CHAPTER 1.1.

HISTORY OF THE STERILE INSECT TECHNIQUE

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TABLE OF CONTENTS

1. PROLOGUE.....	2
2. SEREBROVSKII AND POSSIBLE USE OF CHROMOSOMAL TRANSLOCATIONS TO CAUSE INHERITED PARTIAL STERILITY	5
3. VANDERPLANK AND USE OF HYBRID STERILITY TO COMBAT TSETSE FLIES	6
4. KNIPLING AND USE OF STERILITY INDUCED BY IONIZING RADIATION	7
4.1. <i>New World Screwworm</i>	7
4.1.1. <i>Early Attempts at Control, and Importance of Correct Identification</i>	8
4.1.2. <i>Studies on Reared Screwworms in the 1930s, and Conception of the SIT</i>	8
4.1.3. <i>Sterility Based on Radiation-Induced Dominant Lethal Mutations</i>	9
4.1.4. <i>Sanibel Island Field Evaluation Pilot Test</i>	10
4.1.5. <i>Curaçao Eradication Trial — Proof of Concept</i>	10
4.1.6. <i>Florida Eradication Programme</i>	10
4.1.7. <i>Eradication and Area-Wide Population Management in South-Western USA</i>	11
4.1.8. <i>Managing Screwworm Population along the US-Mexico Border</i>	12
4.1.9. <i>Programmes in Central America: the Drive to Panama</i>	13
4.1.10. <i>Screwworm Eradication Programme in North Africa</i>	13
4.1.11. <i>Screwworm Programmes in the Caribbean</i>	14
4.2. <i>Tephritid Fruit Flies</i>	14
4.2.1. <i>Mexican and Queensland Fruit Flies</i>	16
4.2.2. <i>Moscamed</i>	16
4.2.3. <i>Melon Fly Eradication in the South-Western Islands of Japan</i>	17
4.2.4. <i>Mediterranean Fruit Fly Genetic Sexing Strains</i>	17

Pages 1–44

V. A. Dyck, J. Hendrichs and A. S. Robinson (eds.), Sterile Insect Technique. Principles and Practice in Area-Wide Integrated Pest Management. Second Edition.

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4.2.5.	<i>Sterile “Genetic Sexing Strain” Males Alleviate Mediterranean Fruit Fly Crises in California and Florida, USA</i>	18
4.2.6.	<i>Jordan-Israel-Palestine Mediterranean Fruit Fly Programme</i>	18
4.2.7.	<i>Trend is Suppression, not Eradication, of Fruit Flies</i>	19
4.3.	<i>Onion Maggot</i>	19
4.4.	<i>Tsetse Flies</i>	20
4.5.	<i>Mosquitoes</i>	22
4.6.	<i>Coleoptera</i>	26
4.6.1.	<i>Field Cockchafer</i>	26
4.6.2.	<i>Sweetpotato Weevils</i>	26
4.7.	<i>Lepidoptera</i>	27
5.	TRANSBOUNDARY SHIPMENT AND INTERNATIONAL RECOGNITION OF THE SIT	28
6.	EPILOGUE	29
7.	REFERENCES.....	31

SUMMARY

During the 1930s and 1940s the idea of releasing insects of pest species to introduce sterility (sterile insect technique or SIT) into wild populations, and thus control them, was independently conceived in three extremely diverse intellectual environments. The key researchers were A. S. Serebrovskii at Moscow State University, F. L. Vanderplank at a tsetse field research station in rural Tanganyika (now Tanzania), and E. F. Knipling of the United States Department of Agriculture. Serebrovskii's work on chromosomal translocations for pest population suppression could not succeed in view of T. D. Lysenko's opposition to Mendelian genetics and the catastrophic conditions in the USSR during World War II, after which he died. Vanderplank used hybrid sterility to suppress a tsetse population in a large field experiment, but lacked the resources to develop this method further. Knipling and his team exploited H. J. Muller's discovery that ionizing radiation can induce dominant lethal mutations, and after World War II this approach was applied on an area-wide basis to eradicate the New World screwworm *Cochliomyia hominivorax* (Coquerel) in the USA, Mexico, and Central America. Since then very effective programmes integrating the SIT have been mounted against a number of tropical tephritid fruit fly species, some species of tsetse flies *Glossina* spp., the pink bollworm *Pectinophora gossypiella* (Saunders), the codling moth *Cydia pomonella* (L.), the cactus moth *Cactoblastis cactorum* (Berg), the painted apple moth *Teia anartoides* Walker, and the false codling moth *Thaumatotibia leucotreta* (Meyrick). In non-isolated onion fields in the Netherlands, the onion maggot *Delia antiqua* (Meigen) has since 1981 been suppressed by the SIT. In the 1970s there was much research conducted on mosquito SIT, which then went into “eclipse”, but has been reviving during the last decade; a number of pilot trials are ongoing or in preparation, in conjunction with the *Wolbachia*-based incompatible insect technique (IIT) against mosquitoes, including *Aedes aegypti* (L.), *Ae. albopictus* (Skuse), *Ae. polynesiensis* Marks, and *Anopheles arabiensis* Patton. Development of the SIT for use against the boll weevil *Anthonomus grandis grandis* Boheman, the horn fly *Haematobia irritans* (L.) (Eschle et al. 1973), and the gypsy moth *Lymantria dispar* (L.) has ended, but it is in progress for two sweetpotato weevil species, *Cylas formicarius* (F.) and *Euscepes postfasciatus* (Fairmaire), the small hive beetle *Aethina tumida* Murray, the brown marmorated stink bug *Halyomorpha halys* Stål (Welsh et al. 2017), the navel orangeworm *Amyelois transitella* (Walker), the African sugarcane borer *Eldana saccharina* Walker, the European grapevine moth *Lobesia botrana* (Denis and Schifferrmüller), the carob moth *Ectomyelois ceratoniae* (Zeller), the leafminer *Liriomyza bryoniae* (Kaltenbach) (Walker 2012) and other greenhouse pests, the Old World screwworm *Chrysomya bezziana* (Villeneuve), additional *Glossina* spp., other *Anastrepha* spp. and *Bactrocera* spp. fruit flies, and other pests. New technologies and continuous research support for ongoing programmes, including molecular, microbial and information technology approaches, are resulting in improved methodologies and processes, and thus in enhanced cost-effectiveness for all aspects of SIT application.

1. PROLOGUE

When using the sterile insect technique (SIT), it is applied usually as a component of area-wide integrated pest management (AW-IPM) (Hendrichs et al. 2007; Klassen and Vreysen, this volume). The density of the target insect pest population is

initially reduced, eliminating already mated females, with auxiliary control methods (Mangan and Bouyer, this volume). Then the SIT imposes birth control on the population to further reduce its numbers (Klassen and Vreysen, this volume).

The SIT involves rearing large numbers of the target species, exposing them mainly to gamma rays (but increasingly also to X-rays to avoid the transport, security, and regulatory issues related to radioactive sources (Bakri et al., this volume)) to induce sexual sterility (Bakri et al., this volume; Robinson, this volume), and then releasing them into the target population. The released sterile males mate with wild females to prevent them from reproducing (Knipling 1955).

Runner (1916) found that large doses of X-rays applied to the cigarette beetle *Lasioderma serricorne* (F.) rendered it incapable of reproduction. Soon afterwards H. J. Muller (1927) showed that ionizing radiation induced visible mutations in *Drosophila*, and also a much larger number of dominant lethal mutations, which were expressed through a reduction in the hatch of eggs laid by treated females or fathered by treated males. In 1946 he received the Nobel Prize in Physiology or Medicine (Fig. 1); however, only after 1950, when Muller made a special effort to publicize the biological effects of radiation, did economic entomologists become aware that, through gamma or X-ray irradiation, sexual sterility in male insects was quite easily achieved (Bakri et al., this volume).

The fact that chemicals could also produce genetic changes in the same way as radiation was only discovered during the Second World War by Charlotte Auerbach, a German-Jewish zoologist and geneticist, who fled to the UK and had been introduced to mutation research by H. J. Muller. She found in 1941 that mustard gas was mutagenic in *Drosophila*, and also affected fertility (Auerbach et al. 1947). Most of the dominant lethal mutation-producing chemicals are alkylating agents, producing carbonium ions which in living tissues combine with the nucleic acids of cells, causing point mutations and chromosome breakage (LaChance 1967). Nevertheless, the potential of alkylating agents as chemosterilants was not recognized for at least another ten years (Davidson 1974). Then, in view of their low cost compared with radiation sources, much research was done on over 125 pest species of public health and agricultural importance (Knipling 1968; LaBrecque and Smith 1968; Davidson 1974).

The great disadvantage of alkylating agents is that their sterilizing and mutagenic effects extend to higher animals, including humans. Attempts to find safer chemosterilants resulted in the discovery of non-alkylating chemicals. Nevertheless, methods to apply them uniformly were largely impractical for large-scale conditions. Furthermore, the residues on insect bodies, resulting from chemosterilization, can result in their bioaccumulation in natural food chains (Nagel and Peveling, this volume). As a result, their application was largely discontinued in the 1970–80s, although the use of juvenile hormone analogues and other compounds in autosterilization devices in the field, to attract and sterilize individuals that then disseminate these chemosterilants to other individuals of the target population, is being reconsidered (Bouyer and Lefrançois 2014; Baxter 2016).

Nevertheless, besides the means of achieving sterilization in insects, the idea of releasing pest insects to introduce sterility into wild populations, and thus control them, had already been conceived independently in the 1930s and 1940s by A. S. Serebrovskii at Moscow State University, F. L. Vanderplank at a tsetse field

research station in rural Tanganyika (now Tanzania), and E. F. Knipling of the United States Department of Agriculture (USDA) (Fig. 1). However, Serebrovskii and Vanderplank both sought to achieve pest control through the sterility that arises when different species or genetic strains are hybridized (Robinson, this volume).

*Figure 1. Upper left: Hermann J. Muller; upper right: Aleksandr S. Serebrovskii; lower left: Frederic L. Vanderplank; lower right: Edward F. Knipling.
Photo Credits: Muller – Nobel 2018; Serebrovskii and Vanderplank – Gould et al. 2006; Knipling – World Food Prize Foundation.*

2. SEREBROVSKII AND POSSIBLE USE OF CHROMOSOMAL TRANSLOCATIONS TO CAUSE INHERITED PARTIAL STERILITY

Beginning in 1922, Muller encouraged and assisted Serebrovskii's genetic studies on *Drosophila*. In 1933, Muller became the director of a genetics laboratory, a position created for him by N. I. Vavilov, head of the Lenin All-Union Academy of Agricultural Sciences. Serebrovskii became embroiled in the fierce controversy with T. D. Lysenko about the validity and usefulness of Mendelian genetics in advancing Soviet agriculture (Medvedev 1969), whether genes exist, and whether the Lamarckian concept of inheritance of acquired traits is correct. Lysenko had gained the support of Stalin, and he attempted to force Vavilov, Serebrovskii, Muller, and other geneticists to recant their adherence to Mendelian genetics. In December 1936, exponents of the two trends in Soviet biology confronted each other at a special session of the Lenin All-Union Academy of Agricultural Sciences, and the geneticists vigorously defended their science. Subsequently several prominent geneticists were arrested. Probably Serebrovskii was motivated to develop the concept of using chromosomal translocations for pest population suppression as a means to deflect Lysenko's strident criticism that research in genetics was devoid of promise to benefit Soviet agriculture (Carlson 1981).

Serebrovskii (1940) noted that it was already well known in 1940 that a translocation of segments between two chromosomes caused an abnormal association of four chromosomes during meiosis in heterozygotes, resulting in the formation of gametes with lethal genetic duplications and deficiencies. These abnormalities manifested themselves as partial sterility in the translocation heterozygote. Such partial sterility tended to be passed on from one generation to the next (Curtis 1985; Marec et al., this volume). Those translocations that were viable in the homozygous state had normal meiotic pairing, and were fully fertile. Serebrovskii appreciated that, in such conditions of negative heterosis (or underdominance as it has more recently been called (Davis et al. 2001)), natural selection would favour whichever chromosome type was initially in the majority, with a point of unstable equilibrium, which would be at a frequency of 50% if the viability of the two homozygous karyotypes were equal. At a frequency of 50%, the proportion of heterozygotes, and hence of sterility in the population, would be maximal.

On the basis of Mendelian principles, Serebrovskii worked out: (1) the extent to which sterility would continue to appear in a population in the generations after a single release of translocation homozygotes, (2) ways of enhancing levels of sterility by using several different translocations, and (3) the effects of releasing only males to avoid a temporary increase in the breeding population. A single release into a wild population of strains each with two translocations would cause 93.75% of the embryos to die; correspondingly, three translocations would cause 98.4% of the embryos to die. Years later the alternative possibility was proposed — the deliberate release of a majority of insects with translocations as a means of "driving" into a vector population a gene that would render it harmless to man, e.g. a gene for inability to transmit disease (Curtis 1968, 1985).

Serebrovskii (1940) started practical work on translocations in *Musca domestica* L. and *Calandra granaria* L., but presumably it was impossible to continue it in the

catastrophic conditions in the USSR during World War II. Unlike some other opponents of Lysenko, Serebrovskii was not arrested, but he died of natural causes in 1948. Before his death he expanded his ideas in a book (Serebrovskii 1971), but which could not be published until after the fall from power of N. S. Khrushchev and of Lysenko (whom Khrushchev also supported).

3. VANDERPLANK AND USE OF HYBRID STERILITY TO COMBAT TSETSE FLIES

In the 1930s and 1940s, Vanderplank and his colleagues developed and field-tested an entirely different system of insect control, based on sterility from species crosses and in the hybrids from such crosses. Based on field studies on the *Glossina morsitans* Westwood group of tsetse flies in East Africa, they had discovered the subtle, but unequivocal, differences between *G. morsitans sensu stricto* and *G. swynnertoni* Austen. Laboratory crosses between *G. morsitans* and *G. swynnertoni* were made by Corson (1932), Potts (1944), and Vanderplank (1944, 1947, 1948), but the cross-matings had low fertility. Vanderplank (1947) reported that the genitalia of the hybrids were distinguishable from both parent species, the hybrid males were sterile, and the female hybrids partially sterile. Hybrid sterility in tsetse flies has been studied further by Curtis (1971), and extensively by Gooding (1985, 1993).

Vanderplank (1944) proposed that sterility from crosses could be used for tsetse control, and Jackson (1945) showed that there was random mating between the two species in the field. On this basis, Vanderplank organized the mass-collection of *G. morsitans* pupae and then released the flies in a 26-km² area occupied only by *G. swynnertoni*. This habitat was separated by at least 19 km from other tsetse populations, and was considered too arid for *G. morsitans* to establish itself permanently.

Vanderplank (1947) briefly described the success of this experiment, noting that the initial effects were as theoretically expected. Surprisingly, he never published the detailed results, but he kindly gave them to C. F. Curtis. After F. L. Vanderplank's death, his son, R. J. R. Vanderplank, gave permission that these remarkable data be published (Table 1). The releases of *G. morsitans* did indeed virtually eliminate the less numerous *G. swynnertoni*, and there was a period in which hybrids could be identified, before they also declined in numbers.

Finally, the predicted decline of *G. morsitans* also occurred, presumably because of its lower tolerance of aridity than that of *G. swynnertoni*. When the density of tsetse flies had been reduced to a low level, local people moved into the area, and apparently completed tsetse eradication by bush clearance. It is unfortunate that the details of this remarkable trial have remained almost unknown for so long, and were not followed up.

*Table 1. Effect of releasing *G. morsitans* pupae into a 26-km² *G. swynnertoni* habitat in Tanzania on the density of these two species and of the interspecific hybrids (*G. morsitans* habitat separated from other tsetse habitats by at least 19 km) (data from F. L. Vanderplank and C. H. N. Jackson, 1944–1946, reproduced with permission)*

Date	<i>G. morsitans</i> released (number)	Average catch of old males (per 5 hours of catching)		
		<i>G. morsitans</i>	<i>G. swynnertoni</i>	Hybrids
June 1944	0	0	54	0
July	0	0	69	0
August	27000	64	50	0
September	25000	138	25	0
October	26000	169	16	5 ¹
November	11000	54	15	7 ¹
December	4500	39	12	11 ¹
January 1945	5200	49	9	19
February	2300	68	5	21
March	0	40	4	28
April	0	22	4	20
May	0	17	3	10
June	0	16	1.2	9
July	0	13	1.1	7
August	0	15	0	4
September	0	11	0.2	2.4
October	0	7	0.1	2.1
November 1945 – March 1946	No surveys: local inhabitants now grazing cattle in the area			
April 1946	0	0.6	0.4	0.8
After April 1946	Area given over to local inhabitants who cut down most of the bush			

¹In this period, not all males were examined under the microscope, so the numbers recorded as hybrids were possibly inaccurate.

4. KNIPLING AND USE OF STERILITY INDUCED BY IONIZING RADIATION

4.1. *New World Screwworm*

The debut of the development and practical application of the SIT occurred in the 1950s in the USA under Knippling's leadership. It culminated in the most successful AW-IPM programme integrating the SIT to date. It was started in 1958 to rid the south-eastern USA of the New World screwworm, a deadly parasite of livestock. During the next 48 years the technique was used to eradicate this pest from the USA, Mexico, and Central America to Panama (Vargas-Terán et al., this volume).

4.1.1. Early Attempts at Control, and Importance of Correct Identification

Since ancient times, the tropical and semi-tropical New World screwworm has been a serious enemy of warm-blooded animals, including humans, in an area extending from Argentina to the southern USA. Descendants of European settlers learned to manage their herds and flocks so that the birth of most calves and lambs, as well as castration, branding, and dehorning operations, occurred only during months when screwworms were scarce (Cushing and Parish 1938). Each animal was checked for wounds at least twice per week, and each wound was treated with an insecticidal “smear” (Knipling 1985).

The correct identity of the insect concerned was established in 1858 by French medical doctor and entomologist C. Coquerel who collected larvae in the frontal sinuses of a convict, who later died, in the French penal colony of Cayenne (Devil's Island), off the coast of French Guiana. He published an accurate description of the New World screwworm in the Annals of the Entomological Society of France (Coquerel 1858) where he reported similar human cases with high mortality, describing science as powerless to prevent “these terrible ravages”. Coquerel assigned the name *Lucilia hominivorax* Coquerel to this parasite; “hominivorax” literally means “man eater”.

North American entomologists were, unfortunately, unaware of Coquerel's paper. Indeed, until 1933, North Americans confused the identity of the New World screwworm with the more abundant scavenger of dead carcasses, *Cochliomyia macellaria* (F.). Due to this inability to recognize that a different species was involved, livestock producers wasted much energy in burying or burning the carcasses of dead animals, and trapping adult flies, in the vain hope of reducing the population of what was believed to be the myiasis-causing screwworm.

E. C. Cushing, under the guidance of W. S. Patton of the Liverpool School of Tropical Medicine, discovered that the genitalia of adult flies that had developed in carrion were different from those of most flies collected from wound-reared specimens, and named the latter species *Cochliomyia americana* (Cushing and Patton 1933). Later this species was found to be the *C. hominivorax* described 75 years earlier by Coquerel (Laake et al. 1936). *C. hominivorax* is now referred to as the New World screwworm, and the scavenger *C. macellaria* (F.) as the secondary screwworm. As soon as the true identity of *C. hominivorax* had been clarified, Knipling and his colleagues made a concerted effort to elucidate its biology and ecology. They concluded that the number of screwworm flies that survives the winter as pupae in the soil was very low, perhaps only 40–80 per km² (Cushing and Parish 1938; Lindquist 1955; Meyer and Simpson 1995).

4.1.2. Studies on Reared Screwworms in the 1930s, and Conception of the SIT

C. hominivorax was the first obligate insect parasite to be reared on an artificial diet (Melvin and Bushland 1936), and this enabled very large numbers of screwworms to be available for study. Knipling observed the extreme sexual aggressiveness of male screwworms, as well as the refusal of females to mate more than once, and he realized that, if sexual sterility could be induced in males, and if vast numbers could be sterilized and released in the field, then the screwworm population would be suppressed. He also realized that, if releases continued for several successive

generations, and the wild population density decreased, the ratio of the number of sterile males to that of fertile wild males would increase sharply. Provided that the target wild population was isolated, the sterile:fertile ratio would become so great that probably not even a single fertile mating would occur, and thus the wild population would be eradicated (Knipling 1955, 1985). Knipling introduced simple mathematical models to assess the effects of the SIT and the integration with insecticides and other measures on the dynamics of screwworm populations (Barclay, this volume; Klassen and Vreysen, this volume).

The idea of the SIT may well have been triggered in part by the observation of monogamy in female screwworms (Knipling 1955). Thus, initially, there was the widespread belief that the SIT could only be applied to pest species in which the females mated only once. Consequently, there was a certain reluctance to consider the method for pest control of other species. However, Knipling (1959a, b) reconsidered that a monogamous mating system may not always be required, and von Borstel and Knipling (1960) described in detail why, independent of how many times the female mates, it is the competition between normal and lethal sperm that counts. Therefore, as long as irradiated sperm is competitive and can still penetrate eggs, female mating frequency is unimportant for effective SIT application (Bushland 1960; Knipling 1979; Lance and McInnis, this volume; Whitten and Mahon, this volume).

Nevertheless, in the 1930s, mass-rearing was not developed, and no method to induce sexual sterility was known. For a decade, the paramount urgency of World War II prevented Knipling from pursuing this sterile-male concept (Klassen 2003), but R. C. Bushland made a few attempts to induce sterility using chemicals.

4.1.3. Sterility Based on Radiation-Induced Dominant Lethal Mutations

In 1946, after H. J. Muller was awarded the Nobel Prize in Physiology or Medicine for his discovery of induced mutagenesis, he used his prestige to lead a vigorous campaign against the atmospheric testing of atomic weapons. He wrote a popular article in the *American Scientist* in which he used tombstones as symbols to depict graphically the dead progeny from matings of irradiated *Drosophila* (Muller 1950). A. W. Lindquist recognized that Muller had developed a means of sexually sterilizing insects, and drew Knipling's attention to this paper (Lindquist 1955).

Knipling wrote to Muller, asking if ionizing radiation could be used to induce sexual sterility in the New World screwworm. Upon receiving Muller's confident assurance, Bushland and D. E. Hopkins used the X-Ray Therapy Section of Brooke Army Hospital to conduct the first screwworm irradiations in 1950. They found that, when 6-day-old pupae were exposed to 50 Gy, the adults that emerged appeared to be normal. However, when irradiated males were mated with untreated females, none of the eggs hatched. Females that had been irradiated and mated to untreated males produced almost no eggs, and none hatched. When untreated and irradiated males were caged together with untreated females, the irradiated males competed about equally with untreated males (in accordance with Knipling's model) (Bushland and Hopkins 1953).

4.1.4. Sanibel Island Field Evaluation Pilot Test

Sanibel Island (47 km²), 4 km from the Gulf coast of Florida, was selected for a release-recapture experiment (Bushland 1960; Itô et al., this volume) using ³²P-labelled flies. In addition, the ratio of radioactive egg masses to non-radioactive masses was assessed. The release in 1951 of approximately 39 sterile male flies per km² per week for several weeks resulted in up to 100% sterility of the egg masses in wounded goats, and it greatly reduced the wild population. However, eradication was not achieved, apparently because wild fertile flies were flying to the island from the nearby mainland (Baumhover 2002).

4.1.5. Curaçao Eradication Trial — Proof of Concept

In 1954, Knipling was informed that screwworms were causing severe damage to the dairy industry on the island of Curaçao, 65 km from Venezuela, with an area of only 435 km². For the eradication trial, flies were reared in Orlando, Florida, and irradiated pupae were packaged in paper bags, air freighted to Curaçao, and released by air twice per week. On Sanibel, the release of 39 sterile males per km² per week had been effective, but on Curaçao this rate caused only 15% sterility of egg masses, and it had little effect on the incidence of myiasis cases due to the presence of thousands of unattended goats and sheep. Since wounds on these animals were not treated, they supported a high screwworm population. The release rate was increased to about 155 sterile males per km² per week, whereupon egg sterility increased to 69%, and then to 100% by the time two generations had elapsed. Subsequently, only two more fertile egg masses were found, and so sterile-fly releases were continued for another 8 weeks. Evidently eradication had been accomplished within 14 weeks, and the releases were halted after 22 weeks (Baumhover et al. 1955).

4.1.6. Florida Eradication Programme

At a meeting of the Florida Livestock Association in 1956, A. H. Baumhover suggested that eradication of the screwworm in Florida might eventually be possible, and he outlined a plan that called for the release of 50 million sterile flies per week. However, Knipling was reluctant to implement immediately a high-risk USD 10-million programme on the mainland — there were too many unknown factors, with problems in mass-rearing and distribution requiring several more years of applied research (which might reduce the eventual cost of the programme by USD 2 million). However, the governor T. L. Collins noted that the agricultural economy of Florida was losing more than USD 20 million per year due to the screwworm, and he pressed for immediate implementation. Nevertheless, to upgrade the rearing and release methodology, a further trial was conducted in 5000 km² along the Atlantic coast (Baumhover et al. 1959; Graham and Dudley 1959). Meanwhile, in July 1957, the Florida Legislature appropriated USD 3 million to match federal funds for an operational programme.

A mass-rearing facility was constructed at an Air Force Base at Sebring, Florida, with the production capacity of 60 million flies per week, and the programme was scheduled to begin in July 1958 (Scruggs 1975; Meyer and Simpson 1995). However, it was decided to accelerate this schedule following the unusually cold

winter of 1957–1958, which eliminated all screwworms in the south-eastern states, except for the southern one-third of Florida. To contain the surviving screwworm population, the production was rapidly increased in the research facilities at Orlando and Bithlo, from 2 to 14 million sterile flies per week, and by May 1958 sterile flies were being distributed north of the infested area to the border with Georgia using 10 aircraft. The programme also established a quarantine line across central Florida to prevent the shipment of any infested livestock out of southern Florida, and any localized concentrations of screwworm cases in northern Florida were quickly eliminated by treating infested wounds, spraying herds, and releasing large numbers of sterile flies.

The mass-rearing facility at Sebring reached full production in August 1958, and 20 aircraft were used to distribute sterile flies throughout Florida and parts of neighbouring states. The Florida Cooperative Extension Service conducted a public information programme, and trained county agents to educate livestock producers. Field inspectors assisted and trained producers in treating cases and submitting larvae from wounds for identification at eradication headquarters in Sebring. Cases of myiasis in each county were plotted each day. The number of sterile flies released per km² per week was increased at persistent “hot spots” from about 155 to 1160. The last autochthonous case occurred on 19 February 1959 (Baumhover 2002). All sterile fly releases were terminated in November 1959. The total cost of the programme was USD 11 million, about 50% of the annual losses in Florida (Meadows 1985).

4.1.7. Eradication and Area-Wide Population Management in South-Western USA

The Florida programme aroused the interest of cattle producers in Texas, the western states, and Mexico. In 1959 the presidents of the USA (D. D. Eisenhower) and Mexico (A. López Mateos) agreed to a feasibility study to eradicate the New World screwworm in Mexico.

The strategy for dealing with the USA south-west was a by-product of the use of the 160-km-wide sterile-fly barrier across Florida, with the release of sterile flies only in the overwintering area, and to let the cold weather destroy the screwworms to the north of this area. Following eradication from that area, sterile flies would be deployed to create a barrier zone along the US-Mexico border to protect against reinvasion (Bushland 1985).

A mass-rearing facility was established at a former air base converted to an insectary, fly sterilization and dispersal centre, near Mission, Texas, and releases began in 1962. By 1964 no screwworms were found in Texas or New Mexico for a period of two or three generations, and USDA officials declared the screwworm eradicated from these states. In 1965, the programme was extended to the Pacific, and in 1966 the entire USA was declared free of screwworms; the federal government took full responsibility to maintain the barrier zone from the Gulf of Mexico to the Pacific. However, no agreement with Mexico to proceed southward had been reached, and the USA remained highly vulnerable to the influx of screwworms from Mexico. At this point in time, the goal of the programme was no longer eradication in the true sense, but had become population containment (Klassen 1989, 2000; Hendrichs, Vreysen et al., this volume).

4.1.8. *Managing Screwworm Population along the US-Mexico Border*

Both US and Mexican cattle producers were anxious to push the screwworm population south to the narrow Isthmus of Tehuantepec, where a barrier of only 220 km would be needed. In 1972 the Mexico-United States Screwworm Eradication Agreement was signed, with the aim of eradicating the screwworm to the north of the Isthmus of Tehuantepec, and to establish a sterile-fly barrier there.

In the meantime, many difficulties arose. Screwworm cases occurred as much as 480 km north of the US-Mexico border. In 1968 almost 10 000 cases were recorded in the USA, and in 1972 such cases rose to 95 000. Knipling (1979) noted that, before the programme began, the maximum flight range of screwworm adults was estimated at 80 km. It was planned that the width of the sterile-fly barrier be twice this figure. However, Hightower et al. (1965) demonstrated that natural fly movement can occur up to at least 290 km, and the pattern of screwworm movement during the spring indicated that dispersal in a single generation was up to 480 km. In addition, Knipling (1979) concluded that the main reasons for the “breakdown” of the containment programme in 1972 were the unusually favourable conditions for winter survival of screwworms, the abandonment by ranchers of traditional animal husbandry practices needed to counter screwworm infestations (including the twice-weekly inspection and treatment of animals), and the explosion of the population of white-tailed deer as a result of almost no screwworm-induced mortality during the previous decade (Nagel and Peveling, this volume).

Critics of the programme postulated changes in the behaviour of the native population through inadvertent genetic selection during mass-rearing, making wild adults prone to avoid matings with the released strain, and the existence of cryptic species in the field (Bush et al. 1976; Richardson et al. 1982). However, no data were generated to support these views (Krafsur 1998; Krafsur and Ouma, this volume), which were strongly rebutted (LaChance et al. 1982). Another important factor was the unwise attempt to reduce sterile fly distribution costs by releasing flies on parallel flight lanes spaced 8 or 16 km apart, and this failed to deliver adequate numbers of sterile flies to all locations where wild virgin females were present (Krafsur 1978; Hofmann 1985).

The Mexico-United States Screwworm Eradication Commission began field operations in Mexico in 1974. A mass-rearing facility, with a capacity of 500 million sterile flies per week, was built at Tuxtla Gutiérrez, Chiapas (south of the Isthmus of Tehuantepec), and it reached full production in January 1977. Nevertheless, as late as 1976, almost 30 000 cases occurred in the USA. Major relief came when fly production at Mission, Texas, was supplemented from the new factory in Mexico (Meyer and Simpson 1995). Subsequently, the need for the Mission facility diminished rapidly, and in 1981 it was closed. The last autochthonous case in the USA occurred in August 1982.

Knipling (1979) stated:

Had scientists known of the long flight range of the insect, they would not have recommended a sterile fly release programme in the south-west. This would have been unfortunate. By taking this gamble, up to a billion [1000 million] dollars [USD] have been saved. We have learned that despite the long-range movement of the insect, a high degree of pest population suppression can be achieved even against non-isolated populations.

4.1.9. Programmes in Central America: the Drive to Panama

By 1984 the Commission had achieved the goal of eradicating the screwworm to Mexico's Isthmus of Tehuantepec (Peneda-Vargas 1985). Nevertheless, at the request of ranchers in southern Mexico and Central America, in 1986 operations were extended to the Yucatán Peninsula and the countries bordering Mexico (Irastorza et al. 1993). Eradication was declared as follows: Mexico 1991, Belize and Guatemala 1994, El Salvador and Honduras 1996, Nicaragua and Costa Rica 1999, and Panama 2006 where since 2004 a permanent sterile-fly barrier is being maintained in the Darien Gap along the border with Colombia (Wyss 2000; Maxwell et al. 2017; Skoda et al. 2017; Vargas-Terán et al., this volume). A smaller mass-rearing facility was constructed in the early 2000s at Pacora, Panama, and the larger facility at Tuxtla Gutiérrez was closed in 2013.

4.1.10. Screwworm Eradication Programme in North Africa

In 1988, the New World screwworm was discovered at Tripoli, Libya, where it rapidly spread over 28 000 km². Many feared that the insect would spread throughout North Africa, the Middle East and southern Europe, and migrate up the Nile River to sub-Saharan Africa, with serious consequences for the African people, livestock, and the already endangered large mammals.

In 1989, the Government of Libya asked the Food and Agriculture Organization of the United Nations (FAO) for assistance in eradicating the screwworm. The operational programme was planned in detail by consultants assembled by the Joint FAO/IAEA Division, and Libya and various donor countries provided the funding (FAO 1992; Vargas-Terán et al., this volume).

The infested area was partially isolated by the Mediterranean Sea, desert to the south, and barren areas with few livestock to the east and west. One hundred teams, each consisting of two individuals equipped with a jeep, inspected all livestock every 21–28 days, applied insecticide to every wound, and sprayed many of the animals. About 80 swormlure-baited wing traps were deployed across the lines of flight of the aircraft from which the sterile screwworms were dropped.

Sterile screwworms were supplied from Mexico — mating studies showed that the factory-strain flies were sexually compatible with the Libyan strain. Some differences in the mitochondrial DNA were observed, but they were not considered to indicate a barrier to applying the SIT (FAO 1992). Each weekly flight from Tuxtla Gutiérrez to Tripoli carried 40 million sterile screwworm pupae. In Tripoli, adult emergence was controlled to allow two early morning releases per week.

The attack on the pest population was planned for the early winter of 1990, since by then cool weather would have greatly reduced the density and the reproductive capacity of this insect. Also, cool weather would synchronize the life stages, and eliminate generation overlap. The number of sterile flies released was quickly increased to the maximum to saturate all suitable niches with sterile males. Thus, from the time that indigenous females emerged from under the soil, they would be in the company of sexually sterile males.

The impact of this strategy was dramatic. Only six instances of wounds infested with screwworm larvae were found in 1991, compared with more than 12 000 cases in 1990. Releases of sterile flies were continued until October 1991, and surveillance of all livestock until June 1992 (Lindquist et al. 1993). Eradication was declared in June 1992 (FAO 1992). As previously in Texas, where critics cast doubt on the effectiveness of the sterile insect technique, claiming that eradication was caused principally by cold winters and hot, dry summers (Richardson 1978; Readshaw 1986, 1987, 1989), there were again voices that affirmed that weather, instead of sterile male releases, had been decisive in screwworm elimination from Libya. These arguments were clearly rebutted, not only for Texas (Krafsur et al. 1986; Krafsur 1987), but also for Libya, where it was shown that all of the conditions for successful screwworm overwintering and dispersal existed in a 15–25-km-wide zone along the Mediterranean coast (Krafsur and Lindquist 1996; Kouba 2004).

4.1.11. *Screwworm Programmes in the Caribbean*

By 1975 the screwworm had been eradicated from Puerto Rico and the United States Virgin Islands. In 1999, the Government of Jamaica initiated a programme to eradicate the screwworm that was terminated without reaching eradication (Vreysen et al. 2007; Dyck, Reyes Flores et al., this volume; Vargas-Terán et al., this volume).

No eradication programmes have been initiated on Cuba and Hispaniola, even though they can easily be sources of *C. hominivorax* reintroduction into areas that have been cleared of this pest (Vargas-Terán et al., this volume). This threat has been confirmed by multiple interceptions of screwworm-infested animals at ports of entry, as well as significant outbreaks in Aruba, Curaçao, Mexico, and most recently in Florida, that were efficiently eliminated applying the SIT (Skoda et al. 2018; Vargas-Terán et al., this volume).

4.2. *Tephritid Fruit Flies*

Currently, the SIT is most widely applied against tephritid fruit flies (Enkerlin, this volume). Already in 1955, immediately after the successful screwworm eradication trial in Curaçao, investigations were initiated by the USDA in Hawaii into the possibility of developing and integrating the SIT to eradicate populations of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann), melon fly *Zeugodacus* (*Bactrocera*) *cucurbitae* (Coquillett), and oriental fruit fly *Bactrocera dorsalis* (Hendel) (Steiner and Christenson 1956; Steiner et al. 1970). Also, prior to 1960, pioneering investigations were underway on the Queensland fruit fly *Bactrocera tryoni* (Froggatt) in Australia, and on the Mexican fruit fly *Anastrepha ludens* (Loew) in Mexico and the USA (Klassen et al. 1994; Enkerlin, this volume). Furthermore, extensive research and development was started in the early 1960s at the FAO/IAEA Laboratory in Seibersdorf, Austria, to develop the SIT for the Mediterranean fruit fly and other fruit fly pests (Klassen et al. 1994).

The first successful use of the SIT against an insect pest, other than the screwworm fly, was the eradication in 1963 of the melon fly from Rota in the Mariana Islands (Steiner et al. 1965). The first large-scale programme, established by Mexico and the USA in the late 1970s, stopped the invasion of the Mediterranean fruit fly from Central America into southern Mexico (Hendrichs et al. 1983). In Japan, the SIT was employed in the 1980s and 1990s to eradicate the melon fly in Okinawa and all of Japan's south-western islands, permitting access for fruits and vegetables produced in these islands to the main markets in the Japanese mainland (Kuba et al. 1996). In Chile, the SIT was used to rid the north of the country of the Mediterranean fruit fly; thus by 1995 the entire country had become a fly-free zone, and a joint programme with Peru operates in northern Chile and southern Peru. Since then Chilean fruits have entered the US market in huge volumes without the need for any quarantine treatment, providing a major benefit to the Chilean economy (Enkerlin, this volume). Argentina also has developed significant SIT Mediterranean fruit fly programmes in several fruit-producing provinces, some of which have succeeded in establishing pest free areas. Mexico has also applied the SIT to get rid of various *Anastrepha* species from northern Mexico (Enkerlin, this volume).

The SIT is increasingly being applied with the objective to reduce losses and pesticide use rather than fruit fly eradication, with suppression programmes ongoing in Brazil, Croatia, Israel, South Africa, Spain and Thailand, and in preparation in Morocco and Vietnam. To prevent Mediterranean fruit fly establishment in the continental USA through infested imported (smuggled) fruit, sterile males are being released preventively in the Los Angeles Basin, Tampa, and Miami. Consequently, there is no longer a need to spray these urban areas with malathion insecticide to suppress and eliminate incipient pest populations each time there are outbreaks.

Several species of tropical fruit flies are extremely destructive pests of fruits and vegetables. Tephritid fruit flies are major economic pests because they have:

- A multivoltine life cycle with an explosive reproductive capacity,
- A polyphagous behaviour with the capacity to exploit a large number of hosts,
- The ability to disperse widely as adults or to be moved in fruit as larvae,
- The ability (adults) to survive several months of inclement weather.

Tropical fruit flies not only cause great losses in fruit and vegetable production, but they also seriously impede international trade because of quarantine regulations designed to avoid cross-border introductions. Consequently, efforts to remove, suppress, or exclude these pests have been made in at least 32 countries (Klassen et al. 1994; Hendrichs 2001; Enkerlin, this volume).

The mating behaviours of tropical fruit flies are very different from the aggressive behaviour of male screwworms, involving complex courtship behaviours with males aggregating in mating arenas or leks, and where receptive females determine mate choice (Hendrichs et al. 2002; Robinson et al. 2002). Thus, special attention in terms of product quality control must be given to the effects of colony-holding conditions, artificial diets, irradiation, and handling procedures on the acceptability to wild females of released sterile males (Cayol 2000; Hendrichs et al. 2002).

4.2.1. *Mexican and Queensland Fruit Flies*

In 1964, the SIT was used to eradicate the Mexican fruit fly from outbreaks in southern California, and as a containment measure to prevent the pest from re-entering California from Baja California Norte in Mexico, and a decade later to exclude the pest from the Rio Grande Valley of Texas. Both SIT containment programmes have continued since then, but the programme on the California-Mexico border was terminated after the Mexican states of Baja California Norte, Baja California Sur, Chihuahua, and Sonora, following successful SIT projects in the 1990s against *A. ludens* and the West Indian fruit fly *Anastrepha obliqua* (Macquart), were converted into fruit fly-free zones from which citrus, stone fruits, apples, and vegetables are now being exported without any postharvest treatment (Reyes F. et al. 2000; Enkerlin, this volume).

Field trials of the SIT against the Queensland fruit fly began in 1962 in New South Wales, Australia. Although the population was suppressed strongly, it could not be eradicated because of long-range immigrants. Since the mid-1990s, an SIT containment programme has tried to protect a “Fruit Fly Exclusion Zone” comprising the “Tri-State” major fruit production area (southern New South Wales, northern Victoria, and eastern South Australia), although the Queensland fruit fly has been increasingly extending its range southward into this free area (Capon et al. 2017). In 1990, use of the SIT resulted in the eradication of this pest from an incipient infestation in 125 km² at Perth, Western Australia (Fisher 1996). Also, the SIT was used to eradicate the Mediterranean fruit fly in Carnarvon in Western Australia (Fisher et al. 1985), and is now used to eradicate recurrent outbreaks of this pest in South Australia (Smallridge et al. 2002).

4.2.2. *Moscamed*

In 1955, the Mediterranean fruit fly was found in Costa Rica. After the pest had established a small foothold in Nicaragua, and a pilot programme conducted in 1967 (Rhode 1970), an operational programme to contain this pest was initiated to prevent it from invading countries to the north (Rhode et al. 1971). However, very unfortunately, a review team concluded that the Mediterranean fruit fly is not economically important to Central America, and recommended that the programme be terminated (Rhode 1976; Dyck, Reyes Flores et al., this volume). Thus, by 1976 the pest had expanded its range into Honduras, El Salvador, and Guatemala, and by 1979 it already occupied 15 000 km² in southern Mexico.

In the meantime, to meet this emergency, the Government of Mexico entered into cooperative agreements with Guatemala and the USA to establish the first large-scale fruit fly AW-IPM programme using the SIT. Construction of a rearing facility at Metapa, Mexico, to produce 500 million sterile flies per week, began in 1977 and initiated production in early 1979 (Schwarz et al. 1985). By 1982, pest eradication in the infested area of Mexico was achieved (Hendrichs et al. 1983), and a containment barrier was created through Guatemala (Villaseñor et al. 2000; Enkerlin, this volume). For approximately 40 years, this programme has kept Mexico, the USA, and half of Guatemala free of the Mediterranean fruit fly, allowing Mexico over this period to significantly expand its fruit and vegetable exports, mainly to the USA (Enkerlin et al. 2015, 2017). Mexican horticulture export earnings since 1994 have

tripled to more than USD 9000 million per year (Enkerlin, this volume). In the meantime, the production capacity of the Moscamed programme has increased to over 4000 million sterile males per week, the majority of which are produced at the El Pino facility in Guatemala (Rendón et al. 2004).

4.2.3. *Melon Fly Eradication in the South-Western Islands of Japan*

Between 1919 and 1970, the melon fly gradually invaded most island groups in the south of Japan, including Okinawa. The shipment of fruits and vegetables to markets in mainland Japan was strictly forbidden. Consequently, the Japanese National Government assisted the Prefectural Governments of Kagoshima and Okinawa to conduct two separate programmes to eradicate the melon fly from all of the south-western islands.

A pilot eradication experiment on small Kume Island (60 km²) began in 1972, and eradication was declared in 1978. In 1984, an operational programme was undertaken in the Miyako Islands. The capacity of the rearing facility was 30 million flies per week. Since the wild population was estimated at 34.4 million, male annihilation (using cotton strings impregnated with cuelure and insecticide) was used to reduce it to 5% of its original level. The production of high-quality flies, and supplementary releases in high-density areas, were critically important (Yamagishi et al. 1993; Kakinohana 1994). By 1986 the production capacity had been expanded to almost 200 million sterile flies, and the programme gradually moved from island group to island group until eradication of the melon fly from all of Japan was achieved in 1993 (Kuba et al. 1996; Koyama et al. 2004).

4.2.4. *Mediterranean Fruit Fly Genetic Sexing Strains*

In the early 1960s, the Citrus Marketing Board of Israel developed an insecticide-based area-wide programme against the Mediterranean fruit fly that was able to meet the certified quarantine security requirements of fruit importing countries (Cohen and Cohen 1967). Bisexual releases of sterile flies were avoided for this programme because sexually sterile female Mediterranean fruit flies can cause (with their ovipositors) cosmetic damage in some varieties. However, in work with the Australian sheep blow fly *Lucilia cuprina* (Wiedemann), Whitten (1969) found that male and female pupae of a strain, in which the segment of the autosome bearing a gene for black puparium is translocated to the Y chromosome, could be separated mechanically, as all males are brown, and all females black.

This encouraged Rössler (1979) to construct a similar strain of the Mediterranean fruit fly in which male pupae (brown) could be separated from female pupae (white). This special strain was mass-reared and pupae sorted by a seed-sorter at the FAO/IAEA Seibersdorf Laboratory in Austria; it performed well in large-scale tests in Israel (Franz et al., this volume).

Subsequently, this laboratory developed a genetic sexing strain in which a segment of an autosome bearing the dominant wild type allele of a temperature-sensitive lethal (*tsI*) mutant was translocated to the Y chromosome (Franz and Kerremans 1994; Caceres et al. 2004). This enabled the elimination of females at the

egg stage, thereby saving significant costs during mass-rearing, handling, and release, and increasing sterile male production in the same facility.

In addition, this laboratory developed a “filter rearing system” to maintain strain stability in the mass-rearing of such genetic sexing strains (Fisher and Caceres 2000; Franz et al., this volume; Parker, Mamai et al., this volume).

4.2.5. *Sterile “Genetic Sexing Strain” Males Alleviate Mediterranean Fruit Fly Crises in California and Florida, USA*

Until 1980, the Mediterranean fruit fly invaded California and Florida at only infrequent intervals. Outbreaks, occurring usually in urban areas, were eliminated mainly by applying malathion-bait sprays. It cost more than USD 100 million to eradicate the infestations in California detected in 1980 and 1982.

In the decade 1987–1997, multiple new infestations were encountered annually in California and Florida. Since each outbreak was addressed independently, this non-area-wide approach often resulted in continuous new satellite infestations, and there was a real threat that the pest would become established. Therefore, in 1994, an area-wide SIT eradication programme was initiated, with twice-weekly releases of sterile Mediterranean fruit flies over the entire Los Angeles Basin. This programme was so successful and cost-effective that, in view of the many introductions, in 1996 a permanent preventive release programme was established over this area (Dowell et al. 2000; Barry et al. 2004). The same preventive approach has also been followed since 1998 in three Florida counties that are at high-risk in terms of introductions.

These preventive release programmes have now been in operation for over 20 years, maintaining the Mediterranean fruit fly-free status of the United States (although this is disputed by Carey et al. 2017, but see rebuttals by McInnis et al. (2017) and Shelly et al. (2017)). Sterile males of the *tsI* sexing strain VIENNA 7 or VIENNA 8, mainly produced by the Moscamed programme in Guatemala, are used for these preventive release programmes. Sexing strains are also used in most Mediterranean fruit fly suppression, containment, or eradication programmes (Caceres et al. 2004; Franz et al., this volume; Augustinos et al. 2017).

4.2.6. *Jordan-Israel-Palestine Mediterranean Fruit Fly Programme*

The signing of the Oslo Peace Accord created an opportunity for the international community to assist Middle East countries, notably the Hashemite Kingdom of Jordan, the Palestinian Authority, and Israel, to undertake joint projects that would foster cooperation. An economic analysis of three area-wide programme alternatives was conducted (with the support of the FAO/IAEA) (Enkerlin and Mumford 1997). In the operational programme, initially focused on the Arava/Araba region between Israel and Jordan, the genetic sexing strain VIENNA 7 (Franz et al., this volume) has been used for population suppression rather than eradication (at present, there is no intention to establish disruptive quarantines along a major highway). As a result of this suppression programme, the export of fresh vegetables from the Arava region has reached more than USD 30 million per year (Cayol et al. 2004; Enkerlin, this volume). Initially, the sterile pupae for this programme were shipped from the

Moscamed facility in El Pino, Guatemala, but then BioBee (the largest producer of biological control agents in Israel) constructed a commercial mass-rearing facility, with the goal of expanding suppression to other fruit and vegetable production areas in Israel, West Bank, and Jordan, and to sell sterile flies internationally, for example, to the Mediterranean fruit fly suppression programme in the Neretva Valley in Croatia (Bassi et al. 2007; Bjeliš et al. 2016).

4.2.7. *Trend is Suppression, not Eradication, of Fruit Flies*

For technical and economic reasons, including the undesirability of establishing quarantines that interfere with trade, or difficulties in maintaining them effectively, today many fruit fly AW-IPM programmes that integrate the SIT aim to suppress the pest populations (Mumford 2004; Enkerlin, this volume; Hendrichs, Vreysen et al., this volume; Mumford, this volume). Examples of suppression programmes using sterile flies as an additional IPM tool are:

- Mediterranean fruit fly
 - Costa Rica (Reyes et al. 2007)
 - Arava, Israel (Cayol et al. 2004)
 - Hex River Valley, South Africa (Barnes et al. 2004; Venter et al. 2021)
 - San Francisco Valley, Bahia, Brazil (Malavasi et al. 2007)
 - Valencia, Spain (Generalitat Valenciana 2003)
 - Neretva Valley, Croatia (Bjeliš et al. 2016)
 - Souss Valley, Agadir, Morocco (Enkerlin, this volume)
 - Southern Brazil, Brazil (Kovaleski and Mastrangelo 2021)
- Mexican fruit fly
 - Mexico (Orozco-Dávila et al. 2017)
- Oriental fruit fly and *Bactrocera correcta* (Bezzi)
 - Ratchaburi Province, Thailand (Sutantawong et al. 2004).

4.3. *Onion Maggot*

Since 1981, the SIT has been applied by a private firm (now de Groene Vlieg Bio Control b.v.) in The Netherlands to control the onion maggot *Delia antiqua* (Meigen) on an aggregate area of ca. 10 000 hectares (Loosjes 2000; Everaarts 2016). The flies are reared year-round, and stockpiled in diapause for release during the onion-growing season. Individual farmers contract for the service of population monitoring and releasing the sterile flies independently of their neighbours, many of whom use chemical control (the relevant insecticides were eventually banned by the European Union in the 2000s but the industry lobby managed to get exemptions for the onion crop). As a result of this uncoordinated approach, much efficiency is lost because the sterile flies are not applied on an area-wide basis (protected fields do not form a contiguous block). Some growers in the general area of sterile-fly releases benefit from them, but do not contribute to the programme (free-riders). Nevertheless, the programme has been able to expand to ca. 40% of the onion production area.

4.4. *Tsetse Flies*

Tsetse flies are confined to sub-Saharan Africa where they transmit the disease trypanosomiasis [trypanosomiasis] to humans (sleeping sickness) and livestock (nagana). They are regarded as a major cause of rural poverty because they prevent mixed farming. Crops have to be cultivated manually with hoes because nagana kills draught animals. The surviving cattle produce little milk, and manure is not available to fertilize the worn-out soils. The conquest of sleeping sickness and nagana would be of immense benefit to rural development in sub-Saharan Africa.

Understanding this fundamental role of tsetse at the root of rural poverty, it was E. F. Knipling who in the early 1960s assigned D. A. Dame from the USDA to lead a research effort in Southern Rhodesia (Zimbabwe), in collaboration with the University of Rhodesia, to determine the feasibility of applying the SIT against tsetse flies and to develop mass-rearing technology. Also, the FAO/IAEA, and other institutions from the previous colonial nations, initiated studies to assess the potential of the SIT for tsetse species. Of the over 30 tsetse species, only some (6 or 7) are of economic importance, and since then have been the subject of SIT development (Feldmann et al., this volume).

Tsetse flies are unique among pest insects in being larviparous, i.e. females do not lay eggs but gestate a larva in a uterus (one larva at a time), with a gestation period of about 9 days. Thus, these flies have extraordinarily low rates of reproduction. Therefore, relatively low release rates should be sufficient, compared with those required for highly fertile oviparous pests (Hendrichs, Vreysen et al., this volume). However, rearing tsetse flies is relatively laborious and expensive because adults of both sexes require frequent blood feeding. The development in the 1980s at the FAO/IAEA Laboratory in Seibersdorf, Austria, of an *in vitro* rearing system with membranes and heated abattoir-collected blood (that is previously irradiated to eliminate any microbial contamination) to replace the use of live animals, represented a major breakthrough that enabled the upscaling of mass-rearing (Parker, Mamai et al., this volume).

Table 2 summarizes the SIT trials that have been conducted on tsetse flies. (Data from the trial by Vanderplank are shown above in Table 1.) In a trial on *G. m. morsitans* in 1969 on an island (5 km²) in Lake Kariba, Zimbabwe, pupae collected in the field were chemosterilized in the laboratory, and then returned to the field to permit adult flies to emerge. The sterile flies were fully competitive, but adult flies that were sterilized after emergence and held in captivity suffered an 80% loss in field competitiveness. These studies were followed in 1977–1978 by a larger-scale (195 km²) trial in Tanzania using mass-reared *G. m. morsitans* fed on live animals, which demonstrated full sterile-fly competitiveness following irradiation and release in the pupal stage.

Among the other releases (conducted in the 1970s and 1980s) were several that successfully integrated releasing sterile males with deploying recently developed attractant traps and insecticide-treated targets. Three tsetse species were eradicated simultaneously in 3000 km² in Burkina Faso (Politzar and Cuisance 1984), and one species in 1500 km² area in Nigeria (Takken et al. 1986). The technology was successfully applied, but unfortunately the programmes were not conducted area-wide and thus the pest free status of the areas was not sustainable.

Table 2. Summary of SIT trials with tsetse flies *Glossina* spp.

Species, habitat, and location	Method	Outcome and objectives	References
<i>Glossina swynnertoni</i> , savannah, north-western Tanzania	Release of <i>G. morsitans</i> , which mated with <i>G. swynnertoni</i>	99% suppression in 256 km ² , permitted development of the area for agricultural production	Vanderplank 1947, and hitherto unpublished data shown in Table 1
<i>G. morsitans morsitans</i> , savannah, Lake Kariba, Zimbabwe	Insecticidal suppression followed by release of chemically sterilized pupae	> 99% suppression on 5-km ² island, feasibility study	Dame and Schmidt 1970; Dame et al. 1981
<i>G. tachinoides</i> Westwood, riverine, Chad	Radiation-sterilized, transport from France, ground release sterile ♂	Feasibility study, sterilization, transport, release	Cuisance and Itard 1973
<i>G. palpalis gambiensis</i> Vanderplank, riverine, Burkina Faso	Suppression by aerial insecticide treatment, ground release sterile ♂	Feasibility study (16 linear km) to control sleeping sickness	Van der Vloedt et al. 1980
<i>G. palpalis palpalis</i> Robineau-Desvoidy with <i>G. tachinoides</i> as a control, riverine, Lafia, Nigeria	Suppression with traps and targets followed by ground release of radiation-sterilized adults	Eradication of <i>G. p. palpalis</i> in 1500 km ²	Takken et al. 1986; Oladunmade et al. 1990
<i>G. morsitans morsitans</i> , savannah, Tanzania	Insecticidal suppression followed by ground release of radiation-sterilized pupae	90% suppression (195 km ²), feasibility study	Dame et al. 1975; Williamson et al. 1983
<i>G. morsitans morsitans</i> , and <i>G. pallidipes</i> Austen, savannah, Lake Kariba, Zimbabwe	Autosterilization of wild flies with pyriproxyfen	Suppression (12 km ²), feasibility study	Hargrove and Langley 1990
<i>G. morsitans submorsitans</i> Newstead, <i>G. palpalis gambiensis</i> , <i>G. palpalis palpalis</i> , <i>G. tachinoides</i> , riverine and savannah, Burkina Faso, Nigeria	Insecticide application and trapping suppression followed by ground release of radiation-sterilized adults	Eradication (3000 km ² - Burkina Faso, 1500 km ² - Nigeria)	Politzar and Cuisance 1984; Takken et al. 1986
<i>G. austeni</i> Newstead, bushland and forest, Unguja, Zanzibar, Tanzania	Suppression with insecticide on livestock and attractive devices followed by aerial release of radiation-sterilized adults	Eradication (1650 km ²), trypanosomosis transmission ceased	Msangi et al. 2000; Vreysen et al. 2000; Feldmann et al., this volume
<i>G. fuscipes fuscipes</i> Newstead, forest, Buvuma Islands, Uganda	Autosterilization of wild flies with triflumuron vs. insecticide-impregnated traps	Suppression (5 km ²), abandoned because of funding shortfall	Oloo et al. 2000

Traps were also used on a small island (12 km²) in Lake Kariba, Zimbabwe, to attract wild flies that were autosterilized by coming into contact with the traps, and then departed (Hargrove and Langley 1990). This, and another failed eradication trial, also in a small island in a Ugandan lake, are almost the only attempts to date to apply the autosterilization principle which avoids or minimizes the need for a rearing facility.

The eradication in 1997 of the tsetse fly *G. austeni* in Unguja Island, Zanzibar, Tanzania, confirmed the feasibility of the area-wide integration of aerial sterile-male releases with other suppression methods to create sustainable tsetse-free areas (Vreysen et al. 2000). This successful programme freed cattle from the burden of nagana, resulting in major socio-economic benefits (Msangi et al. 2000; Feldmann and Jannin 2001; Feldmann et al., this volume). In response, in 2001, the African Heads of State and Government committed their countries to rid Africa of this disease (Feldmann and Jannin 2001). However, the dream to conquer nagana will require many decades of concerted effort. Furthermore, there is a debate about the desirability of using the SIT with other approaches to eradicate populations of major tsetse species from large areas of the African mainland (DFID 2002; Hargrove 2003; Nagel and Peveling, this volume), and the perceived high cost of applying the technique.

Currently ongoing programmes to free selected areas from tsetse are under way against *G. pallidipes* and *G. fuscipes* in the Deme valley in southern Ethiopia, and against *Glossina palpalis gambiensis* in the Niayes area of Senegal (Zerihun 2017; Vreysen et al. 2021; Feldmann et al., this volume).

4.5. Mosquitoes

Mosquito-borne diseases (malaria, dengue, filariasis, yellow fever, chikungunya, Zika) annually cause severe mortality and morbidity. For mosquito SIT, since females bite, blood-feed and may transmit major human pathogens, it is essential that releases of female mosquitoes be reduced to an absolute minimum. Therefore, efficient sexing is needed on a large scale, and genetic sexing systems are the preferred approach (Gilles et al. 2014; Franz et al., this volume). Naturally occurring pupal size difference between males and females, for example in some *Aedes* mosquitoes, are currently exploited for mechanical sexing, although it is difficult to achieve a 100% pure separation under operational conditions and is very labour-intensive when applied on a large scale.

As shown in Table 3 and in Benedict and Robinson (2003), in the 1960s and 1970s there was considerable interest and activity developing the SIT for mosquitoes, and several release trials were conducted, some of them integrating the *Wolbachia*-based incompatible insect technique (IIT), based on the ground-breaking work by Hannes Laven on cytoplasmic incompatibility (CI) (Laven 1958, 1967). The largest-scale trials were conducted in El Salvador and India. Unfortunately, in both countries, political factors in the mid-1970s interrupted further work — civil war in El Salvador, and in India false accusations that the project was intended to collect data on biological warfare (Nature 1975; WHO 1976).

Table 3. Summary of release trials with sterile or semi-sterile male mosquitoes

Target species	Location	Sterilization and sex-separation method	Outcome	References
<i>Anopheles quadrimaculatus</i> Say	Lakes in Florida, USA	Pupal irradiation, adult release, sex separation by pupal size	Poor competitiveness of colonized males for wild females, which may have been mismatched for sibling species	Weidhaas et al. 1962; Dame et al. 1964
<i>Culex quinquefasciatus</i> Say	Okpo, Myanmar	Cytoplasmic incompatibility	Eradication of small village population	Laven 1967
<i>Anopheles gambiae</i> s.s. Giles	Pala, Burkina Faso	<i>An. melas</i> Theobald x <i>An. arabiensis</i> Patton cross yielding sterile hybrid males and few females	Poor competitiveness of hybrid males	Davidson et al. 1970
<i>Culex quinquefasciatus</i>	Sea Horse Key, Florida, USA	Chemosterilization with thiotepa	Sterilization of small island population, moderate competitiveness	Patterson et al. 1970
<i>Culex pipiens</i> L.	Village near Montpellier, France	Chromosome translocations	Persistent semi-sterility in wild population	Laven 1972; Cousserans and Guille 1974
<i>Culex quinquefasciatus</i>	Villages near Delhi, India	Thiotepa sterilization or cytoplasmic incompatibility plus translocations, sex separation by pupal size	300 000 released per day, 99.8% male, adequate competitiveness in the field for females of wild origin, but high egg sterility not achieved by mass-release due to immigration	Sharma et al. 1972; Singh et al. 1975; Curtis 1976; Grover et al. 1976a; Yasuno et al. 1978; Curtis et al. 1982
<i>Aedes aegypti</i> (L.)	Urban areas in or near Delhi, India	Thiotepa sterilization or sex-ratio distorter plus translocations, sex separation by pupal size	Rearing and sex separation as for <i>Culex quinquefasciatus</i> above, high competitiveness in the field for females of wild origin	Curtis et al. 1976; Grover et al. 1976b; Ansari et al. 1977; Suguna et al. 1977
<i>Aedes aegypti</i>	Mombasa, Kenya	Chromosome translocations	Partial sterility detected in wild population	McDonald et al. 1977

Table 3. Continued

Target species	Location	Sterilization and sex-separation method	Outcome	References
<i>Anopheles albimanus</i> Wiedemann	Lake Apastapeque, El Salvador	Chemosterilization of pupae with bisazir, inaccurate sex separation based on pupal size	100% sterility induced in wild population, which fell below detection level after 5 months	Lofgren et al. 1974
<i>Anopheles albimanus</i>	Pacific coast of El Salvador	Bisazir sterilization, sex separation originally by pupal size + feeding on malathion-treated blood, later by a Y chromosome propoxur-resistance translocation inversion (MACHO strain)	Eventually 1 million MACHO released per day and found competitive, a natural population increase was suppressed, but eradication prevented by immigration in spite of a barrier zone	Seawright et al. 1978; Dame et al. 1981
<i>Culex tritaeniorhynchus</i> Giles	Village near Lahore, Pakistan	Pericentric inversion plus translocation, sex separation by temperature-sensitive lethal	Assortative mating — competed for females of colony origin but not for females of wild origin	Baker et al. 1978, 1979
<i>Anopheles culicifacies</i> Giles	Village near Lahore, Pakistan	Bisazir sterilization, sex separation by Y chromosome dieldrin translocation	Released males behaved normally in the field but showed subnormal mating competitiveness	Baker et al. 1980, 1981; Reisen et al. 1981
<i>Culex tarsalis</i> Coquillett	Kern County, California, USA	Adult irradiation after separation of males by hand	Partial assortative mating — reduced competitiveness for wild females, but supercompetitiveness for colony females	Reisen 1982

The work in India showed that two important vector species of culicine mosquitoes could be mass-reared, and the sexes separated (according to pupal size) to ensure that 99.8% of the released mosquitoes were males. Males were chemosterilized in the pupal stage, or by male-linked chromosome translocations combined either with cytoplasmic incompatibility or sex-ratio distortion due to meiotic drive. Field tests showed that the mating competitiveness of the males of both species was acceptable. However, the mass release of *Culex quinquefasciatus* males in villages achieved only limited levels of sterility in eggs laid by wild females. This was attributed to the influx of already-mated females from outside the target release area. A planned mass release of sterile male *Aedes aegypti*, aimed at

the eradication of this urban mosquito from a whole town, was prevented by the political problem mentioned above.

In El Salvador the target was the malaria vector *Anopheles albimanus*. It was multi-resistant to insecticides (partly due to the agricultural use of insecticides), and therefore difficult to control by conventional means. In the initial study, releases during 5 months around Lake Apastapeque were successful in inducing 100% sterility in eggs laid by wild females (Lofgren et al. 1974; Weidhaas 1974). Sex separation in that trial was based on pupal size differentiation; however, it was very imperfect, yielding 15% females among the released males. In a second larger trial, a second separation was added; adults were offered malathion-laced blood through a membrane. This effectively eliminated most of the females, but the males were debilitated from being caged and handled. Therefore, a genetic sexing strain was developed — a chromosome translocation was induced, linking a propoxur-resistance gene to the Y chromosome, and this was combined with a crossover-suppressing chromosome inversion. Propoxur treatment at the egg stage selectively eliminated all but 0.2% of females, thereby allowing a doubling of the male production for release (Seawright et al. 1978). By eliminating the handling losses in the adult stage, the net release was increased from 200 000 males per day to over 1 million, and these males, when released as sterile pupae, were almost fully competitive in the field. Compared with the seasonal upward trend of the untreated population, the releases reduced the target field population by more than 97% (Dame et al. 1981; Benedict and Robinson 2003). However, complete control was thwarted by immigration, and political unrest and war caused the trials to be terminated.

As a result of the increase in the global burden of mosquito-borne diseases, the unsustainability of relying on insecticides for vector control due to increasing insecticide resistance, and the absence of vaccines and efficient, safe and inexpensive drugs to combat malaria, dengue, chikungunya, Zika, and other emerging diseases, the idea of genetic control of mosquitoes is now undergoing a revival (Häcker et al., this volume; Lees et al., this volume).

During the last 15 years considerable progress has been made in developing the SIT as a potential new tool in the arsenal to manage mosquitoes. Recent developments enable efficient mass-rearing and irradiation for male release (Lees et al. 2015; FAO/IAEA 2017b, c, 2018). Equipment and protocols have been developed and validated for efficient mass-rearing, irradiation and release of *Aedines* and *Anophelines*. Assessment of male quality is becoming more sophisticated, showing that mosquitoes are not different in their radiation-sensitivity, a common misconception. For example, the radiation doses to sterilize male *Aedes albopictus* (Skuse) and *Aedes aegypti* range between 35–40 Gy and 60–80 Gy, respectively, and have a negligible effect on the biological quality of the mosquito (Bourtzis et al. 2016).

Several institutions and governments are currently evaluating the feasibility of mosquito SIT in various pilot settings and stages of development, including in Brazil, China, Cuba, French Polynesia, Italy, Mauritius, Mexico, Reunion, Singapore, Spain, Sudan, Thailand, and USA (Lees et al., this volume).

Until perfect sexing mechanisms exist, the SIT in combination with *Wolbachia*-induced cytoplasmic incompatibility and pathogen interference is considered the safest solution for *population suppression* (Zhang et al. 2015; Bourtzis et al. 2016;

Bown 2019; Zheng et al. 2019). Being *Wolbachia*-infected, any accidentally released females cannot result in population establishment because they are irradiated and therefore sterile, but at the same time because of *Wolbachia* they will also be unable to transmit human pathogens. This is not the case with transgenic or only symbiont-based approaches that are also under development (Thomas et al. 2000; Alphey and Andreasen 2002; Itô et al. 2002; Hoffmann et al. 2011; Bourtzis et al. 2014; Carvalho et al. 2015; Häcker et al., this volume), where released females can either vector disease (will result in *population replacement*) or leave an “ecological footprint” (Evans et al. 2019). For such approaches, issues such as stability, sustainability, and biosecurity need to be addressed. Regulatory issues and those relating to intellectual property and the economic cost of application must also be overcome (Bourtzis et al. 2016).

4.6. Coleoptera

4.6.1. Field Cockchafer

Cockchafer (Scarabaeidae) are important pests of root vegetables. The flight period can be accurately forecast, and is restricted to a few weeks every third year, with males emerging before females. In 1959 and 1962, Horber (1963) conducted two field trials on *Melolontha vulgaris* F. in 30 hectares of agricultural land in Switzerland. He collected adult males in light traps, and gave them a sterilizing dose of 33 Gy. In the two trials, 3109 and 8594 sterile males were released, and the wild populations were reduced by 80% and to eradication, respectively.

Incidentally, in another family of beetles, the SIT is under development for application against the small hive beetle *Aethina tumida* Murray (Coleoptera: Nitidulidae), a serious threat to bee-keeping (Downey et al. 2015).

4.6.2. Sweetpotato Weevils

Two weevil species are found in Okinawa Prefecture in south-western Japan — sweetpotato weevil *Cylas formicarius* (F.) and West Indian sweetpotato weevil *Euscepes postfasciatus* (Fairmaire) (Yasuda 2000). These are invasive alien pests that threaten agricultural production, and have been designated as plant quarantine pests. Consequently, the transport of fresh sweet potatoes from Okinawa to mainland Japan is prohibited. Currently, both species are the targets of pilot AW-IPM eradication trials integrating the SIT on Kume Island.

Radiation has detrimental effects on these weevils. Digestive obstruction following the collapse of the epithelial tissue of the midgut has been suggested as the cause of the short lifespan of irradiated adults. Nevertheless, mitigation measures, including partial sterility and fractionated-dose irradiation at low temperature, successfully overcame these effects (Kumano et al. 2010, 2012).

From 1994 to 1999, the male annihilation technique (MAT), using synthetic sex pheromone and insecticide in wood fibreboard squares, was applied. The population of *C. formicarius* was suppressed by about 90%, and the plant infestation level dropped from 9.5 to less than 1%. Subsequently, sterile weevils were aerially released, and “hot spots” were treated with additional ground releases (Kohama et

al. 2003). In 2013 *C. formicarius* was declared eradicated from Kume Island (Haraguchi et al. 2014).

Following a successful SIT trial in 1995, and using weevils reared on artificial diet (Shimoji and Miyatake 2002; Shimoji and Yamagishi 2004), an island-wide AW-IPM programme integrating the SIT against *E. postfasciatus* is ongoing on Kume Island.

4.7. *Lepidoptera*

Throughout the world, lepidopteran larvae cause immense damage to food and forage crops, forests, and stored products. However, there are several problems when applying the SIT against moths (Bakri et al., this volume; Lance and McInnis, this volume; Marec et al., this volume; Simmons et al., this volume):

- Some tolerance to dominant lethal induction by ionizing radiation, because of the holokinetic chromosomes of Lepidoptera,
- Reductions in ability to mate when inducing full sterility,
- Production of eupyrene and apyrene sperm,
- Spermatophore formation,
- Complex sperm transfer.

For species (such as the codling moth) that undergo diapause, the potential exists to mass-rear year-round and stockpile the pupae, and then activate them later in the spring for release in synchrony with the wild population (Parker, Mamai et al., this volume). However, on the whole, the large-scale rearing of moths is more difficult than that of most flies. For these reasons, the development of the SIT against moths has lagged behind work with flies. Nevertheless, the potential to use the SIT against lepidopteran pests appears to be very great (Marec et al., this volume), and its application is increasing (Simmons et al., this volume).

M. D. Proverbs (1962, 1982) in British Columbia, Canada, developed the SIT to suppress the codling moth, an economic pest of apples and pears. He found that very high and debilitating doses of ionizing radiation (about 400 Gy) are required to induce 100% sterility. However, considerably lower and less debilitating doses induce inherited sterility (IS), and the level of sterility of the F₁ progeny is greater than that of the irradiated parent (North 1975). Simulation models showed that released males with IS would suppress the wild population to a greater extent than the release of equal numbers of fully sterile males (Marec et al., this volume). In 1994, releases of irradiated codling moths were initiated in the Okanagan Valley of British Columbia, and continue with the objective of permanent area-wide population suppression (Dyck et al. 1993; Bloem and Bloem 2000; Simmons et al., this volume). Overall, codling moth populations have been reduced by 94% relative to pre-programme levels and damage to less than 0.2% of fruit in more than 90% of the orchards in the programme area (Nelson et al. 2021).

Another AW-IPM programme integrating the SIT, which has been implemented as a large-scale operational programme, is for the pink bollworm. Since 1967 sterile moths have been released in 0.4 million hectares of cotton fields in the San Joaquin Valley of California to prevent the establishment of this pest by moths migrating from southern California (Staten et al. 1993; Walters et al. 2000). This programme,

largely funded by growers, has been key to the survival of cotton production in California. More recently, in conjunction with the extensive planting of *Bt*-cotton in the mid-2000s, the programme succeeded in eliminating this pest from south-west USA and northern Mexico (Staten and Walters 2021; Simmons et al., this volume).

The SIT is also being applied for continuous suppression of the false codling moth in citrus orchards in South Africa (Boersma 2021). It has also been applied successfully to eradicate outbreaks of invasive moth pests (Hendrichs, Enkerlin et al., this volume) such as the painted apple moth in New Zealand (Suckling et al. 2007) and the cactus moth in Mexico (Bello-Rivera et al. 2021). Extensive SIT/IS application on the gypsy moth was made in the past (Simmons et al., this volume). Furthermore, it is under development for application against a number of other moth pests (Vreysen et al. 2016; Simmons et al., this volume) including the African sugarcane borer in South Africa (Conlong and Rutherford 2017), the navel orangeworm in California, the European grapevine moth in Chile, and the carob moth in North Africa.

5. TRANSBOUNDARY SHIPMENT AND INTERNATIONAL RECOGNITION OF THE SIT

Over the years, the transboundary shipment of sterile insects across borders increased significantly, with cumulative numbers shipped reaching approximately 600 thousand million pupae by 2015 (see Appendix 3 on History of Transboundary Shipments of Sterile Tephritid Fruit Flies in FAO/IAEA 2017a). Also, mass-production of sterile insects has become semi-commercial or fully commercial in several situations (Loosjes 2000; Barnes 2007; Bassi et al. 2007; Everaarts 2016). Consequently, there were increasing demands for guarantees that sterile insects can be safely and legally shipped internationally, as well as for harmonized international regulations to facilitate this trade in order to reduce the need for independent development of national regulations that often hinder insect control programmes. However, even though sterile insects are non-invasive agents that leave no “ecological footprint” because of their sterility (contrary to insecticides or other measures that are toxic or pathogenic, or to most other biological agents whose establishment is irreversible once they are released), they were not formally accepted as biological control agents by the International Plant Protection Convention (IPPC) because they did not fit the IPPC definition of “reproducing” biological control agents (IPPC 1995).

In response to these requests, the FAO/IAEA Division organized a consultant’s meeting to quantify transboundary movement of sterile insects and to assess their risks (they were found to be negligible) (see Appendix 4 on Transboundary Shipment of Sterile Insects in FAO/IAEA 2017a). Therefore, at the request of the FAO/IAEA, when the original International Standard for Phytosanitary Measures Number 3 (ISPM 3) was revised by the IPPC in 2005, sterile insects were included in the updated standard (IPPC 2017a). Consequently, as a result of the significant international recognition, positive track record, and innocuous character of the SIT, sterile insects were officially categorized among *beneficial organisms* by the IPPC to which most countries are parties. Furthermore, the terms “sterile insect” and

“sterile insect technique” were formally included in the IPPC Glossary (IPPC 2017b):

Sterile insect: An insect that, as a result of a specific treatment, is unable to reproduce [ISPM 3, IPPC 2017a]

Sterile insect technique: Method of pest control using area-wide inundative release of sterile insects to reduce reproduction in a field population of the same species [ISPM 3, IPPC 2017a].

6. EPILOGUE

Krafsur (1998) noted that many scientists view the SIT and related genetic methods negatively (Whitten and Mahon, this volume). For example, Hargrove (2003) cast doubt on the potential value of the SIT for tsetse eradication. Especially academic researchers tend to be opposed to programmes they perceive as costly, and would rather see instead more funding of research at universities and research institutions. They are also critical of the scarcity of data clearly linking releases with induced sterility in wild females and population suppression. Krafsur (1998) identified the fundamental problem as follows:

There is a paucity of published data that relate sterile male releases to population suppression. It would lend much credibility to the efficacy of SIT if sterile mating frequencies were estimated in challenged populations. Numerous models have been constructed that relate sterility and genetic deaths to population density but few were tested with field data. Studies in which target population dynamics are evaluated in terms of sterile mating rates and other covariates are badly needed. In this way, useful mathematical models could be made and tested with actual data.

Nevertheless, in the screwworm programmes, sterile and fertile egg masses were collected routinely in the Sanibel Island, Curaçao, and Florida programmes, and these data were related to target population decline (Baumhover 2002). Vreysen et al. (2000, 2018) described a clear connection between the release of sterile tsetse males and induced sterility in wild females, and between induced sterility and subsequent population decline in the field. Also Rendón et al. (2004) established this relationship on a large scale for the Mediterranean fruit fly.

Regarding lepidopteran pests, North and Snow (1978) confirmed the interaction of released irradiated moths and the wild population by capturing wild females, allowing them to oviposit, dissecting them to determine whether or not the spermatophores were coloured with the dye from the rearing medium, and examining their progeny cytogenetically for chromosomal aberrations. Others have adopted this approach for other species (Simmons et al., this volume; Marec et al., this volume; Vreysen, this volume). All these data confirm the relationship between sterility and pest suppression, yet much remains to be done to further address the paucity of field data identified by Krafsur.

AW-IPM programmes that integrate the SIT serve a very useful role in focusing attention on the need for area-wide strategies in managing major pest problems (Klassen and Vreysen, this volume). They are difficult to manage (Dyck, Reyes Flores et al., this volume), but those that exist have shown that the conventional IPM

programmes tend to be conducted on too small a scale for optimum efficiency, and often employ insecticides in a way that destroys natural enemies.

Progress in developing and implementing the SIT for AW-IPM programmes has been slow in some cases but rapid for others (such as fruit fly pests). The SIT is being or has been practised on an industrial and area-wide scale against the New World screwworm, Mediterranean fruit fly (and other fruit fly species, e.g. *Anastrepha ludens*, *A. obliqua*, *Zeugodacus cucurbitae*, *B. dorsalis*, *B. tryoni*), pink bollworm, false codling moth and codling moth (Hendrichs 2000; Hendrichs and Robinson 2009). Mass-rearing facilities in several countries produce several thousand million sterile Mediterranean fruit flies per week. Currently, the infrastructure to rear the pink bollworm is being adapted for the production of the navel orangeworm for the suppression of this pest in almond and pistachio orchards in California. The codling moth programme in Canada has weathered major concerns (Myers et al. 1998), and has significantly reduced insecticide use (local pesticide sales indicate a 96% reduction since 1991 in the amount of active ingredient used against the codling moth) (Nelson et al. 2021). The small onion maggot programme releasing sterile flies in The Netherlands survives, even without authority for a mandatory area-wide application, and the citrus production areas in South Africa that are under the false codling moth programme continue to expand. The African Union is attempting to facilitate the integrated use of the SIT to establish tsetse-free zones in selected areas (Feldmann et al., this volume). The SIT has been shown to be valuable in dealing with certain transboundary pest problems, and in eliminating outbreaks of invasive pests (Hendrichs, Enkerlin et al., this volume), as demonstrated again by the recent eradication of a large Mediterranean fruit fly outbreak in the Dominican Republic (Zavala-López et al. 2021).

Programmes continue to receive research support, resulting in improving technologies and thus in enhanced cost-effectiveness for all aspects of the SIT (Abd-Alla et al. 2013; Beier et al. 2014; Bourtzis and Hendrichs 2014; Ready and Feldmann 2014; Vreysen et al. 2014, 2016; Scott et al. 2017). This includes improved colony management, strains and sexing systems (Augustinos et al. 2017; Sánchez-Rosario et al. 2017; Franz et al., this volume), and better mass-rearing, sterilization, shipment, holding and release systems (Bakri et al., this volume; Dowell et al., this volume; Parker, Mamai et al., this volume), a better understanding and management of pathogens and symbionts in mass-rearing (Abd-Alla et al., this volume; Augustinos et al., this volume), post-factory treatments to improve sterile male performance based on the integration of semiochemicals, hormones and symbionts (Pereira et al. 2013; Pereira et al., this volume), and the incorporation of population genetics, GIS, satellite imagery, information technologies and habitat analysis in project planning and implementation (Bouyer et al., this volume).

Finally, the accelerating development and application of modern biotechnology tools are being exploited to develop self-sustaining as well as self-limiting approaches. While the former aim at population replacement strategies using gene drive or *Wolbachia*-based approaches, SIT-based control systems are self-limiting strategies that aim at leaving no “ecological footprint” (Häcker et al., this volume).

Molecular technologies have already been applied to create sterility and sexing strains, and to introduce stable markers for population monitoring purposes (Bourtzis and Hendrichs 2014). Several such strains have undergone an initial

evaluation under mass-rearing scenarios or in open-field trials, although their wider adoption has so far been slow because of low public acceptance of transgenic approaches, and the regulatory requirements and approvals that are required in most countries for their application (Häcker et al., this volume).

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