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APPROACHES TO THE BIOLOGICAL CONTROL OF WHITEFLIES

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ABSTRACT

Biological control has been successful for some whitefly species but not for others. Natural enemies available for control of whiteflies include fungi, predators and parasitoids. Each of these groups has an important place in the ecosystem, but knowledge of their biology and utilization is limited and available mainly for parasitoids. There is no proven method for predicting the success of natural enemies. However, the number of host stages that are not vulnerable to enemy attack, as well as the host refuges, should be reduced in both time and space. This can be accomplished by integrating the use of different natural enemies, plant resistance and selective insecticides. Comparative studies of successful cases of whitefly biocontrol are suggested as a means to increase our knowledge of the necessary attributes of successful natural enemies.

RESUMEN

El control biológico de moscas blancas ha resultado exitoso para algunas especies y no para otras. Los enemigos naturales que se encuentran a disposición para dicho control son hongos, depredadores y parasitoideos. Cada uno de estos grupos ocupa un lugar importante en el ecosistema, pero el conocimiento de su biología y modo de utilización es limitado, y existe mayormente para los parasitoideos. Parte de los problemas actuales de plagas se tipifican por extensas áreas de esparción de las moscas blancas, alrededor de las cuales se forman los complejos de enemigos locales. No hay un método probado para la estimación a-priori del éxito de un enemigo natural; la eficacia de un enemigo tal debe ser verificada en el campo. No obstante, se sugiere que la selección del enemigo sea guiada por la necesidad de reducir el número de estados hospederos que no son vulnerables al ataque del enemigo y de reducir los refugios del hospedero en el tiempo y el espacio. Esto puede realizarse integrando el uso de diferentes enemigos naturales, de la resistencia de las plantas y de insecticidas selectivos. Se sugieren estudios comparativos de casos exitosos en control biológico de moscas blancas, como medio para aprender más acerca de los atributos necesarios para enemigos naturales exitosos.

Biological control of arthropods, the utilization of organisms (or natural enemies) to control arthropod pests, has been practiced for over 100 years. During the last decade notable contributions have been made to the theory and practice of such control. Critical issues dealing with insect behavior, competition, diversity, and aggregation, as well as models and their relevance to biological control have been examined (Waage & Greathead 1986, Mackauer et al. 1990). Likewise, much information about whitefly pest status, ecology, and biological control agents has been reviewed (Gerling 1990a). Drawing upon this body of knowledge, I shall present some of the approaches to biological control of whiteflies.

For practical purposes, biological control has been divided into two categories: Inoculative (or classical), in which the natural enemy is usually introduced only once and is then expected to continue to multiply and control the pest; and inundative, in which the natural enemy is seen as a "biological insecticide", may be introduced repeatedly, and is primarily aimed at producing immediate pest suppression. Recently, van Lenteren (1986) employed the term "seasonal inoculative release method" for repeated releases with a long-term effect.

Whiteflies have been the subject of biological control attempts since early this century; first using the classical approach, and later also through the inundative or seasonal inoculative methods. Some attempts have been successful (Clausen 1978, van Lenteren & Woets 1988), whereas others (Gerling 1986) have failed, with the species involved causing severe economic damage (Byrne et al. 1990). In addition, formerly successful biological control is now being challenged due to the need (or apparent need) for insecticidal treatments against other pests (Dowell 1990).

The proper utilization of natural enemies depends upon an adequate understanding of whitefly and enemy taxonomy, ecology and behavior. While ecological and behavioral traits will be discussed here, taxonomy is beyond the scope of this review; however, its importance should not be underestimated. The taxonomy of both whiteflies (Bink-Moenen & Mound 1990) and their enemies (Viggiani & Mazzone 1979, DeBach & Rose 1982, Hayat 1989) is currently in a state of flux. Consequently, accurate determinations are not always available.

THE WHITEFLY-ENEMY COMPLEX

Whiteflies are homopterans belonging to the suborder Sternorrhyncha. Their life cycle includes an egg, four nymphal instars, a so-called pupal instar, and winged adults.

All of the immature stages except for the young first instar "crawler" are sessile. Whiteflies usually have from 2 to 7 generations per year, most of which occur during the summer, since they are mainly warm climate insects (Bink-Moenen & Mound 1990). In addition to direct plant damage caused by sucking its sap, whiteflies also cause damage through honeydew production and virus transmission.

Because of the relatively long period which they spend as sessile insects, whiteflies are often considered suitable objects for biological control. Their known natural enemies include fungal pathogens, and arthropod predators and parasitoids.

Fungi occur principally in climates with high relative humidity. They usually attack the host nymphs, but some species (e.g. *Paecilomyces fumosoroseus*) may attack all of the stages (Fransen 1990). Host specificity varies; the genus *Aschersonia* is specific to whiteflies whereas *Verticillium*, *Poecilomyces* and *Aegerita* are not.

Fransen (1990) reviewed the known species of *Aschersonia* and other whitefly-infecting fungi and their host association. When they are grouped by host ranges (Fig. 1), two extremes become evident. Twenty one species of whiteflies have only one recorded fungus species attacking them, while 15 species of fungi are known from a single whitefly host. On the other hand, a few well studied species have extensive host-pathogen associations (*T. vaporariorum* and *Dialeurodes citri* are recorded as being attacked by 16 and 10 fungus spp. respectively and *Aschersonia aleyrodis* is recorded from 10 whitefly species). Such relationships often indicate insufficient study of some of the organisms. This is supported by the fact that, for the 1200 known species of whiteflies (Mound & Halsey 1978), only 37 species of fungi have been described.

Fungi can be utilized by transferring infected branches from one plant to the next, or by the more modern methods of mass producing fungal spores and applying them with commercial spray equipment. To date, this has been limited to *V. lecanii*, where strain selection and improvement have produced a marketable commercial product (Ravensberg et al. 1990). Research leading to the commercial utilization of *P. fumosoroseus* is in progress (Osborne et al. 1990).

Predators belong mainly to four insect orders: Heteroptera, Neuroptera, Diptera, and Coleoptera, and to the mites (Gerling 1990b). They have not often been credited with whitefly control, and their role has been little investigated. At present, in light of recent field and laboratory observations, the role of indigenous predators is receiving new attention and their potential as controlling agents is being reassessed (Alomar et al. 1990).

From the few studies that have been conducted, it is possible to outline characteristics that may serve as guidelines for future attempts at biological control using predators:

1. Mobility: The adults are mobile and may travel considerable distances. Mobility of immatures ranges from very limited (*Acletoxenus*) (Diptera:Drosophilidae) (Clausen & Berry 1932) to extensive (Heteroptera) (Alomar et al. 1990).
2. Physiological characteristics: Mating and oviposition are often associated with complex behaviors such as premating flights (*Chrysoperla*) (Duelli 1980) or ovipositional diapause (Coccinellids) (Hagen 1962). Adults of some groups pass unfavorable periods (adverse climate or absence of food) in diapause (Hagen et al. 1976), while others migrate.
3. Prey relations: The prey range extends from oligophagy [coccinellids that feed mainly on whiteflies, (Clausen & Berry 1932)] to polyphagy [some mirids feed on plants and insects (Alomar et al. 1990)]. Some species are cannibalistic as larvae and/or adults, and others prey upon parasitized whiteflies. Predators may change their dietary preferences or habits in response to changes in prey availability (Lawton et al. 1974). In the case of whitefly predators, we found that *Chrysoperla carnea* which previously fed on

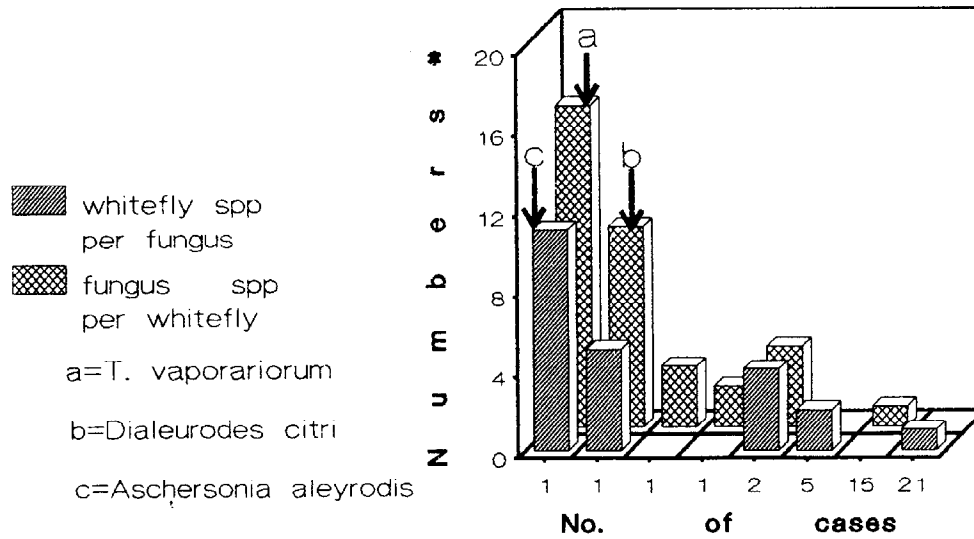


Fig. 1. Frequency distribution of whitefly-fungus host ranges (Data from Fransen 1990). High numbers of whitefly species attacked by the same fungus sp., or high numbers of fungus species associated with a single whitefly species are relatively rare (left side of graph). Conversely, numerous cases exist with a one whitefly-one fungus association (right side of graph).

*Numbers of fungus or whitefly species per associated whitefly or fungus species.

non-whitefly prey because of its relative availability, shifted to include whiteflies in their diet once these became abundant (Or 1986, Gerling personal observations).

These points indicate that predators constitute a very versatile group, and once their particular characteristics are known, different species can be utilized under a multitude of environmental conditions. In particular, predators may be efficient at high prey densities, both because of adult requirements (Hagen et al. 1976), and because their immatures can maximize their potential for development within a limited area. Indeed, several species of predators have been effective as controlling agents, particularly at high whitefly densities (Clausen 1978, Waterhouse & Norris 1989).

Predators have, so far, been used to control whiteflies especially in perennial ecological systems (Clausen 1978, Waterhouse & Norris 1989). However, due to their mobility and relative polyphagy they may also be useful in temporary agricultural systems, such as annual vegetables and field crops, where an unstable, changing environment is not as favorable for the establishment of specific parasitoids (Alomar et al. 1990, Dowell 1990). Consequently, their introduction and encouragement may contribute measurably to manipulative (inundative and short-term inoculative) control. However, as pointed out previously, the utilization of particular organisms requires running a considerable number of specific tests (see Alomar et al. 1990 for a list) in order to establish their characteristics in relation to the control requirements.

Parasitoids are credited with most of the success in the biocontrol of whiteflies. Exploration for parasitoids has been conducted either in the presumed endemic range of the host (Clausen & Berry 1932, Clausen 1978, Onillon 1990, Waterhouse & Norris 1989), or in locations where previous success was achieved (Clausen 1978, Onillon 1990). A notable exception is the fortuitous control of *Parabemisia myricae* by *Eretmocerus* sp. in California (Rose & DeBach 1982) where indigenous parasitoids provided excellent control.

Recent reviews of whitefly parasitoids (Gerling 1990b, Onillon 1990, Waterhouse & Norris 1989) were examined in order to rate the importance of five host/parasitoid traits to the success of biological control programs:

1) Host instar attacked. 2) Plant-host range of the whitefly. 3) Mode of development (arrhenotoky, autoparasitism). 4) Reproductive physiology (synovigenic vs. proovigenic). 5) Host range of the parasitoid.

Of the above, success was not related to the first three criteria, whereas proovigenic *Amitus* were particularly successful under high host densities.

The importance of the fifth trait, host-range, could not be rated unequivocally. Most successful whitefly control was achieved by parasitoids with a limited range that included, at most, a few congeneric species that might have evolved with their hosts in the same region. However, excellent success in greenhouse whitefly control is attained with *Encarsia formosa* that has a wide host range. Moreover, some whitefly species (e.g. *Bemisia tabaci* and *Trialeurodes vaporariorum*) have a very wide geographical range and are often attacked by different species of parasitoids which presumably have moved on to them from local whitefly spp. (Gerling 1986); so much so that looking for an originally evolved "narrow" association becomes meaningless. Such an increase in parasitoid host range can yield excellent control, as has been shown by the fortuitous biological control of *Parabemisia myricae* by *Eretmocerus* sp. in California (Rose & DeBach 1982). Consequently host specificity in itself cannot be taken as a measure in determining the chances for success of the parasitoids.

B. WHITEFLY-ENEMY INTERACTIONS

As pointed out by Price (1984), a population that exists at a low level may reach an outbreak phase due either to the creation of an ecological advantage (e.g. increased reproductive rates), or to the relaxation of an ecological constraint that has been introduced into the population.

In many of the whitefly outbreaks that were controlled biologically, the ecological constraints that had been relaxed, and which were re-established by man were the natural enemies. Often multiple introductions of enemies were carried out (Clausen 1978, Onillon 1990) and one or more of these became established and reduced the whitefly populations sufficiently. However, the outbreak-inducing ecological conditions may also be climatic (man-made or natural), or due to the availability of new crops as host plants, or the extension of the agricultural season through the introduction of protected plants, or the use of agrochemicals. Some of these practices and conditions, such as the use of insecticides, can and should be changed in order to facilitate biological control, whereas others, such as the type of crop or the use of greenhouses, can not.

Many of the current acute whitefly outbreaks do not involve the transfer of a whitefly species from a place in which it is under satisfactory natural control to a location where its enemies are lacking. Rather, other natural or man-made ecological conditions can usually be blamed for the outbreaks. Such outbreaks, e.g. of *B. tabaci* or *T. vaporariorum* may reach monumental proportions. The pests are often widely distributed and their economic damage varies in accordance with the crop grown, the agricultural practice, the geographic locality, and the duration of the species' residence in the area.

These invading whitefly populations may show considerable genetic variability and an increasing host range—features that often accompany an out-break phase (Price 1984). The natural enemy complex of these whiteflies usually consists of some parasitoid species that apparently migrate with them through very extensive ranges (e.g. *Eretmocerus mundus* is recorded from Spain in the west to Pakistan in the east, and from Africa in the south to Turkemanistan in the north, without any intended human assist-

ance), and of other species that moved on to the pest from the local fauna (Gerling 1986). In addition, local predators may adapt gradually to the newly abundant food source.

The efficiency of controlling the whitefly population by each of these local enemy complexes is usually quite specific, incorporating, in addition to human activities, the nature of the pest outbreak, and the attributes of the enemies and climate. At times, situations occur in which whitefly control has been achieved by indigenous enemies (e.g. Rose & DeBach 1982). Thus, both, endemic and introduced whitefly species may be controlled by either locally occurring or introduced natural enemies (e.g. Dowell et al. 1979, Onillon 1990). Consequently, almost any place in which host-enemy associations of whiteflies take place may be considered as a potential source of natural enemies to be used for biological control. However, it should be kept in mind that since uncertainties exist in the classification of both hosts and parasitoids, not all of the apparent specific associations may prove to involve the host species that we are seeking.

APPROACHES TO BIOLOGICAL CONTROL

1. The Host-refuge Consideration

Murdoch (1990) in his suggestions for maintaining low host populations and fluctuations, stressed the need for elimination of host refuges. These can take the form of: a) Invulnerable host stages, b) refuges in time or c) refuges in space.

a. Differential vulnerability of insect stages to natural enemies is a common occurrence. In whiteflies, it is expressed through preference of many predators to feed on eggs and young larvae which are easier to overcome and/or differ in their nutritive value (Gerling 1990b). Likewise, parasitoids prefer to attack certain nymphal host instars (e.g. many *Encarsia* prefer instars 3 and 4 and seldom attack the first two instars, whereas *Amitus* may attack instars 1 and 2 and leave eggs and older instars unaffected (Gerling 1990b).

b. Temporal refuges often occur where pests become established in a new area or crop, before natural enemies reach the new location in sufficient numbers. With whiteflies, this is especially acute in annual crops and greenhouses to which *B. tabaci* and *T. vaporariorum* migrate each season and where their natural enemies must follow (Gerling et al. 1980, van Lenteren & Woets 1988).

c. Spatial refuges may take numerous forms. They may be associated with plant architecture, as for example, when whiteflies cover certain parts of the plant whereas the enemies search on others. This has been suggested as a factor limiting the effectiveness of *Encarsia formosa* on Gerbera plants infested by the greenhouse whitefly (van Lenteren pers. comm.). Climatic and other regional characteristics may also furnish hosts with refuges from enemies, and finally, host density itself may act in that capacity. Above a certain host density, parasitization may act in an inverse density dependent manner because, 1. The physical environment on a heavily infested leaf is not conducive to parasitoid activity due to the copious amounts of honeydew and exuviae present (van Lenteren pers. comm., Gerling pers. obs.); and 2. There is no evidence for long-distance attraction of parasitoids to infested leaves (Gerling 1990b). Thus, less parasitoids per whitefly would arrive on densely infested leaves than on sparsely infested leaves. Inverse density dependence would follow since the daily rate of oviposition by parasitoids cannot exceed a fixed, species specific, level (Vet & van Lenteren 1981, Shimron 1991). Arrestment alone cannot compensate for this shortcoming.

The practical field situations usually involve more than one kind of refuge and may require unique solutions. The introduction of multiple species of natural enemies, each having a somewhat different host preference and developmental niche, the use of "banker plants" (Osborne et al. 1990), and the development of whitefly-resistant plants are usually the most profitable approaches to reduce these refuges.

2. Plant Resistance

The fact that some plant species or varieties are more hospitable to insects than others can be used to reduce pest refuge areas. Although complete resistance is rare, partial resistance is common (DePonti et al. 1990). Differential susceptibility to whitefly attack was demonstrated at the specific and varietal levels (DePonti et al. 1990, van Lenteren & Noldus 1990). Thus, certain plant species or varieties will support only low whitefly populations; this may suffice as a control method in itself, or at least facilitate parasitoid activity by reducing the detrimental effects of high whitefly density.

3. Integration

To achieve maximum benefits, and to overcome some of the host-refuge problems, biological control of whiteflies must be integrated within itself and with other control methods. A strategy that combines different natural enemies, predators (especially mites, coccinellids and Heteroptera) (Avilla et al. 1990, Gerling 1990b) and fungi with parasitoids, can deal with most host stages and habitats in a complementary fashion. However, the compatibility and complementary action of the different organisms must be examined in order that they may be employed most effectively. For example, Waterhouse and Norris (1989) reported that in the campaign against *Aleurodicus dispersus* the predator *Nephaspis oculatus* was effective at high host densities whereas the parasitoids of the genus *Encarsia* were effective at low densities. Smith et al. (1964) introduced several species of parasitoids against *Aleurocanthus woglumi* and each became established in a different climatic zone. Franssen (1990) discussed the interactions and utilization of fungi together with parasitoids in controlling whiteflies. Whereas broad spectrum fungi like *P. fumosoroseus* and *Beauveria bassiana* may infect parasitoids and predators, the integration of the whitefly specific *Aschersonia aleyrodis* and *Aschersonia 'Cuba red'* with parasitoids gave better control than the use of parasitoids alone.

The use of natural enemies with insecticides can often be achieved through the choice of the right materials and proper timing, as has been elaborated by Dowell (1990). He concluded that the improvement of biological control of whiteflies, depends upon the development of new control measures for pests currently under chemical control. Recently, a relatively new group of insecticides, the Insect Growth Regulators (IGRs) have come into use. These include molting inhibitors and chitin synthesis inhibitors. Their action is selective so that their use in whitefly management may be valuable. Laboratory experiments with Buprofezin, a chitin synthesis inhibitor, conducted with *E. formosa* and the greenhouse whitefly have shown that while the pest was affected the development of the parasitoid and percent parasitization were not (Garrido et al. 1984, Wilson & Anema 1988, van de Veire & Vacante 1989). Garrido et al. (1984) have also shown that *Cales noacki* and its host *Aleurothrixus floccosus* responded similarly. Laboratory experiments in Israel demonstrated that Buprofezin is effective mainly against first and second instar *B. tabaci* nymphs but that it also had some detrimental effects on young larvae of *Eretmocerus* sp. and on pupae of *Encarsia deserti* (Sinai 1990).

Complementary field experiments with Buprofezin were conducted in cotton fields for three years. Since the IGR affects mainly whitefly instars that are too young to serve as hosts for parasitoids, the trials were run with the expectation that parasitoid/host ratio (and consequently, percentage parasitization) would be higher in the treated field than in the corresponding untreated plots. However, although, they resulted in

good whitefly control, only an occasional and limited increase in percent parasitism occurred (Sinai 1990, Gerling, pers. obs.). These results might be partially explained by the parasitoid mortality that has been demonstrated in the lab, and partially by other factors, such as predators, whose activity had not been adequately monitored. However, the overall success of control without decline in percent parasitism is indicative of the potential of IGRs in whitefly pest management.

A LOOK TO THE FUTURE

One of the main limitations to cheap and efficient biological control is our inability to preselect natural enemies and determine their future qualities as controlling agents prior to their field utilization. Recent studies on host-enemy interaction, parasitoid behavior and developmental strategies (e.g. van Alphen & Vet 1986, Waage & Godfray 1984, Walde & Murdoch 1988) as well as studies of practical natural enemy implementation (Dowell et al. 1979, van Lenteren 1986, van Lenteren & Woets 1988), explored in depth desirable attributes of natural enemies. Such studies also led to the production of a flow chart for natural enemy selection (van Lenteren 1986).

However, the guidelines provided in the flow chart are mainly relevant for greenhouses, where the artificial conditions require continual interference and provide relatively stable and predictable environmental conditions. In inoculative, out-of-door control, where the relative involvement per crop plant is lower, and the risks of changing and/or unpredictable environmental conditions may be high, it is still simpler and cheaper to utilize the "introduce and see what happens" method than to run a series of tests on the host and its natural enemies. Moreover, the complexity of the ecological conditions that may influence the efficiency of a natural enemy, hinder the formation of a simple and effective method to predict the quality of a natural enemy that will be used for whitefly control out-of-doors.

In the absence of a general testing method to estimate the quality of a natural enemy, the role of guesswork can be reduced by studying the dynamics of whitefly-enemy interactions and by learning from previous successes (and failures) in the biological control of whiteflies. Such studies should be conducted in both the area of the pest's origin and in the country in which the control took place. These should elucidate the role of the physical and trophic components in the ecological system, and may shed light on factors that facilitated the natural enemy's success. A step in this direction was taken by Southwood & Reader (1976) when they studied the population dynamics of the *Aleurotrachelus* (*Aleurotuba*) *jelinekii*, at times a pest in Britain.

It seems only natural that in present times, when man has learned to change natural processes through genetic engineering, and to manipulate biological organisms in ways that would have been unthinkable only a short time ago, extensive efforts should be expanded towards the manipulation and improvement of natural enemies. The goal is to obtain a natural enemy that we can recognize as being better adapted to control its host under specified conditions, and that can be used with considerable chances for success. At the same time, it should be resistant to insecticides that may be applied in the agroecosystem. It is also necessary to improve the techniques of rearing, mass producing, storing, and releasing enemies.

Many of the abovementioned desiderata have been considered in detail (van Lenteren 1986, Mackauer et al. 1990). Unfortunately, only limited successes have been obtained so far, especially in the field of insecticide resistance and artificial rearing (Roush 1990). However, the pace at which science is advancing gives hope that much more can be achieved if we, as consumers of natural enemy 'high tech', will make our priorities better known and venture to experiment using the newly discovered techniques.

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BIOLOGICAL CONTROL OF WHITEFLIES WITH ENTOMOPATHOGENIC FUNGI

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ABSTRACT

This paper is a review of 3 fungi (*Aschersonia aleyrodis* Webber, *Verticillium lecanii* (Zimmerman) Viégas and *Paecilomyces fumosoroseus* (Wize) Brown & Smith) that are being evaluated for the management of injurious polyphagous whiteflies and was presented as part of a conference on the potential for biological control in the Caribbean. The prospect for the utilization of biopesticides based on entomopathogenic fungi is promising. The need to develop alternatives to conventional pesticides has become apparent in recent years because two of the major whitefly pest species, *Bemisia tabaci* (Gennadius) and *Trialeurodes vaporariorum* (Westwood), have developed resistance to many of the insecticides used for their control.

RESUMEN

Se revisan en este manuscrito 3 especies de hongos: *Aschersonia aleyrodis* Webber, *Verticillium lecanii* (Zimmerman) Viégas y *Paecilomyces fumosoroseus* (Wize) Brown