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MEDFLY AREAWIDE STERILE INSECT TECHNIQUE PROGRAMMES FOR PREVENTION, SUPPRESSION OR ERADICATION: THE IMPORTANCE OF MATING BEHAVIOR STUDIES

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ABSTRACT

The Sterile Insect Technique (SIT) is amongst the most non-disruptive pest control methods. Unlike some other biologically-based methods it is species specific, does not release exotic agents into new environments and does not even introduce new genetic material into existing populations as the released organisms are not self-replicating. However, the SIT is only effective when integrated on an areawide basis, addressing the total population of the pest, irrespective of its distribution. There has been considerable progress in the development and integrated application of the SIT against the Mediterranean fruit fly (medfly), *Ceratitis capitata*, as reflected by operational programs for prevention, suppression and eradication of this pest. There is however, considerable scope for improving the efficiency of medfly SIT, an indispensable requirement for increased involvement of the private sector in any future application. One way to achieve this has been the development of genetic sexing strains, making it possible to release only sterile males. Another is improving sterile male performance through a better understanding of the sexual behavior of this insect. Unlike other insects for which the SIT has been successfully applied, medfly has a complex lek-based mating system in which the females exert the mate choice selecting among aggregated and displaying wild and sterile males. With the objective of developing a better understanding of medfly mating behavior, an FAO/IAEA Coordinated Research Project was carried out from 1994 to 1999. Some of the resulting work conducted during this period with the participation of research teams from ten countries is reported in this issue.

Key Words: Mediterranean fruit fly, medfly, *Ceratitis capitata*, areawide IPM, sterile insect technique, SIT, mating behavior, lek, quality control

RESUMEN

La técnica del insecto estéril (TIE) está entre los métodos de control de plagas menos perjudiciales. A diferencia de otros métodos con base biológica, la TIE es específica a nivel de especie, no transfiere agentes exóticos hacia nuevos ambientes y ni siquiera introduce nuevo material genético dentro de las poblaciones existentes debido a que los organismos liberados no se pueden auto replicar. Sin embargo, la TIE es solamente efectiva cuando se integra en forma extensiva, considerando el total de la población de la plaga, sin importar su distribución. Ha habido considerable progreso en el desarrollo y la aplicación integral de la TIE contra la mosca del Mediterráneo, *Ceratitis capitata*, tal como lo reflejan los programas operacionales para la prevención, supresión y erradicación de esta plaga. Existe sin embargo, un considerable campo para mejorar la eficiencia de la TIE de la mosca del mediterráneo, un requerimiento indispensable por aumentar la participació del sector privado en cualquier aplicación futura. Una forma de lograr esto ha sido a través del desarrollo de razas genéticamente sexadas, haciendo posible la liberación solamente de machos estériles. Otra es el mejoramiento del desempeño de los machos estériles por medio de un mejor entendimiento del comportamiento sexual de este insecto. A diferencia de otros insectos para los cuales la TIE ha sido aplicada exitosamente, la mosca del Mediterráneo presenta un complejo sistema de apareamiento basado la agregación de machos en un “lek”, deutro del cual la hembra ejerce la selección de pareja escogiendo entre el total de los machos salvajes y estériles en cortejo. Con el objetivo de desarrollar un mejor entendimiento del comportamiento de apareamiento de la mosca del Mediterráneo, un proyecto de investigación coordinado por FAO/IAEA se llevó a cabo de 1994 a 1999. En esta edición se reportan algunos de los trabajos conducidos durante este periodo con la participación de equipos de investigación pertenecientes a diez países.

The effectiveness of integrating compatible pest control methods is significantly increased by coordinated implementation over larger contiguous areas to address whole target pest populations (Knipling 1979). This areawide IPM approach to pest management is gaining acceptance for some key insect pests (Tan 2000). Important tephritid fruit fly pests, such as the Mediterranean fruit fly (medfly), *Ceratitis capitata*, a notorious pest of quarantine importance because of its extremely wide host range (Liquido et al. 1991), are such key pests that invariably cause economic damage if left uncontrolled. The case for an areawide IPM approach arises for these key pests as they cannot be effectively controlled at the local orchard level without the systematic use of insecticide that disrupts the biological control of secondary fruit pests and also interferes with the use of other biologically-based control methods (Ehler & Endicott 1984).

Among biologically-based methods, the Sterile Insect Technique (SIT) is the most target-specific and non-disruptive method. Unlike some other biologically based methods it is species specific, does not release exotic agents into new environments and does not even introduce new genetic material into existing populations as the released organisms are not self-replicating. However, to be effective the released mass-reared and sterile males have to successfully transfer their sperm carrying dominant lethal mutations to a large majority of females of the target population. As when mating disruption using pheromones is applied, already-mated females that move into an area under treatment, are largely unaffected by the presence of sterile males, and proceed to lay their eggs into fruit. As a result, SIT is only effective when applied on an areawide basis addressing the pest simultaneously over urban, commercial, non-commercial and wild host areas. The areawide integration of SIT with other control methods, results in significant benefits for growers, providing them with enough incentives to associate and to cooperate.

Status of SIT for Medfly

Over the last quarter century there has been considerable progress in the development and integrated application of SIT against medfly, as reflected by ongoing operational programs for eradication, prevention, and suppression leading to a rapid increase in sterile fruit fly production capacity (Fig. 1). The expanding use of medfly SIT is followed by similar trends for other fruit flies, particularly economically-important *Anastrepha* and *Bactrocera* species. The benefits accruing to the domestic and export markets for fruit and vegetable of all these programs have been of the order of hundreds of millions of U.S. dollars annually (Hendrichs 2000).

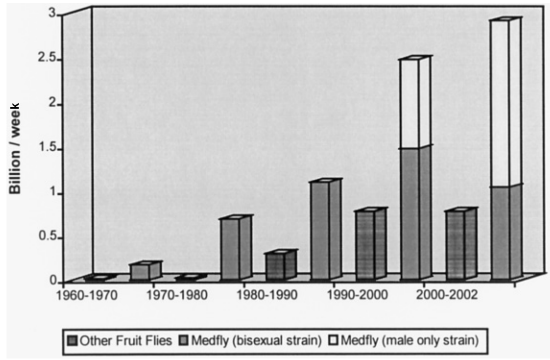

Fig. 1. Current worldwide production capacity of sterile fruit flies.

Medfly SIT Eradication Programs

The application of SIT against medfly focused initially on the concept of eradication, following the successful example of the screwworm, *Cochliomyia hominivorax*, which over the last fifty years has been eradicated from the U.S., Mexico and recently also from all of Central America and most of Panama (Wyss 2000). A number of medfly SIT eradication programs have eliminated populations of this species, succeeding in the establishment of medfly-free regions or whole countries. The first large SIT program against medfly was initiated in southern Mexico in 1977, with the construction of a 500 million sterile fly mass rearing facility in Tapachula. The aim of the Moscamed program was to prevent the spread of medfly, which had become established in Central America, into Mexico and the U.S.A. Establishment of medfly in Mexico would have threatened a multi-million fruit and vegetable export trade with the U.S.A. The program succeeded in 1982 in eradicating medfly from areas it had already infested in southern Mexico (Hendrichs et al. 1983) and since then a sterile fly barrier has been maintained from southern Belize through Guatemala to southern Mexico to assure the fly-free status of Mexico, U.S.A. and a large part of Guatemala (Villaseñor et al. 2000). In Chile, following many unsuccessful attempts to eradicate the pest using insecticides (Olalquiaga & Lobos 1993), eradication from the northern part of the country was achieved in 1995 with the integration of SIT, opening trade opportunities estimated over five years at a benefit to the Chilean fruit industry of ca. U.S.$ 500 million (SAG 1996). In Argentina, also as a result of SIT programs against medfly that started in the early 1990's, fly-free areas have been developed in various Patagonia valleys, and Argentina recently succeeded in negotiations with Chile to transport fruit from Mendoza and Patagonia provinces through medfly-free Chile for export from Chilean ports (De Longo et al. 2000).

Medfly SIT Prevention Programs

There are a number of examples were SIT is being applied as a preventive control to avoid the establishment of exotic or invasive fruit flies. These include Southern Australia, where sterile males are being released near Adelaide to prevent the establishment of medfly coming from Western Australia (Bill Woods, personal communication), and Okinawa, Japan where preventive releases of sterile melon flies are in progress along the southern-most islands of the archipelago to avoid re-establishment of melon fly coming from Taiwan (Kuba et al. 1996).

Probably most visible, are the repeated medfly introductions into high-risk areas in California and lately also Florida, threatening the exports of a multi-billion dollar fruit industry (Siebert & Cooper 1995). These have required recurrent emergency eradication actions, mainly consisting of insecticide applications, costing annually millions of U.S. dollars (Penrose 1995). Allowing the establishment of medfly in California would cost California ca. U.S.$ 1.5 billion a year and result in a drastic increase of insecticide use (Siebert 1999). In view of the public opposition to recurrent aerial bait-spraying over urban areas (CDFA 1994), and the failure to eradicate these outbreaks with insecticides, authorities embarked on the area-wide use of SIT over the whole Los Angeles basin (LAB) starting in 1994, involving the aerial release of over 300 million sterile flies per week (Dowell & Penrose 1995). The SIT strategy was so successful technically, politically and environmentally, but also from the economic point of view (costing on average less than half that of recurrent emergency programs), that after eradication in 1996, areawide aerial releases were continued on a permanent basis over 5,500 km^2 of high risk areas in the LAB (Dowell et al. 1999; Dowell et al. 2000).

This Preventive Release Program (PRP) has been in operation since 1996 without major outbreaks of medfly occurring in the LAB. It has been expanded to ca. 6400 km^2 to include additional high-risk areas contiguous to the LAB. From 1987 until the inception of the PRP, the State of California faced repeated major medfly infestation in the LAB, with an average of 7.5 medfly infestations detected each year. Since the inception of the PRP this has dropped to 0.2 infestations per year (97% reduction) in the PRP area (CDFA, 2000). The few very confined medfly detections within the PRP boundaries prove the assumptions on which the PRP is based: a) that California, especially southern California is under constant threat of medfly invasion and b) that the PRP can prevent the development of medfly populations from these invasions. There is not a more biologically efficacious, environment-friendly and cheaper method to exclude medfly from southern California (CDFA 2000).

Medfly SIT Suppression Programs

Two factors have been responsible for an increasingly more cost-effective application of medfly SIT. The first factor is the development of strains for male-only release, made possible by continuing research supported and co-ordinated by the IAEA and FAO over the last two decades (Franz et al. 1996). Improved genetic sexing strains with higher production, increased stability and which are molecularly marked are now in use in almost all operational SIT programs (Robinson et al. 1999). The use of male-only strains is now the state of the art for medfly SIT and has resulted in a number of benefits among which are increased applicability of the SIT and also increased effectiveness of the sterile males in the absence of sterile females (Hendrichs et al. 1995, Rendon et al. 2000). The economic implications are significantly reduced costs of applying SIT per square kilometer per week in comparison to the use of bisexual strains (Enkerlin et al. in preparation).

Second, as is the case in any industrial production, biological or non-biological, significant economies of scale can be derived from larger mass rearing factories. Whereas the cost per million for sterile flies in small facilities producing tens of millions per week is relatively high, this cost decreases by more than half when mass rearing facilities reach a capacity of hundreds of millions per week (Enkerlin, unpublished data). The El Pino facility in Guatemala, which has reached a weekly production of over one billion sterile males, actually has a sliding scale of costs for their sales of sterile medfly males, that is inversely related to the production levels (Table 1).

Some of the initial medfly pilot SIT projects in the 1960s and early 1970s confirmed the effectiveness of SIT (De Murtas et al. 1970, Mellado et al. 1970, Ros et al. 1981, Rhode 1970, Kamburov et al. 1975, Cheikh et al. 1975); nevertheless, application of the SIT against medfly did not expand mainly because sterile fly costs were higher at that time when compared to conventional insecticide sprays. However, progress on both of the above factors has opened the possibility of using of SIT for routine medfly suppression, rather than only for eradication programs that are of a limited duration. Using SIT for suppression has the major advantage of not requiring the establishment of quarantines to protect free areas. In addition, in view of the increasing sensitivity to environmental concerns, there is new interest in using the SIT, particularly in the Mediterranean region where tourism and commercial fruit orchards coexist, with the aim of producing low-insecticide or organic fruit. Sales of organically produced food, though still small, have been growing by 20% a year in the U.S.A. and in some European countries as much as 40% a year (The Economist 2001). This has stimulated the initiation of pilot SIT suppres-

TABLE 1. COSTS PER MILLION STERILE MALES AT VARYING PRODUCTION LEVELS AT THE MOSCAMED MEDFLY MASS REARING FACILITY, EL PINO, GUATEMALA.[1]

Level of sterile male medfly production	Running costs[2] per million sterile males	Production costs[3] per million sterile males	Total cost per million sterile males
300 million per week	$199.29	$178.67	$377.96
400 million per week	$149.47	$178.67	$328.14
500 million per week	$119.47	$178.67	$298.24
600 million per week	$ 99.64	$178.67	$278.31
700 million per week	$ 85.41	$178.67	$264.08
800 million per week	$ 74.73	$178.67	$253.40
900 million per week	$ 66.43	$178.67	$245.10
1.0 billion per week	$ 59.78	$178.67	$238.45
1.1 billion per week	$ 54.35	$178.67	$233.02
1.2 billion per week	$ 49.82	$178.67	$228.49
1.3 billion per week	$ 45.99	$178.67	$224.98
1.4 billion per week	$ 42.76	$178.67	$221.43
1.5 billion per week	$ 39.87	$178.67	$218.54
1.6 billion per week	$ 37.50	$178.67	$216.17

[1]From Vollmershausen 2001.
[2]Includes direct administrative costs, depreciation, maintenance utilities, security and R&D.
[3]Includes diet materials, supplies, personnel and transportation.

sion programs in Tunisia (Cayol & Zarai 1999), Israel and Jordan (Rössler et al. 2000), Madeira (Pereira et al. 2000), and South Africa (Barnes et al. 2001). These SIT pilot projects have been effective in reducing insecticide applications and fruit losses, as well as rejections of transboundary shipments due to pest presence in fresh fruit exports (Barnes et al. 2001).

The economic feasibility of using SIT for medfly suppression has been confirmed by benefit-cost analyses (Enkerlin & Mumford 1997; Mumford 2000). Even without including the environmental benefits, costs per hectare per year of protecting orchards is now lower for an integrated areawide approach with SIT than for non-areawide conventional cover sprays, and approximately equal to the areawide application of bait-sprays. These savings to the fruit industries and the general environmental benefits already indicate the potential for the establishment of commercial SIT mass rearing facilities. The continuous demand for sterile males in SIT suppression programs should open the way for commercialization of the SIT. Nevertheless, further increases in the cost-effectiveness of medfly SIT are a precondition before serious private sector investment takes place in mass rearing facilities and sterile fly production.

There is a third area, in addition to the use of genetic sexing strains and the implementation of economies of scale, where there is considerable scope for improving the efficiency of medfly SIT. This is the relatively poor performance of the mass produced sterile males, which on average are approximately only one third to one half as competitive as the wild males (FAO/IAEA/USDA 2002). To compensate for this low effectiveness, high sterile to wild over-flooding ratios are routinely applied. A better understanding of medfly sexual behavior and the way it is affected by the processes of colonization, mass rearing and irradiation, could lead to improvements in sterile male performance, thus lowering current over-flooding ratios and overall costs of SIT application.

MATING SYSTEMS AND SIT

The nature of mating systems in any given species is determined primarily by ecological factors such as the distribution of resources (Emlen & Oring 1977). Based on resource distribution, male mating systems of insect pests that are the target of the SIT can be divided into three broad polygynous categories (Thornhill & Alcock 1983). First, there are the resource-defense systems where the potential for mate monopolization by males is high due to a clumped distribution of females and the resources that are attractive to receptive females (Table 2). Here, male mating success is largely determined by *intra-sexual* competition at these resources required by females, both to intercept females and to prevent other males from gaining access to females. Second, there are non-resource-based mating systems where mating takes place away from resources required by females. The potential for males to economically defend resources and females is rather low in this case because the resources and females are more widely dispersed, and intra-male selection involves a prolonged searching polygyny. Males participate in a type of continuous scramble competition, attempting to out-race their competitors to receptive females

TABLE 2. COMPARISON OF MALE MATING SYSTEMS OF INSECT PEST SPECIES THAT ARE THE TARGET OF APPLICATION OF THE STERILE INSECT TECHNIQUE.

Type of male mating system[1]	Male intra-sexual selection	Defense of female-required resources	Potential for monopolization of females	Pheromone release	Non-resource-based mating territories	Visual sound and tactile male courtship behaviors	Inter-sexual selection and female mate Choice	Examples of insect pest targets of SIT application
Resource defense polygyny	Yes	Yes	High	No	No	No	No	New and Old World Screwworm; Tsetse spp.
Prolonged searching polygyny	Yes	No	Low	Females	No	No	No	Codling Moth; Pink Bollworm; etc.
Lek polygyny	Yes	No	Low	Males	Yes	Yes	Yes	Medfly and other Tephritid fruit flies

[1]Classification of mating systems after Thornhill & Alcock 1983.

that are releasing pheromones. Third, there are lek-mating systems, also non-resource-based, where the potential for males to monopolize resources and females is also rather low. However, in these cases, males establish "symbolic" mating territories, and compete by attracting females and attempting to exclude competitors from the mating arenas. In lek mating systems, unlike the two previous mating systems, *inter-sexual* selection components are also involved, with females exerting mate choice by visiting aggregated males and selecting a mate from amongst them.

Tsetse flies, *Glossina* spp. and screwworm flies *Cochliomyia hominivorax* and *Chrysomyia bezziana*, are examples of the first type of mating system that are mainly resource-based (Table 2). Males seek mates on animal hosts where females forage for food (blood in the case of tsetse) or food and oviposition sites (animal wounds in the case of screwworms). In these species, the interaction between the sexes is relatively simple in view of the absence of any courtship and males compete at such encounter sites trying to get hold of females (Jaensson 1979). Once a male manages to grab a female, and confirms through tarsal contact species-specificity of the female based on her cuticular hydrocarbon profile particular to each species, copulation takes place (Pomonis et al. 1993, Carlson et al. 2000). Mating success in these species is therefore largely determined by the sexual aggressiveness of the males, sterile or wild, in intercepting receptive females at these important resources.

On the other hand, the mating system of such pest Lepidoptera as codling moth (*Cydia pomonella*) and pink bollworm (*Pectinophora gossypiella)* is non-resource based, however, also generally involves no male courtship, nor direct female mate choice (Table 2). Sterile and wild males participate in a type of scramble competition following pheromone trails originating from receptive females, with the winner being first in reaching the females and transferring the spermatophore (Snow et al. 1976).

A majority of the tropical and subtropical tephritid fruit flies, including medfly and a majority of *Anastrepha* and *Bactrocera* spp. have a lek polygyny, involving both male *intra-sexual* selection and also *inter-sexual* selection (Prokopy 1980). Males have to find and join leks (male aggregations in mating arenas) within which they have to participate in aggressive encounters with other males to defend sites from which to signal and court females. Receptive females are attracted by male pheromone to the leks for the sole purpose of soliciting courtships from various males, thus comparing their performance and eventually accepting one for mating.

While in tephritids with a lek mating system the population as a whole has a sex ratio of close to 1:1, females are not synchronized in their sexual maturation and thus only a small proportion of females will visit leks at any given time. Therefore the operational sex ratio, the number of courting males for each attracted mature and receptive female in a lek, is largely biased in favor of males. As a result, male intra-sexual competition is intense and the differential mating success can be large, with many males getting no mates, and a few males obtaining many matings (Arita & Kaneshiro 1985, Hendrichs 1986). Bisexual releases of sterile flies, half of which include sterile virgin females that all become receptive within a short time period, decrease the operational sex ratio of males to females at leks. On the other hand, the use of male-only strains for sterile fly releases results in operational sex ratios that increase even further the male bias at mixed leks compared to wild male leks and thus the need for releasing higher quality sterile males. Increasing sterile to wild male over-flooding ratios in species with a lek polygyny is less effective in overcoming reduced sterile male competitiveness than in species with the other mating systems. As wild females actively select and discriminate in favor of males releasing timely pheromone of the adequate profile (Heath et al. 1994) and performing properly visual, sound and tactile courtship behaviors (Eberhard 2000), they may still favor the courtship of a wild male even though he may represent a minority within a mixed lek. Thus the effective application of the SIT for lek species requires a more detailed understanding of the mating systems. They also require a much more sophisticated quality control system to measure and assure the sterile male performance.

Status of Medfly Sexual Behavior Studies and Quality Control of Sterile Flies

Even though various workers had studied various aspects of medfly behavior in the pre-SIT era (Féron 1962), it was the implementation of SIT that stimulated most research into medfly sexual behavior. Concerns about whether mass-reared, or even any laboratory-reared, medfly strains were exhibiting wild-like characters in terms of sexual behavior and competitiveness motivated research as early as the 1970s. Pilot SIT activities against medfly in Central America, Hawaii, Israel and elsewhere resulted in assessments of the mating competitiveness of irradiated and non-irradiated medflies (Causse 1970, Holbrook & Fujimoto 1970, Fried 1971, Rössler 1975), and the publication of a collection of quality control tests for fruit flies in general (Boller & Chambers 1977), which included various tests relevant to medfly mating behavior.

The initiation of the Moscamed program in the late 1970s, resulted in the renewed interest in medfly mating studies. This program, required a quality control system for a weekly production of

500 million sterile flies. As part of this effort, the description of the lek mating behavior of wild medflies, observed under semi-natural conditions in field cages, was provided (Prokopy & Hendrichs 1979), and the first medfly mating compatibility test on a field-caged host tree was carried out to measure female mate choice by allowing wild females to select among competing wild and sterile males under natural conditions (Zapien et al. 1983). In addition, a collection of field tests was developed for confirming and extending a series of laboratory tests (Boller et al. 1981, Chambers et al. 1983) and the first quality control manual for medfly mass rearing and field evaluation was produced (Orozco et al. 1983), which has been used extensively to measure quality of mass produced flies. These publications formed the basis for a USDA quality control manual, compiled to ensure that sterile medflies for SIT programs with USDA involvement met certain quality standards (Brazzel 1986).

Further refinements have come with behavioral studies in the open field to validate the medfly behaviors observed on field-caged host trees (Hendrichs & Hendrichs 1990, Hendrichs et al. 1991, Whittier et al. 1992). More recent studies addressed many other aspects including the various effects of mass-rearing (Calkins et al. 1994, Calkins et al. 1996), male size (Orozco & Lopez 1993), nutritional status (Blay & Yuval 1997), mating-induced changes in female behavior (Jang 1995, Jang et al. 1998), strain differences (Liedo et al. 1996), and behavioral incompatibility between wild and mass reared flies (McInnis et al. 1996).

The conclusion from all these studies has been that although sterile mass reared medflies do join and compete within leks, achieve a portion of matings with wild females, and transfer sperm and induce female refractoriness and sterility in offspring, they are clearly less competitive than their wild counterparts. These behavioural changes appear not to be caused by mating incompatibility among different medfly populations (Cayol 2000a), but rather by mass-rearing conditions, the irradiation process and the years a strain is held in colonization (Cayol 2000b).

FAO/IAEA Sponsored Coordinated Research Project

The Joint Division of Nuclear Techniques in Food in Agriculture of the Food and Agriculture Organization (FAO) and the International Atomic Energy Agency (IAEA) sponsors Coordinated Research Projects (CRPs) or research networks that focus participating scientists from both developing and developed countries on applying nuclear techniques to specific problems relevant to agriculture. A CRP entitled "Medfly Mating Behavior Studies under Field Cage Conditions" was initiated in 1994 with three objectives: a) to develop a detailed understanding of medfly courtship behavior and female choice through experimentation and slow-motion video analysis, b) to measure mating compatibility worldwide among medfly populations, and c) to develop harmonized mating tests to measure competitiveness and compatibility of sterile flies. This CRP concluded in 1999 and four Research Coordination Meetings (RCMs) were held to review results and plan future research, Vienna, Austria (4-7 October, 1994), Tapachula, Mexico, (19-23 February 1996), Tel Aviv, Israel (15-19 September) and Antigua, Guatemala (29 June-03 July 1999). Twelve research teams from ten countries (Argentina, Austria, Costa Rica, France, Greece, Guatemala, Israel, Kenya, Mexico, U.S.A.) participated and conducted research on different aspects of medfly sexual behavior. The research findings resulting from this CRP, published as refereed publications in scientific journals and as a series of papers in this issue are included in the listing of relevant references in Table 3.

Application of Research Findings: International Fruit Fly Quality Control Manual

On the basis of all the above studies, as well as information from various fruit fly quality control manuals, a concerted effort was made to develop an FAO/IAEA/USDA manual on "Product Quality Control and Shipping Procedures for Sterile Mass-Reared Tephritid Fruit Flies" (FAO/IAEA/USDA 2002). The objective was to incorporate the improved understanding of medfly mating behavior into quality control protocols, to harmonize procedures and thus allow comparison of sterile fly quality over time and across rearing facilities and field release programs.

Based on the CRP findings, the FAO/IAEA/USDA international manual emphasizes mating competitiveness, sexual compatibility and post-mating factors and de-emphasizes the widely used laboratory mating propensity test. This test is carried out only with mass reared males and females, under high densities and in small Plexiglas cages, all conditions that favor sterile males and thus it routinely overestimates sterile male performance. Even worse, it measures the wrong parameter, namely speed of pair formation between mass-reared males and females, even though sterile males trying to achieve fast mating, short-cutting steps in the courtship sequence, are only successful under crowded colony rearing conditions but are unsuccessful in mating with wild females (Briceño et al. 1996, Briceño & Eberhard 1998).

The international manual recognizes that the most important indicator of sterile male quality control is their successful interaction with wild females of the target population. Thus a standard field-cage test is required as an ultimate measure of quality, where wild females of the target population

TABLE 3. LISTING OF RELEVANT STUDIES CONDUCTED ON VARIOUS ASPECTS RELATED TO MEDFLY SEXUAL BEHAVIOR AND MATING COMPETITIVENESS.

Field of Study	Relevant References
Courtship behavior in relation to sexual competitiveness	Feron 1962; Sivinski et al. 1989; Whittier et al. 1994; Whittier & Kaneshiro 1995; Briceño et al. 1996; Liimatainen et al. 1997; Briceño & Eberhard 1998; Lance et al. 2000; Briceño & Eberhard 2002; Briceño et al. 2002; Lux et al. 2002b
Lekking behaviour in relation to sexual competitiveness	Prokopy & Hendrichs 1979; Arita & Kaneshiro 1985; Arita & Kaneshiro 1989; Shelly et al. 1993; Shelly & Whittier 1995; Yuval et al. 1998; Kaspi & Yuval 2000; Field et al. 2002
Field cage evaluations in relation to sexual competitiveness	Wong et al. 1983; Zapien et al. 1983; Rendon et al. 1996; Cayol et al. 1999; Katsoyannos et al. 1999; Calcagno et al. 2002; Economopoulos & Mavrikakis 2002
Open field studies and evaluation of field competitiveness	Hendrichs & Hendrichs 1990; Whittier et al. 1992; McInnis et al. 1994; Rendon et al. 2000; Shelly 2000
Feeding behavior and nutritional status in relation to sexual competitiveness	Hendrichs et al. 1991; Warburg & Yuval 1997; Blay & Yuval 1997; Cangussu & Zucoloto 1997; Bravo & Zucoloto 1998; Field & Yuval 1999; Kaspi & Yuval 2000; Papadopoulos et al. 2001; Shelly et al. 2002; Yuval et al. 2002
Predation in relation to sexual behavior	Hendrichs et al. 1993; Hendrichs & Hendrichs 1994; Hendrichs & Hendrichs 1998
Morphometric traits in relation to sexual competitiveness	Churchill-Stanland et al. 1986; Orozco & Lopez 1993; Hunt et al. 1998; Menez et al. 1998; Blay & Yuval 1999; Hunt et al. 2002; Hasson & Rossler 2002; Rodriguero et al. 2002
Irradiation in relation to sexual competitiveness	Causse 1970; Holbrook & Fujimoto 1970; Hooper 1971; Hooper 1972; Calkins et al. 1988; Heath et al. 1994; Lux et al. 2002a
Age in relation to sexual competitiveness	Liedo et al. 1996b; Papadopoulos et al. 1998; Taylor et al. 2001; Liedo et al. 2002
Factors affecting female post-mating and re-mating behavior	Boller et al. 1994; Jang 1995; Hendrichs et al. 1996; Jang et al. 1998; Jang 2002; McInnis et al. 2002; Vera et al. 2002
Effects of mass-rearing in relation to sexual competitiveness	Liedo et al. 1996a; Calkins 1991; Calkins et al. 1994; Calkins et al. 1996; Cayol 2000b
Inter-population compatibility and isolation studies	McInnis et al. 1996; Cayol 2000a; Cayol et al. 2002;
Comparative approaches to sexual behavior in Tephritidae	Myburgh 1962; Prokopy 1980; Sivinski et al. 2000; Yuval & Hendrichs, 2000; Quilici et al. 2002

are the final arbiters of sterile male quality. This test is carried out on a routine basis under semi-natural conditions on field-caged host trees. Further fine-tuning of the manual is a continuous process through which the procedures evolve as new findings emerge. In support of this process, a new 6-year FAO/IAEA Coordinated Research Project on "Quality Assurance of Mass Produced and released Fruit Flies" has been initiated involving participants from all major fruit fly SIT programs.

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