THREE TARGETS OF CLASSICAL BIOLOGICAL CONTROL IN THE CARIBBEAN: SUCCESS, CONTRIBUTION, AND FAILURE

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INTRODUCTION

Three examples of classical biological control in Florida and the Caribbean basin are compared and contrasted. Use of the encyrtid parasitoids *Anagyrus kamali* Moursi and *Gyranusoidea indica* Shafee, Alam and Agarwal against the pink hibiscus mealybug, *Maconellicoccus hirsutus* Green, in the Caribbean exemplifies a well conceived and successful program. Islands where the parasitoids have been introduced in a timely manner have avoided the major agricultural and economic losses suffered on islands where the mealybug invaded without its parasitoids. Population regulation of the mealybug by its parasitoids appears to limit the pest to its primary host, *Hibiscus* spp., leaving the pest's broad range of potential secondary host plants largely unaffected.

In contrast, the classical program using the encyrtid wasp *Ageniaspis citricola* Logviniskaya against the gracillariid citrus leafminer, *Phyllocnistis citrella* Stainton, in Florida is an example of successful establishment of an exotic parasitoid with more ambiguous results. Objective evaluations indicate that the parasitoid does inflict mortality on the pest population, but that similar levels of control might well have been provided by indigenous natural enemies. Parasitism by native species declined following introduction of *A. citricola*; ants and other generalist predators remain the primary source of mortality for juvenile stages. Furthermore, levels of biological control similar to those obtained in Florida are provided by native predators and parasites in dry regions where *A. citricola* has failed to establish.

A third program of classical biological control, one directed against the brown citrus aphid, *Toxoptera citricida* (Kirkaldy), in Florida, has been largely a failure. All available ecological literature indicates that this pest is controlled by various combinations of generalist predators throughout its range and that it lacks specialized parasitoids, making it a dubious candidate for a classical biological control program. Nevertheless, considerable effort has been expended since 1997 to introduce a series of unproven parasitoids of questionable effectiveness even in their countries of origin. Despite the failure of any these parasitoids to establish, populations of the brown citrus aphid have declined dramatically in the years subsequent to its introduction, due entirely to the actions of generalist predators. In spite of this "success", introductions of unproven parasitoids against the brown citrus aphid continue. I suggest that natural enemy introductions should not be the first response to every invasive pest, but rather that each pest should be carefully evaluated as a potential, rather than automatic, target for classical biological control.

PINK HIBISCUS MEALYBUG

The pink hibiscus mealybug, *Maconellicoccus hirsutus* Green, was first detected in the Caribbean on the island of Grenada in 1993 (Persad, 1995). It spread to Trinidad and Tobago in 1993, and subsequently to other islands of the Lesser Antilles, reaching Puerto Rico in 1997 (Michaud and Evans, 2000). Presently, 27 Caribbean islands are infested, with the apparent exceptions of Dominica, Antigua, and Barbuda. Early in 2001, pink hibiscus mealybug was detected in the Bahamas, and its arrival on the Florida mainland appears imminent.

The basic life history and biology of the pink hibiscus mealybug have been described by Ghose (1972) and literature on the insect has been reviewed by Mani (1989). Crawlers of pink hibiscus mealybug typically initiate colonies on the growing terminals of *Hibiscus* spp. If uncontrolled, the mealybugs quickly spread until whole branches are covered with mature females and their egg sacs. Toxins injected by the growing nymphs during feeding cause severe distortion of growing plant parts including flowers and vegetative shoots. This permanent damage is characterized by shortened internodes and "rosetting" of foliage. Dense pink hibiscus mealybug populations ultimately result in death of the plant.

A highly effective classical biological control program has been implemented by personnel of the USDA Animal and Plant Health Inspection Service (APHIS) against the pink hibiscus mealybug in the Caribbean employing two exotic parasitoids–*Anagyrus kamali* Moursi, imported from China and Hawaii and *Gyranusoidea indica* Shafee, Alam, and Agarwal (Hymenoptera: Encyrtidae), imported from Egypt. Classical programs against the pink hibiscus mealybug have a long history dating back to the 1920s in Egypt (Hall, 1926; Moursi, 1948). The key parasitoid is *A. kamali*, a species presumed to be of Asian origin (Williams, 1996). Its apparent effectiveness arises from a very short generation time (just half that of its host) that facilitates a very rapid numerical response to mealybug populations. *Gyranusoidea indica*, a species of African origin, appears to be of secondary importance.

On some Caribbean islands, innundative releases of *Cryptolaemus montrouzieri* Mulsant were employed to provide supplemental control of heavy mealybug populations until parasitoids could be established. On other islands, such as Puerto Rico, this ladybeetle was already present as a consequence of previous importation and responded well to pink hibiscus mealybug infestations. A number of other coccinellids, some native, others introduced, were also observed to prey on pink hibiscus mealybug in Puerto Rico. These included *Cycloneda sanguinea limbifer* Casey, *Coelophora inaequalis* (F.), *Diomus* sp., *Scymnus* sp., and *Zilus eleutherae* (Casey) (Michaud and Evans, 2000).

The implementation of a classical biological control program, the introduction of exotic natural enemies for purposes of suppressing populations of an invasive pest, represents a large-scale experiment on the ecosystem. If pest populations decline, this may or may not be a consequence of establishment of the introduced natural enemy. Too often there are no means of inferring what would have happened to the pest population in the absence on the introduced biocontrol agent, especially when exotic species are released upon first discovery of an invasive pest. We cannot know the ultimate outcome in the absence of the exotic species unless the introductions fail to establish, or unless non-release plots are established and monitored. However, in the case of pink hibiscus mealybug in the Caribbean, we have islands that effectively approach experimental replicates, providing an opportunity to contrast the economic impact of the pest on islands where the parasitoid introductions occurred early versus where they occurred late. For example, Grenada and the islands of Trinidad and Tobago estimated agricultural losses of U.S.$10,000,000 and $18,000,000, respectively in the first year after invasion of pink hibiscus mealybug. In contrast, early detection of pink hibiscus mealybug on Vieques off the coast of Puerto Rico, combined with early release of both parasitoid species by personnel of the USDA APHIS, effectively prevented any agricultural losses in Puerto Rico. The same was true in Hawaii where *A. kamali* was introduced concurrently with pink hibiscus mealybug in 1983, resulting in fortuitous biological control. The impact of parasitism also appears to significantly slow geographic range expansion by the mealybug. After more than 4 years the pest has yet to reach western regions of Puerto Rico, an island only 100 miles in length.

Although the pink hibiscus mealybug has been recorded from plants in over 200 genera (Chang and Miller, 1996), the majority of these plants may be only secondary hosts. Michaud and Evans (2000) examined a wide range of reportedly susceptible host plants growing directly adjacent to infested hibiscus without finding any evidence of pink hibiscus mealybug damage or colonization. Thus it would appear that many of the host plants reported as susceptible to pink hibiscus mealybug attack, including most of the annual crop plants, are secondary hosts that are colonized only when mealybug populations overwhelm a primary woody host plant, typically hibiscus, carob, or mulberry.

The classical programs against pink hibiscus mealybug have been very successful in the Caribbean and we may conclude that this pest is an appropriate target for the classical approach. It has two highly specific and effective parasitoids that not only suppress pink hibiscus mealybug populations, but appear to limit the pest's effective host range to *Hibiscus* spp., the primary woody host plant in this region. When biological control is established promptly upon detection of pink hibiscus mealybug, secondary hosts, including most agricultural crops, remain largely unaffected. Although pink hibiscus mealybug remains a quarantine problem for nurseries and ornamentals, major economic losses associated with damage to agricultural crops are effectively averted.

CITRUS LEAFMINER

The citrus leafminer, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), was first detected in Florida in 1993 and spread to infest virtually all citrus-producing regions of the state within six months (Pomerinke, 1999). Although recorded from a number of related Rutaceous plants, the citrus leafminer is a relatively specialized feeder on citrus. The female moth lays its eggs on very young foliage and the developing larvae form serpentine mines on the upper and lower surfaces of the leaves, sometimes even on the fruit. The economic impact of this direct damage is highest on nursery stock, where cosmetic appearance is important, and on young trees where significant reduction of photosynthetic surface area can stunt growth.

An endoparasitic wasp of Asian origin, *Ageniaspis citricola* Logviniskaya (Hymenoptera: Eulophidae), was imported from Australia and released against citrus leafminer at 53 different sites in Florida during 1994 and 1995 (Hoy and Nguyen, 1997), and within six months it had established throughout the state. The parasitoid attacks egg and early larval instars and emerges from the pupal stage, occupying the host for its entire period of development. Anywhere from two to six larvae can mature per host. In October 1996, Hoy *et al*. (1997) surveyed for *A. citricola* by collecting pupae from some 28 Florida counties and reported that rates of parasitism averaged 66%, and ranged as high as 90%. By comparison, native parasitoids emerged from pupae at rates of 0 to 24%. However, to sample pupae exclusively while ignoring all other sources of mortality acting on earlier life stages produces a highly biased post-release evaluation, since predation on earlier life stages may inflict equal or greater mortality on the pest population. Furthermore, the publication of these findings in a trade journal appeared to promote *A. citricola* as the primary source of leafminer mortality to citrus producers who had invested heavily in supporting the parasitoid introductions.

It is fortunate that other, more comprehensive studies provide us with a broader picture of leafminer biocontrol in Florida. Pomerinke (1999) conducted cohort-type studies in which potted citrus trees infested with known numbers of citrus leafminer eggs were set out in established citrus groves in southwestern Florida and monitored daily for survival. Amalin *et al.* (2001) conducted a four-year study in lime groves in south Florida that assessed predation in addition to parasitism by tallying the frequency of unfinished mines. These two studies concurred in their findings that predation by generalist predators (e.g., ants, spiders, lacewings) was the most important source of mortality to developing leafminers, accounting for 50% or greater mortality to citrus leafminer populations, and that parasitism by *A. citricola* caused only 3-5% mortality, with another 2-3% contributed by native ectoparasitoids. Amalin *et al.* (2001) also showed that predation had a better density-dependent response to leafminer populations than did parasitism. Even more notable is that Pomerinke's (1999) data indicate that parasitism of citrus leafminer by native species declined from 18% to 2%

after establishment of *A. citricola*. This result suggests that *A. citricola* only replaced mortality that would have been provided by the native parasitoids that were just beginning to provide control of citrus leafminer when *A. citricola* was released and began to compete with them for hosts (Browning and Peña, 1995).

The list of native parasitoids that attack citrus leafminer is substantial and includes *Closterocerus cinctipennis* Ashmead, *Horismenus sardis* (Walker), *Horismenus fraternus* (Walker), *Elasmus tischeriae* (Howard), *Pnigalio minio* (Walker), and *Zagrammosoma multilineatum* (Ashmead) (Browning and Peña, 1995). Although *P. minio* is the most abundant of the native species in Florida, *Z. multilineatum* can become important during dry weather that impedes the survival and dispersal of adult *A. citricola*. It is also apparent that very similar levels of citrus leafminer biocontrol have been achieved in regions such as Texas and Mexico where *A. citricola* was either never released, or failed to establish (Legaspi *et al.*, 1999). Pupal parasitism of citrus leafminer by native species has been reported to approach 100% in Nicaragua (Llana, 1996), and recent reports from Spain indicate that biological control of citrus leafminer by native parasitoids is developing well despite the failure of *A. citricola* to establish in the dry Mediterranean climate (Urbaneja *et al.*, 2001).

Superficially, the citrus leafminer represented a reasonable target for classical biological control, although in retrospect, given its general suitability as a host for diverse and abundant native parasitoids, it would perhaps have been advisable to delay introduction of *A. citricola* until the full impact of these indigenous species could have been thoroughly assessed. Whether the introduction of *A. citricola* improved levels of citrus leafminer control in Florida or merely displaced native parasitoids will remain a matter for conjecture. The project as designed had no control and thus we cannot say what would have ultimately happened to citrus leafminer populations in Florida without the presence of *A. citricola*. However, the biased nature of the post-release evaluation conducted by those responsible for the classical program, and its publication in a trade journal, as opposed to a more appropriate, peer reviewed publication, points to a more fundamental problem. Exotic species introductions represent large investments by those conducting them and professional reputations may hinge on a public perception of success. This generates a considerable vested interest in demonstrating the effectiveness of the introduced species, with little concurrent incentive for measuring the contributions of indigenous natural enemies. Biological control would perhaps be better served if post-release evaluations were entrusted to third party investigators with no vested interest in the program.

BROWN CITRUS APHID

The brown citrus aphid, *Toxoptera citricida* (Kirkaldy) (Homoptera; Aphididae), is the primary vector of citrus tristeza virus, one of the most serious diseases of citrus in the world. The aphid has been present in South America since the 1920s, gradually moving northward from Argentina through Brazil, reaching Venezuela in the 1970s. It was first discovered in south Florida in 1995 and infested virtually all citrus-growing regions of the state within two years.

The brown citrus aphid was selected as a target for a biological control program before it even arrived in Florida, despite the fact that all existing literature on brown citrus aphid ecology indicated that biological control of this insect was broad based and brought about by the combined actions of a wide range of generalist predators (Michaud, 1998). Based on a single laboratory study from Japan (Takanashi, 1990), the parasitoid *Lysiphlebia japonica* Ashmead (Hymenoptera: Aphidiidae) was selected and approved for introduction. It was released at over 30 sites throughout Florida in 1996 and, although it was recovered once, it failed to establish. Subsequent releases of *L. japonica* in Puerto Rico and Belize were also unsuccessful. Although the introduction of *L. japonica* was widely publicized, no peer-reviewed research was ever produced by the program, and no record of its failure was ever published. It seems reasonable to assume that if we are to improve our success rate with the classical approach, we should scrutinize our failures just as carefully as we do our successes. It is difficult to understand how we can be expected to learn from our mistakes if they leave no published record in the literature.

The legacy of the program against brown citrus aphid actually represents an important lesson in biological control; we may be seriously underestimating the ability of our established ecosystems to respond to invasive insects. Large populations of brown citrus aphid occurred in comercial citrus during 1997 and 1998, but became far less common in 1999. The period of peak brown citrus aphid abundance in Florida afforded a unique window of opportunity to examine sources of aphid mortality on a relatively large scale. A comprehensive series of cohort studies were conducted in both Florida and Puerto Rico that followed the survival of aphid colonies from their initial stages of colonization to their ultimate extinction (Michaud, 1999). The results clearly revealed that several species of coccinellids (primarily *Cycloneda sanguinea* L. and *Harmonia axyridis* [Pallas]), along with the syrphid fly *Pseudodorus clavatus* (F.), were the primary biological control agents, not only in Florida, but also in Puerto Rico (Michaud and Browning, 1999). Subsequent laboratory studies revealed that these three species were all capable of successful development on a diet of brown citrus aphid (Michaud, 2000; Belliure and Michaud, 2001), whereas many other predators were not. Field data revealed that *C. sanguinea* and *H. axyridis* together comprised more than 75% of all the adult coccinellids observed on brown citrus aphid colonies during the period of peak aphid abundance (Michaud, 2000).

By 1999, brown citrus aphid infestations were quite rare in Florida citrus. The last cohort study was performed in October 1998 and followed 328 colonies, only one of which survived to produce the migrant alatae of economic importance in transmission of citrus tristeza virus (Michaud, 2001). Brown citrus aphid currently remains under generally good biological control in Florida, although isolated outbreaks may occur if biological control is disrupted. Granted, citrus tristeza virus remains a problem, but pesticides are no longer applied against the brown citrus aphid in mature citrus groves. Thus certain preadapted native predators eventually suppressed populations of this invasive pest, although they required more than two years before their maximum impact was achieved. Note that two to three years is the same time frame typically required for evaluating the effectiveness of introduced species, and it is tempting to suspect that credit for biological control of brown citrus aphid may well have been attributed to *L. japonica* had it established. The brown citrus aphid experience in Florida provides us with an important lesson; native natural enemies can and do respond to some invasive pests. Whenever we introduce exotic species at the very onset of a pest invasion, we risk underestimating the ultimate impact of indigenous species.

By conservative estimates more than $500,000 of targeted grant funding was spent on classical biological control programs against brown citrus aphid, while the problem essentially took care of itself, albeit with a little advice to citrus growers to avoid pesticide applications. It is notable that the classical programs have focused exclusively on individual parasitoid species and have yet to generate any unbiased ecological studies of sources of aphid mortality in the field. In my view, the value of such "rear and release" programs should be questioned if they fail to generate any understanding of how biological control is ultimately achieved, with or without exotic species introductions.

Even more disconcerting is the fact that proponents of the classical approach apparently refuse to accept defeat and continue to lobby Florida citrus producers for funding to introduce yet more unproven parasitoid species. The latest candidate is *Lipolexis scutellaris* Mackauer (Hoy and Nguyen 2000). There is no literature to indicate that *L. scutellaris* has any impact on brown citrus aphid populations, or any other aphid populations, even in Asia, its region of origin. Although *L. scutellaris* can be reared on the brown citrus aphid in the laboratory, adult wasps are very small and capable of attacking only the smallest brown citrus aphid nymphs in a colony. Adults are extremely short-lived, even under low temperature conditions that maximize their longevity. Furthermore, aphids parasitized by *L. scutellaris* tend to drop from the plant prior to mummification, a pathological symptom indicative of a non-coadapted parasitoid-host relationship (Chow and Mackauer 1999). Thus the introduction of *L. scutellaris* appears not only inadvisable and ill-conceived, but completely unnecessary, given the current levels of biological control of brown citrus aphid provided by indigenous predators.

CONCLUSIONS

There are several problems with the way that the classical biological control method is currently applied as a pest control formula in Florida. First, classical introductions are increasingly used as a first line of defense against invasive pests, regardless of need or the availability of suitable candidate species for introduction. Thus, new pests are treated as automatic, rather than potential, targets for the classical approach and no time frame is allocated for assessing the responses of indigenous natural enemies before the introduction of exotic species. Second, many parasitoid species selected for importation have either very low probabilities of establishment, or no track record as effective biological control agents even in their countries of origin, leading to many failed introductions. Third, large investments in classical biological control programs can generate a vested interest in demonstrating "success" and when establishment is achieved, biased post-release evaluations may exaggerate the importance of the exotic species in suppressing the pest population. At the same time, the contributions of native predators to suppression of the pest may go unreported and unrecognized. The "apparency" of parasitism relative to predation (predation being far more difficult to observe and measure) tends to facilitate this disparity since introduced species are now almost invariably parasitoids. Finally, classical biological control is sometimes heavily promoted to commodity groups in trade journals as a formulaic solution, both before and after the fact. Claims of success, including research findings of dubious validity, are sometimes published in such journals, effectively circumventing the peer review process and potentially biasing databases with respect to the true success rate of classical biological control programs.

I conclude that the application of the classical approach as an automatic response to every new pest causes us *a priori* to underestimate the potential resilience of our native ecosystems to pest invasions. Moreover, the indiscriminate application of the classical approach is environmentally irresponsible as it exposes our ecosystems to an undue risk of non-target effects, including the potential disruption of biological control systems already in place.

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