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Mealybug Wilt, Mealybugs, and Ants on Pineapple

Mealybug wilt (Fig. 1), with its associated mealybugs and ants, has been a continuing problem in Hawaiian pineapple production for more than 75 years. Mealybug wilt control and, therefore, ant and mealybug control in pineapple fields has become increasingly more critical for the profitable production of pineapple in the state of Hawaii. Registrations for mirex and heptachlor for ant control were canceled by the Environmental Protection Agency in 1977 and 1982, respectively; the industry is being permitted to utilize existing stocks until the supply is exhausted. While a new ant control product, Amdro, has been registered for noncrop use, control by applications to field borders has not been adequate or consistent. For the Hawaiian pineapple industry to remain economically viable and to control mealybugs and mealybug wilt, the ant control problem must be solved. This article summarizes the history and biology of the ant, mealybug, and mealybug wilt association and the current situation regarding control.

History of the Problem

Scientists at the Hawaiian Sugar Planters Association (HSPA) Experiment Station in 1910 were the first to describe pineapple wilt. At that time, the only research on pineapple was being done at HSPA under the general supervision of Harold Lyon. Starting in the early 1920s, the Association of Hawaiian Pineapple Canners started their own experiment station, initially as part of the University of Hawaii and later (1931) as a independent research organization, which eventually became the Pineapple Research Institute of Hawaii (PRI).

As early as 1912, Higgens (15) of the University of Hawaii noted that wilt was limited to only a few fields. By 1920, entire fields were being devastated by wilt (17). In 1925, A. Horner, Jr., from Hawaiian Canneries on Kauai, was the first to point out the association between wilt and both mealybugs and ants and the first to suggest a means of controlling the ants. By 1930, some companies seriously considered relocating their pineapple plantations in areas outside Hawaii. It was generally observed at that time that wilt started at edges of fields, around weedy rock piles, and near grassed waterways and ditches. "Edge wilt" was the term used to describe the disease, clearly indicating that it occurred as a result of movement of some factor into the field.

Although Illingworth (17) was the first person to suggest that mealybugs were directly implicated in pineapple wilt, he also suggested that ants were a beneficial factor. This latter pronouncement was unfortunate because it put the emphasis on the control of mealybugs while ignoring the control of ants.

Walter Carter, who became head of the Entomology Department at PRI in 1930, supplied the definitive evidence for the relationship between mealybug feeding on pineapple plants and wilt (5). In subsequent publications (6,8), he described the initial invisible step, which was the cessation of root growth followed by wilt symptoms on the leaves. Carter spent two decades attempting to determine the nature of mealybug wilt, and he terminated his work with a reappraisal (7), which is discussed later in the text. In addition, he spent an equal amount of time developing successful control measures.

History of Control

Physical. The first control measure suggested by Horner from Kauai in 1925 was an ant fence around fields (Fig. 2). The fence consisted of a 1 × 12 in. (2.54 × 30.48 cm) board sunk 6 in. (15.24 cm) edgeways into the soil. This board was sprayed at appropriate time intervals with one part Carbolineum and two parts gasoline. Horner described this mixture as having a very strong tarry smell (creosote?). Later these fences were sprayed with heavy oil residue. Carter indicated that when these fences were scrupulously maintained, movement of ants into the field was significantly reduced (*personal communication* between Carter and W. Sanford, 1967).

The second method, developed by California Packing Corporation (CPC), later to become Del Monte Corporation, consisted of planting border or "guard" beds (a bed being two adjacent rows of plants) that ran parallel to the periphery of the field (Fig. 2). This was done because it was discovered that ants, if given the choice, would move down instead of across the bed. Guard beds were still being used in some pineapple fields as late as the 1950s.

K. Ito (in PRI files, 1959) suggested that since weed seeds constitute the main

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Fig. 1. Pineapple mealybug wilt: (A) In the field. (B) Close-up showing reddened leaves and wilted appearance. (C) Loss of root system of infected plant (left).

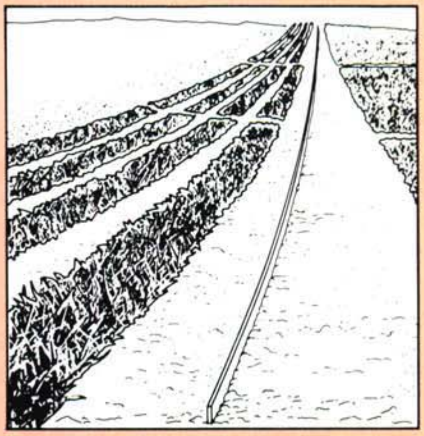

Fig. 2. Drawing of ant fence and border beds running perpendicular to field beds used to control ant movement into the field.

source of food for the fire ant (*Solenopsis geminata* (Fabricius)), which also attends mealybugs in pineapple fields, good weed control should keep down the population of this ant.

Finally, there was a suggestion by several authors that keeping edges of fields and rock piles within fields free from weeds helped to reduce the movement of ants into the fields.

Chemical. Starting in the late 1920s, direct control of mealybugs by spray applications of Volck oil was successful but expensive. Maxwell Johnson of CPC developed the concept of using oil emulsions, which permitted the use of less purified and cheaper oils. Unfortunately, this ran into patent infringements with the Volck oil manufacturers. W. Carter in 1935 developed the use of diesel oil emulsified with Wyoming bentonite, which proved to be cheaper and more effective. These diesel oil sprays were the primary basis for development of the boom spray rig and were used for the control of mealybug wilt from the mid-1930s until shortly after World War II, when dichlorodiphenyltrichloroethane (DDT) became available for the direct control of ants.

Following the use of DDT for ant control, parathion, a highly effective but dangerous organic phosphorus insecticide, became available for the control of mealybugs. Later, malathion, a much less dangerous organic phosphorus insecticide, became the basis of mealybug control. Finally, malathion was displaced by another organic phosphorus compound, diazinon, which combined relatively low toxicity to humans and high toxicity to mealybugs.

W. Carter (*personal communication* between Carter and W. Sanford, 1967) was of the opinion that frequent applications of insecticides to control mealybugs were not necessary. The objective should be to keep mealybug populations low, since the incidence of mealybug wilt is directly proportional to mealybug numbers. Carter said that "the emphasis should be complete elimination of ants because without the ants, mealybug populations cannot build up in a field." Unfortunately, the chlorinated hydrocarbons such as DDT, benzene hexachloride, heptachlor, lindane, and chlordane that were previously used in pineapple fields to successfully control ants can no longer be used. Even mirex, which was a very successful ant bait, can no longer be used in Hawaiian pineapple fields despite the small amounts required for control and its low mammalian toxicity.

Biological. Several attempts have been made to introduce natural enemies of mealybugs as a means of control, but none has had any great success without ant control. D. T. Fullaway, an entomologist at the Board of Agriculture and Forestry (currently the Hawaii State Department of Agriculture [DOA]), introduced natural enemies from Mexico and Panama in the early 1920s, but none became established. Later, in the 1930s, W. Carter, K. Sakimura, and K. Schmidt

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from PRI and entomologists from the DOA conducted expeditions to tropical areas in the world where cultivated and wild pineapples were found to locate possible natural enemies. Although some showed promise in the laboratory, only a small percentage were successfully established in pineapple fields. The introduction of modern insecticides after World War II brought an end to this program, and, according to Carter, "the parallel development of insecticide treatments worked against the predators' effectiveness," presumably because the insecticides killed the predators.

The major predators of a given species of ant are other species of ants. Usually within a given field, one species of ant will dominate and drive away any other species. For example, two more recent ant introductions into Hawaii, the Argentine ant (*Iridomyrmex humilis* (Mayr) and the long-legged ant (*Anoplolepis longipes* Jerdon), have successfully displaced the big-headed ant (*Pheidole megacephala* (F.)) where environmental conditions are favorable (14). In contrast, Carter (*personal communication* between Carter and W. Sanford, 1967) stated that the sugar ant (*Plagiolepis alluaudi* Forel) is "tolerated by *Pheidole* and this might be *Pheidole*'s undoing," the idea being that *Plagiolepis* might be able to move into and destroy *Pheidole* colonies. However, *Plagiolepis* has been in Hawaii since 1912 and there is no evidence that any competitive displacement of *Pheidole* by *Plagiolepis* has occurred. Since each of these species of ants nurses and transports mealybugs within pineapple fields, there is no particular advantage to the displacement of one by the other.

There are no reports in the PRI literature regarding control of ants in pineapple by parasites and diseases. Natural enemies of other ant species are known, but no work in this area has been attempted with the ant species found in Hawaiian pineapple fields.

Breeding and roguing. Hybrids have been developed at the PRI that have had some degree of resistance to mealybug wilt, especially when compared with most Smooth Cayenne clones (8). The most resistant hybrids showed mild symptoms of wilt after a single infestation of mealybugs and severe wilt when infestations were repeated. Collins and Carter (10) demonstrated that some clones of Smooth Cayenne were resistant to mealybug wilt and that this resistance could be transmitted to progeny through seed production. Breeding and selection for mealybug wilt resistance was not pursued because it offered only partial resistance and because it would have further complicated an already complex breeding program.

Roguing of positive source plants was given consideration but was never implemented because scientists at PRI disagreed about whether plants that recovered from wilt could be recognized by symptoms. M. Linford, a plant pathologist at PRI, felt that terminal or tip dieback symptoms, which occurred chiefly during the fruit development period, probably were manifestations of recovery from mealybug wilt. K. Ito, an associate entomologist at PRI, presented experimental evidence showing that: 1) terminal mottle (Fig. 3) was a leaf dieback symptom of chronically diseased pineapple plants and that such symptoms did not appear on healthy plants, 2) plants that had recovered from mealybug wilt and all their vegetative progenies were chronically diseased and were positive sources of mealybug wilt, 3) the so-called resistant Cayenne clones were all chronically diseased and positive sources of mealybug wilt, and 4) all such positive source plants were infected with the mealybug "virus." W. Carter disagreed with Linford's theory that terminal mottling was a chronic symptom of mealybug wilt and with Ito's evidence that terminal mottling was a specific symptom on plants infected with mealybug "virus." The three scientists were probably not as far apart as it would appear. Linford and Ito were probably correct that terminal mottle was a symptom of both wilt-recovered plants and positive source plants. Carter was probably equally correct that such a symptom was an indication of low vigor regardless of its cause, i.e., mealybug wilt, nematode damage, drought, nutrient deficiencies, etc., making it highly impractical to rogue out positive source plants on the basis of leaf symptoms. Only under optimum growth conditions could one expect to be able to rogue out all positive source plants from a population of pineapple plants.

Current Status of the Problem

Ants. Ants are a problem in pineapple fields only because of their association with mealybugs (Fig. 4). It is the ants' caretaking behavior that allows the mealybug species *Dysmicoccus brevipes* (Cockerell) and *D. neobrevipes* Beardsley to prosper (6,22,26). Two hypotheses attempt to explain why mealybugs flourish as a result of ant tending. The first is that ants protect mealybugs from any potential parasites and predators (22). The big-headed ant will build mud encasements around the mealybugs (Fig. 4) that afford added protection from predation, parasitization, desiccation, and adverse weather conditions. The second hypothesis is that benefits to the mealybugs result from the ants' removal of honeydew. Honeydew-feeding prevents the accumulation of honeydew on the plant and mealybugs and impedes sooty mold buildup, both of which may be detrimental to mealybugs (22). We are of the opinion that both hypotheses are valid.

The ants do not restrict their activities to the caretaking of mealybugs already on plants but also carry mealybugs to other plants as they extend their territory (24). Beardsley et al (3) found that the percentage of mealybug-infested pineapple plants was highly correlated with the number of ants caught in pitfall traps. Beardsley's work confirmed earlier work and observations that the incidence of mealybug wilt was highest on field edges, reflecting the greater abundance of mealybugs and ants in these areas. Wilt spread into the field from the edges in a contagious manner, with the number of diseased plants increasing at a logarithmic rate over time.

Three species of ants are important in Hawaiian pineapple fields. The big-headed ant (Fig. 5A and B) is the dominant species in fields below 700 m. The Argentine ant (Fig. 5C) may be dominant at elevations above 600 m. In very dry, lowland areas, the fire ant (Fig. 5D) may dominate.

Much of the work in pineapple in Hawaii has been concentrated on the big-headed ant (BHA), since this species is found on more hectares of the crop than other mealybug-tending ants. The adults of BHA occur as males and three castes of females: minor workers, major workers (soldiers), and queens. The greatest proportion of a colony is minor workers. They perform most of the work of the colony, which includes gallery excavation, searching for and recruitment to food, and grooming, feeding, and moving of the immatures and queens. It is generally the older minor workers that perform duties outside the nest, including the caretaking of mealybugs, while younger workers specialize in in-nest duties. The soldier caste specializes in colony defense and prey dismemberment. The queens and males, which are the reproductives of the colony, are produced by the colony during winter and early spring. BHA typically has many queens per colony, each capable of ovipositing an average of 100–300 viable eggs per month on random days. This is a major obstacle to control efforts, since the survival of a single queen ensures the survival of the colony.

The winged queens disperse from the colony between September and March on a mating flight. Upon alighting, the queen must be accepted by workers, since she cannot establish a colony by herself (9,24). Chang (9) found that a minimum of 10 newly eclosed minor workers and one queen are needed for colony survival; colonies with a queen and 10 older minor workers do not prosper. In Chang's study (9), all colonies with a solitary queen, or one queen with 10 majors, or one queen with 10 larvae died within 7 weeks. Minor workers are essential, since this is the only caste that will feed and groom immatures and other castes including queens. Therefore, BHA colonies cannot become established in ant-free pineapple fields unless the fields are bordered by an ant-infested area. A common method of colony dispersal is for workers and queens to leave a nest and establish a nest nearby, often with galleries attached to the old nest. Ratoon pineapple fields may eventually contain a network of interconnected nests.

A viral etiology of mealybug wilt is supported by the discovery of double-stranded RNAs in infected pineapple plants that led to isolation and characterization of a virus proposed to be named pineapple wilt virus

The diet of the omnivorous BHA includes arthropods (16), honeydew, seeds, and fruit. Honeydew excreted by pineapple mealybugs is an important BHA food source. The principal components of honeydew are amino acids and carbohydrates (13). Gray (13) demonstrated that the number of amino acids in honeydew increases with the period of feeding. Also, honeydew contains at least five additional amino acids not found in pineapple leaves, upon which the mealybugs feed.

Sanders (25) studied the acceptance, distribution, and storage of three food types (oils, carbohydrates, and proteins) in an attempt to find a suitable attractant for use in an ant bait. Current commercial baits use a soybean oil attractant based on studies with red imported fire ant (*Solenopsis invicta* Buren). BHA accepted all three food types, but their distribution and storage in the colony varied. Oils with higher unsaturated fatty acid content were preferred above other oils. All oils were consumed by minor workers and regurgitated among themselves, then stored within this caste for several hours before being fed to larvae. It is felt that workers must predigest oils before regurgitating to the larvae (25). The

Fig. 3. Terminal mottle symptom showing reddening of older leaves, leaf tip burning, and normal-appearing young leaves.

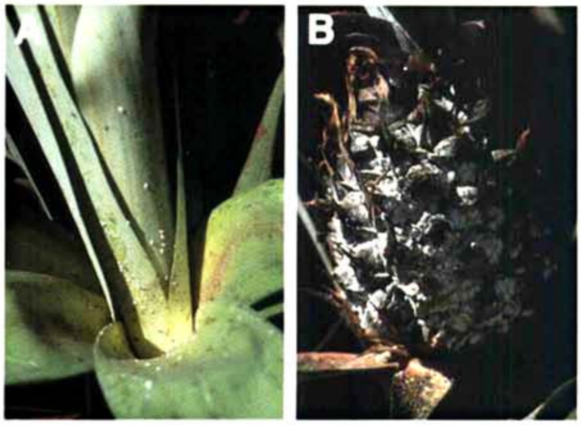

Fig. 4. Mealybug-infested plant showing mealybugs and ants nesting on (A) base of leaves and (B) developing fruit.

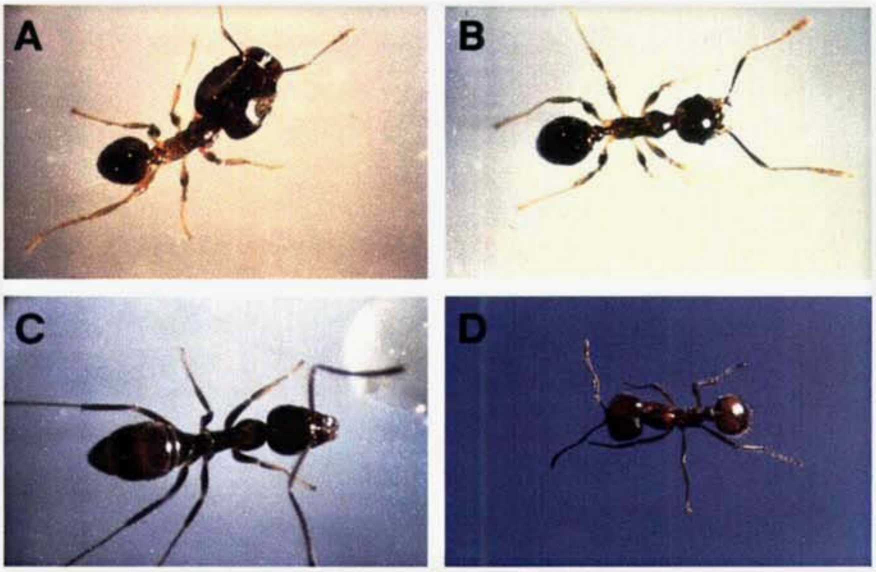

Fig. 5. Three ant species of major importance in Hawaii for care and movement of mealybugs responsible for pineapple mealybug wilt: (A) Big-headed ant (*Pheidole megacephala*), soldier; (B) big-headed ant, worker; (C) Argentine ant (*Iridomyrmex humilis*), worker; and (D) fire ant (*Solenopsis geminata*), worker.

queens were fed oils by minor workers after the majority of larvae were fed. Therefore, if an oil attractant is used, the toxicant must be slow-acting and effective at low concentrations. Carbohydrates were fed to all castes by minor workers. However, acceptance of honey bait by workers ceased after 2 days. This was not observed with glucose bait. Solid protein was readily accepted and distributed throughout the colony when its moisture content reached an acceptable level. Minor workers did not feed on solid protein but did cut up and distribute the solid particles to the larvae and possibly the queens. Minor workers consumed the liquid portion of the protein, since both larvae and queens received regurgitated liquids containing marked liquid protein from minor workers. Carbohydrate and protein attractants may work well with faster-acting toxicants, since both are fed directly to larvae and queens. However, carbohydrates have the disadvantage of being attractive to some beneficial insects.

Mealybugs. Several different species of mealybugs have been associated with mealybug wilt of pineapple in Hawaii and in other areas where pineapple is grown. Because the taxonomy of these mealybugs was not well understood until relatively recently, some confusion exists in the published literature dealing with these pests.

Early references (e.g., 4,5,30) to the mealybugs associated with wilt generally refer to *Pseudococcus brevipes* (Cockerell) as the pineapple mealybug. However, Ito (18) pointed out that there were two distinct types of pineapple mealybugs associated with wilt disease in Hawaii, which he referred to as the pink form and the gray form. He showed that these two forms, in addition to their color difference, possessed other distinctive biological characteristics, such as mode of reproduction (bisexual in the gray form and obligately parthenogenetic in the pink form) and the gray form's ability to produce green spots on pineapple foliage (Fig. 6). Ferris (11) removed the pineapple mealybug from the genus *Pseudococcus* and placed it in the new genus *Dysmicoccus* as *D. brevipes* (Fig. 7A). Beardsley (1) demonstrated that there were valid morphological differences between Ito's pink and gray forms and recognized the gray form as a distinct new species, *D. neobrevipes* (Fig. 7B). In Hawaii, *D. neobrevipes* (gray species) occurs primarily on the crown of the pineapple plant, including the developing fruit. *D. brevipes* (pink species) is confined largely to the lower portions of the pineapple plant, near ground level or below.

Both the pink and the gray species of pineapple mealybugs originated in tropical America and probably were brought to Hawaii on planting material sometime before effective plant quarantine regulations were established. Both species can infest many other host plants besides pineapple. The gray species commonly occurs on sisal, banana, and several other hosts. The pink species is often found on perennial grasses, including sugarcane, and has been recorded from more than 50 species of plants.

Both pink and gray pineapple mealybugs are now widely distributed throughout the pineapple-growing areas of the world. The gray species was known only from Hawaii at the time it was described, although there is good evidence it was more widely distributed but unrecognized. It is now known to occur in Fiji, Micronesia, Philippines, Taiwan, Malaysia, Mexico, and Jamaica.

In some other pineapple-growing areas of the world, the pineapple mealybug situation is further complicated by the existence of a third form, which is very similar to *D. brevipes*. This form, which has not yet been distinguished taxonom-

Fig. 6. Green spotting symptom on pineapple leaf indicating feeding of the gray form of mealybug.

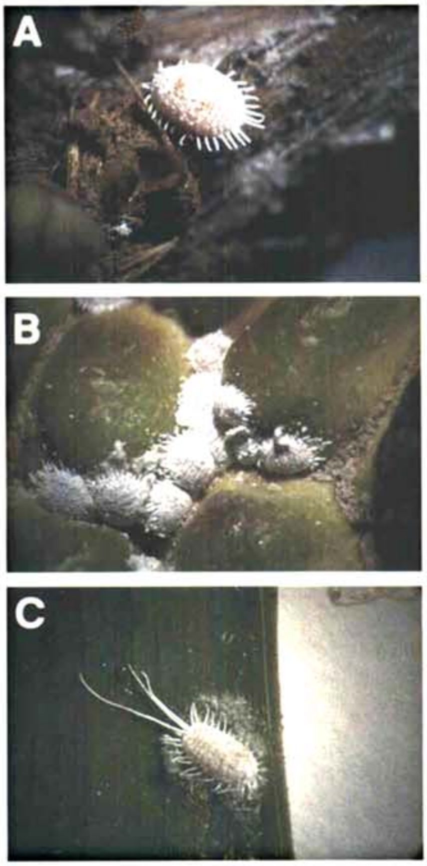

Fig. 7. Three species of mealybug found in Hawaii that are capable of spreading mealybug wilt: (A) Pink mealybug (*Dysmicoccus brevipes*), (B) gray mealybug (*D. neobrevipes*), and (C) long-tailed mealybug (*Pseudococcus longispinus*).

ically from *D. brevipes*, differs from the pink pineapple mealybug of Hawaii in being bisexual and producing green spotting on pineapple leaves. Also, it apparently infests the crown of the pineapple plant. In these respects it is similar to *D. neobrevipes*, the gray species, but it is quite distinct morphologically, the females being virtually indistinguishable from those of *D. brevipes*. This mealybug, which we have referred to as the bisexual *D. brevipes*, is, on the basis of its biology, a distinct species. It is known to occur in West Africa (Ivory Coast), Madagascar, Dominican Republic, and Martinique. Other mealybug species that are related to the pink and the gray species found in Hawaii are known to occur on pineapple and other hosts in tropical America (2).

Ito (18) studied the life history of the pink and gray pineapple mealybugs in Hawaii, and Carter also has summarized this information. The life histories of the two species are quite similar in most respects, except that the pink species is always parthenogenetic, males being unknown, while the gray species is bisexual and mating must occur in order for young to be produced. Neither species lays eggs, the young emerging from the mother as fully developed first-stage larvae, called crawlers. The crawler stage is the primary dispersal stage in all mealybug species. Crawlers have flattened bodies and long hairs that are believed to aid in their dispersal by wind. Crawlers move about actively for a short period, probably no more than a day, during which they may be blown off the plant on which they were born and deposited on other plants at distances up to several hundred yards. This is probably the principal way in which mealybug infestations spread; the role of ants in moving mealybugs from infested plants to adjacent uninfested plants has been postulated but not well documented.

One other mealybug species occasionally infests pineapples in Hawaii and can cause wilt. This is the long-tailed mealybug (*Pseudococcus longispinus* (Targioni-Tozzetti)) (Fig. 7C), which gets its name from the long waxy filaments extending, taillike, from the posterior end of the insect. Unlike the pink and the gray species, the long-tailed mealybug apparently can survive fairly well without being tended by ants, and because of this, spotty infestations occasionally develop even in fields where ants have been controlled. The long-tailed mealybug has a number of natural enemies, however, and once these have located an infestation, they will generally eliminate the population within a few weeks.

Predators and parasites of mealybugs are numerous on infested pineapple plants in Hawaii in the absence of ants. Those that were purposely introduced to control mealybugs and are known to have become established are *Anagyrus ananatis* Gahan, *Euryrhopalus propinquus* Kerrich, *Hambeltonia pseudococcina* Compere, *Lopodiplosis pseudococci* Felt, *Nephus bilucenarius* Mulsant, and *Scymnus uncinatus* Sicard (20). Of these, the three encytid parasitoids (first, second, and third) and the cecidomyiid predator (fourth) are the most effective. In addition to these species, there are several more natural enemies of mealybugs, either accidentally introduced or introduced to combat other pest species. Several ladybird species in the genera *Scymnus* and *Nephus* have been reported feeding on mealybugs in Hawaii. Laboratory work in South Africa indicated that one ladybird beetle (*Exochomus concavus*) could consume 155 mealybugs throughout it's life span (23). In Hawaii, the natural enemies that have become established do control mealybug colonies but not in the presence of ants. Observations by the authors on numerous occasions have demonstrated that when ants are eliminated from mealybug-infested pineapple plants, natural enemies will move in and clean up the mealybugs.

Wilt. For more than 50 years the wilt disease of pineapple has been associated with mealybug feeding (Fig. 4) and was thought to be caused by the secretion of toxins from mealybugs as they fed on the plants. This concept was reinforced by the relationship of mealybug numbers to the incidence of wilt and by the excellent control that could be obtained by reducing the number of mealybugs on plants. This "toxin" hypothesis espoused by Carter (5–8) was the genesis for the name mealybug wilt of pineapple, which is still used to describe the characteristic symptoms of the disease. Carter described the aboveground symptoms of mealybug wilt as follows:

1. The preliminary reddening of the leaves (Fig. 1).

2. A definite color change from red to pink and with an inward reflexing of the leaf margins.

3. Loss of rigidity of affected leaves (wilted appearance).

4. A recovery state in which the center of the plant grows out with fresh, apparently normal leaves. This stage was called "terminal wilt, normal leaves."

Carter (7) later modified the toxin hypothesis because of the observation that healthy plants do not become diseased when they are infested by mealybugs from certain negative source plants such as seedling pineapple plants never previously infested with mealybugs, sisal, yucca, and grasses. Disease will occur, however, if mealybugs are placed on healthy plants after feeding on certain positive source plants such as wilt-tolerant pineapple clones or clones not previously infested by mealybugs. Thus, the new hypothesis included the concept of a transmissible factor that Carter called a latent virus infection, which he proposed would interact with the mealybug to produce the toxin.

The following summary of the data from Carter (5), Ito (18), and Singh and Sastry (27) seems to support the concept that the wilt disease is caused by a virus transmitted by mealybugs:

1. Mealybugs must first feed on a plant that is designated as a positive source, since mealybugs fed on artificial media for more than 4 hours cannot transmit the disease when transferred to healthy plants.

2. The mealybugs must move to another plant, which is normally accomplished with the help of ants.

3. The amount of wilt within a field is very dependent on the average number of mealybugs per plant and the average length of time these mealybugs feed on each plant.

4. Aboveground symptoms appear faster after mealybugs feed on young plants (i.e., symptoms peaked at 75 days after feeding on 5-month old-plants vs. about 120 days on 9-month-old plants).

5. Recovered plants do not become symptomatic when reinfested with mealybugs from positive source plants (cross-protection via a mild strain?).

Recent results (14) further support the notion that the disease has a viral etiology. The discovery of double-stranded RNAs (dsRNAs) in infected pineapple plants led to the isolation and characterization of a virus proposed to be named pineapple wilt virus. The virus can consistently be recovered from plants with mealybug wilt symptoms. The extremely long, flexuous shape of the virus particles, the molecular weight of the largest dsRNA (about 4.4×10^6 daltons), the presence of multiple smaller dsRNAs, and the molecular weight of its coat protein (23×10^3 daltons) are consistent with the properties of subgroup II closteroviruses (12). Interestingly, this is the only virus group that contains a known example of a flexuous rod-shaped virus transmitted by mealybugs.

Recently, a specific antiserum has been prepared and an enzyme-linked immunosorbent assay developed (U. B. Gunasinghe and T. L. German, *unpublished*) that will be used to study disease incidence, search for virus sources outside the crop, and study the relationship between the virus and mealybugs. Because it has not been possible to mechanically transmit the virus for unequivocal proof that it is the etiologic agent of the disease, results of epidemiological studies will be used.

In the search for control strategies, screening of chemicals to control ants should be continued, ant ecology and behavior should be studied in detail, and ant predators and parasites should be investigated

Potential Controls

Currently, ants are controlled by use of the remaining supplies of mirex and heptachlor. As discussed above, mealybugs are generally controlled by controlling ants. Since the supplies of mirex and heptachlor are essentially exhausted, new control strategies must be found.

A review of the information available on ants, mealybugs, and mealybug wilt suggests that the following possibilities for control should be considered:

1. Obtain an in-field use label for Amdro, since only a noncrop-use registration currently exists. Use of Amdro on field borders only has not resulted in adequate or consistent ant control. A petition for a tolerance and in-field use label was submitted in 1981, but apparently data gaps or problems with interpretation of data still exist. A petition for an experimental label was submitted in May 1986 but no action has been taken. Work should continue to determine what data gaps and/or problems with interpretation of existing data are delaying registration of Amdro. Studies should be initiated to determine the reasons for variability in control (unpublished work by A. Hara with Amdro on ants on ornamental *Protea* indicates variability in attractiveness of baits).

2. Screening of chemicals to control ants should be continued. Bait formulations such as Logic, Affirm, Amdro, and Prodrone are more desirable than sprays because of their low hazard to the applicator, minimal impact on nontarget organisms and the environment, and selectivity to ants. Any formulation showing promise should be tested, however. To date, in two major efficacy trials only Logic has shown considerable promise (J. W. Beardsley and N. J. Reimer, *unpublished*).

3. Detailed studies on ant ecology and behavior should be conducted. Little is known about the in-migration rate of big-headed ants into fields, survival after tillage, food source in fallow fields, foraging behavior and foraging distance, recruitment to food, seasonality, and population trends with plant phenology, among others. Information in these areas may reveal a point of vulnerability in the biology of the ants that can be manipulated for better control.

4. Studies should continue on the role of a virus in disease development, to identify alternate hosts of the virus and explore the removal of these from areas adjacent to pineapple as a means of control. Virus-free vegetative "seed" material should be identified and studied for use as disease-free propagative material for planting.

5. Biological control of mealybugs should be reconsidered. It probably never was given a fair trial because of the introduction of diesel oil sprays in 1935 that not only destroyed the mealybugs but also reduced mealybug predator populations. Biological control of mealybugs will not be effective without control or suppression of ant populations. A program integrating the management of ant populations with biological control of mealybugs should be initiated.

6. Ant predators and parasites should be studied. Researchers have discovered a number of natural enemies of fire ants (19,28,29). It appears that little has been done in this area with big-headed ants.

7. Physical barriers such as ant fences or rows of beds running parallel to the field periphery have been partially successful in the past and should be considered. Whether these particular barriers are used or not, they do illustrate that ant behavior can be modified by changing their physical environment.

8. Reconsideration of the use of mirex could serve as a stopgap control until more suitable chemicals and/or biological control methods are developed.

Literature Cited

1. Beardsley, J. W. 1959. On the taxonomy of pineapple mealybugs in Hawaii, with a description of a previously unnamed species (Homoptera: Pseudococcidae). Proc. Hawaii Entomol. Soc. 17:29-37.
2. Beardsley, J. W. 1965. Notes on the pineapple mealybug complex, with descriptions of two new species (Homoptera: Pseudococcidae). Proc. Hawaii Entomol. Soc. 19:55-68.
3. Beardsley, J. W., Su, T. H., McEwen, F. L., and Gerling, D. 1982. Field investigations on the interrelationships of the big-headed ant, the grey pineapple mealybug, and the pineapple mealybug wilt disease in Hawaii. Proc. Hawaii Entomol. Soc. 24(1):51-67.
4. Carter, W. 1932. Studies of populations of *Pseudococcus brevipes* (Ckl.) occurring on pineapple plants. Ecology 13:296-304.
5. Carter, W. 1933. The pineapple mealybug, *Pseudococcus brevipes* (Ckl.) and wilt of pineapples. Phytopathology 23:207-242.
6. Carter, W. 1935. Studies on the biological control of *Pseudococcus brevipes* (Ckl.) in Jamaica and Central America. J. Econ. Entomol. 28:1037-1041.
7. Carter, W. 1963. Mealybug wilt of pineapple; a reappraisal. Ann. N.Y. Acad. Sci. 105:741-764.
8. Carter, W., and Collins, J. L. 1947. Resistance to mealybug wilt of pineapple with special reference to a Cayenne-Queen hybrid. Phytopathology 37:332-348.
9. Chang, V. C. S. 1985. Colony revival, and notes on rearing and life history of the big-headed ant. Proc. Hawaii Entomol. Soc. 25:53-58.
10. Collins, J. L., and Carter, W. 1954. Wilt resistant mutations in the Cayenne variety of pineapple. Phytopathology 44:662-666.
11. Ferris, G. F. 1948. Atlas of Scale Insects of North America, Series 5, Pseudococcidae. Stanford University Press, Stanford, CA. 278 pp.
12. Francki, R. I. B., Milne, R. G., and Hatta, T. 1985. Atlas of Plant Viruses. Vol. 2. CRC Press, Boca Raton, FL. 284 pp.
13. Gray, R. A. 1952. Composition of honeydew excreted by pineapple mealybugs. Science 115:129-133.
14. Gunasinghe, U. B., and German, T. L. 1986. Association of virus particles with mealybug-wilt of pineapple. (Abstr.) Phytopathology 76:1073.
15. Higgens, J. E. 1912. The pineapple in Hawaii. Hawaii Stn. Press Bull. 36:1-34.
16. Illingworth, J. F. 1916. Economic aspects of our predacious ant, *Pheidole megacephala*. Proc. Hawaii Entomol. Soc. 3:349-368.
17. Illingworth, J. F. 1931. Preliminary report on evidence that mealybugs are an important factor in mealybug wilt. J. Econ. Entomol. 24:877-889.
18. Ito, K. 1938. Studies on the life history of the pineapple mealybug, *Pseudococcus brevipes* (Ckll.). J. Econ. Entomol. 31:291-298.
19. Jouvenaz, D. P. 1986. Diseases of fire ants: Problems and opportunities. Pages 327-338 in: Fire Ants and Leaf Cutting Ants: A Synthesis of the Current Knowledge. C. S. Lofgren and R. K. VanderMeer, eds. Westview Press, Boulder, CO. 428 pp.
20. Lai, P. Y., and Funasaki, G. Y. 1986. List of beneficial organisms purposely introduced for biological control in Hawaii: 1890–1986. Hawaii State Dep. Agric. Rep. 78 pp.
21. Muir, F. 1921. The sugarcane leafhopper and its parasites in Hawaii. Hawaii Plant. Rec. 25:108-123.
22. Nixon, G. E. J. 1951. The association of ants with aphids and coccids. Commonwealth Institute of Entomology, London. 36 pp.
23. Petty, G. J. 1985. H.15 The pineapple mealybug. Farming in South Africa. Republic of South Africa Government Printer, Pretoria. 8 pp.
24. Phillips, J. S. 1934. The biology and distribution of ants in Hawaiian pineapple fields. Univ. Hawaii Exp. Stn. Pineapple Prod. Coop. Assoc. Bull. 15:1-57.
25. Sanders, D. A. 1981. The acceptance and rate of distribution of food substances among different castes and larvae of the big-headed ant, *Pheidole megacephala* (F.). M.S. thesis. University of Hawaii, Honolulu. 61 pp.
26. Serrano, F. B. 1934. Pineapple mealybug-wilt in the Philippines. Philipp. J. Sci. 55:363-377.
27. Singh, S. J., and Sastry, K. S. M. 1974. Wilt of pineapple—a new virus disease in India. Indian Phytopathol. 27:298-303.
28. Wojcik, D. P. 1986. Observations on the biology and ecology of fire ants in Brazil. Pages 88-103 in: Fire Ants and Leaf Cutting Ants: A Synthesis of the Current Knowledge. C. S. Lofgren and R. K. VanderMeer, eds. Westview Press, Boulder, CO. 428 pp.
29. Wojcik, D. P. 1986. Status of the search for natural control agents in South America. Pages 29-37 in: Proc. Fire Ant Conf.
30. Zimmerman, E. C. 1948. Insects of Hawaii. Vol. 5. Homoptera: Sternorhyncha. University of Hawaii Press, Honolulu. 464 pp.