

# Biological Pest Control in Mexico

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## Abstract

Mexico is a megadiverse country that forms part of the Mesoamerican biological corridor that connects North and South America. Mexico's biogeographical situation places it at risk from invasive exotic insect pests that enter from the United States, Central America, or the Caribbean. In this review we analyze the factors that contributed to some highly successful past programs involving classical biological control and/or the sterile insect technique (SIT). The present situation is then examined with reference to biological control, including SIT programs, targeted at seven major pests, with varying degrees of success. Finally, we analyze the current threats facing Mexico's agriculture industry from invasive pests that have recently entered the country or are about to do so. We conclude that despite a number of shortcomings, Mexico is better set to develop biological control-based pest control programs, particularly on an area-wide basis, than many other Latin American countries are. Classical and augmentative biological control and SIT-based programs are likely to provide effective and sustainable options for control of native and exotic pests, particularly when integrated into technology packages that meet farmers' needs across the great diversity of production systems in Mexico.

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**Sterile insect technique (SIT):** an area-wide technique involving the release of sterile male insects to achieve continuously high densities of sterile males in the field so that they greatly outnumber wild (fertile) males

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## INTRODUCTION

Mexico is one of the world's megadiverse countries, with a land area of almost 2,000,000 km<sup>2</sup>, over half of which is used for rearing livestock and just 22 million ha (11%) are under cultivation (128). The most important field crops are maize, beans, sorghum, cereals, potatoes, and vegetables that are grown on 72% of the cultivated area, with the remaining land given over to perennial crops such as coffee, sugarcane, and citrus. Some regions have become highly specialized in the production of certain crops, such as tomatoes in Sinaloa State, broccoli in Guanajuato State, and chili peppers in Chihuahua State.

With the world's thirteenth largest economy, paradoxically, Mexico is a wealthy country in which almost half of the population lives in poverty. Many resource-poor farmers (*campesinos*) live in communities known as *ejidos*. The majority (58%) of *ejido* farmers cultivate an area of 3 ha or less (64). Moreover, *campesinos* often speak indigenous languages, which represents a challenge to farmer education programs in remote rural areas where Spanish is not widely understood. This contrasts with production over large areas using modernized intensive techniques in certain parts of Mexico (95).

In this review we examine the influence of the biogeographical characteristics of Mexico, between North and South America, that have placed it at risk from exotic invasive insects, and how the country's geography has proved immensely valuable in controlling some devastating pests. We describe the rise of biological control in Mexico following some notable successes, including early use of the sterile insect technique (SIT), an autocidal method of biological control designed for area-wide application (50, 149) (see the **Supplemental Glossary**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). We then analyze the current situation by examining several examples of major pests and the role of biological control in their management. We pay particular attention to how Mexico's phytosanitary authorities are placed to respond to the threats posed by exotic pests that are invading the country or look set to do so. Finally, we examine the factors that favor and oppose biological control-based pest management programs in Mexico and find they exist in almost equal measure.

## Biogeographical Situation

Mexico's geography is dominated by two mountain ranges (Sierra Madre Oriental and Sierra Madre Occidental) that run along the eastern and western sides of the country. These ranges generate a diversity of ecosystems that include the arid and semiarid zones of northern Mexico, a temperate subhumid central plateau, and humid or subhumid tropical regions of the southeast. The mountainous terrain and arid areas restrict the zones that can be used for agricultural production to the coastal plains and central plateau. Climatic conditions, particularly precipitation levels, have been highly influential in the performance of numerous natural enemies released in Mexico (see **Supplemental Figure 1**, **Supplemental Figure 2**). The volcanic soils are fertile, although plagued by erosion problems in many places, exacerbated by deforestation, particularly where crops are grown on inclines.

As part of the Mesoamerican biological corridor that connects continental North and South America, Mexico's geographic location places it in danger from exotic pests invading from the northern and southern borders, including the Caribbean islands. Examples of pests that have recently invaded include the Asian citrus psyllid (*Diaphorina citri*), which spread south from the US border; the coffee berry borer (*Hypothenemus hampei*), brown citrus aphid (*Toxoptera citricida*), and Guatemalan potato moth (*Tecia solanivora*), which spread north from the southern borders

with Guatemala and Belize; and the cactus moth (*Cactoblastis cactorum*), which is threatening to invade from the Caribbean. However, the marked narrowing of the southern part of the country forms a 200-km-wide isthmus between the Atlantic and Pacific Oceans, creating a natural funnel-like structure that has proved to be of crucial importance to the success of SIT-based programs against screwworm (*Cochliomyia hominivorax*) and Mediterranean fruit fly (*Ceratitidis capitata*) by greatly reducing the area over which sterile flies are released.

## History of Biological Control in Mexico

Biological control in Mexico began and has evolved alongside that of the United States (15, 33). The Mexican governmental Commission on Agricultural Parasitology was formed in 1900, and from then until 1945 a number of natural enemies were collected in Mexico to combat exotic pests in Hawaii (37). During this period several natural enemies were introduced into Mexico to combat the citrus mealybug (*Planococcus citri*), the sugarcane stem borers (*Diatraea saccharalis* and *D. lineolata*), and the cottony cushion scale (*Icerya purchasi*), the last of which was controlled by the vedalia ladybeetle (*Rodolia cardinalis*) introduced in 1939 (15).

Between 1945 and 1990 the situation changed radically. The success of the citrus blackfly (*Aleurocanthus woglumi*) program established biological control as an enormously valuable tool against exotic pests. From 1950 to 1965 a series of introductions of natural enemies were made against a diversity of pests with varying levels of success, often as a last resort when chemical insecticides were failing to provide adequate pest control (28). By the 1970s courses on biological control were being taught in Mexican universities, and by 1975 a total of 15 federally funded Centers for the Production of Beneficial Organisms were producing natural enemies, particularly *Trichogramma* species for control of lepidopteran pests (52). The honorees of the Mexican Society for Biological Control, José Luis Carillo-Sánchez, Dieter Enkerlin-Schallenmuller, Silverio Flores-Cáceres, Eleazar Jiménez-Jiménez, and Hiram Bravo-Mojica, all made their principal achievements during this period (113).

From 1990 the role of biological control has been formalized at the federal and state government levels and within the academic community. In 1991, the National Reference Center for Biological Control (CNRCB) was opened in Tecomán, Colima, Mexico, and was recognized by the International Organization for Biological Control as an international reference center. Similarly, the state-level plant health committees (Comité Estatal de Sanidad Vegetal) recognized biocontrol as an option that should be considered when designing integrated pest management (IPM) programs, and began to earmark a certain percentage of their annual budgets to finance biocontrol activities.

The academic community began to grow in number and expertise; an increasing number of scientists and researchers were returning to Mexico having obtained their master's or doctoral degrees in biocontrol-related disciplines from US or European universities. These individuals formed the Mexican Society for Biological Control in 1989 and launched the Society's scientific journal, *Vedalia*, in 1994 (113). The most significant activity of the Society is the annual conference and preconference courses and workshops in biological control, which attract several hundred people every year. Students, technicians, and an increasing number of farmers take these courses that are taught by prominent Mexican and foreign scientists. Growing interest in the discipline has also been reflected in the increasing number of publications on biological control from researchers at Mexican institutions. The number of scientific papers published on biological control in Mexico in the 1990s exceeded the total production of the previous nine decades and appeared set to double during the following decade (2001–2010) (112).

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**Integrated pest management (IPM):** a multifaceted pest control method based on knowledge of the pest's biology and likely impact on yields to establish action thresholds at certain pest densities

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**Classical biological control:** the introduction of an exotic (nonnative) natural enemy to reduce and maintain exotic pest populations at acceptable densities indefinitely

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## NOTABLE EARLY SUCCESSES

The period between 1950 and the mid-1980s saw four remarkably successful programs of SIT-based and classical biological control (**Supplemental Text**). The first of these programs involved the classical biological control of the citrus blackfly (*Aleurocanthus woglumi*), which was first reported in Sinaloa State in 1935. The blackfly spread rapidly, causing massive losses in citrus-growing areas of the country (10). A joint project between the Mexican Department of Agriculture and USDA involving the introduction and release of the aphelinid *Encarsia perplexa* from south Asia resulted in effective biological control of the pest by 1955 (69). This program provided a clear example of the value of searching for biological control agents in regions that are climatically similar to that of the country that is seeking the enemies for biological control. The importance of the US-Mexico alliance in meeting the program's objectives was also key to the program's success (69, 132). Classical biological control of this pest has also been achieved in the United States and the Caribbean (73, 137).

A second classical biological control program was targeted at the Rhodesgrass mealybug, *Antonina graminis*, an exotic pest of pastures. Two encyrtid parasitoids, *Anagyrus antoninae* and *Neodusmetia sangwani*, from south Asia were released in Mexico in 1957–1959 in a program that ran in parallel to a USDA program in Texas (44). The latter species provided effective biological control over all parts of the country affected by the pest (38, 111).

The third program, which involves the eradication of the New World screwworm (*Cochliomyia hominivorax*) from North and Central America, is a textbook case of successful pest control using SIT (49, 146). Following a successful program in the southeastern United States, a joint US-Mexico Commission was formed in 1972 and charged with the task of eradicating this devastating pest of livestock from the US border to the narrowest point of Mexico at the Isthmus of Tehuantepec (**Supplemental Figure 1**). A mass-production plant was constructed near the center of the isthmus and began operating in 1976. The release of sterile flies, in combination with intensive programs of farmer education and animal inspection, was effective in progressively extending the screwworm-free zones down through Mexico until the whole country was declared screwworm free in 1991. The eradication zone was subsequently moved through Central America until its present location in Panama (146). The economic benefits have been estimated at US\$328 million per year for livestock producers in Mexico (152). A combination of remarkable levels of international cooperation and a number of biological and ecological factors, in addition to the reproductive biology of the fly, have been identified as contributing to the success of the SIT-based screwworm eradication program (91) (**Supplemental Text**).

The fourth program among the early successes of pest control in Mexico is that of the Mediterranean fruit fly (medfly, *C. capitata*), which has also involved a strong SIT component. This polyphagous exotic tephritid was first detected in Mexico in Chiapas State in 1977, close to the border with Guatemala (45). In response to the rapid northward spread of the fly Mexican and Guatemalan authorities and the USDA formed a commission in collaboration with the FAO and International Atomic Energy Authority (IAEA). An area-wide program was implemented, known as the Moscamed Program, involving the application of insecticidal baits, mechanical and cultural control of hosts, and restrictions on the movement of fruits and vegetables. These measures were combined with the release of sterile males produced in the Moscamed plant at Metapa, Chiapas, which has the capacity to produce 500 million flies per week. The pest was eliminated from Chiapas by 1982, although the barrier zone between Guatemala and Mexico is under continuous pressure of reinvasion due to the abundance of host plants in this region, particularly coffee (119).

The production process at the Moscamed plant and area-wide release of sterile males have been described in detail (3, 88, 123), and research to improve male mating success in the field is continuously reviewed (**Supplemental Text**). An economic analysis performed for the 30-year period 1978–2008 indicated a cost/benefit ratio estimated at 1/112, based on a combination of direct and indirect benefits of US\$40.5 billion and US\$19.6 billion, respectively (119). The Moscamed plant, now over 30 years old, is set to be completely rebuilt and will double its capacity over the next few years.

### Common Aspects of the Early Successful Programs in Mexico

These four programs shared at least six characteristics that jointly contributed to their success. (a) In all cases, the scale of the problem was recognized as a national crisis. Necessary legislation and operational responsibilities were swiftly defined at the federal government level and applied to all states. (b) Federal funding was made available to deal with the crisis. (c) Highly effective natural enemies were employed, and the target stages of the pest were not cryptic, i.e., they did not feed within plant structures that provide a physical refuge against natural enemies. In the case of SIT programs, the technique was highly effective because of the mating behavior of the pest. (d) USDA staff provided know-how and participated in all key aspects of the programs from their outset until their objectives were accomplished. (e) Each program was run by a small autonomous group of motivated and experienced personnel that dedicated 100% of their effort to running the program. (f) Finally, each program involved a combination of farmer education, training of field personnel, and continual monitoring of the program's efficacy. In addition, chemical- and biological-control-based measures in combination with quarantine restrictions were applied within the country and across national borders. These characteristics should prove useful in guiding the development and implementation of biological control programs elsewhere.

### Mexico as a Source of Natural Enemies

As a source of natural enemies, Mexico's contribution to biological control programs in the world exceeds the number of natural enemies that it has imported from elsewhere. Clausen (37) lists 23 parasitoids, 13 predators (mainly coccinellids), and 10 species of insects with other roles that were obtained from Mexico for 15 pest control programs between 1890 and 1970. Hawaii seems to have benefited significantly from Mexican natural enemies: Six of the 15 programs targeted pests in Hawaii. In the same period natural enemies were imported into Mexico to control eight species of pests. Why has Mexico played this important role? As a megadiverse country on the doorstep of the United States, searching for biological control agents in Mexico's many different ecosystems and diverse climatic conditions was likely an attractive option for USDA researchers wishing to identify candidate natural enemies for use in their programs.

The story is similar for weed control agents. CSIRO (Commonwealth Scientific and Industrial Research Organisation) researchers have released 18 species of phytophagous insects from Mexico for control of exotic weeds in Australia but have recently closed their Biological Field Station in Veracruz, Mexico, which has been operating since 1984 (124). In contrast, the weevils *Neochetina eichborniae* and *N. bruchi* were imported and released in Mexico in 1977 and 1994, respectively, but failed to control the water hyacinth *Eichhornia crassipes* at any site (77).

As a source of pests, Mexico has been identified as the point of origin of several pernicious species, notably the Mexican bean beetle (*Epilachna varivestis*), the boll weevil (*Anthonomus grandis*

*grandis*), and the Mexican fruit fly (*Anastrepha ludens*), and a few other pests of lesser or sporadic importance such as the coconut mealybug (*Nipaecoccus nipae*) (37).

## BIOLOGICAL CONTROL IN MEXICO: CURRENT SITUATION

The National Service for Agroindustrial Food Quality and Safety (SENASICA) is a decentralized branch of the Secretary of Agriculture, Livestock, Rural Development, Fisheries and Food (SAGARPA). SENASICA is responsible for plant and animal health, food safety, and inspection of agricultural produce and animals at national borders and inspection points. The current director of plant health in SENASICA is a founder and ex-President of the Mexican Society for Biological Control, so that biocontrol options are invariably considered when planning governmental responses to emerging pest problems. In such cases, SENASICA calls on the CNRCB reference center to evaluate possible options. Pests that represent major threats to agriculture become the subject of nationwide programs of monitoring and legal controls. In 2011–2012 a total of 65 organisms, of which 42 were insects and mites, including 27 species of exotic tephritid fruit flies, were classified as requiring national vigilance and quarantine measures (**Supplemental Table 1**).

### Current Programs of Biological Pest Control: Seven Case Studies

The effectiveness of biological control and IPM practices has been the subject of multiple studies targeted at native and exotic pests (11, 90), including lepidopteran pests (*Heliothis/Helicoverpa* spp., *Spodoptera* spp., *Plutella xylostella*, *Pectinophora gossypiella*), homopteran pests (*Bemisia tabaci*, *Planococcus ficus*), and a number of coleopteran pests such as the boll weevil (*Anthonomus grandis grandis*), Mexican bean beetle (*Epilachna varivestis*), whitegrubs (*Phyllophaga* spp.), and weevil pests of avocado (*Copturus aguacatae*, *Conotrachelus aguacatae*, *Heilipus lauri*). The factors that determine the varying degrees of success of such programs are illustrated in the following case studies, which were selected on the basis of the scale of the program, the national importance of the pest, and the spectrum of biocontrol strategies employed.

**Case 1: Pink hibiscus mealybug.** Since the CNRBC opened in 1991, the country is now well placed to respond to pest threats through the development of management programs with a strong biological control component. The recent control of the pink hibiscus mealybug (*Maconellicoccus hirsutus*) is a clear example. This mealybug is a polyphagous pest of fruit and timber trees and a number of horticultural crops. Originally from south Asia, the mealybug was detected in California and around the city of Mexicali, Baja California, Mexico, in 1999. Based on previous successes in several Caribbean islands (70), two encyrtid parasitoids, *Anagyrus kamali* and *Gyranusoidea indica*, were imported from Puerto Rico and were released in small numbers around Mexicali in September 1999 (122). By 2004 the pest was detected in high numbers infesting teak and *Acacia* spp. in the west coast state of Nayarit (122). SAGARPA immediately initiated an emergency phytosanitary program involving restrictions on the movement of infested produce and chemical and cultural control measures. These actions were complemented by the rearing and release of *A. kamali* and *G. indica*. An exotic coccinellid predator, *Cryptolaemus montrouzieri*, was also obtained from laboratories in the United States, Canada, and Mexico and released in large numbers (>6.5 million individuals) (122). Importantly, training was provided by USDA-APHIS workers who had experience controlling the pest in the Caribbean (78).

Under the auspices of the CNRCB, a parasitoid-rearing facility began operating in Nayarit, and between August 2004 and April 2008, 25 million *A. kamali* individuals were reared and released in the states of Nayarit and Jalisco. Releases of *G. indica* were discontinued in 2005 as there was no

evidence of their establishment at field sites. The coccinellid *C. montrouzieri* was highly effective at controlling all stages of the mealybug in high-density infestations. However, the beetle tended to migrate away from low-density infestations in search of more abundant prey. The opposite occurred for the parasitoid *A. kamali*, which was effective in controlling early instars of the pest in areas of moderate- or low-density infestations. Because of this, high-density infestations were targeted for release of the coccinellid, which despite interference by ants in some areas (141) resulted in rapid control of the pest. In areas with moderate pest densities or following partial control by the coccinellid, releases of *A. kamali* resulted in high levels of parasitism (>90%) and sustained control of the pest at very low densities (**Supplemental Figure 3**). By mid-2008 it was no longer necessary to release the coccinellid because the incidence of high-density infestations was minimal. Current production of *A. kamali* fluctuates around 20 million wasps per year and an additional production facility opened in Nayarit in 2010. Both enemies are now well established and provide effective control of the pest except in areas where broad-spectrum insecticides are applied to control other pests of field crops and fruit trees (122).

Echoing the factors that were determinantal in historical programs, the following features contributed to the success of this program. (a) Federal funding to address the problem was provided promptly and administered efficiently. (b) SENASICA responded rapidly following detection of the pest in Nayarit, and the CNRCB was effective in coordinating natural enemy rearing and field release activities. (c) USDA-APHIS researchers with experience of candidate natural enemies collaborated from the outset of the program. (d) Highly effective natural enemies were available: The complementary action of the coccinellid and the parasitoid permitted a two-step strategy of natural enemy releases at field sites (141) (**Supplemental Figure 3**).

**Case 2: *Anastrepha* spp. fruit flies.** Biological control of *Anastrepha* spp. in Mexico involves a combination of SIT and parasitoid-based control measures. Tephritid fruit flies of the genus *Anastrepha* are major pests of cultivated and wild fruits in Latin America (1). As part of the National Campaign Against Fruit Flies, control of *Anastrepha* species in Mexico has gained much from the experience of the medfly program. Indeed, adjacent to the Moscafruit plant is a smaller Moscafruit plant, which opened in 1994, that currently produces 175 million *Anastrepha ludens* pupae and 40 million *Anastrepha obliqua* pupae per week (55). The polyphagous Mexican fruit fly, *A. ludens*, is the most damaging fruit fly pest in Mexico and requires the use of postharvest quarantine treatment measures (3). The activities of the SIT program in Mexico have been reviewed (88, 96) (**Supplemental Text**).

The use of SIT is complemented by the action of native and exotic parasitoids. Of the nine exotic species introduced in the 1950s, *Diachasmimorpha longicaudata* (Braconidae), *Aganaspis indica* (Figitidae), and *Pachycrepoideus vindemmiae* (Pteromalidae) are still recovered in field-collected samples, although the last two species occur at a low prevalence (5). Initial field studies on the solitary larval-pupal parasitoid *D. longicaudata* indicated generally low levels of parasitism (5). However, its use in augmentative biological control was re-evaluated in the early 2000s. Weekly releases of 940 parasitoids per hectare resulted in a 70% reduction in *Anastrepha* populations in mango orchards in southern Mexico (87). Since then, the use of mass-reared *D. longicaudata* has been incorporated into the National Campaign Against Fruit Flies and releases are targeted at backyard orchards, urban zones, and areas of wild fruit trees with difficult access (86). The parasitoid has also been used to control outbreaks of *C. capitata* in Chiapas (85). The *D. longicaudata* colony is maintained in the Moscafruit plant using irradiated *A. ludens* larvae (30, 84) and is producing 26 million parasitoids per week at the time of writing. In Chiapas, average field parasitism rates are greater than 30% (86). However, sampling fruit in the field underestimates rates of parasitism

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#### Augmentative biological control:

the practice of increasing the numbers of natural enemies in a particular site or area to reduce the density of exotic or native pest populations

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**Conservation biological control:**

the practice of providing the conditions that favor the presence and reproduction of natural enemies in a particular area

(107) and does not estimate parasitoid-induced mortality from stinging larvae. A cost analysis for the production of *D. longicaudata* is needed.

*Anastrepha* flies are attacked by a guild of native parasitoids, some of which are maintained in laboratory colonies (5, 6, 31). Native parasitoid species vary widely in host specificity (72), distribution and guild composition (131), and parasitism behavior (130). Forest fragments represent reservoirs of native and exotic parasitoid species for conservation biological control of *Anastrepha* species (4). For example, native tropical plum trees (*Spondias mombin*) can be a source of large numbers of native parasitoids (2).

In general, the program to control *Anastrepha* spp. in Mexico has been highly successful. To date, 85,000 ha of fruit-growing areas in nine states along the border with the United States have been declared as fruit fly-free zones and an additional 186,000 ha of fly-infested fruit crops have been declared areas with a low prevalence of pestiferous tephritids (55). Additional areas have been certified as temporarily free of tephritids during the fruit production period. The cost/benefit ratio has been calculated for each of the states that participate in the fruit fly-free program (120).

**Case 3: Coffee berry borer.** From a biological control perspective, one of the most intensely studied pests in Mexico is the coffee berry borer, *Hypothenemus hampei* (40, 147). Coffee is grown in the mountainous areas of southern Mexico, and 282,000 farmers depend on this crop (64). Shade-grown coffee also contributes to a diversity of ecosystem services, including pest control (104). The coffee berry borer is a scolytid beetle of African origin that is considered the most serious pest of coffee worldwide. This insect entered Mexico from Guatemala in 1978 and rapidly spread to all the principal coffee-growing regions (16, 23). Given the economic and social importance of coffee production, a national campaign against the pest was initiated by SAGARPA in 1995 (110, 126).

The adult female beetle bores into the coffee berry, lays her eggs, and guards the developing progeny until they are ready to emerge (18). Three species of African parasitoids have been imported into Mexico: *Prorops nasuta* (65, 66), *Cephalonomia stephanoderis* (20), both of which are solitary bethylid ectoparasitoids of larvae and pupae within infested berries, and *Phymastichus coffea* (46, 67), a gregarious eulophid that parasitizes adult beetles as they tunnel into the berries. Native natural enemies, including ants (103), pathogenic fungi (42, 43), and a native bethylid parasitoid that is also a facultative hyperparasitoid of *P. nasuta* and *C. stephanoderis* (100, 101), also attack *H. hampei*.

Researchers in Chiapas have worked intensively on this pest. A unique system of on-farm rearing of parasitoids has been developed using naturally infested berries that would otherwise be destroyed (22). Studies have also been performed on the chemical ecology of (36) and interactions between natural enemies (26, 34), on the pest's symbiotic microorganisms (99), and on the development of cheap traps for monitoring *H. hampei* populations (21). However, the physical refuge provided by the coffee berry, the parental care behavior provided by the female, and the short temporal window during which the female beetle is susceptible to control measures outside the fruit are characteristics that severely hinder biological control (16, 41, 66, 68). The use of *Beauveria bassiana* as a biological insecticide received passing support from state phytosanitary committees (110) but was discontinued.

In reality, it is the price of coffee that determines the management of each plantation and therefore the magnitude of the coffee berry borer infestations (19, 23). When prices are low, harvesting the crop may not be economically viable, infested berries remain unpicked, and pest populations soar. In contrast, high prices lead to high rates of harvesting and plantation care and pest populations fall. As a result, the National Campaign has suspended all biocontrol measures and now stipulates that the pest should be controlled by plant sanitation procedures (17), including



the disposal of unpicked and fallen berries. The degree of implementation of this practice depends largely on fluctuations in the price of coffee (23).

**Case 4: Velvetbean caterpillar.** Stimulated by the success of a baculovirus-based control program against the noctuid velvetbean caterpillar, *Anticarsia gemmatalis*, in Brazil (89) and the results obtained in the southern United States (51), researchers at Mexico's National Institute for Agriculture, Forestry and Livestock Research (INIFAP) began studying the use of the virus for control of this pest in soybean in the northern state of Tamaulipas. An in-field production system was used to generate large quantities of the virus. This involved the application of a Brazilian isolate of the virus to soybean plants heavily infested by *A. gemmatalis* larvae. Several days later, when larvae were at the late stages of infection, the larvae were manually collected and frozen until required for processing. Application of  $\sim 1 \times 10^{11}$  virus occlusion bodies per hectare results in almost 100% mortality of the pest (13).

The cost of the virus produced by the INIFAP experimental station is US\$4.0 per hectare (plus US\$10 in application costs), and a single application provides control of *A. gemmatalis* for the entire crop cycle, compared to an average of three applications of pyrethroid insecticides per crop cycle (14). Densities of natural enemies in baculovirus-treated soybean crops were on average five times higher than densities observed in cypermethrin-treated fields, and the incidence of secondary pests was significantly lower in virus-treated than in pyrethroid-treated crops (12). The virus is now used regularly over an area of 15,000 ha of soybean, with major reductions in the use of chemical insecticides (14). From a project costing US\$184,000, the cost/benefit ratio has been estimated at 1/27, a very favorable result (14).

**Case 5: Maize and sugarcane stalk borers.** A complex of stalk-boring lepidopteran pests of maize and sugarcane has been the target of numerous attempts at biological control. Seven species are responsible for the majority of economically important infestations in maize and sugarcane. *Diatraea grandiosella*, *D. lineolata*, and *D. muellerella* are mainly pests of maize; *D. considerata* and *D. magnifactella* prefer sugarcane; and two additional species, *D. saccharalis* and *Eoreuma loftini*, are found at similar levels on both crops (117). The relative importance of each of these pests in northeastern Mexico has changed markedly over the past 70 years (115).

A total of 37 species of parasitoids have been reported to attack this pest complex in Mexico (117). In addition to native parasitoids, the release of *Trichogramma* spp. against these pests has been occurring since the 1920s. Approximately 35% of the total production of *Trichogramma* spp. in Mexico is targeted at the control of stalk-boring Lepidoptera (8). Reports on the effectiveness of these parasitoids vary from generally favorable (9, 58) to decidedly poor or highly seasonal (116, 148). The need for a detailed and systematic evaluation of the effectiveness of *Trichogramma* spp. for stalk borer control has been highlighted repeatedly (27, 117). Studies on the natural prevalence of parasitism by all species have indicated generally low or variable levels (114), which motivated the introduction of the braconid *Cotesia flavipes* in 1985. This wasp has proved useful against *D. saccharalis* and *D. lineolata* (133, 150) but performed poorly against other *Diatraea* spp., possibly due to differences in the host encapsulation response (151).

In an enduring collaborative effort involving researchers from INIFAP, Texas A&M University, and the sugar refinery at Los Mochis, Sinaloa, 13 species of parasitoids were redistributed, released, and monitored between 1990 and 2006, resulting in a 30% average reduction in pest-damaged sugarcane and corresponding savings in insecticide use. Despite growing take-up of biocontrol practices in sugarcane production since the 1990s (9), management of stalk borer populations with effective biocontrol agents remains an elusive goal (117).

**Case 6: Orthopteran pests.** The Central American locust *Schistocerca piceifrons piceifrons* is a sporadic but serious pest in the southeastern states of Tabasco, Campeche, and Yucatán and also affects the Huasteca region, which includes the states of Hidalgo, San Luis Potosi, Tamaulipas, and northern Veracruz (61). Following the successful use of fungal pathogens elsewhere (71), trials in the Yucatán using native isolates of *Metarhizium anisopliae* var. *acridum* ( $4 \times 10^{12}$  conidia per hectare) in a mineral oil formulation provided effective control of gregarious swarms of the locust (60). Similar trials in the La Huasteca region resulted in 70–90% mortality in swarms following applications of the pathogen (25). The use of this fungus has been incorporated into the National Campaign against the locust and is undergoing registration in Mexico as a biological insecticide. The fungus is produced in two state-run laboratories, in Guanajuato and Yucatán, and a privately owned business in Puebla and was applied to 4,000 ha of locust infestations in 2010 at a cost of approximately \$US10 per hectare (106). The use of fungal insecticides is expected to increase fourfold over the coming years.

A complex of grasshopper species, particularly *Brachystola magna*, *B. mexicana*, *Melanoplus differentialis*, and *Sphenarium purpurascens*, is the subject of a SENASICA-funded campaign in the center of the country and the northern state of Chihuahua (24). Maize, beans, sorghum, soybean, and pumpkin are the most seriously affected crops (127). In 2011, between 500 and 4,000 ha of crops in Guanajuato and 8,000 ha in Tlaxcala were to be treated with *M. anisopliae* var. *acridum* (125). The use of this pathogen has been reported as highly effective, with levels of pest control that consistently exceed 70% (61).

**Case 7: Brown citrus aphid.** The brown citrus aphid (*Toxoptera citricida*), a vector of *Citrus tristeza virus*, was first detected in the Yucatán in 2000 (82). Between 1998 and 2002, 18 million individuals of the exotic coccinellid *Harmonia axyridis*, plus several million individuals of two species of native coccinellids and the predatory chrysopid *Chrysoperla carnea* s.l., were released in the Yucatán in a SAGARPA-funded control program; however, their impact on brown citrus aphid populations was not monitored (75). Studies in Florida and elsewhere with exotic parasitoids have given variable results (63, 80), and trials with fungal pathogens have been similarly variable in their efficacy (59, 98). In contrast, the conservation of natural enemies, particularly predatory coccinellids, syrphids, and chrysopids, with reduced use of insecticides has produced favorable results in Florida (79, 81, 83) and may be a useful model to follow. Accordingly, a technology package involving applications of the entomopathogen *Isaria fumosorosea* (formerly *Paecilomyces fumosoroseus*), liberation of *Chrysoperla rufilabris* or a native coccinellid, and supplementary food sprays to favor the retention and reproduction of predatory insects has been developed for Mexican citrus growers (75).

## CURRENT AND FUTURE PEST THREATS WILL REQUIRE BIOLOGICAL CONTROL

Megadiverse tropical countries are at high risk from invasive species that threaten their unique biodiversity (76, 94). Mexico is no exception and is currently being invaded, or about to be invaded, by a handful of serious pests. The risks associated with releasing exotic natural enemies for classical biological control have been analyzed (144), but studies on nontarget impacts of biocontrol agents in megadiverse regions are rare. Recent arrivals include the Guatemalan potato moth (*Tecia solanivora*) in Chiapas (39); melon thrips (*Thrips palmi*) established in the states of Chiapas, Campeche, Yucatán, and Quintana Roo (93); and red palm mite (*Raoiella indica*), a pest of palms and banana, which invaded the Yucatán (32).

Serious threats close to Mexico's borders include the redbay ambrosia beetle (*Xyleborus glabratus*), currently present in Florida and Alabama, which vectors a fungal pathogen that

could damage Mexico's avocado industry (48), and the cactus moth (*Cactoblastis cactorum*), which provided rapid control of prickly pear cactus (*Opuntia* spp.) in Australia, South Africa, and elsewhere in the 1920s and 1930s. The moth was introduced to a number of Caribbean islands from 1957 onwards (129, 153), was detected in Florida in 1989 (97) and is now spreading across the southeastern United States with serious consequences for local *Opuntia* (135, 136). Mexico harbors the highest diversity of *Opuntia* species, which are of great ecological, cultural, and culinary importance (29, 134). A small outbreak of the moth in 2006 on Mexico's Caribbean coast was rapidly eradicated by physical destruction of larval infestations and egg masses (92). A large-scale monitoring program is now under way as part of a US-Mexico joint program (57), but if *C. cactorum* manages to invade the country, classical biological control and SIT-based area-wide programs are likely to be the principal control options given the diversity and geographical distribution of cactus species attacked by the moth (62).

The final threat is among the most serious: The recent arrival of the Asian citrus psyllid (*Diaphorina citri*) is expected to have a devastating effect on citrus production. This psyllid is the principal vector of Huanglongbing, a destructive bacterial disease of citrus. The pest was reported in southern Texas in 2001 and was subsequently found in many parts of Mexico (118). The Huanglongbing pathogen followed shortly after, with the first report in 2009 in the Yucatán; the disease is now present in 13 states and is the most serious threat to citrus production in Mexico.

Research in Florida has indicated that native and exotic coccinellids could be important agents for the control of *D. citri* (109). In Mexico, however, the principal focus of attention has been the exotic eulophid ectoparasitoid *Tamarixia radiata* (56). The wasp has provided excellent control of the psyllid on Réunion Island and good results on the islands of Guadeloupe and Puerto Rico (47, 105), although its performance in Florida has been mediocre (108).

The strategy developed in Mexico involves mass production of the parasitoid in the CNRCB laboratories in Colima using psyllids reared in cages with orange jasmine (*Murraya paniculata*) (53). Current production in Colima is 1.2 million wasps per year. A new facility in Yucatán is producing 3 million parasitoids per year for release in Quintana Roo, Yucatán, and Campeche. Laboratories for parasitoid production are also being built in the citrus-growing areas of Veracruz, San Luis Potosí, and Tamaulipas. Initial results in Colima have been promising, with a 90% reduction in psyllid populations in orchards following weekly releases of 400 wasps per hectare (121). The next few years will be decisive: If the parasitoid proves effective, a campaign of farmer education would be required to promote reduced use of insecticides and increase the areas over which parasitoid-mediated control could be applied.

## PRODUCTION OF NATURAL ENEMIES FOR AUGMENTATIVE BIOLOGICAL CONTROL

Currently, 74 laboratories distributed across 25 states are producing natural enemies in Mexico. Of these laboratories, 69 are run by local and regional grower organizations in collaboration with state committees for plant health. These laboratories produce 11 species of parasitoids, 3 species of predators, and 6 entomopathogens (**Supplemental Table 2**), as well as a range of biocontrol agents and antagonists for plants and plant pathogens. *Trichogramma* spp. are produced in 27 of the 69 laboratories. In fact, Mexico is the world's third-largest producer of *Trichogramma* after Russia and China (145). In addition, commercial suppliers of natural enemies offer approximately 20 species of predators, parasitoids, and entomopathogens mostly for use in greenhouses and covered crops. The commercial suppliers are responsible for the majority of requests to SENASICA for importation of natural enemies (**Supplemental Table 2**).

The commercialization of parasitoids and predators is not regulated in terms of quality or performance (142). Moreover the efficacy of using natural enemies for augmentative biocontrol has not been systematically evaluated for the majority of crop-pest-enemy combinations in Mexico (28, 74, 117). This should be considered a priority given the current investment of resources in the mass production of *Trichogramma* spp. in many parts of the country. A notable exception is control of lepidopteran pests on field-grown tomatoes in Sinaloa, in which releases of *Trichogramma pretiosum* in combination with biorational insecticides and mating disruption pheromones resulted in significant reductions in pest densities and a generally lower prevalence of pest-damaged fruit (139, 140). The IPM approach was also consistently cheaper than chemical control.

## CONCLUSIONS AND RECOMMENDATIONS

This review has focused on past and present successes and failures in biological pest control and revealed great challenges from native and exotic pests that are established or in the process of invading the country. Additional threats come from exotic pests approaching the northern and southern borders; experience tells us that these pests will arrive sooner than expected. Climate change is also likely to exacerbate issues with exotic and native pests over the coming decades (54, 138).

Dealing with these pests requires a national policy that promotes biological control in IPM programs as one of the few sustainable options available to farmers and extension workers (28). The development of such a policy needs to build on the strengths already present in the country. Our analysis of the factors that favor biocontrol in Mexico (**Table 1**) reveals that Mexico is better positioned than many other developing countries in having scientific, operational, and administrative infrastructure, a small but active academic community with links to international collaborators, and funding bodies willing to support biocontrol research and implementation. For farmers wishing to access lucrative markets in the United States and Europe, pesticide residue regulations in those countries are an additional factor that favors low pesticide inputs in agriculture.

However, the same analysis indicates that the factors that impede biocontrol programs exist in almost equal measure to those that promote such practices (**Table 1**). We could only identify 12 Mexican scientists whose current work has a clear and consistent impact on the development of biological pest control. Indeed, Mexico has a paucity of scientists and low investment in R & D compared with regional counterparts such as Brazil. Funding agencies have tended to fund small, short-term projects from individual scientists. However, because of reduced competition among scientists, projects with modest advances can obtain sequential periods of funding despite a low likelihood of a successful outcome.

Broad-spectrum pesticides are still widely used, and monitoring of residues in food for consumption within Mexico is inadequate. With a few notable exceptions (14, 119, 120), analyses of the economic benefits of pest management programs that include a biocontrol component are lacking, leaving farmers with no firm information on which to base their management decisions. The same applies to natural enemies from the national network of mass-production laboratories, for which studies on quality control and efficacy in the field are few in number and often contradictory.

Despite this scenario, the outlook is hopeful and there are signs that a number of the shortcomings are being addressed. First, the number of active scientists registered in Mexico's National System of Researchers is growing at a rate of 11% per year across all disciplines. Second, the need for interinstitutional collaboration among scientists and medium- to long-term funding for effective research projects is becoming recognized. SAGARPA and the National Science and Technology Council (CONACYT) recently awarded multimillion-dollar funding to networks of researchers in different academic and extension institutions to address the problems of

**Table 1** Factors that favor and impede biological pest control in Mexico

Factors that favor biocontrol	Factors that impede biocontrol
1. Notable successes in the past	1. Mostly short-term funding (2–3 years) for research projects
2. Funding bodies becoming aware of the value of interinstitutional and multidisciplinary collaborations	2. Most funding directed at small, single-institution projects (US\$10,000–50,000)
3. A handful of highly experienced biocontrol scientists	3. Paucity of active experienced scientists in general
4. Area-wide programs (SIT) in use	4. Highly divergent production systems: large, technologically intensive systems versus small, traditional systems
5. Federal government (SAGARPA) interested in funding effective biocontrol programs	5. Widespread use of broad-spectrum pesticides that affect natural enemy populations
6. Ready access to international collaborators (e.g., USDA-APHIS)	6. Limited monitoring of pesticide residues in foods destined for consumption within Mexico
7. Mexican Society for Biological Control provides training and facilitates collaboration within Mexico	7. Major threats from invasive pests in a range of crops
8. Natural enemy production laboratories and commercial suppliers present in many parts of the country	8. Limited expertise in the evaluation of the potential impact of exotic natural enemies on native species
9. CNRCB and various academic institutions involved in developing biocontrol programs	9. No clear incentives for farmers to adopt biocontrol or IPM practices
–	10. Insufficient evaluation of the efficacy of natural enemies currently being released in different crops
–	11. Cost-benefit analyses lacking for many biocontrol/IPM programs
–	12. Inadequate dissemination on the value of biocontrol at all levels (farmers, academics, general public)

Abbreviations: SIT, sterile insect technique; SAGARPA, Secretary of Agriculture, Livestock, Rural Development, Fisheries and Food; CNRCB, National Reference Center for Biological Control; IPM, integrated pest management; USDA-APHIS, US Department of Agriculture–Animal Plant Health Inspection Service.

Huanglongbing/Asian citrus psyllid and to a project targeted at pests of sugarcane. Third, growing public demand for food with minimal pesticide residues is expected to influence large supermarket chains to favor products grown under IPM.

Promoting IPM with natural enemy conservation or augmentation will require the support of the pesticide industry. The incidence of chronic and acute pesticide poisoning (35) and the continued use of chemicals that have been phased out in developed countries are issues of concern in Mexico (102). The new generation of biorational insecticides, which can be used in combination with natural enemies, represents important new markets for agrochemical companies in Mexico.

Improved take up of augmentative biocontrol faces a series of challenges, including indifference from the agrochemical industry, farmer's risk-averse attitudes to changes in their habitual use of pesticides, inertia by governmental institutions, and the need for simplified and harmonized international guidelines for the importation and release of natural enemies (143). We suggest that the way forward should consider the development of crop protection packages tailored to meet the needs and capabilities of farmers across different sectors. These packages should include measures to conserve natural enemy populations, such as the use of biorational insecticides and pheromones where available, in combination with natural enemy augmentation and cultural control measures where possible. Farmers and extension workers will need to become involved in education and training programs that are appropriate to their experiences and understanding of crop-pest relationships. Experience with a small but growing number of pests indicates that such packages can be highly effective if developed and implemented with farmer participation (7, 90).

## SUMMARY POINTS

1. Case studies reveal considerable variation in the success of biological control in Mexico, from highly successful classical biological control and SIT-based area-wide programs to continued challenges facing augmentative and conservation-based programs.
2. Mexico faces major threats from exotic pests that have recently entered the country or are about to do so.
3. The factors that favor or impede biological control exist in almost equal measure. New programs should build on the strengths in SIT and classical biocontrol but also strengthen shortcomings in augmentative control within IPM programs. This will require considerable investment in infrastructure but cost/benefit analyses performed to date indicate highly favorable returns on investments in biological control.
4. Few scientists in Mexico have a tangible impact on the development and practice of biological control in the country. Funding multidisciplinary networks of researchers across multiple institutions or scientists with an established record of achievements could be an effective means of assigning limited resources.
5. The efficiency of mass-produced natural enemies needs to be validated across a range of pest-crop systems, and the economic benefits of biocontrol-based IPM programs should be made clear to farmers and extension workers.
6. The development of technology packages involving farmer participation from the outset could provide a number of effective and sustainable solutions to many of the current pest problems, but the advantages of such technologies must be clear to growers if they are to be widely adopted.

## DISCLOSURE STATEMENT

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## Supplemental Text

# BIOLOGICAL PEST CONTROL IN MEXICO

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This document provides additional information that complements the text in the main body of the review. The document is divided into five sections:

1. The New World screwworm, *Cochliomyia hominivorax*
2. The medfly, *Ceratitis capitata*
3. The Citrus blackfly, *Aleurocanthus woglumi*
4. SIT-based control of *Anastrepha* spp.
5. Literature Cited

## THE NEW WORLD SCREWWORM, *COCHLIOMYIA HOMINIVORAX*

Eradication of the New World screwworm (*Cochliomyia hominivorax*) from North and Central America has become a textbook example of the effectiveness of the sterile insect technique (SIT) applied on an area-wide basis (17, 29, 49). This program involved rearing billions of flies that were sterilized and released over large areas. Continuously high densities of sterile males ensured that the large majority of wild females would be mated by sterile males and would not produce viable offspring leading to a rapid decline in the natural population. SIT was employed progressively to eradicate this devastating pest of livestock from the southeastern United States between 1958 and 1966. A US-Mexico border zone was established to prevent reinfestation from populations in Mexico; which was effective until a mild winter contributed to a major outbreak in Texas in 1972. This led US and Mexican livestock owners to lobby jointly for a SIT-based eradication program in Mexico. In 1972, a joint US-Mexico commission was formed and charged with the task of eradicating the pest from the US border to the narrowest point of Mexico at the Isthmus of Tehuantepec. A screwworm production plant was constructed close to Tuxtla Gutiérrez, Chiapas State, near the center of the isthmus barrier zone. The plant began operating in 1976 and has the capacity to produce over 500 million flies per week. Release of sterile flies, in combination with intensive programs of farmer education, insect trapping, animal

inspection points on commercial livestock routes, case reporting, and rapid treatment of infested animals with organophosphate powder, was effective in progressively extending the screwworm-free zones down through Mexico until the Isthmus of Tehuantepec was reached in 1984. The release of flies then continued over southeastern Mexico and the whole country was declared screwworm free in 1991, although an outbreak in 1992, which was quickly controlled by additional releases of sterile flies, underlined the importance of imposing strict quarantine restrictions on the movement of livestock from infested areas of Central America. Between 1994 and 2001 the screwworm eradication zone was subsequently moved through each of the countries of Central America until its present location in Panama, where a production facility with a capacity of 80 million flies per week maintains the biological barrier between Central and South America (49). Estimates of the economic benefits of the program in Mexico vary (28, 47), but benefits have been estimated at US\$328 million per year for livestock producers in Mexico (53), in addition to the elimination of the significant risk of human morbidity and mortality from myiasis in Mexico and Central America.

The screwworm plant at Tuxtla Gutiérrez is currently producing approximately 8 million flies per week, just enough to maintain the colony. There are several opportunities for eradication on Caribbean islands, which represent a continual threat of reinvasion for the neighboring screwworm-free countries. At the time of writing, feasibility study is under way for the Dominican Republic that, if funded, would require the establishment of a new colony and the ramping of production to operational program levels. However, given that the capacity of the Panamanian plant is only sufficient to maintain the current biological barrier, the strategic value of the Mexican plant as an instrument for rapid response to new outbreaks is clear. This was thoroughly demonstrated during an outbreak of *C. hominivorax* in Libya in which the Mexican plant supplied a total of 1,300 million flies that were released over an area of 41,000 km<sup>2</sup> in Libya between December 1990 and October 1991, resulting in the rapid elimination of the pest (17). In contrast, a recent program in Jamaica failed (20), apparently due to a series of operational difficulties on the island (15).

### **THE MEDFLY, *CERATITIS CAPITATA***

The eradication of the medfly, *Ceratitis capitata*, from the southern state of Chiapas was achieved by the rapid response to this invasive pest, the application of a SIT-based program in



combination with quarantine measures on the movement of potentially infested produce and intensive trapping, and the application of insecticidal baits. The principal aspects of the program are described in the main body of the review, but it is important to note that the Moscamed program is undergoing a continual process of improvement aimed at reducing production costs and improving the sexual competitiveness of the sterile male flies (21). For example, the original bisexual strain was replaced in 2002 with a genetic sexing strain that carries a temperature sensitive lethal (TSL) allele (18). Exposure to elevated temperature during embryonic development results in death of female embryos, meaning that diet resources and handling of developing larvae and pupae are fully dedicated to male rather than female production, effectively doubling the production capacity of the Moscamed plant. The TSL strain (named Vienna 7/Toliman 99) is sexually competitive compared to wild males (31, 40).

Since 2002, the Moscamed plant receives all *C. capitata* eggs for rearing in daily truck deliveries from a very large production plant located at El Pino Medfly Rearing Facility in Guatemala (9). However, this dependence on the production of eggs in Guatemala will soon end as Mexico's Moscamed plant, now over 30 years old, is set to be completely rebuilt and will double its capacity over the next few years. The new facility should contribute to future plans to extend the biological barrier toward the south of Guatemala over the coming decade, greatly extending the size of the contention zone and markedly reducing the risk of medfly outbreaks in Mexico and the United States (16).

A visit to the Moscamed facilities reveals that a series of quality control checks have been implemented at every step of the process (22), from the transport and receipt of eggs produced in Guatemala to the temperature and humidity conditions experienced by flies during the aircraft liberation process. As a result, potential problems can be rapidly detected and corrected to ensure the continued success of the program. Recent improvements include the redesign of the cages used to hold adult flies that favor male sexual competitiveness (13, 34) and the use of orange oil aromatherapy during adult sexual development (44), both of which improve the mating success of males in the field. Similarly, improvements have been made to adult eclosion procedures and the release of sterile flies from GPS-guided aircraft. The current fly release machine includes a refrigeration unit, a box containing 15 million chilled flies and a lower rotating band that moves the flies to the aircraft's liberation chute at a calibrated rate (48). Three chilled boxes, containing a total of 45 million flies, are loaded into each aircraft that flies a GPS-guided route that is

subsequently verified when the flight data are downloaded upon return to the extensive new adult eclosion and liberation facilities next to the Tapachula International Airport. Particular attention is paid to controlling humidity prior to the release of adults, as flies tend to clump together and suffer high mortality if moisture levels in the aircraft fly release machines exceed specified values.

As a caveat, the effectiveness of the Moscamed program is faced by three additional obstacles. First, the success of the program is continually challenged by the richness and abundance of plants that are hosts to medfly larvae, so that SIT-based control will continue to require insecticidal bait spraying measures (involving the use of the biorational compound, spinosad GF-120) as an additional means to reduce pest population densities. Second, medfly females are prone to remating, particularly when the first mating occurred with a sterile male (7, 30, 50, 51). This places an additional requirement on the SIT program to maintain sterile male densities at continuously high levels to minimize the frequency of matings with wild males. Finally, perhaps one of the most influential factors determining the success of the area-wide control of medfly in the region is the international price of coffee. This issue revolves around the management of coffee plantations: When prices are low, coffee berries are not harvested and fallen berries are not cleared away, resulting in a dramatic increase in the abundance of hosts for the development of *C. capitata* (36).

### **THE CITRUS BLACKFLY, *ALEUROCANTHUS WOGLUMI***

The importation and liberation of natural enemies of the citrus blackfly, *Aleurocanthus woglumi*, in Mexico provides an outstanding example of (a) the importance of compatibility in climatic conditions in the areas of natural enemy prospection, and (b) the effectiveness of releasing multiple natural enemies against a pest in a classical biological control program. It also highlights the pivotal role of international collaboration in achieving the program objectives (10, 16, 46). The pest, native to south Asia, was first reported in Mexico in the west coast state of Sinaloa, from where it spread rapidly, causing massive losses in many citrus-growing areas of the country. The blackfly was also capable of developing on more than 75 additional species of host plants, including coffee, mango, sapote, pear, and quince. A joint project between the Mexican Department of Agriculture and the United States Department of Agriculture (USDA) was initiated and resulted in the introduction of *Eretmocerus serius* from the USDA laboratory in

Panama, which had successfully controlled the blackfly in Cuba some years earlier (45). The parasitoid became established in Mexico in 1943 but only provided effective control in certain areas of continuously high humidity. Prospection by H.D. Smith in Malaysia was unsuccessful, but a subsequent trip to citrus-growing areas of India and Pakistan, which were climatically similar to conditions present in Mexico, resulted in the shipment of eight species of parasitoids and two predators. Of these, three parasitoid species proved to be highly effective in controlling the blackfly. The platygastriid *Amitus hesperidum* was the most effective natural enemy at reducing heavy infestations but performed poorly in hot, dry areas. The aphelinid *Encarsia clypealis* was effective in humid conditions and at low pest densities. In contrast, *Encarsia perplexa* (originally misidentified as *Prospaltella opulenta*) (23) is better adapted to a wide range of climatic conditions including hot dry areas, and this is now the most important species in controlling the blackfly in many parts of the country, whereas *Encarsia clypealis* and *Eretmocerus serius* are now of minor importance. Another species released during the program, *Encarsia smithi*, was initially abundant but appears to have been displaced by the other species and is now uncommon (6, 37).

The importance of each of these species in Mexican citrus production areas contrasted with their relative abundance in their native regions in India and Pakistan. Moreover, both *Encarsia* species are autoparasitoids in which females develop as primary parasitoids of blackfly, whereas males develop as secondary parasitoids (hyperparasitoids) of females of their own or closely related species (25, 52). As observed in other autoparasitoid systems (24, 54), their unusual biology did nothing to destabilize host suppression by parasitoid populations in the field.

Once established in the field, parasitized material was collected and redistributed to colonize infested areas as part of a national campaign that was financed by a modest tax on gasoline. The national campaign was headed by a Presidential committee that coordinated the program between 1951 and 1958. At the peak of its activities, over 1,600 field and laboratory personnel were organized into brigades to collect information on infestation and parasitism levels and coordinate the redistribution of parasitized material (26). By the end of 1953, over 242 million parasitoids had been released (10). The native coccinellid predator *Delphastus pusillus* was also found to contribute to parasitoid-mediated control of the blackfly in areas with heavy infestations. Blackfly populations were considered to have been brought under effective biological control in 21 of the 24 affected states of Mexico by 1955. Periodic outbreaks due to

excessive use of insecticides continued to be treated by the release of parasitoids collected in other parts of the country (27). Both Mexican and US biocontrol practitioners have underlined the vital importance of the Mexico-USDA alliance in natural enemy prospection, field evaluations, worker training, and operational aspects of the blackfly program.

### **SIT-BASED CONTROL OF *ANASTREPHA* SPP.**

The success of the SIT-based program targeted at *Anastrepha ludens* and *A. obliqua* involves a continuous process of improvement in the sexual competitiveness of the sterile male flies released in the field. Here we summarize a number of the current activities of the Moscafrut program and their collaborators. In an effort to maintain genetic diversity in the insect colonies, wild flies reared from fruits collected at various points in the country have been periodically introduced into the production colonies. Both *A. ludens* and *A. obliqua* are bisexual strains, but a genetic sexing strain of *A. ludens* is also being produced at the Moscafrut plant. This new strain, Tapachula-7, allows males to be separated from females on the basis of pupal color (11).

Quality control measures are applied at all steps of the rearing process (41), and the performance of these flies in the field is tested at least once a year using IAEA-defined criteria (9). In the case of *A. ludens*, there is disagreement on whether mass-reared males are as attractive as wild males to wild females (35, 38, 42). However, one arm of the National Campaign Against Fruit Flies coordinates a diversity of research projects for the improvement of the quality of mass-reared flies via reduced doses of radiation used for sterilization (43), the use of probiotics during rearing (32), pre-release adult diets (33), reduced stress caused by high adult densities (39), photoperiod and adult habitat manipulation (12, 13), and hormone-mediated improvement of male attractiveness (19) for improved mating success in the field.

Additional efforts to improve the effectiveness of control measures targeted at *Anastrepha* spp. include intensive research on fly mating (14) and host fruit selection behavior (4), including the evolutionary, biological, and physiological factors that determine host use (2). The selection of fruit cultivars, the intelligent design of orchards in response to diurnal fluctuations in fly displacement (5), and the development of products based on the fly's host-marking pheromone (1) look set to provide new and valuable tools for crop protection that are fully compatible with biological and integrated control measures. Moreover, long-term population studies in Mexican

orchards subject to chemical pest control suggest that area-wide techniques are more likely to provide effective pest control than measures applied at the level of individual orchards (3).

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## Supplemental Glossary

# BIOLOGICAL PEST CONTROL IN MEXICO

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**Augmentative Biological Control:** increasing the numbers of natural enemies in a particular site or area to reduce the density of exotic or native pest populations. This strategy may be inoculative, for which enemies are released early in the crop cycle and allowed to reproduce, or inundative, for which enemy releases are performed on various occasions to maintain high densities of natural enemies in the crop.

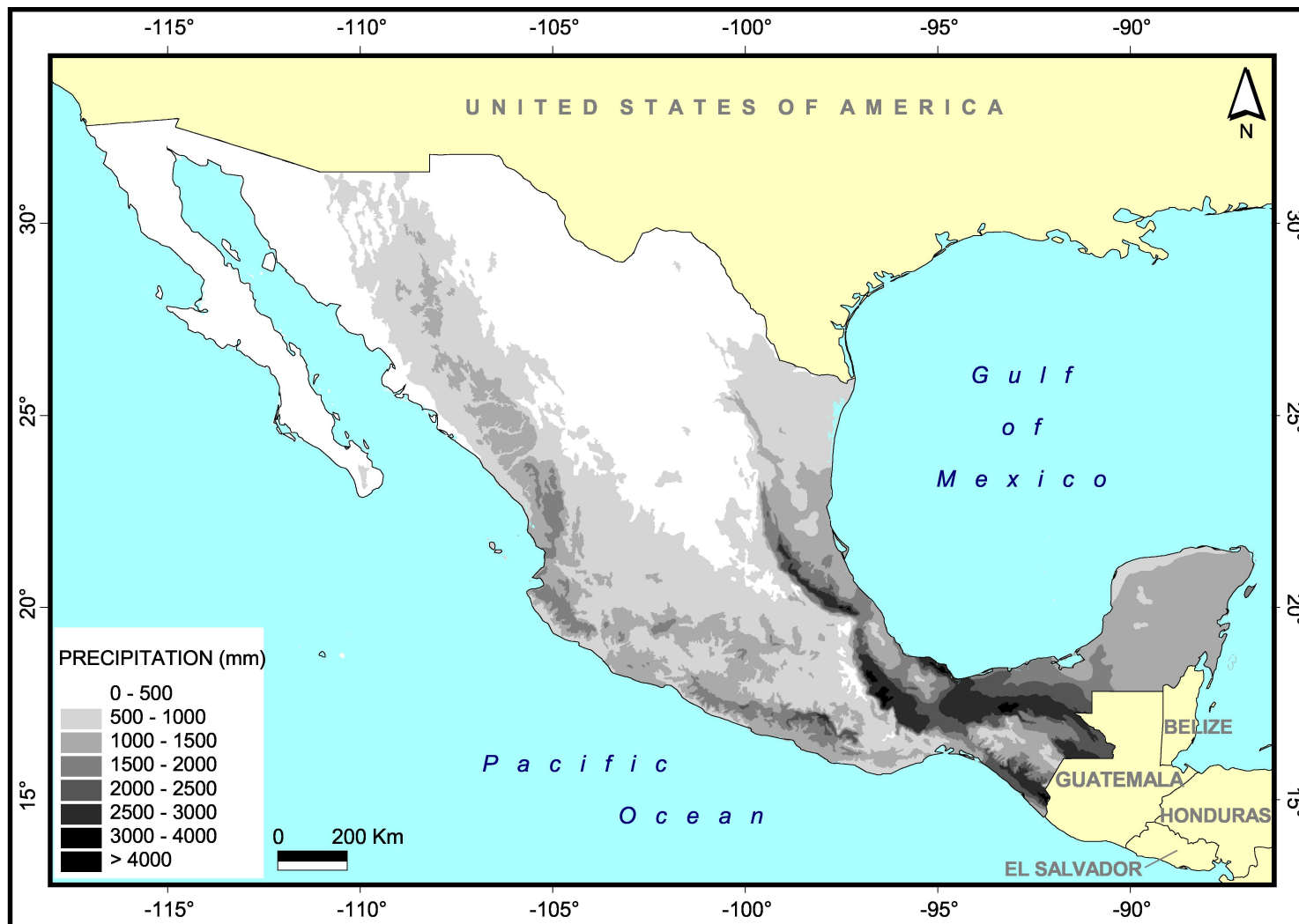
**Classical Biological Control:** the introduction of an exotic (nonnative) natural enemy to reduce and maintain exotic pest populations at acceptable densities indefinitely. Natural enemies are usually obtained from the region of origin of the pest.

**Conservation Biological Control:** to provide the conditions that favor the presence and reproduction of natural enemies in a particular area. This usually involves reducing or eliminating the use of broad-spectrum insecticides, providing physical refuges and supplementary food sources. Classical and augmentative biological control are often more effective when combined with natural enemy conservation practices.

**Sterile Insect Technique (SIT):** an area-wide technique involving the release of sterile male insects produced in a mass-rearing facility to achieve continuously high densities of sterile males in the field so that they greatly outnumber wild (fertile) males. Wild females that mate with sterile males do not produce viable offspring, leading to a rapid decline in the natural population.

**Integrated Pest Management (IPM):** a multifaceted pest control method involving a series of evaluations, decisions, and controls based on knowledge of the pest's biology and likely impact on yields to establish action thresholds at certain pest densities. Natural enemy conservation or augmentation is a valuable component of IPM systems, particularly when combined with the use of pest-resistant crop varieties, pheromone-based mating disruption, cultural control methods, and, if necessary, the application of selective biorational insecticides that have low impact on natural enemy populations.

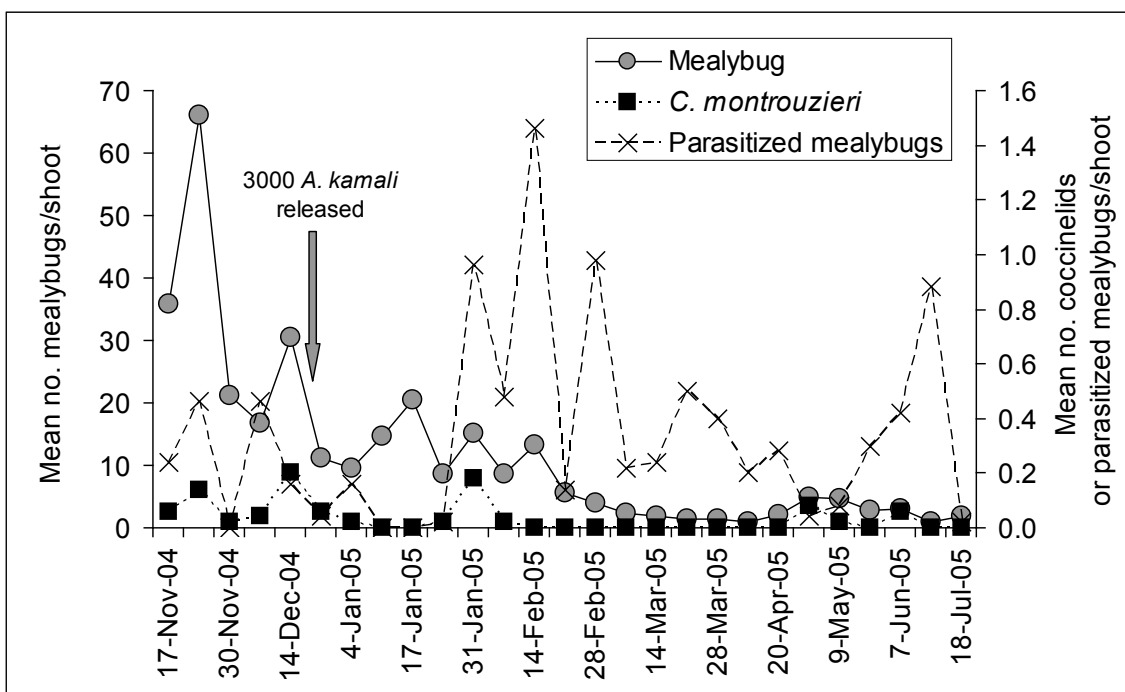
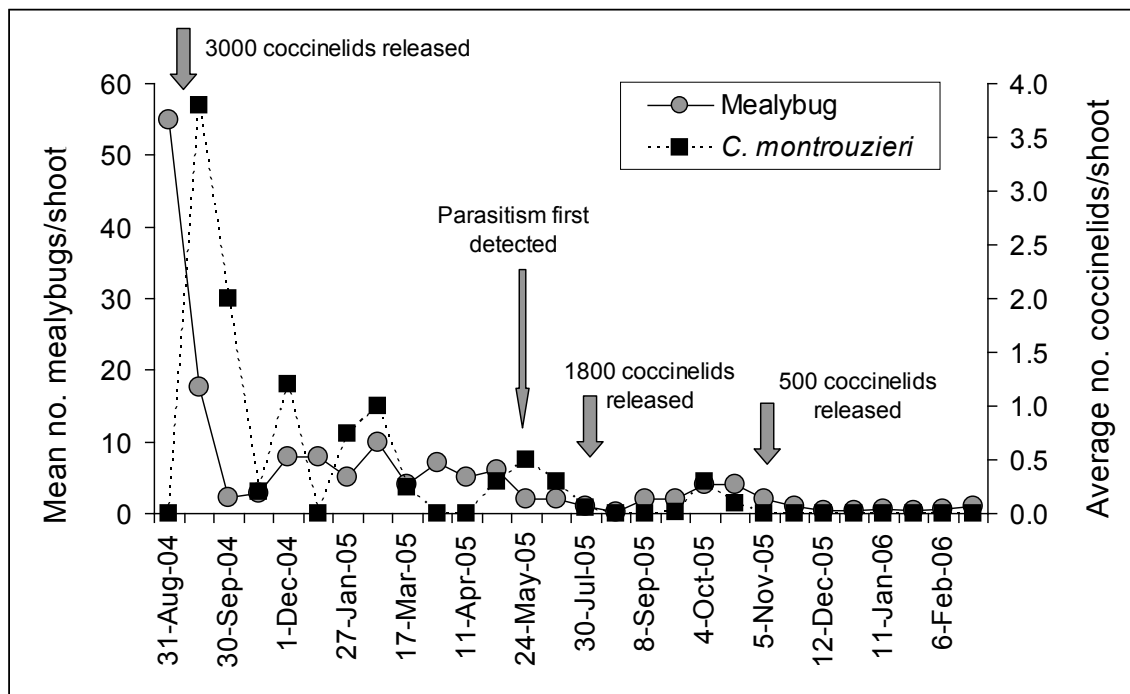
**Supplemental Figure 1.** Distribution of mean precipitation in Mexico.



Map prepared by H. Weissenberger (ECOSUR)



**Supplemental Figure 3.** Classical biological control of the pink hibiscus mealybug (*Maconellicoccus hirsutus*) following the release of the exotic coccinellid predator *Cryptolaemus montrouzieri* followed by the exotic encyrtid parasitoid *Anagrus kamali* at two sites in Nayarit State. (Top) High densities of the mealybug were rapidly controlled following release of *C. montrouzieri*; parasitism by *A. kamali* was detected approximately nine months later (El Porvenir, Nayarit). (Bottom) *A. kamali* parasitoids were released when high mealybug densities had been controlled by *C. montrouzieri*. The parasitoid provided stable control of the pest population at very low densities within approximately three months (San Vicente, Nayarit).



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*Biological Pest Control in Mexico*  
Williams, Arredondo-Bernal, and Rodríguez-del-Bosque

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**Supplemental Table 1.** Pests under phytosanitary vigilance and quarantine measures in Mexico 2011--2012<sup>a</sup>

Species	Family	Crops at risk	Number of states under phytosanitary vigilance
<b>Acari</b>			
<i>Raoiella indica</i>	Tenuipalpidae	Palms and banana	11
<b>Coleoptera</b>			
<i>Curculio caryae</i> <sup>b</sup>	Curculionidae	Nuts	2
<i>Euplatypus segnis</i>	Platypodidae	Fruit and nut trees	1
<i>Rhynchophorus ferrugineus</i> <sup>b</sup>	Curculionidae	Palms	13
<i>Rhyssomatus subtilis</i>	Curculionidae	Soya	2
<b>Diptera</b>			
<i>Drosophila suzukii</i>	Drosophilidae	Berries and soft fruits	2
<i>Ceratitis capitata</i> <sup>c</sup>	Tephritidae	Fruits and vegetables	All
<b>Hemiptera</b>			
<i>Maconellicoccus hirsutus</i>	Pseudococcidae	Fruits and vegetables	5
<i>Toxoptera citricida</i>	Aphidiidae	Citrus	8
<b>Lepidoptera</b>			
<i>Argyrotaenia franciscana</i> <sup>b</sup>	Tortricidae	Fruit trees	1
<i>Epiphyas postvittana</i> <sup>b</sup>	Tortricidae	Fruits and vegetables	6
<i>Grapholita molesta</i> <sup>b</sup>	Tortricidae	Fruits (Rosaceae)	4
<i>Lobesia botrana</i> <sup>b</sup>	Tortricidae	Vine	2
<i>Tuta absoluta</i> <sup>b</sup>	Gelechiidae	Solanaceae	9
<i>Helicoverpa armigera</i> <sup>b</sup>	Noctuidae	Field crops	1
<i>Cactoblastis cactorum</i> <sup>b</sup>	Pyralidae	Cactaceae	12

<sup>a</sup>These species are subject to legal restrictions on the movement of potentially infested material and continual monitoring as components of control programs implemented at the national level by Dirección General de Sanidad Vegetal (SENASICA-DGSV 2012:

<http://www.senasica.gob.mx>).

<sup>b</sup>Not present in Mexico at the moment of writing; classified as a phytosanitary threat.

<sup>c</sup>In addition to *C. capitata*, which is detected sporadically in the border buffer zone between Mexico and Guatemala, the following species of tephritids are listed as potential invasive threats for which the importation of potentially infested produced is restricted: *Anastrepha grandis*, *A. suspensa*, *Bactrocera invadens*, *B. dorsalis*, *B. carambolae*, *B. correcta*, *B. cucurbitae*, *B. latifrons*, *B. minax*, *B. musae*, *B. oleae*, *B. ornatissimus*, *B. papayae*, *B. passiflorae*, *B. tryoni*, *B. tsuneonis*, *B. zonata*, *Ceratitis cosyra*, *C. rosa*, *Dacus ciliatus*, *Rhagoletis cerasi*, *R. fausta*, *R. indifferens*, *R. mendax*, *R. tomatum*, and *Trirhithrum coffeae*.



**Supplemental Table 2.** Species of natural enemies produced in laboratories in Mexico for control of insect pests, or most commonly imported for augmentative biological control

Natural enemy	Principal target pests
<b>Parasitoids</b>	
<i>Anagyrus kamali</i> (Encyrtidae)	Pink hibiscus mealybug
<i>Diachasmimorpha longicaudata</i> (Braconidae)	Tephritid fruit flies
<i>Dirhinus giffardii</i> (Chalcididae)	Stable flies
<i>Habrobracon</i> sp. (Braconidae)	Stored grain pests
<i>Lixophaga diatraeae</i> (Tachinidae)	Lepidopteran stalkborers
<i>Muscidifurax raptor</i> (Pteromalidae)	Stable flies
<i>Spalangia endius</i> (Pteromalidae)	Stable flies
<i>Tamarixia radiata</i> (Eulophidae)	Asian citrus psyllid
<i>Trichogramma atopovirilia</i> (Trichogrammatidae)	Lepidopteran stalkborers
<i>Trichogramma exiguum</i> (Trichogrammatidae)	Lepidopteran stalkborers
<i>Trichogramma pretiosum</i> (Trichogrammatidae)	Lepidoptera
<b>Predators</b>	
<i>Chrysoperla carnea</i> s.l. (Chrysopidae)	Whiteflies, aphids
<i>Cryptolaemus montrouzieri</i> (Coccinellidae)	Pink hibiscus mealybug
<i>Geocoris punctipes</i> (Geocoridae)	<i>Tetranychus urticae</i> , <i>Bactericera cockerelli</i>
<b>Pathogens</b>	
<i>Bacillus thuringiensis</i>	Lepidoptera
<i>Beauveria bassiana</i>	Coffee berry borer, pepper weevil
<i>Isaria fumosorosea</i>	Whiteflies
<i>Lecanicillium lecanii</i>	<i>Aphis</i> spp., <i>Toxoptera citricida</i>
<i>Metarhizium anisopliae</i>	Whitegrubs ( <i>Phyllophaga</i> spp.)
<i>Metarhizium anisopliae</i> var. <i>acridum</i>	Locusts and grasshoppers
<b>Most commonly imported natural enemies<sup>a</sup></b>	
<i>Aphidius colemani</i> (Aphidiidae)	Aphids
<i>Aphidoletes aphidimyza</i> (Cecidomyiidae)	Aphids
<i>Chrysoperla rufilabris</i> (Chrysopidae)	<i>Bemisia tabaci</i> , <i>Aphis</i> spp.
<i>Cryptolaemus montrouzieri</i> (Coccinellidae)	Pink hibiscus mealybug
<i>Dacnusa sibirica</i> (Braconidae)	Leafminers
<i>Diglyphus isaea</i> (Eulophidae)	Leafminers
<i>Encarsia formosa</i> (Aphelinidae)	<i>Trialeurodes</i> spp.
<i>Iphiseius</i> (= <i>Amblyseius</i> ) <i>cucumeris</i> (Phytoseiidae)	Thrips
<i>Muscidifurax raptor</i> (Pteromalidae)	Stable flies
<i>Phytoseiulus persimilis</i> (Phytoseiidae)	<i>Tetranychus urticae</i>
<i>Spalangia endius</i> (Pteromalidae)	Stable flies
<i>Tamarixia triozae</i> (Eulophidae)	<i>Bactericera cockerelli</i>

<sup>a</sup>Species list based on number of importations requests received by SENASICA (2006-2011). Natural enemies sold by commercial suppliers in Mexico are listed on the company websites, for example, <http://www.koppert.com.mx> (Koppert México) and [http://imex.mx/folletos/Insectos\\_1344447176.pdf](http://imex.mx/folletos/Insectos_1344447176.pdf) (Imex Distribuciones SA de CV).

## Supplemental Text

# BIOLOGICAL PEST CONTROL IN MEXICO

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This document provides additional information that complements the text in the main body of the review. The document is divided into five sections:

1. The New World screwworm, *Cochliomyia hominivorax*
2. The medfly, *Ceratitis capitata*
3. The Citrus blackfly, *Aleurocanthus woglumi*
4. SIT-based control of *Anastrepha* spp.
5. Literature Cited

## THE NEW WORLD SCREWWORM, *COCHLIOMYIA HOMINIVORAX*

Eradication of the New World screwworm (*Cochliomyia hominivorax*) from North and Central America has become a textbook example of the effectiveness of the sterile insect technique (SIT) applied on an area-wide basis (17, 29, 49). This program involved rearing billions of flies that were sterilized and released over large areas. Continuously high densities of sterile males ensured that the large majority of wild females would be mated by sterile males and would not produce viable offspring leading to a rapid decline in the natural population. SIT was employed progressively to eradicate this devastating pest of livestock from the southeastern United States between 1958 and 1966. A US-Mexico border zone was established to prevent reinfestation from populations in Mexico; which was effective until a mild winter contributed to a major outbreak in Texas in 1972. This led US and Mexican livestock owners to lobby jointly for a SIT-based eradication program in Mexico. In 1972, a joint US-Mexico commission was formed and charged with the task of eradicating the pest from the US border to the narrowest point of Mexico at the Isthmus of Tehuantepec. A screwworm production plant was constructed close to Tuxtla Gutiérrez, Chiapas State, near the center of the isthmus barrier zone. The plant began operating in 1976 and has the capacity to produce over 500 million flies per week. Release of sterile flies, in combination with intensive programs of farmer education, insect trapping, animal

inspection points on commercial livestock routes, case reporting, and rapid treatment of infested animals with organophosphate powder, was effective in progressively extending the screwworm-free zones down through Mexico until the Isthmus of Tehuantepec was reached in 1984. The release of flies then continued over southeastern Mexico and the whole country was declared screwworm free in 1991, although an outbreak in 1992, which was quickly controlled by additional releases of sterile flies, underlined the importance of imposing strict quarantine restrictions on the movement of livestock from infested areas of Central America. Between 1994 and 2001 the screwworm eradication zone was subsequently moved through each of the countries of Central America until its present location in Panama, where a production facility with a capacity of 80 million flies per week maintains the biological barrier between Central and South America (49). Estimates of the economic benefits of the program in Mexico vary (28, 47), but benefits have been estimated at US\$328 million per year for livestock producers in Mexico (53), in addition to the elimination of the significant risk of human morbidity and mortality from myiasis in Mexico and Central America.

The screwworm plant at Tuxtla Gutiérrez is currently producing approximately 8 million flies per week, just enough to maintain the colony. There are several opportunities for eradication on Caribbean islands, which represent a continual threat of reinvasion for the neighboring screwworm-free countries. At the time of writing, feasibility study is under way for the Dominican Republic that, if funded, would require the establishment of a new colony and the ramping of production to operational program levels. However, given that the capacity of the Panamanian plant is only sufficient to maintain the current biological barrier, the strategic value of the Mexican plant as an instrument for rapid response to new outbreaks is clear. This was thoroughly demonstrated during an outbreak of *C. hominivorax* in Libya in which the Mexican plant supplied a total of 1,300 million flies that were released over an area of 41,000 km<sup>2</sup> in Libya between December 1990 and October 1991, resulting in the rapid elimination of the pest (17). In contrast, a recent program in Jamaica failed (20), apparently due to a series of operational difficulties on the island (15).

### **THE MEDFLY, *CERATITIS CAPITATA***

The eradication of the medfly, *Ceratitis capitata*, from the southern state of Chiapas was achieved by the rapid response to this invasive pest, the application of a SIT-based program in

combination with quarantine measures on the movement of potentially infested produce and intensive trapping, and the application of insecticidal baits. The principal aspects of the program are described in the main body of the review, but it is important to note that the Moscamed program is undergoing a continual process of improvement aimed at reducing production costs and improving the sexual competitiveness of the sterile male flies (21). For example, the original bisexual strain was replaced in 2002 with a genetic sexing strain that carries a temperature sensitive lethal (TSL) allele (18). Exposure to elevated temperature during embryonic development results in death of female embryos, meaning that diet resources and handling of developing larvae and pupae are fully dedicated to male rather than female production, effectively doubling the production capacity of the Moscamed plant. The TSL strain (named Vienna 7/Toliman 99) is sexually competitive compared to wild males (31, 40).

Since 2002, the Moscamed plant receives all *C. capitata* eggs for rearing in daily truck deliveries from a very large production plant located at El Pino Medfly Rearing Facility in Guatemala (9). However, this dependence on the production of eggs in Guatemala will soon end as Mexico's Moscamed plant, now over 30 years old, is set to be completely rebuilt and will double its capacity over the next few years. The new facility should contribute to future plans to extend the biological barrier toward the south of Guatemala over the coming decade, greatly extending the size of the contention zone and markedly reducing the risk of medfly outbreaks in Mexico and the United States (16).

A visit to the Moscamed facilities reveals that a series of quality control checks have been implemented at every step of the process (22), from the transport and receipt of eggs produced in Guatemala to the temperature and humidity conditions experienced by flies during the aircraft liberation process. As a result, potential problems can be rapidly detected and corrected to ensure the continued success of the program. Recent improvements include the redesign of the cages used to hold adult flies that favor male sexual competitiveness (13, 34) and the use of orange oil aromatherapy during adult sexual development (44), both of which improve the mating success of males in the field. Similarly, improvements have been made to adult eclosion procedures and the release of sterile flies from GPS-guided aircraft. The current fly release machine includes a refrigeration unit, a box containing 15 million chilled flies and a lower rotating band that moves the flies to the aircraft's liberation chute at a calibrated rate (48). Three chilled boxes, containing a total of 45 million flies, are loaded into each aircraft that flies a GPS-guided route that is

subsequently verified when the flight data are downloaded upon return to the extensive new adult eclosion and liberation facilities next to the Tapachula International Airport. Particular attention is paid to controlling humidity prior to the release of adults, as flies tend to clump together and suffer high mortality if moisture levels in the aircraft fly release machines exceed specified values.

As a caveat, the effectiveness of the Moscamed program is faced by three additional obstacles. First, the success of the program is continually challenged by the richness and abundance of plants that are hosts to medfly larvae, so that SIT-based control will continue to require insecticidal bait spraying measures (involving the use of the biorational compound, spinosad GF-120) as an additional means to reduce pest population densities. Second, medfly females are prone to remating, particularly when the first mating occurred with a sterile male (7, 30, 50, 51). This places an additional requirement on the SIT program to maintain sterile male densities at continuously high levels to minimize the frequency of matings with wild males. Finally, perhaps one of the most influential factors determining the success of the area-wide control of medfly in the region is the international price of coffee. This issue revolves around the management of coffee plantations: When prices are low, coffee berries are not harvested and fallen berries are not cleared away, resulting in a dramatic increase in the abundance of hosts for the development of *C. capitata* (36).

### **THE CITRUS BLACKFLY, *ALEUROCANTHUS WOGLUMI***

The importation and liberation of natural enemies of the citrus blackfly, *Aleurocanthus woglumi*, in Mexico provides an outstanding example of (a) the importance of compatibility in climatic conditions in the areas of natural enemy prospection, and (b) the effectiveness of releasing multiple natural enemies against a pest in a classical biological control program. It also highlights the pivotal role of international collaboration in achieving the program objectives (10, 16, 46). The pest, native to south Asia, was first reported in Mexico in the west coast state of Sinaloa, from where it spread rapidly, causing massive losses in many citrus-growing areas of the country. The blackfly was also capable of developing on more than 75 additional species of host plants, including coffee, mango, sapote, pear, and quince. A joint project between the Mexican Department of Agriculture and the United States Department of Agriculture (USDA) was initiated and resulted in the introduction of *Eretmocerus serius* from the USDA laboratory in

Panama, which had successfully controlled the blackfly in Cuba some years earlier (45). The parasitoid became established in Mexico in 1943 but only provided effective control in certain areas of continuously high humidity. Prospection by H.D. Smith in Malaysia was unsuccessful, but a subsequent trip to citrus-growing areas of India and Pakistan, which were climatically similar to conditions present in Mexico, resulted in the shipment of eight species of parasitoids and two predators. Of these, three parasitoid species proved to be highly effective in controlling the blackfly. The platygastriid *Amitus hesperidum* was the most effective natural enemy at reducing heavy infestations but performed poorly in hot, dry areas. The aphelinid *Encarsia clypealis* was effective in humid conditions and at low pest densities. In contrast, *Encarsia perplexa* (originally misidentified as *Prospaltella opulenta*) (23) is better adapted to a wide range of climatic conditions including hot dry areas, and this is now the most important species in controlling the blackfly in many parts of the country, whereas *Encarsia clypealis* and *Eretmocerus serius* are now of minor importance. Another species released during the program, *Encarsia smithi*, was initially abundant but appears to have been displaced by the other species and is now uncommon (6, 37).

The importance of each of these species in Mexican citrus production areas contrasted with their relative abundance in their native regions in India and Pakistan. Moreover, both *Encarsia* species are autoparasitoids in which females develop as primary parasitoids of blackfly, whereas males develop as secondary parasitoids (hyperparasitoids) of females of their own or closely related species (25, 52). As observed in other autoparasitoid systems (24, 54), their unusual biology did nothing to destabilize host suppression by parasitoid populations in the field.

Once established in the field, parasitized material was collected and redistributed to colonize infested areas as part of a national campaign that was financed by a modest tax on gasoline. The national campaign was headed by a Presidential committee that coordinated the program between 1951 and 1958. At the peak of its activities, over 1,600 field and laboratory personnel were organized into brigades to collect information on infestation and parasitism levels and coordinate the redistribution of parasitized material (26). By the end of 1953, over 242 million parasitoids had been released (10). The native coccinellid predator *Delphastus pusillus* was also found to contribute to parasitoid-mediated control of the blackfly in areas with heavy infestations. Blackfly populations were considered to have been brought under effective biological control in 21 of the 24 affected states of Mexico by 1955. Periodic outbreaks due to

excessive use of insecticides continued to be treated by the release of parasitoids collected in other parts of the country (27). Both Mexican and US biocontrol practitioners have underlined the vital importance of the Mexico-USDA alliance in natural enemy prospection, field evaluations, worker training, and operational aspects of the blackfly program.

### **SIT-BASED CONTROL OF *ANASTREPHA* SPP.**

The success of the SIT-based program targeted at *Anastrepha ludens* and *A. obliqua* involves a continuous process of improvement in the sexual competitiveness of the sterile male flies released in the field. Here we summarize a number of the current activities of the Moscafrut program and their collaborators. In an effort to maintain genetic diversity in the insect colonies, wild flies reared from fruits collected at various points in the country have been periodically introduced into the production colonies. Both *A. ludens* and *A. obliqua* are bisexual strains, but a genetic sexing strain of *A. ludens* is also being produced at the Moscafrut plant. This new strain, Tapachula-7, allows males to be separated from females on the basis of pupal color (11).

Quality control measures are applied at all steps of the rearing process (41), and the performance of these flies in the field is tested at least once a year using IAEA-defined criteria (9). In the case of *A. ludens*, there is disagreement on whether mass-reared males are as attractive as wild males to wild females (35, 38, 42). However, one arm of the National Campaign Against Fruit Flies coordinates a diversity of research projects for the improvement of the quality of mass-reared flies via reduced doses of radiation used for sterilization (43), the use of probiotics during rearing (32), pre-release adult diets (33), reduced stress caused by high adult densities (39), photoperiod and adult habitat manipulation (12, 13), and hormone-mediated improvement of male attractiveness (19) for improved mating success in the field.

Additional efforts to improve the effectiveness of control measures targeted at *Anastrepha* spp. include intensive research on fly mating (14) and host fruit selection behavior (4), including the evolutionary, biological, and physiological factors that determine host use (2). The selection of fruit cultivars, the intelligent design of orchards in response to diurnal fluctuations in fly displacement (5), and the development of products based on the fly's host-marking pheromone (1) look set to provide new and valuable tools for crop protection that are fully compatible with biological and integrated control measures. Moreover, long-term population studies in Mexican

orchards subject to chemical pest control suggest that area-wide techniques are more likely to provide effective pest control than measures applied at the level of individual orchards (3).

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## Supplemental Glossary

# BIOLOGICAL PEST CONTROL IN MEXICO

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**Augmentative Biological Control:** increasing the numbers of natural enemies in a particular site or area to reduce the density of exotic or native pest populations. This strategy may be inoculative, for which enemies are released early in the crop cycle and allowed to reproduce, or inundative, for which enemy releases are performed on various occasions to maintain high densities of natural enemies in the crop.

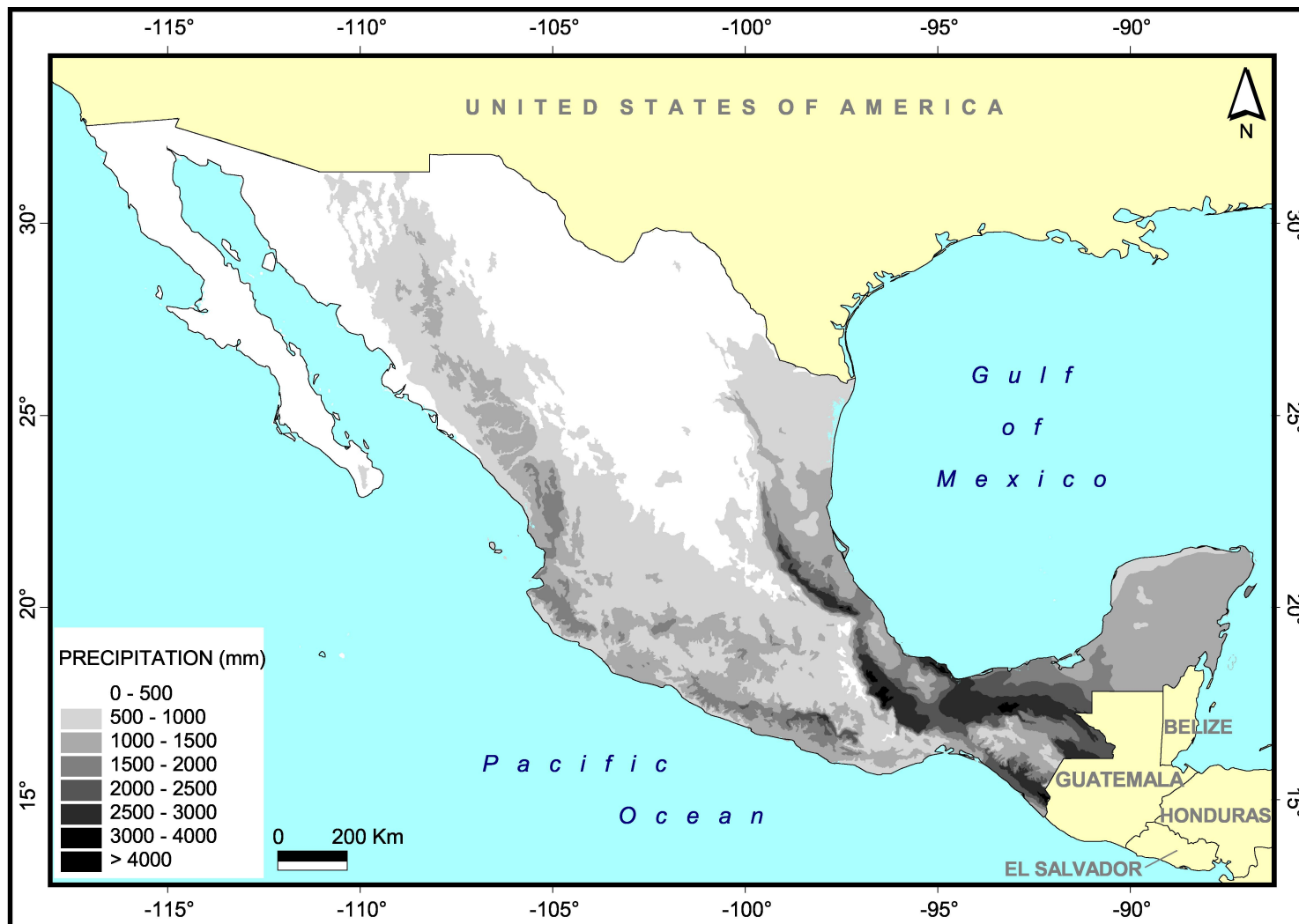
**Classical Biological Control:** the introduction of an exotic (nonnative) natural enemy to reduce and maintain exotic pest populations at acceptable densities indefinitely. Natural enemies are usually obtained from the region of origin of the pest.

**Conservation Biological Control:** to provide the conditions that favor the presence and reproduction of natural enemies in a particular area. This usually involves reducing or eliminating the use of broad-spectrum insecticides, providing physical refuges and supplementary food sources. Classical and augmentative biological control are often more effective when combined with natural enemy conservation practices.

**Sterile Insect Technique (SIT):** an area-wide technique involving the release of sterile male insects produced in a mass-rearing facility to achieve continuously high densities of sterile males in the field so that they greatly outnumber wild (fertile) males. Wild females that mate with sterile males do not produce viable offspring, leading to a rapid decline in the natural population.

**Integrated Pest Management (IPM):** a multifaceted pest control method involving a series of evaluations, decisions, and controls based on knowledge of the pest's biology and likely impact on yields to establish action thresholds at certain pest densities. Natural enemy conservation or augmentation is a valuable component of IPM systems, particularly when combined with the use of pest-resistant crop varieties, pheromone-based mating disruption, cultural control methods, and, if necessary, the application of selective biorational insecticides that have low impact on natural enemy populations.

**Supplemental Figure 1.** Distribution of mean precipitation in Mexico.



Map prepared by H. Weissenberger (ECOSUR)

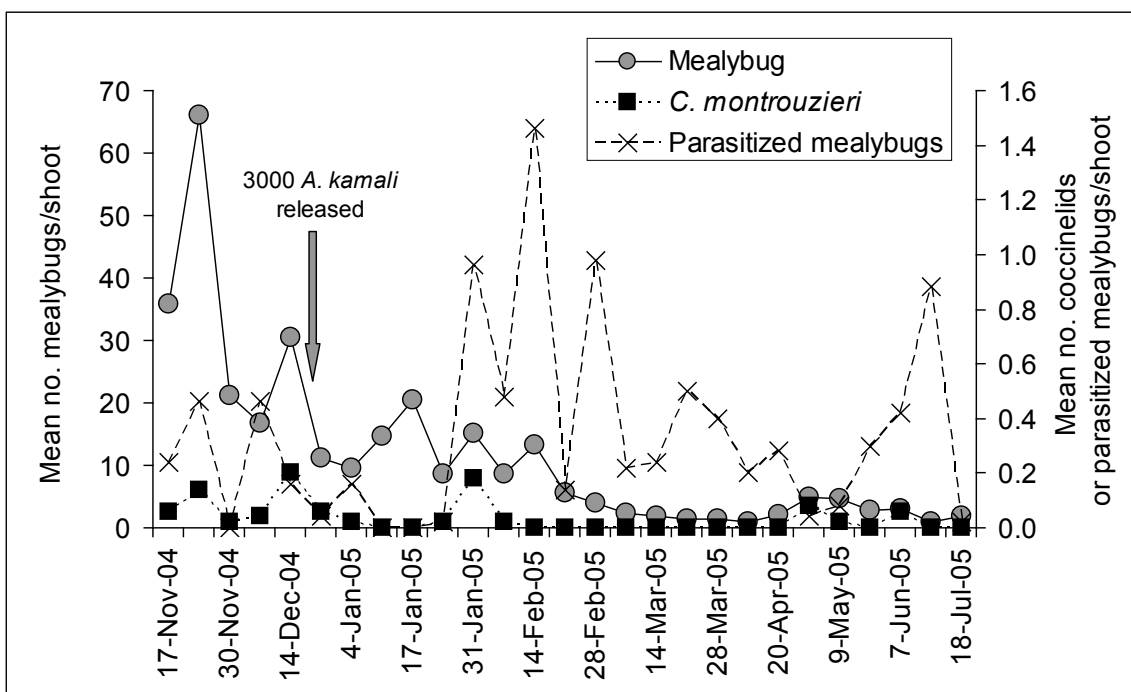
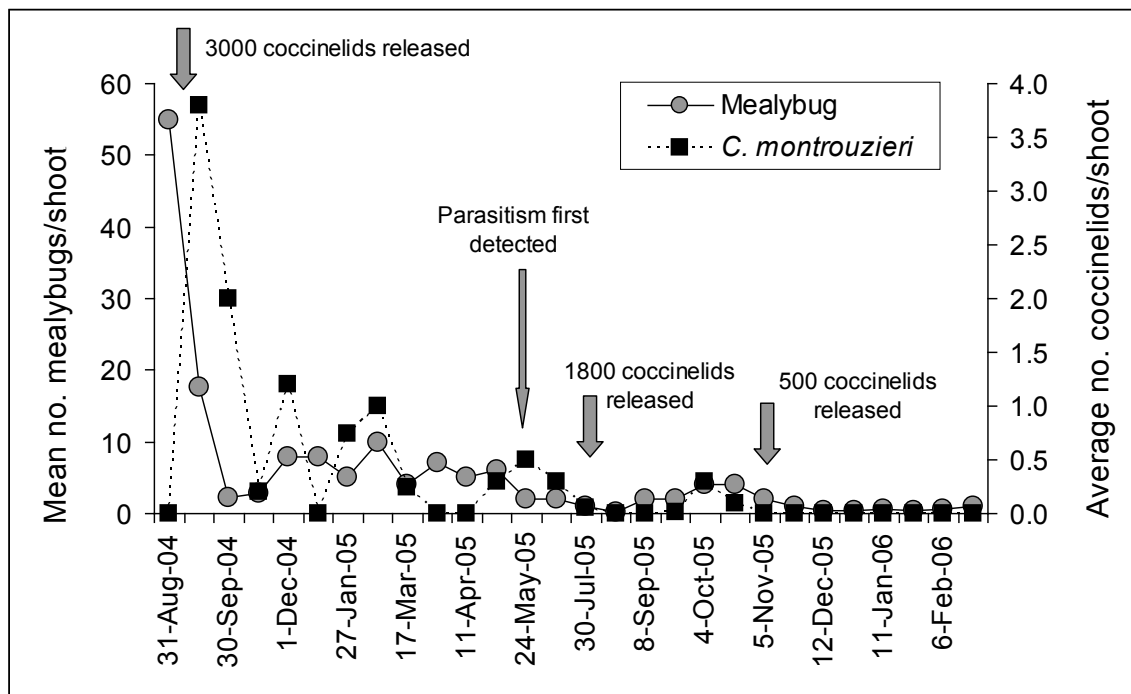
**Supplemental Figure 2.** States of Mexico showing locations of the National Reference Center for Biological Control (CNRCB), the Screwworm, Moscamed, and Moscafrut sterile insect production plants and the Isthmus of Tehuantepec.



Map prepared by H. Weissenberger (ECOSUR)



**Supplemental Figure 3.** Classical biological control of the pink hibiscus mealybug (*Maconellicoccus hirsutus*) following the release of the exotic coccinellid predator *Cryptolaemus montrouzieri* followed by the exotic encyrtid parasitoid *Anagrus kamali* at two sites in Nayarit State. (Top) High densities of the mealybug were rapidly controlled following release of *C. montrouzieri*; parasitism by *A. kamali* was detected approximately nine months later (El Porvenir, Nayarit). (Bottom) *A. kamali* parasitoids were released when high mealybug densities had been controlled by *C. montrouzieri*. The parasitoid provided stable control of the pest population at very low densities within approximately three months (San Vicente, Nayarit).



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**Supplemental Table 1.** Pests under phytosanitary vigilance and quarantine measures in Mexico 2011--2012<sup>a</sup>

Species	Family	Crops at risk	Number of states under phytosanitary vigilance
<b>Acari</b>			
<i>Raoiella indica</i>	Tenuipalpidae	Palms and banana	11
<b>Coleoptera</b>			
<i>Curculio caryae</i> <sup>b</sup>	Curculionidae	Nuts	2
<i>Euplatypus segnis</i>	Platypodidae	Fruit and nut trees	1
<i>Rhynchophorus ferrugineus</i> <sup>b</sup>	Curculionidae	Palms	13
<i>Rhyssomatus subtilis</i>	Curculionidae	Soya	2
<b>Diptera</b>			
<i>Drosophila suzukii</i>	Drosophilidae	Berries and soft fruits	2
<i>Ceratitis capitata</i> <sup>c</sup>	Tephritidae	Fruits and vegetables	All
<b>Hemiptera</b>			
<i>Maconellicoccus hirsutus</i>	Pseudococcidae	Fruits and vegetables	5
<i>Toxoptera citricida</i>	Aphidiidae	Citrus	8
<b>Lepidoptera</b>			
<i>Argyrotaenia franciscana</i> <sup>b</sup>	Tortricidae	Fruit trees	1
<i>Epiphyas postvittana</i> <sup>b</sup>	Tortricidae	Fruits and vegetables	6
<i>Grapholita molesta</i> <sup>b</sup>	Tortricidae	Fruits (Rosaceae)	4
<i>Lobesia botrana</i> <sup>b</sup>	Tortricidae	Vine	2
<i>Tuta absoluta</i> <sup>b</sup>	Gelechiidae	Solanaceae	9
<i>Helicoverpa armigera</i> <sup>b</sup>	Noctuidae	Field crops	1
<i>Cactoblastis cactorum</i> <sup>b</sup>	Pyralidae	Cactaceae	12

<sup>a</sup>These species are subject to legal restrictions on the movement of potentially infested material and continual monitoring as components of control programs implemented at the national level by Dirección General de Sanidad Vegetal (SENASICA-DGSV 2012:

<http://www.senasica.gob.mx>).

<sup>b</sup>Not present in Mexico at the moment of writing; classified as a phytosanitary threat.

<sup>c</sup>In addition to *C. capitata*, which is detected sporadically in the border buffer zone between Mexico and Guatemala, the following species of tephritids are listed as potential invasive threats for which the importation of potentially infested produced is restricted: *Anastrepha grandis*, *A. suspensa*, *Bactrocera invadens*, *B. dorsalis*, *B. carambolae*, *B. correcta*, *B. cucurbitae*, *B. latifrons*, *B. minax*, *B. musae*, *B. oleae*, *B. ornatissimus*, *B. papayae*, *B. passiflorae*, *B. tryoni*, *B. tsuneonis*, *B. zonata*, *Ceratitis cosyra*, *C. rosa*, *Dacus ciliatus*, *Rhagoletis cerasi*, *R. fausta*, *R. indifferens*, *R. mendax*, *R. tomatis*, and *Trirhithrum coffeae*.

**Supplemental Table 2.** Species of natural enemies produced in laboratories in Mexico for control of insect pests, or most commonly imported for augmentative biological control

<b>Natural enemy</b>	<b>Principal target pests</b>
<b>Parasitoids</b>	
<i>Anagyrus kamali</i> (Encyrtidae)	Pink hibiscus mealybug
<i>Diachasmimorpha longicaudata</i> (Braconidae)	Tephritid fruit flies
<i>Dirhinus giffardii</i> (Chalcididae)	Stable flies
<i>Habrobracon</i> sp. (Braconidae)	Stored grain pests
<i>Lixophaga diatraeae</i> (Tachinidae)	Lepidopteran stalkborers
<i>Muscidifurax raptor</i> (Pteromalidae)	Stable flies
<i>Spalangia endius</i> (Pteromalidae)	Stable flies
<i>Tamarixia radiata</i> (Eulophidae)	Asian citrus psyllid
<i>Trichogramma atopovirilia</i> (Trichogrammatidae)	Lepidopteran stalkborers
<i>Trichogramma exiguum</i> (Trichogrammatidae)	Lepidopteran stalkborers
<i>Trichogramma pretiosum</i> (Trichogrammatidae)	Lepidoptera
<b>Predators</b>	
<i>Chrysoperla carnea</i> s.l. (Chrysopidae)	Whiteflies, aphids
<i>Cryptolaemus montrouzieri</i> (Coccinellidae)	Pink hibiscus mealybug
<i>Geocoris punctipes</i> (Geocoridae)	<i>Tetranychus urticae</i> , <i>Bactericera cockerelli</i>
<b>Pathogens</b>	
<i>Bacillus thuringiensis</i>	Lepidoptera
<i>Beauveria bassiana</i>	Coffee berry borer, pepper weevil
<i>Isaria fumosorosea</i>	Whiteflies
<i>Lecanicillium lecanii</i>	<i>Aphis</i> spp., <i>Toxoptera citricida</i>
<i>Metarhizium anisopliae</i>	Whitegrubs ( <i>Phyllophaga</i> spp.)
<i>Metarhizium anisopliae</i> var. <i>acridum</i>	Locusts and grasshoppers
<b>Most commonly imported natural enemies<sup>a</sup></b>	
<i>Aphidius colemani</i> (Aphidiidae)	Aphids
<i>Aphidoletes aphidimyza</i> (Cecidomyiidae)	Aphids
<i>Chrysoperla rufilabris</i> (Chrysopidae)	<i>Bemisia tabaci</i> , <i>Aphis</i> spp.
<i>Cryptolaemus montrouzieri</i> (Coccinellidae)	Pink hibiscus mealybug
<i>Dacnusa sibirica</i> (Braconidae)	Leafminers
<i>Diglyphus isaea</i> (Eulophidae)	Leafminers
<i>Encarsia formosa</i> (Aphelinidae)	<i>Trialeurodes</i> spp.
<i>Iphiseius</i> (= <i>Amblyseius</i> ) <i>cucumeris</i> (Phytoseiidae)	Thrips
<i>Muscidifurax raptor</i> (Pteromalidae)	Stable flies
<i>Phytoseiulus persimilis</i> (Phytoseiidae)	<i>Tetranychus urticae</i>
<i>Spalangia endius</i> (Pteromalidae)	Stable flies
<i>Tamarixia triozae</i> (Eulophidae)	<i>Bactericera cockerelli</i>

<sup>a</sup>Species list based on number of importations requests received by SENASICA (2006-2011). Natural enemies sold by commercial suppliers in Mexico are listed on the company websites, for example, <http://www.koppert.com.mx> (Koppert México) and [http://imex.mx/folletos/Insectos\\_1344447176.pdf](http://imex.mx/folletos/Insectos_1344447176.pdf) (Imex Distribuciones SA de CV).