

A Review of the Association of Ants with Mealybug Wilt Disease of Pineapple

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Abstract. The literature concerning the association between ants and the mealybugs causing pineapple wilt disease is surveyed. A great deal of data on this subject has been published in the relatively obscure technical papers and reports of the defunct Pineapple Research Institute of Hawaii. This review article is an attempt to bring this information to a broader audience and examine it in the context of related research reported in mainstream publications to create a meaningful synthesis. Two species of mealybugs, *Dysmicoccus brevipes* (Cockerell) and *D. neobrevipes* Beardsley, are associated with wilt disease of pineapple under field conditions. A third species, *Pseudococcus longispinus* (Targioni-Tozzetti) induces wilt symptoms in laboratory experiments, but not under field conditions. The symptoms of wilt disease and the geographic distribution of the pineapple mealybug complex are described. The history of the discovery of the disease, the disease etiology, the association of mealybugs with wilt, and the mutualism between ants and mealybugs on pineapple are discussed in detail. At least 28 different species of ants tend mealybugs on pineapples. *Pheidole* and *Solenopsis* are the ant genera most commonly associated with pineapple mealybugs throughout the world. The ants and natural enemies associated with mealybugs on pineapple are reviewed as part of a discussion of the role of ants in promoting mealybug infestations. Finally, management techniques for wilt, including ant and mealybug control, are reviewed.

Introduction

Mealybug wilt disease (also called pineapple wilt or quick wilt) is the leading cause of economic loss in pineapple. Unless the disease is managed, it is not possible to grow pineapple commercially in Hawaii and most other parts of the world (Carter 1934, 1940; Hughes and Samita 1998; Illingworth 1931; Petty and Tustin 1993; Rohrbach and Apt 1986; Rohrbach *et al.* 1988; Singh and Sastry 1974). The disease is apparently caused by a closterovirus spread through mealybug feeding (Sether and Hu 2002a,b).

Three species of mealybugs are associated with mealybug wilt disease of pineapple, though the mealybugs can live on a variety of host plants (Carter 1933a, 1967). These mealybugs have a symbiotic relationship with ants (Phillips 1934, Su 1979).

This literature review is a critical look at the interdisciplinary effort to elucidate the nature of the relationship between pineapples, wilt disease, mealybugs, and ants.

What Is Mealybug Wilt Disease of Pineapple?

Mealybug wilt disease of pineapple is characterized by a loss of turgidity in the leaves. It was first described in Hawaii by Larson (1910). In the 1920s, entire pineapple fields were destroyed by mealybug wilt (Illingworth 1931). By 1930, mealybug wilt had put the Ha-

waiian pineapple industry in serious jeopardy (Carter 1940). Even today, the continued existence of the Hawaiian pineapple industry depends on adequate control of this disease.

Symptoms. Carter (1933a) recognized two types of mealybug wilt disease of pineapple: slow wilt and quick wilt. Quick wilt is now universally known as mealybug wilt (Carter 1967). Most descriptions of pineapple wilt in the scientific literature pertain to quick wilt. Unless otherwise stated, all references to wilt in this review refer to quick wilt. In slow wilt, the symptoms appear after mealybugs have been feeding on the plants for many months. Inner leaves turn brown and dry while outer leaves droop. The yellow-pink leaves associated with quick wilt do not occur in slow wilt (Carter 1933a). In both quick and slow wilt the plant may die, fail to produce fruit, or produced smaller than normal fruit if the plant does not recover. Hu and Sether (2002b) report a 35% reduction in the yield of plants with wilt disease; noting that the earlier the expression of symptoms the greater the impact on fruit yields.

Slow wilt is most likely the result of destruction of leaf tissue resulting from the feeding of large numbers of mealybugs. Recovery from slow wilt is rapid when control measures are taken (Carter 1967).

Quick wilt is observed approximately two months after a sudden period of feeding by a large number of mealybugs. The symptoms of quick wilt in plants up to six months old are: the inner leaves change color (varying from very light, dull green to pale yellow or pink) as rigidity is lost, then the tips of such leaves turn brown and dry up (Carter 1933a). Plants over 6 months old, with quick wilt, (i.e., mealybug wilt) have red leaves that turn pink. The leaf margins bend inwards, and affected leaves lose rigidity and droop. Finally the affected leaves dry up. If the plant recovers at all it is usually before the leaves dry. In some cases, however, apparently normal leaves grow out of the center of the plant after the leaves dry (Carter 1945a, 1967). While localized phytotoxic symptoms of mealybug feeding on pineapple leaves are sometimes associated with wilt, green spotting or striping is not considered a symptom of wilt (Carter 1933b, 1944).

Wilt was once thought to be caused by root damage from various soil organisms. Illingworth (1931) was of the opinion that in pineapples afflicted with wilt, the disease gradually spreads from the leaves to the roots, resulting in root collapse. By growing pineapple plants in water mist boxes, so that the roots could be observed, Carter (1948) determined that the first symptom of mealybug wilt is when the roots stop growing.

Taxonomy and geographical distribution. The literature on the pineapple mealybug complex is taxonomically confusing. Bartlett (1978) and Petty (1978, 1985) call the gray and pink species of pineapple mealybugs two forms of *D. brevipes*. Petty (1978) includes a photograph of *P. longispinus* with a caption describing it as *D. brevipes*. The literature is further complicated because *P. longispinus* was misidentified as *Pseudococcus adonidum* L. for a time. De Lotto (1965) pointed out the misidentification and resurrected the oldest available name, i.e., *P. longispinus* (Targioni-Tozzetti 1867).

Originally, all members of the pineapple mealybug complex were considered a single species named *Pseudococcus brevipes* (Cockerell) (Carter 1933a, Ito 1938), later changed to *Dysmicoccus brevipes* (Cockerell) (Ferris 1950). A pink form and gray form of *D. brevipes* were considered different strains. Beardsley (1959) established the pink form as *Dysmicoccus brevipes* (Cockerell) and the gray form as *Dysmicoccus neobrevipes* Beardsley.

Mealybug wilt of pineapple is only reported from areas of the world where members of the *Dysmicoccus brevipes* species complex occur. All members of the pineapple mealybug complex appear to be of neotropical origin. *Dysmicoccus brevipes* and *D. neobrevipes* are the most important pineapple pests in the world. *Dysmicoccus brevipes* has a greater global distribution than *D. neobrevipes*, occurring almost everywhere that pineapple is grown. The latter species is also widespread, though it is not found on pineapple in parts of Africa, Asia,

and Australia (Beardsley 1993a). Both species first appeared in Hawaii in 1905 (Beardsley 1993b). *D. neobrevipes* was discovered in Thailand in 1988 infesting monkeypod trees (*Albizia saman* (Jacq.) Merr.), but has not been reported on pineapple there (Beardsley 1993a). *D. brevipes* does occur on pineapple in Thailand (Jahn 1992a). Several additional species in the *D. brevipes* complex have been discovered in tropical America, but these species have not yet spread to other regions. Only two of these additional species, *Dysmicoccus mackenziei* Beardsley and *Dysmicoccus probrevipes* (Morrison), occur on pineapple (Beardsley 1965, 1993a).

The relationship of mealybugs to wilt disease. Ehrhorn (1915) first reported that mealybugs were major pests of pineapple. Illingworth (1931) provided the first experimental evidence that mealybug-feeding causes wilt disease symptoms in pineapple. Field studies by Carter (1932) supported this view. Carter (1932, 1942, 1949, 1962) found an association between mealybugs, particularly *D. neobrevipes* and *D. brevipes*, and wilt throughout the pineapple-growing regions of the world. Feeding by the long-tailed mealybug, *Pseudococcus longispinus* (Targioni-Tozzetti), induces wilt symptoms in the laboratory, but is never associated with mealybug wilt outbreaks in pineapple fields. In fact, large colonies of *P. longispinus* have been observed in fields without producing wilt (Carter 1966).

Not every mealybug-infested plant develops mealybug wilt (Carter 1951, Sether and Hu 2002a). Sether and Hu (2002b) found that wilt only develops in plants infected with a closterovirus, designated PMWaV-2, that are also exposed to mealybug feeding.

Mealybug biology. *Dysmicoccus brevipes* is often found below the ground and just above ground level on the roots and stems of pineapple plants. However, in the absence of *D. neobrevipes*, *D. brevipes* may occur on aerial parts of the plant (González-Hernández 1995). In Hawaii, *D. brevipes* reproduces parthenogenetically, and no males are produced in this species. A biparental form, possibly a sibling species of *D. brevipes*, occurs in Brazil, the Dominican Republic, Madagascar, Malaysia, and West Africa. Females of both forms are apparently indistinguishable (Beardsley 1965, 1993a).

Dysmicoccus neobrevipes is only found on the aerial portions of the plant (Beardsley 1960). These mealybugs feed on leaves, the external surface of fruit, and the inside of blossom cups (Jahn 1995). Males are produced in this species, and unmated females cannot reproduce (Beardsley 1960; Ito 1938).

Etiology of wilt disease. Carter's (1933a, 1939b) early experiments led him to the conclusion that mealybug wilt was a toxemia (i.e., the actual saliva of the mealybugs was toxic to the plant) based on these observations: 1. Wilt occurs only when large numbers of mealybugs are present. 2. There is a clear relationship between the number of mealybugs feeding, the length of time they feed, and the intensity of wilt that results. 3. Recovery from wilt by the pineapple plant is common after the mealybugs have been removed.

He also observed that mealybug toxicity is influenced by the kind and condition of the host plant from which the mealybugs are taken.

Carter and Schmidt (1935) conducted experiments to find the minimal number of mealybugs necessary to induce wilt in pineapple plants. They compared plots of pineapple having 0, 1, 5, 10, 20, and 40 mealybugs per plant. In plots having only 1 mealybug per plant, they occasionally saw wilt symptoms. This incidence of wilt, however, was not significantly different from that seen in control plots having no mealybugs. They thought that wilt had a long incubation period (i.e., greater than two months), and that the wilt seen in control plots and in plots with 1 mealybug per plant was actually acquired by the plants before the experiment. Accordingly, they concluded that a single mealybug was not capable of causing wilt. They reported that occasionally as few as 5 mealybugs per plant could produce typical cases of wilt.

Apparently, Carter and Schmidt (1935) did not consider an alternative explanation for

their results: that their control plots were actually contaminated with very small numbers of mealybugs. If mealybugs were present in control plots, then a single mealybug may have actually been sufficient to produce wilt. Since the mealybugs are prone to feed deep in the leaf axils, under sepals, and inside of blossom cups, it would have been very easy for field workers to have missed the presence of single mealybug crawlers (Jahn 1995). To find all the mealybugs on a pineapple plant requires dissection of the plant. Although Carter and Schmidt dissected wilted plants from the plots before the experiment, there is no indication that they dissected any wilted plants from their control plots following the experiment. Furthermore, crawlers of *D. neobrevipes* are transported by the wind (Carter 1967; Jahn and Beardsley 2000). In 1935, this was not known, and Carter and Schmidt probably did not consider wind-borne mealybugs as a possible source of contamination. In any case, Carter and Schmidt found that as the number of mealybugs per plant was increased, the incidence of wilt also increased. They concluded that only a certain percentage of the mealybugs were actually toxic. If a single mealybug could induce wilt, then transmission of a virus or mycoplasma-like organism (MLO) would explain their results equally well, i.e., only a certain percentage of the mealybugs carried virus or MLO. They did not consider this explanation.

Further studies by Carter (1937) demonstrated that single mealybugs could occasionally produce wilt in pineapples. Also, the increase in wilt was not directly proportional to the number of mealybugs. At times, small numbers of mealybugs would cause plants to wilt. There was usually a point beyond which increasing the number of mealybugs would have little or no effect on the increase in wilt. This type of relationship could be evidence of a viral disease, but Carter (1937) did not raise this possibility. At that time, however, viral diseases were poorly understood. The concentration of virus in plant sap was measured as early as 1929 (Holmes 1929). The composition of viruses, however, was not known until 1936 (Bawden *et al.* 1936). Virus particles were seen for the first time in 1939 (Kausche *et al.* 1939).

If mealybugs caused wilt, then they must have been injecting substances into pineapple plants when feeding. Carter (1945c) demonstrated that mealybugs deposited saliva when feeding on pineapple.

By transferring mealybugs from pineapple plant to pineapple plant, and keeping records of which plants mealybugs came from and which plants eventually showed symptoms of wilt, Carter (1951) determined that not all vegetatively produced Cayenne pineapple were positive sources of mealybug wilt. He explained this by postulating the existence of a "latent factor" which must be present in pineapple for mealybugs to develop toxic saliva (Carter 1952). The factor was "latent" because its presence in pineapple, in the absence of mealybug saliva, did not appear to produce wilt symptoms. Because the latent factor was found to be transmissible and to be retained in vegetatively reproduced plants, Carter (1952, 1962) suggested that the latent factor was a virus. Carter and Ito (1956) discovered that pineapple plants showing no symptoms of wilt disease could nevertheless serve as positive sources of mealybug wilt. Thus, Carter (1963, 1967) arrived at a rather complex explanation of mealybug wilt disease. He maintained that certain pineapple plants contain a type of virus that causes mealybugs to produce toxic saliva, which causes pineapple roots to collapse and thus develop the symptoms of mealybug wilt disease. In contrast, Ito (1959, 1962) concluded that mealybugs are not toxicogenic and that mealybug wilt disease of pineapple is a viral disease transmitted by mealybugs.

Flexuous rod-shaped virus particles in the family Closteroviridae, designated *Pineapple Mealybug Wilt-associated Virus* (PMWaV) have been isolated from symptomatic and asymptomatic pineapple plants (Borroto *et al.* 1998; Gunasinghe and German 1986, 1987, 1989; Hu *et al.* 1993, 1996, 1997; Maramorosch *et al.* 1984; Ullman *et al.* 1989; Wakman *et al.* 1995). Symptomatic plants, however, consistently have higher PMWaV infection rates

than symptomless plants of the same cultivar and from the same location (Hu et al. 1997). PMWaV has been detected in mealybugs collected from wilted pineapple plants, but not from mealybugs of the same species reared on squash (Hu et al. 1996). Because PMWaV were consistently associated with pineapple plants affected with mealybug wilt, these particles were proposed as a possible cause of the disease (Ullman et al. 1989; German et al. 1992; Hu et al. 1993). PMWaV can be eliminated from pineapple by a water bath heat treatment (Ullman et al. 1991). PMWaV can be acquired and transmitted by *D. brevipes* and *D. neobrevipes* (Sether and Hu 1997, Sether et al. 1998).

PMWaV is a complex of at least two different closteroviruses, PMWaV-1 and PMWaV-2 (Melzer et al. 2001) that are both transmitted by mealybugs (Sether and Hu 1998, 2000, 2002a; Sether et al. 1998). Both closteroviruses occur throughout the pineapple growing areas of the world (Sether et al. 2001). PMWaV-1 infections are correlated with growth reductions of the plant crop (Sether and Hu 1998) and yield reductions in the ratoon crop (Sether and Hu 2001). PMWaV-2 infection and mealybug feeding are necessary for the development of mealybug wilt disease (Hu and Sether 1999a,b; 2002a,b). All pineapple plants with wilt disease have PMWaV-2 infections, but not necessarily PMWaV-1 infections (Hu et al. 1997, Sether and Hu 2002a). Asymptomatic Smooth Cayenne have been found infected with either virus, both or neither (Sether et al 2001).

A pineapple badnavirus (PBV) has also been found (Wakman et al. 1995). Whether PBV has a role in mealybug wilt disease remains unknown.

Ants Associated with Mealybug Wilt Disease of Pineapple

In the 1920s, pineapple growers in Hawaii noticed that ants were common in the wilted areas of pineapple fields. They assumed that ants were causing wilt disease and took measures to destroy and prevent ant infestations. Based on observations, rather than experimentation, Illingworth (1926a,b) concluded that ants did not cause wilt disease. He recognized the importance of mealybugs as pineapple pests and that ants appeared to benefit mealybugs by deterring natural enemies, but thought that, overall, the predatory nature of ants made them beneficial to pineapple growers. Therefore, he did not recommend ant control. A series of experiments led him to change his mind. Illingworth (1931) demonstrated that ants themselves did not cause wilt disease, but that mealybugs did. He noted that without ants, the natural enemies already present in the field might keep mealybugs under control. In light of this, he suggested that poisoning ants might be an effective means of preventing mealybug wilt disease of pineapple. Since then, mealybug wilt disease has been controlled primarily through ant control. Experiments confirm that ant control reduces mealybug populations and prevents mealybug wilt disease (Beardsley et al. 1982; Carter 1933a, 1960; González-Hernández et al. 1999a,b; Jahn 1990).

While a number of ant species have been found in Hawaiian pineapple fields, the most pestiferous species in pineapple are *Pheidole megacephala* (Fabricius), *Solenopsis geminata* (Fabricius), and *Linepithema humile* (Mayr). *P. megacephala*, the big-headed ant, is the dominant ant species below 600 m elevation, where most Hawaiian pineapple fields are located (Fluker & Beardsley 1970, Reimer et al. 1990a). *P. megacephala* was already common on the Hawaiian island of Oahu in 1879 (Blackburn and Kirby 1880). The ants most commonly associated with pineapple mealybugs throughout the world are species of *Pheidole* and *Solenopsis* (Table 1).

The Role of Ants in Mealybug Wilt Disease of Pineapple

Phillips (1934) hypothesized that mealybugs were associated with ants in pineapple fields

because: 1) ants protected mealybugs from natural enemies; 2) ants protected mealybugs from adverse weather by building earthen shelters around them and moving them to protected places; 3) ants transported mealybugs from plant to plant between and within fields, thus facilitating mealybug dispersal; 4) ants stimulated increased feeding by mealybugs; and 5) ants removed honeydew from mealybugs, thereby preventing fungi from attacking mealybugs. Rohrbach *et al.* (1988) hypothesized that honeydew feeding by ants could benefit mealybugs by preventing the accumulation of honeydew on the mealybugs themselves. Presumably, immature mealybugs get stuck in honeydew and die if ants do not remove it.

Protection from natural enemies. Saying that ants “protect” mealybugs from natural enemies does not necessarily mean that ants are attacking the natural enemies to save honeydew as a food resource. Possibly, ants are consuming the natural enemies as food and mealybugs benefit by happenstance (Jahn and Beardsley 1994). There are numerous examples of ants deterring the predators and parasites of scales, mealybugs, and aphids (e.g., Van der Goot 1916; Way 1954, 1963; Wimp and Whitham 2001). For instance, in the absence of Argentine ants, *L. humile*, parasites suppress populations of lecaniine scale insects (Bartlett 1961). Ants also reduce parasitism of the cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Cudjoe *et al.* 1993). Larval coccinellids eliminate green scales (*Coccus viridis* (Green)) from coffee trees in Hawaii unless *P. megacephala* is present (Reimer *et al.* 1993). Green scales in Sri Lanka also cannot survive without ants (*Oecophylla smaragdina* Fabricius), but the ants apparently do not reduce parasite and predator attacks on the scales (Bess 1958).

A wide variety of natural enemies prey on pineapple mealybugs (Table 2). Ants protect mealybugs from their natural enemies (González-Hernández *et al.* 1999a,b). In laboratory experiments with coccinellids, *D. neobrevipes* did not thrive on pineapples, unless ants were present (Illingworth 1931). In the absence of natural enemies, laboratory populations of *D. neobrevipes* were not significantly different on pineapples with and without ants (Jahn and Beardsley 1996). In the field, *P. megacephala* had a positive association with *D. neobrevipes* and a negative association with the predators of mealybugs (Jahn and Beardsley 1998, 2000). Collectively, these experiments suggest that *P. megacephala* deters predators from attacking *D. neobrevipes*.

Distribution of mealybugs from plant to plant. Ants are known to transport homopterans. In Japan, for example, ants carry rice root aphids, *Anoecia fluviabdominalis* (Sasaki), from wild grasses to upland rice fields (Dale 1994). In an experiment to determine if mealybugs transmit wilt, Illingworth (1931) observed *P. megacephala* carrying mealybugs from one cage of pineapples to another. Carter (1933a) supposed that *P. megacephala* moved mealybugs from alternate hosts to pineapple, as well as among pineapple plants. Laboratory experiments suggest that *P. megacephala* do not move mealybugs from one pineapple fruit to another in significant numbers (Jahn and Beardsley 1996). Sticky trap collections in a Hawaiian pineapple fields demonstrate that first instar pineapple mealybugs are dispersed by the wind (Jahn and Beardsley 2000).

Controlling Mealybug Wilt in Pineapple

Physical and cultural control. The physical and cultural practices used to control mealybug wilt have been aimed at reducing the number of ants, rather than directly managing mealybugs. In the 1920s, the Hawaiian pineapple industry placed ant fences around fields. These fences were 1-foot-wide wooden boards sunk into the ground edgewise about 6 inches. The boards were sprayed regularly with oil. Another technique was to plant pineapple beds parallel to the border around the field, rather than at right angles to the border. This slowed the movement of ants and mealybugs into the field (Carter 1967). Illingworth (1931) sug-

gested removing old pineapple stumps and weed roots from the field and burning them, planting only pineapples without spotting, and destroying wilt-infected plants.

A common cultural practice in Hawaiian pineapple fields is to allow a field to lie fallow for 6 to 12 months after post-ratoon knockdown. This period is referred to as the intercycle. Shortly before replanting, the field is burned to remove pineapple trash. In some areas of Hawaii the burning of pineapple trash has been discontinued because the smoke disturbs residents.

Altering the pineapple: resistance and agronomic practices. The commercial variety of Cayenne pineapple grown by the Hawaiian pineapple industry is one of the most susceptible varieties to mealybug wilt (Carter and Collins 1947). Unfortunately, resistant hybrids are not desirable in other respects (Collins and Carter 1954), and the Pineapple Research Institute eventually halted research on resistance in favor of research on ant and mealybug control.

The severity of some pest problems can be modified by managing soil nutrients (Jahn *et al.* 2001). Carter (1945b) attempted to do this with wilt disease, but he was unable to find any relationship between plant nutrition and the susceptibility of pineapples to mealybug wilt.

Chemical control. Efforts to control mealybugs with insecticides in the 1920s were generally not successful. In the 1930s, wilt was managed by spraying oil emulsions. The advent of the boom spray increased the effectiveness of insecticide applications. After the Second World War, oil sprays were replaced with organophosphorous compounds: parathion, malathion, and diazinon. The safety precautions necessary for using parathion were too costly, and parathion was abandoned for mealybug control (Carter 1967).

Malathion or diazinon is still used for direct mealybug control in pineapple, when ant control does not result in a sufficient reduction in mealybug populations. The chemical control of mealybugs is not easy. Complete coverage of a pineapple plant with an insecticide is not possible. Mealybugs tend to be deep in leaf axils, under the sepals of blossoms, or inside of closed blossom cups where they are protected from insecticidal sprays (Jahn 1995). The thick, waxy coating on mealybugs makes insecticide penetration difficult. Even the use of systemic insecticides is frequently impractical for mealybug control. For example, pink sugarcane mealybugs cease feeding and withdraw their mouthparts just prior to oviposition. These non-feeding females continue to produce offspring beyond the time that the systemic insecticide remains effective (Beardsley 1962). Given these difficulties, Carter (1967) asserted that, to control mealybug wilt, it is essential to first control ants, especially *Pheidole*.

DDT was the first insecticide that made ant control in pineapple possible and it was used extensively. Immediately after planting, DDT was applied at 4 lbs. per acre. Then DDT was applied at 2 lbs. per acre on a monthly basis. Following knockdown, the field was burned and DDT was incorporated into the soil at 10 lbs. per acre (Carter 1967).

After DDT was banned, mirex and heptachlor were used to control ants in pineapple fields. Toxicity studies on rats showed that mirex is excreted in the milk and passes through the placental barrier (Gaines and Kimbrough 1970). Mirex was also reported to cause tumors in nontarget organisms and to have high environmental persistence (Alley 1973). Therefore, in 1977, the registration of mirex was canceled. For similar reasons, the Environmental Protection Agency (EPA) also canceled the registration for heptachlor. The Hawaiian pineapple industry was granted an exemption to the heptachlor ban. The exemption was retracted in 1982 when traces of heptachlor were detected in milk in Hawaii. The Hawaiian pineapple industry was allowed to use up existing stocks of heptachlor for ant control, but not to purchase additional stocks once the ban went into effect.

Control of ants in pineapple fields relies heavily on bait preparations since insecticides are used most efficiently and selectively in this form (McEwen *et al.* 1979). Insecticidal

baits are a common and effective method of controlling ants (Cherrett 1986, Hughes *et al.* 2002). Laboratory and field trials of numerous insecticidal baits indicate that hydramethylnon {tetrahydro-5,5-dimethyl-2-(1H)-pyrimidinoine (3-(4-trifluoromethyl) phenyl)-1-[2-[4 (trifluoromethyl) phenyl] ethenyl)-2-propenylidene] hydrazone}, known by the trade name Amdro, and insect growth regulators are the most promising chemicals for ant control in pineapple (Glancey *et al.* 1990; Reimer and Beardsley 1989a, 1989b, 1990; Reimer *et al.* 1990b, 1990c; Su *et al.* 1980). Under the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) section 18, EPA authorized the use of hydramethylnon on pineapple for control of *P. megacephala* and *L. humile* in Hawaii. An EPA regulation (EPA 2001) extends a time-limited tolerance for residues of hydramethylnon in or on pineapple at 0.05 ppm until June 30, 2003.

Chemical repellents are generally unsuccessful for large-scale ant management. A number of botanical extracts repel ants (e.g., Bueno *et al.* 1990; Chen *et al.* 1983, 1984; Jahn 1991a,b, 1992b; Wiemer and Ales 1981). None, however, has been formulated into a compound that would be practical for preventing ants from entering a pineapple field.

Biological control. In a sense, the pineapple industry already uses biological control to manage wilt disease. When ants are controlled through chemical means, mealybug populations are regulated by the myriad of natural enemies found in pineapple fields (Gonzalez-Hernandez *et al.* 1999a,b) (Table 2).

Carter (1935) searched for biological control agents of pink and gray pineapple mealybugs in Jamaica and Central America. Specific parasites of the mealybugs were extremely rare or entirely absent in the areas he investigated. On an expedition to South Africa, Carter (1939a) found the incidence of mealybugs and wilt to be quite low. He attributed this to climatic conditions rather than biological control. Through explorations by Fullaway, Carter, Sakimura, and Schmidt, a number of parasites and predators were eventually introduced to Hawaii to control pineapple mealybugs (Carter 1967). A small number of these natural enemies became established, e.g., *Lobodiplosis pseudococci* Felt (Diptera: Cecidomyiidae), *Nephus bilucernarius* Mulsant (Coleoptera: Coccinellidae), and *Anagyrus ananatis* Gahan (Hymenoptera: Encyrtidae) (Funasaki *et al.* 1988). None, however, provided adequate control of mealybugs in the presence of ants (Carter 1967). All efforts to control pineapple mealybugs biologically, without ant management, have been unsuccessful (Carter 1959; Rohrbach *et al.* 1988).

No attempt has been made to control ants biologically in pineapple fields. Most research on the natural enemies of ants has focused on fire ants, *Solenopsis* (e.g., Folgarait *et al.* 2002, Jouvenaz *et al.* 1981, Porter & Briano 2000). Microsporidia make up the majority of pathogens of fire ants (Jouvenaz 1983, 1986; Oi & Williams 2002). Microsporidia pose more difficulties than other pathogens as potential biological control agents because of the complexity of their life cycles and their ability to infect hosts of different species (Tanada 1976; Jouvenaz and Hazard 1978; Jahn *et al.* 1986; Oi *et al.* 2001). Only a few parasites of *P. megacephala* are known. *Psilogaster fraudulentus* Reichensperger, an eucharitid parasite from Ethiopia, was discovered on *P. megacephala* (Reichensperger 1913). *Plastophora aculeipes* (Collin), a phorid fly, was discovered on *P. megacephala* subspecies *iligi* (Forel) in Zaire (Schmitz 1915; Wheeler 1922). The most common parasites in *Pheidole* nests in South Africa are goriid worms of the genus *Mermis*, which infest about two percent of excavated nests in the northern transvaal (Petty 1988 personal communication). Fungal and bacterial infections are rare among ants, compared to other insects, due to the antibiotic exocrine secretions of ants (Beattie 1984). The limited research on the natural enemies of *P. megacephala* makes the development of biological control for this ant a long-range goal at best.

Conclusions

The available evidence suggests that mealybug wilt disease of pineapple is a viral disease, though it is possible that wilt is a toxemia induced by a virus that affects the mealybug itself. The disease is managed primarily by controlling ants. In the absence of ants, natural enemies suppress mealybug populations on pineapple. Chemical control of ants allows biological control of mealybugs to occur.

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In Memorium

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Table 1. Ants associated with pineapple mealybugs in various parts of the world.

Region	Ants	References
Australia	<i>Pheidole</i> sp.	Carter 1939
Brazil	<i>Brachymyrmex admotus</i> Mayr, <i>Camponotus cingulatus</i> Mayr, <i>Crematogaster quadriformis</i> Roger, <i>Odontomachus haematoda</i> (L.), <i>Paratrechina fulva</i> Mayr, <i>Prenolepis</i> sp., <i>Solenopsis saevissima</i> (F. Smith) ¹ , <i>Wasmannia auropunctata</i> (Rogers)	de Bartoli 1982, Carter 1949
Cambodia	<i>Tapinoma melanocephalum</i> (Fabricius)	Nickel 1979
Central America	<i>Solenopsis</i> sp.	Carter 1935
Cuba	<i>Camponotus</i> sp., <i>Pheidole</i> sp., <i>Solenopsis</i> sp.	Cuba Ministerio de Agricultura 1989
Fiji	<i>Pheidole megacephala</i> (Fabricius)	Carter 1939, 1942
Guyana	<i>Araucomyrmex</i> sp., <i>Solenopsis</i> sp. ¹	Duodo and Thompson 1992
Hawaii, U.S.A.	<i>Linepithema humile</i> (Mayr), <i>Ochetellus glaber</i> (Mayr), <i>Pheidole megacephala</i> ¹ , <i>Plagiolepis alluaudi</i> Forel, <i>Paratrechina bourbonica</i> Forel, <i>Paratrechina longicornis</i> (Latreille), <i>Solenopsis geminata</i> Jordan, <i>Tapinoma melanocephalum</i> , <i>Tetramorium bicarinatum</i> (Nylander), <i>Tetramorium simillimum</i> (Smith)	Beardsley et al. 1982; Carter 1932, 1967; Fluker and Beardsley 1970; Phillips 1934; Jahn 1992a
Jamaica	<i>Solenopsis</i> sp.	Carter 1935
Kenya	<i>Pheidole</i> sp.	Carter 1939
Malaysia	<i>Solenopsis geminata</i> (Fabricius)	Carter 1939
Mexico	<i>Brachymyrmex</i> sp., <i>Monomorium</i> sp., <i>Pheidole</i> sp., <i>Solenopsis</i> sp.	Zarate 1987, Garcia 1987
Philippines	<i>Pheidole megacephala</i> ; <i>Solenopsis geminata</i>	Serrano 1934

Puerto Rico	<i>Brachymyrmex heeri</i> var. <i>obscurior</i> Forel, <i>Cardiocondyla emeryi</i> Forel, <i>Crematogaster steiheilii</i> Forel, <i>Monomorium floricola</i> (Jerdon), <i>Monomorium carbonarium ebeninum</i> Forel, <i>Paratrechina</i> sp., <i>Paratrechina fulva</i> (Mayr), <i>Paratrechina longicornis</i> , <i>Pheidole megacephala</i> , <i>Solenopsis</i> sp., <i>Solenopsis geminata</i> , <i>Tapinoma melanocephalum</i> , <i>Tetramorium</i> sp., <i>Wasmannia auropunctata</i>	Plank and Smith 1940
South Africa	<i>Pheidole megacephala</i> , <i>Technomyrmex albipes</i> (Fr. Smith)	Petty 1985, 1990
West Africa	<i>Camponotus</i> sp., <i>Crematogaster</i> sp., and <i>Pheidole</i> sp.	Réal 1959

¹ Ant species most commonly associated with mealybugs on pineapple in this region

Table 2. Natural enemies of pineapple mealybugs.

Region	Predators	Parasites	Fungi	References
Australia	COLEOPTERA: Coccinellidae: <i>Cryptolaemus montivivieri</i> Mulsant, <i>Rhizophagus ventralis</i> Erich		unidentified fungi	Chapman 1938, Carter 1939; Petty 1985
Brazil	COLEOPTERA: Coccinellidae: <i>Diomus</i> sp., <i>Hyperaspis c-nigrum</i> Mulsant, <i>H. quinquenotata</i> Mulsant, DIPTERA: Drosophilidae: <i>Pseudiastata brasiliensis</i> Costa Lima	HYMENOPTERA: Encyrtidae: <i>Anagyris ananatis</i> Gahan (formerly identified as <i>A. Coccidivorus</i> Dozier), <i>Hambeltonia pseudococcina</i> Compere		Bartlett 1978; Carter 1949; Chapman 1938
Colombia	COLEOPTERA: Coccinellidae, DIPTERA: Drosophilidae: <i>Pseudiastata nebulosa</i> Coquillett	HYMENOPTERA: Encyrtidae: <i>Aenasius</i> <i>colombiensis</i> Compere, <i>A. cariocus</i> Compere, <i>Anagyris coccidivorus</i> , <i>Hambeltonia pseudococcina</i>		Chapman 1938
Cuba		HYMENOPTERA: Encyrtidae: <i>Pseudaphycus angustifrons</i> Gahan		Cuba Ministerio de Agricultura 1989
El Salvador		HYMENOPTERA: Chalcididae		Chapman 1938
Fiji	NEUROPTERA: Chrysopidae			Chapman 1938
Florida, USA	COLEOPTERA: Coccinellidae: <i>Nephus pictus</i> Gorham	HYMENOPTERA: Encyrtidae: <i>Hambeltonia pseudococcina</i>		Bartlett 1978
Ghana		HYMENOPTERA: Encyrtidae: <i>Tropidophryne</i> <i>africana</i> Compere, <i>Tropidophryne melvillei</i> Compere		Kerrich 1978
Guatemala	COLEOPTERA: Coccinellidae: <i>Nephus pictus</i> , DIPTERA: Cecidomyiidae: <i>Dicroradiplosis</i> <i>guatemalensis</i> Felt, <i>Lobodiplosis</i> (= <i>Vincentodiplosis pseudococci</i> Felt, Drosophilidae: <i>Pseudiastata nebulosa</i> , Syrphidae, LEPIDOPTERA	HYMENOPTERA: Chalcididae, Encyrtidae: <i>T. pretiosus</i> Timberlake		Clancy 1934; Carter 1935; Chapman 1938, Kerrich 1967

Region	Predators	Parasites	Fungi	References
Guyana	COLEOPTERA: Coccinellidae: <i>Hyperaspis</i> sp., <i>Nephus</i> sp. DIPTERA: Drosophilidae: <i>Pseudiastata nebulosa</i>	HYMENOPTERA: Encyrtidae: <i>Eurythopalus propinquus</i> Kerrich, <i>Aenasius tachigallice</i> (Brues)		Chapman 1938
Hawaii, USA	ARANEAE: Araneidae: <i>Argiope appensa</i> Walckner, COLEOPTERA: Coccinellidae: <i>Cryptolaemus montrouzieri</i> , <i>Curinus coeruleus</i> Mulsant, <i>Diomus</i> sp., <i>Hyperaspis sylvestrii</i> Weise., <i>Nephus bilucernarius</i> Mulsant, <i>Rhizobius forestieri</i> (Mulsant), <i>R. ventralis</i> Erich., <i>Scymnus bipunctatus</i> (Klug), <i>S. uncinatus</i> Sicard, <i>Sticholotis ruficeps</i> Weise DERMAPTERA: Carcinophoridae: <i>Euborellia annulipes</i> (Lucas), Chelisochoidae: <i>Chelisochoes morio</i> (Fabricius), Labridae: <i>Labidura riparia</i> (Pallas), DIPTERA: Cecidomyiidae: <i>Dicrodiplosis guatemalensis</i> , <i>Lobodiplosis</i> (= <i>Vincentodiplosis pseudococci</i> , ORTHOPTERA: Tettigoniidae: <i>Conocephalus saltator</i> (Sauss)	HYMENOPTERA: Encyrtidae: <i>Anagyrus ananatis</i> (formerly identified as <i>A. coccidivorus</i> Dozier), <i>Eurythopalus propinquus</i> Kerrich, <i>Hambeltonia pseudococcina</i> . Compere 1936; Funasaki et al. 1988; Gonzalez-Hernandez (1995); Illingworth 1926a,b; Jahn 1992a; Jahn and Beardsley (1998); Williams 1931		Bartlett 1978; Carter 1935, 1949, 1967; Chapman 1938; Chapman 1936; Funasaki et al. 1988; Gonzalez-Hernandez (1995); Illingworth 1926a,b; Jahn 1992a; Jahn and Beardsley (1998); Williams 1931
Indonesia	DIPTERA: Cecidomyiidae		unidentified fungi	Carter 1939
Jamaica	DIPTERA: Cecidomyiidae: <i>Lobodiplosis</i> (= <i>Vincentodiplosis pseudococci</i>)			Carter 1935
Kenya	COLEOPTERA: Coccinellidae, LEPIDOPTERA	HYMENOPTERA: Chalcididae		Carter 1939; Chapman 1938
Malaysia	COLEOPTERA: Coccinellidae: <i>Scymnus apiciflavus</i> Motschulsky	HYMENOPTERA: Chalcididae	unidentified fung	Carter 1939
Mexico	COLEOPTERA: Coccinellidae: <i>Curinus coeruleus</i> , <i>Diomus</i> sp., <i>Hyperaspis lateralis</i> Mulsant, <i>H. sylvestrii</i> , <i>Nephus</i> sp., DIPTERA: Cecidomyiidae: <i>Lobodiplosis</i> (= <i>Vincentodiplosis</i>) <i>pseudococci</i> , NEUROPTERA: Hemerobiidae	HYMENOPTERA: Encyrtidae: <i>Acerophagus debilis</i> Timberlake, <i>Eurythopalus pretiosus</i> (Timberlake)		Chapman 1938, Timberlake 1924
Palau	DIPTERA: Cecidomyiidae			Chapman 1938

Table 2. (continued)

Region	Predators	Parasites	Fungi	References
Panama	COLEOPTERA: Coccinellidae: <i>Diomus</i> sp., <i>Hyperaspis albicollis</i> Gorham, <i>Nephus pictus</i> , <i>Scymnus pictus</i> Gorham	HYMENOPTERA: Chalcididae, Encyrtidae: <i>Anagyris</i> sp., <i>Zaplatycerus fullawayi</i> Timberlake		Carter 1949; Chapman 1938; Kerrich 1978
Philippines	COLEOPTERA: Coccinellidae: <i>Cleodiploxis kozebei</i> (Felt), <i>Hyperaspis silvestrii</i> Weise, <i>Nephus</i> sp. near <i>bipunctatus</i> Kugelann, <i>Scymnus margipallens</i> Mulsant	HYMENOPTERA: Encyrtidae: <i>Anagyris ananatis</i> , <i>Hambeltonia pseudococcina</i>		Bartlett 1978; Chapman 1938
Puerto Rico				Bartlett 1978
Saipan	COLEOPTERA: Coccinellidae: <i>Nephus</i> sp. near <i>bipunctatus</i> , NEUROPTERA: Chrysopidae			Chapman 1938
Singapore	COLEOPTERA: Coccinellidae			Chapman 1938
South Africa	COLEOPTERA: Coccinellidae: <i>Exochomus concavus</i> Fursch		<i>Cladosporium</i> sp.	Petty 1985, 1990
Surinam		HYMENOPTERA: Encyrtidae: <i>Anagyris</i> sp.		Carter 1949
Taiwan	COLEOPTERA: Coccinellidae: <i>Cryptolaemus</i> sp., <i>Diomus fukahoshii</i> Ohta, <i>Nephus</i> sp. near <i>bipunctatus</i> Kugelann, <i>Scymnus</i> sp.	HYMENOPTERA: Encyrtidae: <i>Anagyris</i> sp.		Bartlett 1978; Chapman 1938
Tanzania	COLEOPTERA: Coccinellidae			Chapman 1938
Thailand		HYMENOPTERA: Encyrtidae: <i>Anagyris tenuis</i> sp. nov.		Noyes & Hayat 1994.
Trinidad	COLEOPTERA: Coccinellidae: <i>Nephus</i> sp. DIPTERA: Drosophilidae: <i>Pseudiantata nebulosa</i> Coq.	HYMENOPTERA: Encyrtidae: <i>Acerophagus debilis</i> Timberlake, <i>Aenasius acuminatus</i> Kerrich, <i>Aenasius carticus</i> (A. thobromae) Compere, <i>Anagyris</i> sp., <i>Hambeltonia pseudococcina</i> Compere, <i>Pseudaphycus dysmicocci</i> Bennett		Bennett 1955, 1957; Carter 1949; Chapman 1938; Kerrich 1953, 1967
Venezuela		HYMENOPTERA: Encyrtidae: <i>Aenasius colombiensis</i> , <i>Hambeltonia pseudococcina</i>		Chapman 1938