otherwise inconclusive results neither add nor detract from the theory. For example, Tsai & Thomas (1981) reported that out of a large number of palms exposed to M. crudus in transmission experiments, 15 showed LY symptoms, but "mycoplasmas" were observed in tissue samples from only 2 of the palms. These results are inconclusive. The diagnoses of 13 cases were based on symptoms alone. LY symptoms in young palms, such as those used in the reported experiment, consist of necroses of leaves and death of the meristematic region, i.e., do not clearly distinguish LY from various cultural problems and other maladies of young palms. The 2 palms for which an association with MLO's was shown were not continuously caged (Tsai 1980), so that feeding by unidentified insects other than M. crudus cannot be ruled out. One suspects that the decision to publish this material under the title, "Transmission of lethal yellowing mycoplasma by Myndus crudus" was a hasty one.

M. crudus has been the subject of a number of transmission experiments, most of which were conscientious efforts by highly knowledgeable scientists, but which yielded negative results (Dabek & Waters 1980, Eden-Green 1978, 1979, Eden-Green & Schuiling 1978, Schuiling & Johnson 1973, Tsai 1975, 1977). Our positive results may be attributed to one or more of the following conditions: the insects were captured from palm leaf surfaces by placing the mouth of a bottle over them (aspirators were used in some previous experiments and this may have injured them); insects were captured throughout the year, rather than during a limited period; higher numbers of the susected vector were used, thus increasing the chances of transmission; and insects were captured from palms in all stages of the disease to increase the chances that they had fed on highly infective material. Grasses were planted in the cages to serve as alternate hosts of the insect and thus possibly increase their longevity, however, in a later transmission experiment described below grasses were not planted in the cages, but LY transmission occurred.

The next step in elucidating the transmission of LY was to attempt to determine whether M. crudus transmitted the pathogen to young palms. Insect cages as large as could be practically maintained were used in the experiment described above so as to accomodate the use of large palms, because several researchers had reported that the taller palms in a planting tended to be the first to contract LY, and young palms were reported to be rarely affected by the disease (Bruner & Boucle 1943, Carter 1966, Carter & Suah 1964, Nutman & Roberts 1955). This had long been considered to be an impediment to studying LY transmission and testing palms for resistance to LY. Because young Thurston palms proved to be susceptible in our previous experiment, an experiment involving young palms of 8 different species was conducted. The results were that 8 young palms of 5 different species exposed to M. crudus in screen cages contracted LY. MLO's were observed in sieve tubes in bud tissue samples from all of these palms. The youngest of these was a Chinese windmill palm, Trachycarpus fortunei (W.H. Hooker) H. Wendl., which was 14 months old and about 30 cm. tall when LY symptoms became visible. A coconut palm aged 15 months and a Fiji fan palm, Pritchardia pacifica Seem. & Wendl., aged 19 months were among the remaining palms that contracted

LY in this experiment (Howard et al. 1984c) There were far fewer contaminant insects in this experiment, thus strengthening further the evidence for M. crudus as the vector.

In summary, the predominance of M. crudus on palms in LY-affected areas, its apparently broad host range within the palm family, its geographical distribution in relation to that of LY, its taxonomic affinities to known vectors of MLO-associated disease, and the reduction in the apparent rate of spread of LY where M.crudus populations were suppresssed by insecticides provided field evidence implicating M. crudus as a suspected vector of LY. A total of 20 unequivocal LY transmissions have taken place inside cages into which we introduced M. crudus captured in LY-affected areas. Our work has generated no evidence that any species other than M. crudus transmits LY, although at least 30 species of auchenorrhynchous insects feed on coconut palm in Jamaica (Eskafi 1982).

TAXONOMY AND DISTRIBUTION

The genus Myndus Stål is in the family Cixiidae. One of the largest fulgoroid families, the Cixiidae are distributed from the Tropics to the Temperate Zone. In the few cixiid species for which biological data are available, the immatures develop in or near the root zone of their host plants. Adults feed on the exposed parts of the same or different plants (Kramer 1983, Richards & Davies 1977). Kramer (1983) recognized 172 species in the continental United States; there has not been a recent world review, to our knowledge.

The adults of M. crudus (Fig. 3) are about 4.2 to 5.2 mm long, the female tending to be slightly longer than the male . The ground color is stramineus to light brown. Live females are often darker and have a more robust appearance than the males. The abdomens of live males tend to be greenish. The forewings of both sexes are hyaline with light brown veins (Kramer 1979).

The nymphs (Fig. 4) are white with light gray tergites. They produce minute waxy filaments which are actually coatings of their excretions (Pope 1985). This adaptation apparently facilitates life in a confined nymphal habitat.

M. crudus was described by Van Duzee (1907) from adults collected at Hope Bay and Troja, Jamaica. Paramyndus cocois was described by Fennah (1945) from specimens collected from coconut leaves, sugarcane, and "Guatemala grass" at St. Augustine, Trinidad. Caldwell (1946) considered species of the Western Hemisphere previously referred to as Myndus as belonging to the genus Haplaxius. He referred M. crudis (sic) and P. cocois as well as 22 other species to the genus Haplaxius, and described a new species, H. pallidus, from specimens collected in Miami in 1934. Kramer (1979) syonymized H. crudis (=crudus), H. pallidus and P. cocois with M. crudus.

M. crudus is distributed from the subtropical portions of the Eastern United States (southern Florida and southern Texas), through Mexico and Central America into northern South America, and is present on the Caribbean Islands of Cuba, Cayman Islands, Jamaica, and Trinidad (Kramer 1979, Howard 1983). Presumably, the species is of Central or South American origin and invaded Cuba and the western Caribbean Islands from Yucatan, and Trinidad from northern South America.

THE DISTRIBUTION OF MYNDUS CRUDUS IN RELATION TO THE DISTRIBUTION OF LY

The range of M. crudus greatly exceeds the present range of LY. The insect has been reported in every locality affected by LY in the Americas with the exception of New Providence Island (Bahamas) and the island of Hispaniola.

The insect was collected in a survey for potential LY vectors in Jamaica as early as the 1950's (Farr 1985) and in a similar survey there in the 1970's (Schuil-

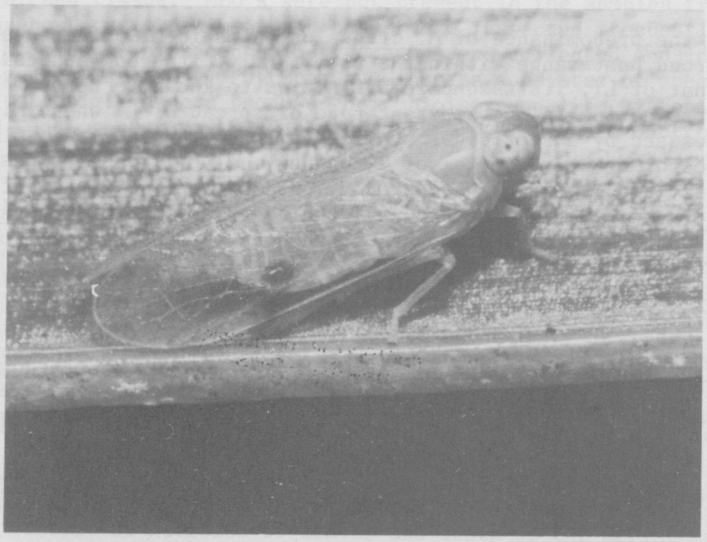

Fig. 3. Myndus crudus adult. Note parasitic mite on right wing.

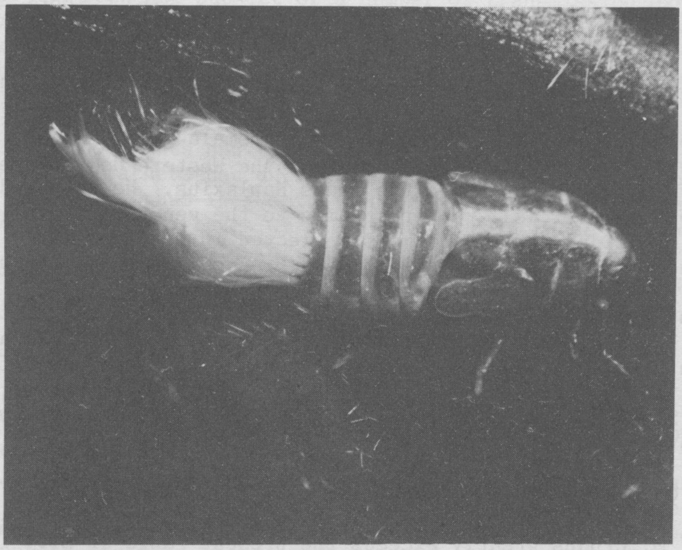

Fig. 4. Nymph of Myndus crudus.

ing 1976). LY is present throughout Jamaica and *M. crudus* is generally distributed on the island.

M. crudus has been collected from various plants in Cuba (Myers 1926, Osborn 1926, Kramer 1979). LY has apparently been generally distributed throughout Cuba and the Isle of Youth for more than 100 years (De La Torre 1906, Harries & Been 1978, Johnston 1912, Mijailova 1967).

LY has also apparently been present in the Cayman Islands since the 1800's and was observed there at epidemic levels by M. Schuiling in 1970 (Howard 1983). *M. crudus* was first reported there by Fennah (1971).

In Florida during the 1970's LY was epidemic in palms in the urban areas along the southeast coast and on certain islands of the Florida Keys. Although coconut palms and other susceptible species were present in several urban areas north of Jupiter Inlet and on the southwest coast, few cases of LY were seen in these areas. Sampling revealed that *M. crudus* populations were about 40 times higher in the LY-affected than in the relatively LY-free areas to the north and on the southwest coast (Howard 1980).

LY was found to be affecting date palms in the Rio Grande Valley of Texas in 1980 (McCoy *et al.* 1980). A survey for potential vectors revealed that *M. crudus* as well as 27 other species of Auchenorrhyncha were associated with Canary Island date palm, *Phoenix canariensis* Hort. *ex* Chab., in this region (Meyerdirk & Hart 1982).

Kramer (1979) reported *M. crudus* from various localities in Mexico. LY was reported for the first time in Mexico in the vicinity of Cancún in 1982 (McCoy *et al.* 1982), and *M. crudus* was subsequently collected from coconut foliage in that area (Howard *et al.* 1984). The disease has been epidemic near the Caribbean coast in Quintana Roo but has not been reported elsewhere in Mexico (Piña & Carrillo 1986). Villanueva *et al.* (1986) found *M. crudus* on various species of palms throughout southern Mexico, and found that populations were generally higher in urban than in rural areas. They suggested that watering of lawns may have made urban habitats more productive of these insects.

LY has apparently been present on the island of Hispaniola (Haiti and the Dominican Republic) since the 1800's, and was reported to occur as scattered cases in the 1960's and early 1970's (reviewed by Howard 1983). No cases of LY were found during a 10-day visit to the Dominican Republic in 1980. Intensive collecting from palms revealed the presence of an undescribed species of *Myndus* very similar externally to *M. crudus* (Howard *et al.* 1981). However, *M. crudus* has not been reported from Hispaniola.

LY may have been present on New Providence as early as the 1920's (Leach 1946) and was diagnosed there in 1974 by G.H. Gwin. R.M. Baranowski found no cases of LY on New Providence in 1980 (Howard 1983). The disease has apparently never been epidemic in the Bahamas, and only limited efforts have been made to determine whether *M. crudus* occurs on any of the Bahama Islands.

A disease of African oil palms in Colombia diagnosed as *marchitez sorpresiva* (sudden wilt) was reported to be transmitted by *Haplaxius pallidus* (=*M. crudus*) (Mena & Martinez 1977) and control of Guinea grass, *Panicum maximum* Jacq., a host of the nymphs, resulted in a reduction in the spread of the disease (Martinez-Lopez *et al.* 1976). It is not known whether there is a connection between this disease in Colombia and LY elsewhere. African oil palms have not shown susceptibility to LY (Howard *et al.* 1979).

THE LIFE HISTORY OF MYNDUS CRUDUS

Zenner de Polania and Lopez (1977) reported on the life history of *M. crudus* (as *M. pallidus*) in Colombia. The eggs of *M. crudus* are laid singly or in rows of 5 in the sheaths of the lower fronds of grasses. Upon eclosion, nymphs (Fig. 4) go to the soil and are said to feed on the roots of their host plants. They are often found in cavities of about 1 cm in diameter lined with their waxy excretions. Photographs and measurements of the 5 nymphal instars along with descriptive information were published by Zenner de Polania and Lopez (*op. cit.*), and detailed descriptions with excellent drawings of the egg and 5 instars were published by Wilson and Tsai (1982). Tsai and Kirsch (1978) reported an average of 61.3 days from egg eclosion to the last nymphal molt at 24° C and 41.5 days at 30°C. Nymphs kept at 15°C did not develop into adults.

Newly emerged adults (Fig. 3) remain a few hours at the bases of the grasses after which they fly to palms. Copulation occurs on palms and the females fly to grasses to oviposit (Zenner de Polania & Lopez 1977). Adults live up to 50 days on palms (Tsai & Kirsch 1978). The sex ratio has been reported as 1♀:1♂ (Tsai & Kirsch 1978) and 1.7♀:1♂ (Reinert 1980). Females are reported to live longer than males (Zenner de Polania & Lopez 1977), and this may bias the sex ratio.

HOST PLANTS

M. crudus is a phloem feeder (Fisher & Tsai 1978, Waters 1976) restricted mostly or entirely to monocotyledenous plants. In Colombia, nymphs of *M. crudus* (as *H. pallidus*) were collected from the roots of 8 species of grasses and 1 species of sedge (Mena & Martinez-Lopez 1977, Zenner de Polania & Lopez 1977). Similar observations were reported in Mexico (Villanueva *et al.* 1986) and Florida (Tsai & Kirsch 1978).

Eden-Green (1978) found St. Augustine grass to be a highly favorable host of the nymphs of *M. crudus*. Reinert (1980) reported that higher numbers of adults were collected in sweep net samples from St. Augustine grass than from Bahia grass or Bermuda grass. *M. crudus* populations were found to be much higher in the southeastern coastal area of Florida than elsewhere in southern Florida. Possibly this is due to the relatively high incidence of St. Augustine grass as a lawn grass in the affected area (Howard 1980). Four species of grasses, 3 of which are known to be hosts of *M. crudus*, and 6 species of dicotyledenous plants which are apparently not hosts of *M. crudus* were found to be consistently present in localities affected by LY in Florida (Howard *et al.* 1984d)

M. crudus has been collected from 26 species of palms in Florida (Howard & Mead 1980). Certain palm species and varieties are more attractive to *M. crudus* adults than others. 'Golden Malayan Dwarf' coconut palms are more attractive than 'Green Malayan Dwarf' or 'Jamaica Tall' cultivars (Tsai & Kirsch 1978). Young coconut palms are more attractive than young date palms, but no difference in numbers of *M. crudus* visiting mature coconut and Canary Island date palms has been detected (Howard 1981a). Field observations suggest that certain palm species, *e.g.*, coconut, *Pritchardia* spp. and *Washingtonia* spp. are more attractive to *M. crudus* than, *e.g.*, the yellow cane palm, *Chrysalidocarpus lutescens* Wendl., but these apparent differences have not been confirmed experimentally (Author, unpublished observations).

SEASONAL AND DIURNAL ACTIVITY

M. crudus flies actively all year in southern Florida (Woodiel & Tsai 1978). Reinert (1980) collected adults in sweep net samples from grasses throughout the year, and found that nymphal populations varied little throughout the year on Bahia grass but during cooler months were greatly reduced on St. Augustine grass. In general, it is possible to find high numbers of *M. crudus* on palms at any time of the year in southern Florida.

Rotary nets were used to sample insects in a planting of cabbage palmetto, Sabal palmetto (Walt.) Lodd., near a large field of grasses, and in a nearby planting of coconut palms over a period of a year (Tsai & Mead 1982). Statistically significant differences were found in the numbers of certain species, including M. crudus, in samples taken at different heights and time periods at the 2 sites, but this information sheds no light on the nature of these species.

Of several colors tested, blue attracted higher numbers of M. crudus, and attracted higher numbers by day than by night (Cherry & Howard 1984). The eyes of M. crudus adapt to light or darkness by movements of eye pigments (Howard 1981b).

NATURAL ENEMIES

Several species of spiders prey on M. crudus (Howard & Edwards 1984), as do red imported fire ants, Solenopsis invicta Buren, tree frogs and lizards (Author, unpublished). A fungus, Hirsutella citriformis Speare (determined by C.W. McCoy, University of Florida) occasionally attacks M. crudus in Florida. A similar or perhaps identical fungus has been observed on M. crudus in Trinidad (Fennah 1945) and in Mexico (Villanueva et al. 1986). Parasitic mites, Leptus sp. and Erythaeus sp. have been found on M. crudus in rare instances in Florida (Fig. 3)(determined by H.A. Denmark, Florida Department of Agriculture and Consumer Services) and similar mites have been found on M. crudus in Mexico (Villanueva et al. 1986). Villanueva et al. 1986 reported that M. crudus are occasionally parasitized by Hymenopterous parasites in Mexico. Since the natural enemies of M. crudus thus far identified occur in LY-affected areas, they are obviously not effective in preventing the spread of the disease.

POTENTIAL CONTROL OF LY THROUGH VECTOR MANAGEMENT

Two methods of management of LY are currently available: (1) periodic antibiotic treatment of palms, and (2) planting of palms that are resistant to LY. These methods are reviewed in detail by McCoy et al. 1983. Subsequent to this review, evidence has been obtained that a date palm cultivar, 'Halawy', may be resistant to LY (Howard et al. 1985).

Research is underway to discover methods of controlling LY through control of the vector. Insecticidal control was attempted experimentally. Reinert (1977) found several insecticides to be effective for short-term control of M. crudus. Two of these compounds were applied in biweekly sprayings of large blocks of palms for 15 months, resulting in only a slight reduction of M. crudus populations and in the spread of LY (Howard & McCoy 1980). Most insecticides currently available are not persistant, and thus treated palms are undoubtedly quickly reinfested. In any case, large scale chemical treatments to palms would be costly and pose an environmental hazard.

Progress has been made in developing ground cover management methods that reduce infestations of peach orchards by leafhopper vectors (McClure et al. 1982) and this approach is being investigated in relation to M. crudus. Tropical grass species are being tested in Florida and in Jamaica in a joint project to attempt to discover grass species or varieties that are tolerant of the shade of coconut canopies, unfavorable as hosts of M. crudus, and aggressive in competition with grasses that do serve as hosts. Included in this study are grasses that would be suitable as turf in tourist areas and forage grasses for use in coconut-cattle farming systems (Howard 1985). Legumes and other dicotyledenous ground covers are also being investigated for use in coconut plantings. Ground-cover management may prove to be only partially successful in reducing the spread of LY, particularly in areas where the diversity of grass species is high and where economic and other factors make weed control particularly difficult. However, it is envisioned that this method could be integrated with other methods, including the use of resistant palms, to successfully manage LY disease.

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