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Mexican Fruit Fly Population Suppression with the Sterile Insect Technique

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ABSTRACT

The Mexican fruit fly is a major quarantine pest of citrus and other fruits in Mexico. Patterns in fly captures by surveillance trapping indicate that a small but persistent population of this pest exists in the Lower Rio Grande Valley of Texas. The mexfly is bivoltine with broods in the spring and fall. Based on 10 yr of data, mild winters and rainfall during the breeding seasons favor increased numbers of flies. Under optimal weather conditions there can be an additional generation in the spring and populations would reach large densities were it not for an intensive control program. In south Texas the USDA releases 25 million sterile flies weekly to suppress the population and minimize the necessity for fumigation of fruit for export. Chemical controls can be integrated with the sterile fly releases but are of limited benefit because they protect groves for only one generation before reinfestation. The suppression program has evolved to meet challenges from urban encroachment, public attitudes deemphasizing chemical controls (both pre- and post-harvest), an increased percentage of abandoned groves, and the threat of invasion by other major citrus pests. The feasability of eradication is being considered but will probably depend on an occlusion of favorable factors such as a population downturn following severe weather (e.g., a hard freeze or drought) and the establishment of a fly free zone in neighboring Mexico.

RESUMEN

La mosca mexicana de la fruta es una plaga importante de la fruta cítrica y de otras frutas en México sujeta a cuarentena. Los patrones de captura de la mosca por medio del trampeo de vigilancia indican que una población pequeña pero persistente de esta plaga existe en el Bajo Valle del Río Grande de Texas. La mosca mexicana de la fruta produce dos descendencias, presentando una progenie en primavera y otra en verano. En base a la información de 10 años, los inviernos benignos y la precipitación durante la estación reproductiva favorecen el aumento en las cantidades de moscas. Bajo condiciones atmosféricas óptimas puede haber una generación adicional en la primavera y las poblaciones alcanzarían densidades altas sino fuera por un programa de control intensivo. En el sur de Texas, el USDA libera semanalmente 25 millones de moscas estériles semanales para suprimir a la población y para reducir al mínimo la necesidad de fumigar la fruta para exportación. Métodos de control químico pueden integrarse con la liberación de moscas estériles pero ofrecen beneficio limitado porque protegen las huertas solamente por una generación antes de la reinfestación. El programa de supresión se ha desarrollado para resolver los desafíos provenientes del crecimiento urbano, de la actitud pública que desenfatiza el control químico (tanto pre como post cosecha), un porcentaje creciente de huertas abandonadas y la amenaza de la invasión por otros parásitos importantes de la fruta cítrica. La viabilidad de la erradicación está siendo considerada pero probablemente dependerá de una conjunción de factores favorables tales como un descenso de la población después de condiciones climáticas severas (por ejemplo una helada o una sequía severa) y del establecimiento de una zona libre de la mosca en el área vecina de México.

Key Words: Anastrepha, quarantine, methyl bromide.

The Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae) is a major pest of citrus and other fruits in Mexico and Central America. Reduction in yield and quality of the fruit crop is caused by the presence of larvae which feed on the fleshy pulp (Baker et al. 1944, Gutierrez- Sampero et al. 1993). A small but persistent population of this pest occurs in the citrus production area of the Lower Rio Grande Valley. The existence of this population poses a unique problem for integrated pest management. No significant damage is inflicted on the commerically harvested citrus in Texas (70% grapefruit, 28% orange). But, because the Mexican fruit fly is an international quarantine pest the detection of even one individual of this species can trigger quarantine protocols (Nilakhe et al. 1991). Most markets will not accept untreated fruit from fruit fly infested areas, thus, the fruit must be fumigated for disinfestation prior to export. Under quarantine protocols the fumigated fruit is boxed separately, labeled for identification, inspected, and certified for export, all of which adds to the post-harvest costs.

An intensive trapping and sterile insect technique (SIT) program has been in operation in south Texas since 1981 administered by the USDA Animal and Plant Health Inspection Service (APHIS). Nonetheless, fertile Mexican fruit flies are detected in the Lower Rio Grande Valley every spring and these fly-finds trigger the expensive quarantine restrictions. The economic benefit of the suppression program derives mainly from the reduction in the percentage of the harvest impacted by the quarantine restrictions, allowing most of the fruit to be shipped without fumigation and the associated expense. Shipment of fruit without regulatory restriction is of economic benefit to Texas growers, but it raises concerns that some fruit infested with larvae might be exported prior to quarantine. To assess the validity of these concerns we herein discuss the life cycle of the insect, the factors influencing population levels, and the effect of the suppression program on infestation rates.

The implementation and goals of the program are described by Holler et al. (1984) and Nilakhe et al. (1991). The SIT program in south Texas is unusual in that the goal is suppression rather than eradication. The program is further unique in that it relies on a combination of SIT and quarantine treatments to maintain production and export of the target commodity. Although the program is unique, it has been cited as a model with potential application to other fruit production areas with similar circumstances. Since its inception the program has been subject to periodic reassessment, and alterations in the program have been adapted as knowledge and technology has expanded. Thus, it is of some importance to detail the rationale behind the program: its functions, failures and achievements. In addition, there are risk assessment and cost/benefit considerations apart from the technical aspects of pest management, population dynamics, and biological control. The present article describes the evolution of the program over the last decade, and updates the status of the fruit fly problem in south Texas.

Detection and Regulation. A detection trapping program is maintained in host plants to achieve a uniform distribution of five McPhail traps per square mile of citrus production area, the level used in California fruit fly detection programs (Gilbert et al. 1984). Each square mile of Cameron, Willacy and Hidalgo County, Texas, is divided equally into fifths, with one trap deployed in each fifth of a square mile, except those square mile sections that are devoid of hosts (rangeland, for example). As the acreage of citrus has increased over the last decade, to a present 35,000 acres, so have the number of traps. A surveillance grid of 2,056 McPhail traps is now in continuous operation in both commercial groves and dooryards with a ratio of 55:41. The traps, baited with torula yeast, borax and water, are serviced by employees of the Texas Department of Agriculture weekly throughout the year. For quality control ten percent of the traps are "salted" with marked flies each quarter year to assure that the traps are being serviced properly.

Flies collected in the traps are screened by USDA-APHIS technicians under ultraviolet light to separate released steriles (marked with red fluorescent dye) from ferals. Unmarked flies are dissected to determine the condition of the gonadal tissues including the spermathecae which are inspected for the presence of sperm. Trap-back of the sterile flies is monitored as a measure of sterile fly survival and to ensure that complete area coverage is being achieved.

Table 1. Fruit and larval interceptions at Texas Ports of Entry. Monthly totals for the period May 1998 to April 1999.

Month	Fruit Interceptions	Anastrepha Larvae
May	22	64
June	32	92
July	20	123
August	20	76
September	3	4
October	0	0
November	3	8
December	1	1
January	10	33
February	21	87
March	5	25
April	12	28
Totals	149	541

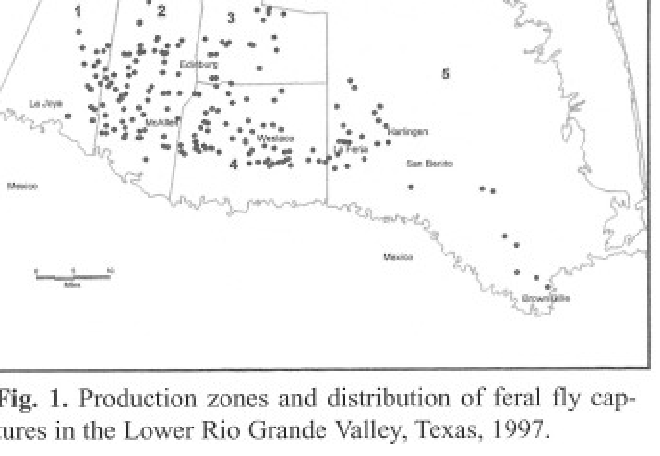

Fig. 1. Production zones and distribution of feral fly captures in the Lower Rio Grande Valley, Texas, 1997.

Table 2. Numbers of A. ludens captured in Santa Rosa Canyon, Nuevo Leon, Mexico, weekly, mid-April to mid-June 1994. Five McPhail traps per site.

	Julian Week											
Location	16	17	18	19	20	21	22	23	24	25	26	27
Parque	6	9	2	14	4	7	21	30	27	10	17	5
Ojo de Agua	–	–	–	–	–	–	–	–	–	–	–	–
Crucitas	4	–	–	–	–	–	–	–	–	1	–	–
Canyon	6	17	2	22	11	6	23	16	39	101	412	211
Palma	4	4	1	1	2	–	9	3	7	3	132	130
Rio Seco	10	5	–	4	3	–	6	2	16	2	33	18
Puente	2	2	2	4	13	3	*z	3	5	5	20	39
Rancho	7	81	4	50	38	16	105	89	39	45	180	266
Penultimo	5	8	10	16	15	3	25	22	7	10	17	25
Iturbide	2	6	7	17	3	8	57	21	19	10	13	10
TOTALS	46	132	28	128	89	43	246	186	159	197	826	704

[z] * - Traps missing.

Table 3. Number of days with freezing temperatures[z] and numbers of flies caught in the lower Rio Grande Valley annually, 1989-1999.

Winter	Nov	Dec	Jan	Feb	Total	Low Temp	MEXFLYS	Flies/ k-traps
89-90	–	10	–	–	10	14°F (McCook)	0	0
90-91	–	5	–	–	5	26°F (McCook)	10	11
91-92	–	–	–	–	0	33°F (McCook)	14	11
92-93	2	–	–	–	2	30°F (Mission)	170	150
93-94	2	–	2	1	5	28°F (McCook)	43	38
94-95	–	1	–	–	1	32°F (McCook)	627	564
95-96	–	–	2	3	5	27°F (McCook)	50	44
96-97	–	2	4	–	6	21°F (McCook)	264	136
97-98	–	2	–	–	2	29°F (Weslaco)	1348	656
98-99	–	1	–	–	1	30°F (La Joya)	21	10

[z]Data from U.S. National Weather Service.

The capture of a feral mexfly in the surveillance traps initiates a delimiting survey. An additional ten McPhail traps are placed within a 1/4 mile radius of the fly-find and fruit within 200 meters of the trap are examined to help determine if the area is infested. The detection of a feral mexfly triggers the quarantine protocol. The protocol defines two categories of infestation: local and general. For regulatory purposes the Lower Rio Grande Valley is divided into five commercial citrus production zones (Fig. 1). A local infestation is declared whenever larvae are found, or whenever two or more feral flies are found within one mile of one another within one projected life cycle (approximately one month depending on degree-days). The protocol requires that any fruit originating within a one mile radius of a feral fly or larval detection must be fumigated with methyl bromide in an APHIS approved chamber monitored by APHIS personnel to obtain certification for export.

A general infestation is declared when five percent of the square mile blocks with traps within a production zone have detections of feral flies, or, when 1.5 percent of the square mile blocks within a zone have two or more fly-finds. The production zones vary from 171 to 606 square miles in area with from 78 to 275 trappable square miles in each zone. With such sensitive triggers all of the zones become regulated in a typical year. In the highest infestation year, 1998, a quarantine was invoked on the 21st of January, well before the end of the harvest season (October to May) and the earliest quarantine date ever. In the current year, 1999, only one of the five zones had to be quarantined and the protocol was not triggered until the 3rd of May, after most harvesting was complete.

When a general infestation is declared all fruit from the entire production zone must be treated for certification. Under general infestation two treatment options are available. Aside from the aforementioned methyl bromide fumigation, groves outside of the one square mile infested core area can be treated with toxic-bait sprays (2.4 oz technical grade Malathion and 9.6 oz of protein hydrolysate, per acre) applied by aircraft. However, to obtain certification the sprays must be initiated within five days and must be reapplied at 6-10 day intervals for no less than 30 days and continued through to the end of harvest. In practice the latter option has never been used, mainly because infestation levels have never reached the point where it would be economically advantageous.

Border Inspections and Fruit Interception. There are seven ports of entry between the Lower Rio Grande Valley of Texas and the adjoining parts of Mexico. In addition, commercial passenger flights arrive from interior Mexico at two Valley airports. USDA-APHIS, Agricultural Quarantine Inspection, Mexican Border Operations, inspects automobiles, buses, commercial trucks, railcars, passengers and their baggage. Products that are fruit-fly hosts are prohibited unless treated at origin under a preclearance program administered by the International Services component of USDA-APHIS. The accepted products are oranges, treated with methyl bromide, and mangoes, treated by hot water dip. Neither passengers or agricultural cargo is moved by train across the border and thus the risk from smuggled perishables is low. Commercial truck cargo moving into the United States is highly regulated and is sampled and inspected at prescribed rates. To ensure compliance with our regulations, trucks are randomly off-loaded and more thoroughly inspected. Based on several years of inspection data the risk of mexfly introduction associated with truck cargo is low. Similarly, airline passengers into our area seldom carry illicit fruit.

Passenger automobiles and their baggage are the source of nearly all interceptions of fruit fly host material and associated insects. Fruit fly larvae are identified only to the genus level. Intercepted citrus and mango account for 98% of the larvae identified as *Anastrepha* spp., with roughly equal numbers of larval interceptions from both types of fruit. Table 1 shows the numbers of host materials intercepted monthly, along with the numbers of larvae determined as *Anastrepha.* These data from a recent twelve month period parallels the pattern from previous years with highest rates from January to August. This last year's total, 541 larvae, is down somewhat from previous years. Over the last seven years the annual totals have ranged from 484 to 1,700 with an average number of slightly more than 1,200 *Anastrepha* larvae intercepted per year. Larvae in mangos are most often *Anastrepha obliqua* (Macquart), the West Indian fruit fly, but those in citrus are always *Anastrepha ludens.* Based on the percentage of automobiles that are actually stopped and searched it is suspected that much illicit fruit is not being intercepted. To improve this situation there are plans to deploy specially trained, fruit detecting dogs at the busiest ports of entry.

Are the Trapped Flies of Indigenous or Exogenous origin? This fundamental question has been debated for years. Flitters (1964) states that adult Mexican fruit flies periodically disperse from northeast Mexico into the citrus areas of the Lower Rio Grande Valley of Texas causing the quarantine and regulatory problems. Williamson & Hart (1989) also attribute the failure of eradication attempts in Texas to the ingress of flies from Mexico. In most years fewer than 50 adult flies are trapped per season in the surveillance grid. Typically, the feral flies are captured in the springtime between February and June with no flies trapped the rest of the year. Prior to initiation of the suppression program feral flies were regularly trapped in November and December (Holler et al. 1984), key months in the harvest period which begins in October. Moreover, no larvae have been found in commercially grown fruit since the program became area-wide in 1985. There is no natural barrier between Texas and Mexico other than the Rio Grande. Although the Mexican fruit fly is not a particularly strong flyer and certainly not a migratory insect, individuals are capable of dispersing up to 10 km, especially if aided by winds (Thomas & Loera-Gallardo 1998). However, while there is approximately 35,000 acres of citrus on the Texas side of the river, there is only about 300 acres of commercial citrus on the Mexican side, all in two isolated orange groves approximately eight km south of the river near Rio Bravo, Tamaulipas. The USDA and its sister agency in Mexico, SAGDR, have jointly operated traps in the larger of the two groves and have found only low numbers of Mexican fruit flies (e.g., two fertile flies in 1996 out of 50 traps). The areas with large indigenous fruit fly populations are ca. 300 km to the south in the state of Nuevo Leon, with inhospitable semi-desert scrub habitat intervening. It seems unlikely, therefore, that any appreciable numbers of adult Mexflies are dispersing into Texas from Mexico unless they are developing in dooryard fruit in towns bordering the river. But if dooryards are the source of the flies, they are as likely to be Texas dooryards as Mexican dooryards. Furthermore, if the fly-finds in Texas were the result of insects flying in from Mexico then one would expect most of the captures to be in traps nearest the river which is not the case. Rather, most captures are scattered in groves well north of the border (Fig. 1).

Alternatively, E.F. Knipling (cited in Nilakhe et al. 1991) opines that the Mexican fruit fly is introduced annually via infested fruit smuggled into Texas from Mexico. Indeed, spot inspections of automobiles crossing the border between the United States and Mexico demonstrate that there is a steady flow of smuggled fruit entering Texas. However, if smuggled fruit were the source of the Texas flies, one would expect them to be captured mainly in traps in urban areas as opposed to the commercial citrus groves. On the contrary, only about 16% of the feral flies are taken in dooryard traps with the great majority taken in commercial groves. This differential cannot be accounted for by a small bias in trap distribution. The ratio of traps in dooryards vs. groves is 41:59. Moreover, the most frequently smuggled fruit are mangoes and the primary pest of Mexican mangoes is *Anastrepha obliqua*. If smuggled fruit were the source of the Texas flies then one would expect numbers of *A. obliqua* to turn up in the traps as well. Yet, *A. obliqua* is rarely found in the surveillance traps and not at all in most years.

One might reason that the adults are not reliably detected because of the limited efficiency of the McPhail trap grid. At a trap density of five traps per square mile only about 0.2 percent of the released steriles are caught. Thus, a local infestation would probably not be detected until one or two generations have built up the population. Because there are few hosts for *A. obliqua* in the Lower Rio Grande Valley (some dooryard mango trees), their populations cannot build up and this factor might account for the paucity of detections of this species. But, there is no evidence of foci or hot spots of the sort expected with localized infestations in the pattern of mexfly captures. Rather, when the mexfly adults first appear in the traps, the fly-finds tend to be scattered throughout the valley, not clustered in adjacent groves. Thus, the pattern in fly-finds is not consistent with the hypothesis that the feral flies are emerging from illicit fruit, nor with the corollary that they might be the progeny of such introductions.

While there is undoubtedly an occasional introduction of individuals from Mexico, the trapping patterns indicate that there is an indigenous if subliminal population in south Texas. That is to say, the absence of flies from the traps during most of the year is not due to the absence of a population, but rather, to a seasonal reduction in active adults.

Life Cycle of the Mexican Fruit Fly. Studies in northern Mexico where the mexfly is indigenous show that the population is typically bivoltine (Fig. 2). The native host of the mexfly is a wild citrus called yellow chapote, *Sargentia greggi* Wats. (Plummer et al. 1941). Yellow chapote normally produces fruit in the late spring but if there is sufficient rain in the autumn months there will be some off-season fruit. The largest numbers of adults are found in the late spring, following maturation of the chapote fruit. Table 2 provides data on captures from ten trapping sites in Nuevo Leon, Mexico with native mots of yellow chapote. These data from only 50 traps give an indication of population densities where the fly population is unimpeded by suppression measures. With the onset of hot summer weather the numbers of flies, measured by trap success, declines sharply. With the onset of moderate temperatures in the fall, around October, the number of adults in the traps begins to increase, although the numbers are always far lower than the numbers trapped at the peak in spring.

Commercial citrus ripens in the late fall and these fruit are targets for ovipositing females. With the onset of cold weather the adult population, measured by trapped numbers, again declines sharply. If the winter is mild, without freezing temperatures, there is no doubt that some adults can survive the winter. In Mexico we have trapped-back sterile flies in January that were released in November. But, the population overwinters mainly in the immature stages; as larvae infesting the fruit and then as puparia in the soil. Adults emerge from these puparia in January-February. These adults mature and oviposit in the spring chapote crop, giving rise to the adults that emerge in the late spring to early summer and the cycle begins anew.

In south Texas wild flies are only trapped in the spring. Yet if the population is indigenous, there has to be a fall generation which is not being detected because of the low densities and limited effectiveness of the traps. Trap-back studies of mass released sterile flies in 1983 at a release density of 3,500 flies per square mile and trap density of five traps per square mile, resulted in only 0.15% of the sterile flies being trapped back (Holler et al. 1984). The ratio of sterile to feral flies in these traps was always greater than 100:1. This suggests that the feral fly population density was only around 40-50 flies per square mile at the spring peak. Under the circumstances, an autumnal population density of around 5-10 flies per square mile, active for only a few weeks, would be virtually undetectable.

A large unknown in this cycle is how the population survives the summer. There is a very high mortality to the immature stages during the summer months, especially in exposed sites (Thomas 1995). Laboratory experiments with the immature stages show that development time is temperature dependent such that warmer temperatures shorten the larval and pupal stages (Leyva-Vazquez 1988). Field studies confirm the temperature effect up to the point where mortality occurs. Development time from egg to adult stretches to 20 weeks during the winter, but can be as short as five weeks in the summer (Thomas 1997). Thus, any oviposition from the spring adults in the early summer should produce adults emerging in mid-summer, yet this is not detected. It has been suggested that there could be a summer diapause. But, we have made many field collections of larvae in Mexico during the spring peak which have been held for emergence (unpublished data) and have seen no instance of delayed development of the sort associated with aestivation or summer diapause. In the absence of evidence for aestivation, or of adult emergence in mid-summer, we believe that some of the adults that emerge in the late spring (April-June) must survive over the summer to oviposit in the fall (October-November) and this is the primary mode of population carryover. In Mexico where populations are indigenous there is a sharp drop off in activity during the late summer (August to October) with only a few adults trapped per week. When activity resumes in the fall the trapped flies are mainly gravid females (Fig. 3). By contrast, the adult

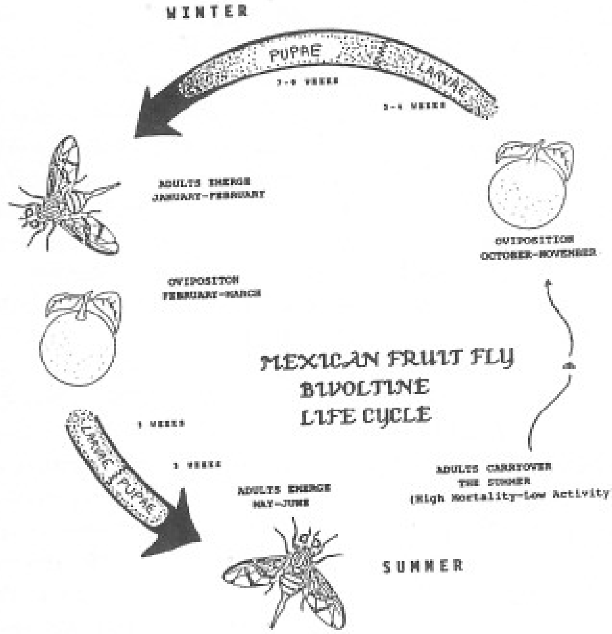

Fig. 2. The bovoltine life cyle of the Mexican fruit fly.

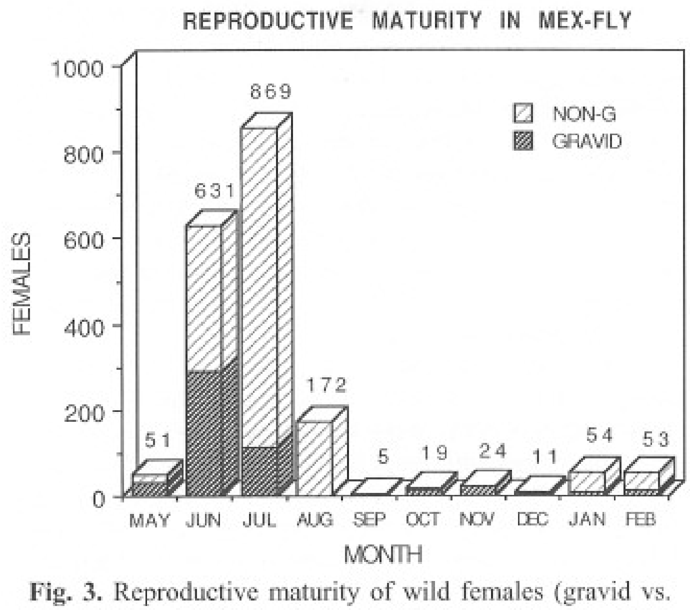

Fig. 3. Reproductive maturity of wild females (gravid vs. non-gravid) captured in traps by month at Santa Rosa Canyon, Nuevo Leon, Mexico.

Table 4. Secondary pest survey in control and treatment zones before and after spray operations. Percent of leaves infested.

	Control Zone		Treatment Zone	
	September	December	September	December
Red Scale				
Aonidiella auranti	26	42	25	35
Purple Scale				
Lepidosaphes becki	5	5	1	7
Citrus mealybug				
Planococus citri	1	2	0	0
Citrus whitefly				
Dialuerodes citri	9	9	2	2
Texas Citrus mite				
Phyllocoptruta oleivora	8	19	18	13

peaks in January and late spring consist mainly of immature flies. Because so few adults are trapped in the late summer we suspect that adult activity is curtailed by the heat and that most adults die with only those in the most optimal habitats able to persist. In the native ecosystem likely refugia would be riparian habitats which offer deep shade, surface water and a more or less dependable supply of carbohydrates from nectar, honeydew and rotting fruit. The largest trees and densest mots of yellow chapote are found on river courses. Commercial groves do not seem to provide good habitat for summer survival because they offer insufficient shade to significantly alter the ambient temperature, no free water and little by way of nectar or honeydew. Because there is no yellow chapote in Texas, we suspect that shady, watered, urban dooryards provide the summer refugia for the fruit fly population, but this is unproven. Dooryard fruit also provides oviposition sites during the offseason. The mexfly is clearly the least stenophagic species in the genus *Anastrepha* (Norrbom & Kim 1988). The wide host acceptance behavior of this insect is undoubtedly an adaptation to survival in a climatically vicarious environment, allowing the population to survive in alternative hosts when the primary host crop fails.

Fly Populations and Weather. Although the Texas population is small when compared to the areas where the fly is indigenous in Mexico, there has been a trend of increasing numbers over the last decade. In 1998 the surveillance program trapped the largest numbers of feral flies since the sterile insect releases began. Moreover, the first flies appeared earlier in the harvest season than in any previous program year. This event raised serious questions about the cost effectiveness of the suppression program. And, if the populations are indigenous to Texas there is concern that the program may not adequately protect the importing states.

It is generally accepted that insect populations undergo density independent fluctuations and that weather is a primary determinant of population size (Andrewartha 1972, Southwood 1976). However, evidence to support this assumption in the case of the mexfly has been elusive. At the present time the only way to census the mexfly is by trapping of the adults. However, trap success reflects activity levels as much as it does population size. Furthermore, McPhail trapping introduces confounding factors. Under drought conditions the traps are more attractive to the flies as a source of moisture. Thus, while dry conditions presumably have a negative effect on population size, it seems to have an enhanced effect on trap success (McPhail 1937). Eskafi (1988) studying mexfly populations in Guatemala was unable to correlate trap success with humidity, temperature or rainfall. Similarly, Aluja et al. (1996) and Celedonio-Hurtado et al. (1995) were unable to find a correlation between weather variables and the numbers of flies in traps. Thomas & Loera-Gallardo (1998) were able to show statistically significant correlations between maximum temperatures (negative) and rainfall (positive) with trap success. But the latter study considered sterile, released flies, not wild populations.

The outbreak of mexflies that occurred in the spring of 1998 was so much larger than in any previous spring that it raised concerns that the sterile release program was failing. These concerns were greatly allayed by the subsequent crash of the population in 1999. While it seems likely that these population fluctuations were unconnected to any flaws in the rearing, release, or viability of the sterile flies, it is still important to understand the factors which contribute to the fluctuations.

There is some data on the effect of climate which fits in with the life cycle. The winter of 1989-90 at the beginning of the decade was an extremely cold winter for the area. Low temperatures hit 14ºF and there were ten days of below freezing temperatures. Most of the citrus trees in south Texas were killed. The following spring, no mexflies were captured in the surveillance traps. Presumably, the hard winter of 1989-90 had all but eradicated the mexfly population in the Rio Grande Valley. The succeeding spring, 1991, a total of only ten feral adults were captured, so either a small number of flies survived or the population was reintroduced from Mexico.
One of the most important predictors of feral fly numbers is the severity of the preceding winter. During the last ten years there have been five cold winters (defined as 4-6 freezing dates) and five mild winters (1-2 freezing dates). All of the fly outbreaks have followed mild winters (Table 3). Specifically, in three springs of those five mild years there was a marked increase in mexfly captures over the preceeding year. The exceptional years were 1992 and 1999. In 1992 the population failed toincrease over the previous year (14 captures vs. 10). But the failure to increase that year might well be attributable to the fact that the newly planted citrus trees following the hard freeze of 89-90, were not yet producing fruit.

The most flies captured in any one spring was 1,348 in the spring of 1998 following a winter with only two freezing dates with the low on those dates of 29 and 32°F. The second largest number of flies, 627, in the spring of 1995, also occurred following an equally mild winter. Actually, the difference in those two years almost disappears when the captures are adjusted for trap numbers. There were almost twice as many traps in operation in 1998. The large outbreak of 1998 followed one of the warmest winters on record, with a mean January temperature of 65.3°F (at Brownsville) as opposed to the expected average of 59.9°F. The correlation with cold weather is not perfect, indicating that other variables are important. Generally, though, outbreaks only follow mild winters. Whenever there are more than 4 freezing dates the following spring population is always low (fewer than 50 total flies trapped).

Rainfall is another factor which appears to exert a favorable influence on the fly population, especially if the rains come during the breeding seasons in the autumn and spring. In four of the five seasons following cold winters there was a sharp decrease in the spring time populations as expected. The exceptional year was 1997 in which the population actually increased slightly over the previous year. Rainfall during the breeding season appeared to be the important factor. February and March 1997 were exceptionally rainy months with 5 inches more than the average 2.1 inch for the Rio Grande Valley, and the moist, humid conditions may have promoted breeding success and made up for the low winter survival. In such an exceptionally moist spring the breeding cycle may be early enough to support a second spring generation. This seems to have happened in the spring of 1997 and may have contributed to the exceptionally large population in 1998. Rainfall during the autumnal oviposition period may also be important. The adults active in October and early November give rise to the overwintering generation. The record population of spring 1998 followed the wettest October (1997) since weather records have been kept in the LRGV, the last 83 years. According to U.S. Weather Service records, the cumulative (13 stations) average for the LRGV is 2.51 inches. Depending on the station, LRGV localities received from 8 to 13 inches in October 1997. The exceptional weather that autumn has been attributed to an El Niño effect.

Conversely, populations crashed in 1999 in spite of a mild winter. The small numbers, only 21 total flies, may be attributable to the fact that there was below average rain at the critical times in October 1998 and the succeeding February and March which received no rain at all, the only time this decade that neither month received rain. The severe drought reversed the long term trend of increasing fly numbers. The effect of a lack of rainfall on mexfly populations is not limited to a scarcity of free water. Rainfall promotes new growth and floration of the citrus trees. The flowers provide nectar and the new growth provides breeding sites for aphids. The aphids produce honeydew which along with nectar is the primary source of carbohydrate essential for survival of the adult flies (Hagen 1956, Christenson & Foote 1960).

In summary, mild temperatures during the overwintering period and moisture during the breeding seasons can explain much of the variation in population size from one year to the next. Thus, the outbreak year of 1998 may be attributed to a combination of favorable weather patterns and not to a breakdown in the suppression program. Likewise, the increasing trend in population size over the last decade is largely attributable to the fact that there has been no prolonged hard freeze since 1989, during which time the citrus acreage has increased, and, with a lag of a few years, more of the trees have come into full fruit production. Inevitably the fruit fly population increases as the host availability increases.

Two other worrisome trends may be contributing factors. Firstly, as fruit production has increased, prices have dropped, resulting in abandoned groves and more unpicked fruit. Abandoned groves are suspected of being refugia for fruit flies, although this is unproven. Secondly, urban sprawl has resulted in the encroachment of housing developments into agricultural areas. Dooryards now interdigitate extensively with commercial groves providing off-season breeding sites and potential over-summering and over-wintering refugia in close proximity to the commercial citrus. Thirty-three of the first 100 feral flies caught in 1998 were captured in dooryard traps, with the percentage over the rest of the season being only about half that, at 16 percent.

Sterile Release Strategy. Currently, 25 million flies per week are reared at the USDA-APHIS facility in Mission, Texas, sterilized, and released by aircraft over 2000 sq. km including 35,000 acres of citrus production, giving a release rate of 700 sterile flies per acre. At the inception of the program in January, 1981, continuing through July, 1988, the sterile flies were released weekly over the entire arable area of the LRGV. One mile lanes were flown north and south with the release altitude at 1000 feet above ground level. The release lanes were offset one-half mile on alternate weeks. Release rates in those years were limited by the availability of sterile flies to as low as six flies per acre per week. These numbers were increased as production technology improved and a new facility in Mission, Texas, became operational in January, 1986.

In July 1988 the program strategy was changed to concentrate releases in commercial citrus. The availability of sterile flies has always been a determining factor for program activities. Concentrating the sterile flies in the groves was done to increase overflooding ratios, and thus improve the efficiency of the suppression program. However, the steady increase in feral fly captures culminating in the outbreak in the spring of 1998 caused concern with program managers. The number of wild flies caught in the neglected urban areas was considerable that winter. Also, trap-back monitoring of the releases indicated that sterile fly longevity was much reduced, especially during the summer months, with mortality as high as 50% only four days after release. The sterile males must attain an age of at least four days to become sexually active.

It was concluded that the strategy of concentrating the flies in groves had drawbacks that were contributing to poor fly survival during the summer. While there are several citrus groves consisting of 1,000 acres or more, the average grove in the LRGV is approximately ten acres. In order for the sterile flies to be released from the aircraft on such a small target, it was necessary to conduct releases at no more than 500 feet above ground level. Because the flies are chilled to 3.3°C prior to release, they are immobile upon release from the aircraft, and often reach the ground before flight capacity is recovered. Soil temperatures in exposed sites can reach 43ºC in the summer and it is known that the flies are immobilized and will die from exposures greater than 38ºC. The release altitude could be increased, but, inasmuch as individual groves cannot be accurately targeted from higher altitude, a change in the release strategy was deemed necessary.

In July 1998 the program was modified to include a combined strategy of area wide releases and targeting of citrus groves. Summertime releases would be confined to the morning hours (from first light to noon) and release altitude changed to 2,500 feet to improve survival. The greatest concentration, approximately 80% of commercial citrus, is located in production zones 1 and 2 in the western portion of the valley. The groves in production zones 3, 4 & 5 are fewer and scattered over a larger area. It was decided to conduct area wide flight lane releases over zones 1 and 2, allowing higher altitude releases, while individual groves would be targeted in zones 3, 4 & 5. The available sterile flies would be distributed according to the acreage of citrus. Thus, 80% of the flies are apportioned to zones 1 and 2 with the remainder in the easterly zones. Initial results from trap-back monitoring have been positive. The recapture rate of sterile flies for August 1998 was 0.03%, triple that of August 1997 and that of September 1998 was 0.024%, more than double that of September 1997.

Mating Behavior and Rearing Adaptation. In order for the SIT program to be effective the released flies must survive to mating age. Males first exhibit mating behavior at age 4 d post-emergence (Dickens et al. 1982). They must then be competitive and compatible with the feral flies. The mexfly has an elaborate courtship and copulatory behavior which is restricted in time and place to crepuscular mating arenas called leks (Robacker et al. 1991). These mating arenas are the real targets of the sterile insect technique. Genetic changes in mass-reared populations of insects and the effects these changes can have on the efficacy of the released insects has been considered for a number of fly species and SIT programs. One of the first reviews that actually examined evidence for the effects of genetic adaptation to mass-rearing across a series of species was that of LaChance (1979). Although there is general agreement that selective pressures are considerable in the processes involved in mass-rearing (Bartlett 1984), the assumption that this will have a negative effect on field performance has been questioned (Mangan 1992). Laboratory strains of the mexfly have been shown to mate more readily, to oviposit more frequently with larger clutches, and female contact with males reduces their longevity (Mangan 1997). Males from mass-reared strains were superior to wild males in attracting wild females under laboratory conditions in "calling" comparisons (Mangan 1996). These tests indicated that there was no general decline in reproductive function of the mass-reared strain, however, these comparisons were all done under similar conditions to which the strain is being reared.

Tests of strain function under more natural conditions were carried out in Nuevo Leon, Mexico by Moreno et al. (1991) in August 1987. They found that, although sterilization with ionizing radiation at the dosage used by the SIT program (70-116 Gy) caused significant reduction in competitiveness, the non-irradiated mass-reared flies were fully competitive with the wild flies. The sterilization process significantly reduced pheromone emission by the treated males. They suggested that changes in the radiation treatment process, for example, by controlling oxygen levels during irradiation, would be more effective in improving sterile fly performance than changing strains.

Subsequent tests were carried out in August 1997 in Weslaco, Texas. In this test sterile and fertile, mass-reared strains were compared against a wild strain. In these tests the total activity (mating with both mass-reared and wild females) of the mass-reared males was significantly lower than that of the wild strains. Again, however, there was no evidence for assortative mating. Conditions in the 1997 tests were considerably more harsh (high temperature about 5ºC higher) than in the 1987 test. All strains were acclimated the same, however, so evidence suggested that the mass-rearing strain was less functional than the wild strain. Based on these data, a decision was made to develop a new strain from wild material collected in Nuevo Leon, Mexico (the nearest significant population to Texas). This strain is expected to be ready for quality control testing in September, 1999.

Integration of SIT and Chemical Controls. One of the advantages of biological control is the reduction in the use of pesticides. As the human population encroaches on the groves this advantage is increasingly important. The reality is, that growers are compelled to treat their groves with chemicals against a variety of pests (Dean et al. 1983) apart from the mexfly. Systemic insecticides are applied routinely in the spring following blossom fall and foliar sprays are applied for mites, especially in the summertime (French & Bruno 1996). Unlike Florida citrus, which is grown primarily for juice, blemishing of the rind causes economic degradation to Texas citrus which is grown primarily for the fresh fruit market.

For our program there are specific situations when chemical control of the fruit fly population may also be appropriate. The sterile insect technique is predicated on high sterile to fertile ratios. With locally high population densities an antecedent chemical application can be desirable to reduce the population to a level where effective overflooding ratios can be achieved. This method has had some success against the medfly in California (Penrose 1993).

A corresponding situation exists in the case of the autumnal oviposition period. Studies of the life cycle of the mexfly suggest that many of the flies that oviposit during the fall are carryovers from the late spring emergence. These flies have already mated, and moreover, it is suspected that many of these flies are moving into the groves from over-summering refuges in dooryards or other amenable habitats. If these flies are already mated and gravid, the sterile fly releases would have minimal impact against this segment of the population at this time in the life cycle. If the autumnal populations, particularly those in the groves, are oriented more to ovipositing than to mating, then a pesticide treatment may be the more effective way to suppress the population and protect the commodity. Therefore, a pilot test of a pre-emptive chemical treatment was conducted in the western part of Hidalgo

County in October, 1995 and October, 1996.

The Texas Gardens area was chosen for the test because of the uniform physiognomy of the groves and surrounding terrain, the paucity of agricultural crops in the acreage between groves, and the low human habitation rate in the area. Three treatment areas of 200 acres each were alternated with three corresponding control areas of equal size. An ultra-low volume of insecticide was applied as an aerial spray of a toxicant-bait mixture of 1:4 parts technical (95%) Malathion and a corn hydrolysate syrup at a rate of 11.5 oz per acre (2.3 oz active ingredient), a rate found to be effective in citrus against mexfly adults (Lopez-Davila et al. 1969) and the only pesticide treatment registered for use against fruit flies in citrus. Three successive applications were made at ten-day intervals, a sequence found to give good control of medfly outbreaks in California (Penrose 1993).

The results of these pilot tests were ambiguous. Effectiveness was judged by the numbers of flies trapped over the succeeding spring (January to June). No feral flies were found in any of the treatment areas in the spring of either year. However, only one feral fly was captured in the three control plots. Fly numbers over the entire valley were so low those two years that it was not possible to credit the treatments for the lack of flies. Thus, in the following year, the test was expanded to include a much larger area, essentially all of the citrus in Zone 1. All of the citrus north of Hwy 107 was marked for treatment, with the exception of a few organic groves; a total of 3,200 acres, nearly ten percent of the citrus acreage in Texas. The disadvantage of expanding the treatment area was the lack of replication. Any difference in fly numbers between the treatment and control zones would have to be on an order of magnitude to conclude that the treatment was successful. As before, three treatments of the toxicant-bait were applied at ten day intervals by USDA-APHIS aircraft in October 1997. The citrus in Zone 1 south of Hwy 107 served as the control. The following spring 100 McPhail traps were dispersed in the control zone and another 100 in the treatment zone, with no more than one trap per grove, which in this area are typically 10 acres each. As before, the traps were operated from January to June.

Because of the size of the area in the test it was undesirable to suspend the scheduled weekly release of sterile flies over the control zone. Therefore, the normal release of sterile flies was continued over the treatment zone without interruption so as to not introduce a variable into the test, although it was recognized that the pesticide would most likely render the releases ineffective.

A major concern was the effect that an area-wide spray might have on beneficial insects. Intensive sprays for fruit-fly eradication in California citrus had sometimes led to outbreaks of secondary pests (Ehler & Endicott 1984). Therefore, we surveyed the treatment and control groves for secondary pests one week before (Sept 29-30) and again one month after (Dec 2-3) the spray operation. We collected 2 leaves from separate trees in fifty separate groves in both the control zone and the treatment zone. Each leaf was placed immediately in a petri dish and sealed with tape. On return to the laboratory each leaf was examined under a microscope and a relative count scored for light, moderate, or heavy infestation levels of each pest.

Basically, there was no evidence of a secondary pest outbreak following the treatments. The most common pests, California red scale and Texas citrus mites were found at equivalent numbers before and after the sprays and in the control and treatment plots (Table 4). In large part the timing of the test, just before the onset of winter, is probably advantageous in this regard.

The results of the pre-emptive spray were less than completely satisfactory. In the spring of 1998, 1,348 wild flies were caught in the APHIS surveillance traps in the LRGV. In our treatment zone the program traps caught only 13 wild flies. Given that the treatment zone included about 10% of all the citrus acreage in the valley one might have expected to catch 10%, or around 130 flies, in this zone. By this comparison there was an order of magnitude in difference between the expected and the observed. However, a more appropriate comparison is between the treatment and the control zones.

During the months of January and February, when the adults emerge from the overwintering generation, no feral flies were found in the treatment zone, while 5 flies were found in the control zone. However, in March, when the populations were peaking in the control zone (40 flies), numbers of ferals (20 flies) did begin to turn up in the treatment zone. The treatment zone was bordered on its east side by a large acreage of citrus and presumably flies had moved into the treatment area from there. By April, as the outbreak declined, there were equal numbers in the control and treatment zone. There is no doubt that the toxic bait kills flies. However, while the pre-emptive sprays may have given protection for one generation, this would not be sufficient to break the life cycle and groves are quickly reinfested when in proximity to untreated groves.

Efficacy and Future of the SIT Program. Because the annual fly numbers trapped in south Texas tend to fluctuate in accord with the prevailing weather patterns it might be surmised that the sterile insect releases are having little effect on the native fly population. Such fluctuations suggest that the fruit fly population is in equilibrium with its physical environment (Meats 1986). However, this does not mean that the sterile releases are not exerting a consistent downward pressure on the population. The numbers in Table 3 from the citrus region in Mexico show what an unimpeded population level might look like. In most years the total number of flies trapped in the LRGV are fewer than the number that can be reared from a single grapefruit.

Krafsur (1999) advocates documenting the efficacy of sterile releases by measuring the proportion of sterile matings as a function of population density and release pressure. Unfortunately, at the present time we lack the technology to distinguish fertile from sterile matings, or an effective way to collect egg masses. One proposal receiving attention is to introduce a genetic marker into the factory strain which will allow us to distinguish the ejaculate of the factory strain from that of the feral flies.

Ultimately, the most important measure of the efficacy of the south Texas protocol, of which SIT is the active ingredient, is the fact that no commerically shipped fruit has ever been found infested with Mexican fruit fly larvae, either at the point of origin in Texas, or at the off-load destinations. This is not to say that the protocols have reduced the risk to zero or near zero levels. Several factors contribute to the risk and the situation is dynamic. In a definitive experiment conducted during the first year of the SIT program, USDA personnel gathered and cut 25,000 individual fruits monthly from all parts of the LRGV throughout the 1981-82 harvest season for a total of 250,000 fruits (mostly grapefruit, but some sour orange). Only 47 infested fruits were found, an infestation rate of fewer than one fruit per 5,000. In our experience, the mexfly prefers ripened fruit for oviposition. Infested grapefruits tend to mature and dehisce earlier, and thus, infested fruit tends to become at least partly segregated from the harvested fruit further reducing the risk of exporting infested fruit.

The upward trend in the numbers of flies trapped each year over the last decade is partly attributable to the larger numbers of traps in operation and partly to the steady increase in the acreage of commercial citrus in production. The latter acreage has now reached about half the pre-freeze level, and as competition depresses prices, some groves are being abandoned. It is suspected but not demonstrated that abandoned groves provide refugia for feral flies because they are not treated with pesticides, nor is fruit or undergrowth removed, as is the case for groves in production.

The encroachment of urban development into the citrus production area poses a double threat. Dooryards provide potential off-season refugia for the pests, while pesticide applications on, or in proximity to, human dwellings are increasingly problematic. Therefore, research has been directed toward development of non-broadcast methods (e.g., bait stations) for delivering safer chemicals (e.g., bacterials, IGR's, photoactive dyes), and baits that better target the pest. As social pressures to reduce pesticide use increase, reliance on the sterile fly releases to suppress the pest population will be greater. Similarly, reliance on methyl bromide as a fumigant for disinfestation treatments is threatened by discovery that this compound is an ozone depleter. Research is focusing on the development of alternative non-chemical disinfestation treatments. These include hot water dips, forced hot-air chambers, vapor-heat, ionizing radiation, and combinations of heat treatments followed by low temperature or controlled atmosphere storage.

Strategies for enhancing delivery of the sterile flies include manipulations in the time of day the flies are released, the altitude and speed of the dispersing aircraft, and, directing the releases toward urban areas or groves depending on the time of year. The change in strategy made in 1998 to achieve better dispersal and survival of the released flies is assumed to be at least partly responsible for the subsequent decrease in the feral population. It is important that the release program not be static in its application. Limited resources demand that the flies be delivered at the place and time where they will be most effective and this varies from season to season.

Feasability of eradication is also being studied. A successful eradication attempt would seem to be conditioned on two eventualities. Firstly, that Mexico is able to maintain a fly-free zone in the states bordering Texas. This would necessitate the establishment of area-wide, integrated pest management programs and the operation of effective quarantine stations at points in the interior preventing the movement of untreated fruit into the northern tier of states (Aluja & Liedo 1986). Secondly, the eradication should be implemented following a climate driven downturn in the feral population, such as a freeze or drought. Without these two conditions it is difficult to envision an effective eradication program that would not have to incorporate extensive fruit stripping in both commercial orchards and private dooryards with follow up pesticide soil drenches. There are statuatory vehicles for dealing with abandoned groves and these would have to be implemented as well.

Another mitigating factor is a threat that another exogenous fruit pest such as the medfly could invade the valley. Any emergency program to eradicate this pest would include the same measures taken to eradicate the mexfly except that the option of waiting for conditions one and two would not be available.

Inasmuch as the present program for exportation does not approach a zero risk, and the fallback methods of pesticides and fumigants will probably be phased out at sometime in the future, there should be planning for an eventual eradication. In any event, the mexfly program must be adaptable to the loss of tools mandated by the changing socio-political milieu as well as those gained by new advances in technology.

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LITERATURE CITED

Aluja, M., H. Celedonio-Hurtado, P. Liedo, M. Cabrera, F. Castillo, J. Guillen and E. Rios. 1996. Seasonal population fluctuations and ecological implications for management of Anastrepha fruit flies (Diptera: Tephritidae) in commercial mango orchards in southern Mexico. J. Econ. Entomol. 89: 654-667.

Aluja, M. & P. Liedo, 1986. Perspectives on future integrated management of fruit flies in Mexico. Pp. 9-42, *in*, M. Mangel, J.R. Carey & R.E. Plant (eds). Pest Control: Operations and Systems Analysis in Fruit Fly Management. Springer-Verlag, Berlin.

Andrewartha, H.G. 1972. Introduction to the study of animal populations, 2nd Ed. Univ. Chicago Press, Chicago, IL.

Baker, A.C., W.E. Stone, C.C. Plummer & M. McPhail. 1944. A review of studies on the Mexican fruit fly and related

Mexican species. USDA Misc. Publ. No. 531, Washington, D.C.

Bartlett, A.C. 1984. Genetic changes during insect domestication. Pp. 2-8, *in*, E.G. King and N.C. Leppla (eds.). Advances and Challenges in Insect Rearing. USDA-ARS, New Orleans, LA.

Celedonio-Hurtado, H., P. Liedo and M. Aluja. 1995. Adult population fluctuations of *Anastrepha* species (Diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. Environ. Entomol. 24: 861-869.

Christenson, L.D. & R.H. Foote. 1960. Biology of fruit flies. Annu. Rev. Entomol. 5: 171-192.

Dean, H.A., J.V. French & D. Meyerdick. 1983. Development of integrated pest management in Texas citrus. Texas A&M Agric. Exp. Sta. Publ. B-1434, 15 pp.

Dickens, J.C., E. Solis & W.G. Hart. 1982. Sexual development and mating behavior of the Mexican fruit fly, *Anastrepha ludens*. Southw. Entomol. 7: 9-15.

Ehler, L.E. & P.C. Endicott. 1984. Effect of malathion-bait sprays on biological control of insect pests of olive, citrus and walnut. Hilgardia 52: 1-47.

Eskafi, F.M. 1988. Infestation of citrus by *Anastrepha* spp. and *Ceratitis capitata* (Diptera: Tephritidae) in high coastal plains of Guatemala. Environ. Entomol. 17: 52-58.

Flitters, N.E. 1964. The effect of photoperiod, light intensity, and temperature on copulation, oviposition, and fertility of the Mexican fruit fly. J. Econ. Entomol. 57: 811-813.

French, J.V. & P.H. Bruno. 1996. Evaluation of BAS 300 11I (Pyridaben) for mite control on Texas citrus. Subtrop. Plant Sci. 48: 10-15.

Gilbert, A.J., R.R. Bingham, M.A. Beavers & R.A. Clark. 1984. Pest detection/emergency projects insect trapping guide. California Department of Food and Agriculture, Sacramento, CA.

Gutierrez-Samperio, J., J. Reyes & A. Villaseñor. 1993. National plan against fruit flies in Mexico. Pp. 419-424, *in*, M. Aluja & P. Liedo [eds.]. Fruit Flies: biology and management. Springer-Verlag, New York, NY.

Hagen, K.S. 1956. Honeydew as an adult fruit fly diet affecting reproduction. Proceedings 10th International Congress of Entomology 3: 25-30.

Holler, T.C., J.L. Davidson, A. Suarez & R. Garcia. 1984. Release of sterile Mexican fruit flies for control of feral populations in the Rio Grande Valley of Texas and Mexico. J. Rio Grande Valley Hort. Soc. 37: 113-121.

Krafsur, E.S. 1999. Sterile insect technique for suppressing and eradicating insect population: 55 years and counting. J. Agric. Entomol. 15: 303-317.

LaChance, L.E. 1979. Genetic strategies affecting the success and economy of the sterile release method. Pp. 8-18, *in*, M.A. Hoy and J.J. McKelvey Jr. (eds.). Genetics in Relation to Insect Management. Rockefeller Foundation.

Leyva-Vazquez, J. 1988. Temperatura umbral y unidades calor requeridas por los estados inmaduros de *Anastrepha ludens* (Loew) (Diptera: Tephritidae). Folia Entomol. Mex. 74: 189-196.

Lopez-Davila, F., D.L. Chambers, M. Sanchez-Rivelo & H. Kamasaki. (1969). Control of the Mexican fruit fly by bait sprays concentrated at discrete locations. J. Econ. Entomol. 62: 1255-1257.

Mangan, R.L. 1992. Evaluating the role of genetic change in insect colonies maintained for pest management. Pp. 269-288, *in*, T.E. Anderson & N.C. Leppla (eds). Advances in Insect Rearing. Westview Press, Boulder, CO.

Mangan, R.L. 1996. Effects of adult chill treatments on mate attracting potential for irradiated Mexican fruit fly males. Entomol. Exp. & Applic. 79: 153-159.

Mangan, R.L. 1997. Effects of strain and access to males on female longevity, lifetime oviposition rate, and egg fertility of the Mexican fruit fly (Diptera: Tephritidae). J. Econ. Entomol. 90: 945-954.

McPhail, M. 1937. Relation of time of day, temperature and evaporation to attractiveness of fermenting sugar solution to Mexican fruit fly. J. Econ. Entomol. 30: 793-799.

Meats, A. 1986. Pests and population models: fluctuations, equilibrium and persistence. Pp. 339-359, *in*, M. Mangel, J.R. Carey & R.E. Plant (eds). Pest Control: Operations and Systems Analysis in Fruit Fly Management. Springer-Verlag, Berlin.

Moreno, D.S., M. Sanchez-Riviello, D.C. Robacker & J. Worley. 1991. Mating competitiveness of irradiated Mexican fruit fly (Diptera: Tephritidae). J. Econ. Entomol. 84: 1227-1234.

Nilakhe, S.S., J.N. Worley, R. Garcia, J.L. Davidson. 1991. Mexican fruit fly protocol helps export Texas citrus. Subtrop. Plant Sci. 44: 49-52.

Norrbom, A. & K.C. Kim. 1988. A list of the reported host plants of the species of *Anastrepha* (Diptera: Tephritidae). USDA-APHIS, 81-52.

Penrose, R. 1993. The 1989/1990 Mediterranean fruit fly eradication program in California. Pp. 401-406, in, M. Aluja & P. Liedo [eds.]. Fruit Flies: biology and management. Springer-Verlag, New York, NY.

Plummer, C.C., M. McPhail & J.W. Monk. 1941. The Yellow Chapote, a native host of the Mexican Fruit Fly. USDA Tech. Bull. 775. 12 p.

Robacker, D.C., R.L. Mangan, D.S. Moreno & A.M. Tarshis-Moreno. 1991. Mating behavior and male mating success in wild *Anastrepha ludens* (Diptera: Tephritidae) on a field-caged host tree. J. Insect Behavior 4: 471-487.

Southwood, T.R.E. 1976. Bionomic strategies and population parameters. Pp. 26-48, *in*, R.M. May [ed.]. Theoretical Ecology: principles and applications. W.B. Saunders, Philadelphia, PA.

Thomas, D.B. 1995. Predation on the soil inhabiting stages of the Mexican fruit fly. Southw. Entomol. 20: 61-71.

Thomas, D.B. 1997. Degree-day accumulations and seasonal duration of the pre-imaginal stages of the Mexican fruit fly (Diptera: Tephritidae). Fla. Entomol. 80: 71-79.

Thomas, D.B. & J. Loera-Gallardo. 1998. Dispersal and longevity of mass-released, sterilized Mexican fruit flies (Diptera: Tephritidae). Environ. Entomol. 27: 1045-1052.

Williamson, D.L. & W.G. Hart. 1989. Current status of Mexican fruit fly research in the Rio Grande Valley of Texas. Pp. 563-569, *in*, R. Cavalloro [ed.]. Fruit Flies of Economic Importance. A.A. Balkema, Rotterdam, the Netherlands.