STERILE INSECT TECHNIQUE

Sterile Insect Technique

Principles and Practice in Area-Wide Integrated Pest Management

Edited by

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Vienna, Austria

Springer

A C.I.P. Catalogue record for this book is available from the Library of Congress.

ISBN-10 1-4020-4050-4 (HB)
ISBN-13 978-1-4020-4050-4 (HB)
ISBN-10 1-4020-4051-2 (e-book)
ISBN-13 978-1-4020-4051-1 (e-book)

Published by Springer,
P.O. Box 17, 3300 AA Dordrecht, The Netherlands.

www.springeronline.com

Printed on acid-free paper

Photo Credits: A.S. Robinson and M.J.B. Vreysen provided some of the photos used on the front and back covers.

Printed in the Netherlands.

PREFACE

It is a challenge to bring together all relevant information about the sterile insect technique (SIT) and its application in area-wide integrated pest management (AW-IPM) programmes; this book is the first attempt to do this in a thematic way. Since SIT practitioners tend to operate in the context of only one insect pest species, it was also a challenge for authors to develop and write their chapters from generic and global points of view, stressing the principles of the technology, and including examples from a range of pest species. We appreciate the understanding shown by the authors in accepting our many suggestions to emphasize the principles of the technology and to minimize details of field programmes. We also thank them for their patience with the prolonged editing process of the book.

We are especially grateful to the authors for writing the chapters without financial compensation. Authors who are retired, or worked on their own time, deserve special commendation.

Each chapter was peer-reviewed, and we thank the reviewers for helping to make the book accurate, complete, up-to-date, and generic in content.

The need for this book has been evident for many years, and now that it has finally been published, it is expected to serve the scientific community for many years to come. We are pleased to have been able to participate in its development.

The Editors
March 2005

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FOREWORD

For several major insect pests, the environment-friendly sterile insect technique (SIT) is being applied as a component of area-wide integrated pest management (AW-IPM) programmes. This technology, using radiation to sterilize insects, was first developed in the USA, and is currently applied on six continents. For four decades it has been a major subject for research and development in the Joint FAO/IAEA Programme on Nuclear Techniques in Food and Agriculture, involving both research and the transfer of this technology to Member States so that they can benefit from improved plant, animal and human health, cleaner environments, increased production of plants and animals in agricultural systems, and accelerated economic development. The socio-economic impacts of AW-IPM programmes that integrate the SIT have confirmed the usefulness of this technology.

Numerous publications related to the integration of the SIT in pest management programmes, arising from research, coordinated research projects, field projects, symposia, meetings, and training activities have already provided much information to researchers, pest-control practitioners, programme managers, plant protection and animal health officers, and policy makers. However, by bringing together and presenting in a generic fashion the principles, practice, and global application of the SIT, this book will be a major reference source for all current and future users of the technology. The book will also serve as a textbook for academic courses on integrated pest management. Fifty subject experts from 19 countries contributed to the chapters, which were all peer reviewed before final editing.

INTRODUCTORY REMARKS

As evidenced by the successful area-wide insect pest control programmes described in this book, the sterile insect technique (SIT), a component of these programmes, has come of age. The technology has expanded rapidly — additional target species, new rearing techniques, studies on genetics and insect behaviour, and especially integration into operational area-wide integrated pest management (AW-IPM) programmes. The SIT has matured to the point where a critical overview of its principles and practice will greatly facilitate further research, development, and application in the field.

The SIT was among the first biological insect control methods designed for area-wide application. While the SIT gained its reputation in insect eradication programmes, it is essential that the scientific community now recognizes its potential as a part of IPM strategies for the area-wide suppression, containment, prevention and, where advisable, eradication of pests.

Insect control methods in the first 70 years of the 20th century were based largely on chemical insecticides; this was especially so after the Second World War with the introduction of synthetic insecticides. The concept of IPM became popular after 1970, and a more selective use of insecticides was emphasized. Attempts to significantly reduce insecticide applications have only gradually become more prominent. Biological control of pest insects, together with the breeding of insect-tolerant or resistant plants, is probably now receiving the major emphasis in IPM programmes. According to an international standard under the International Plant Protection Convention (IPPC), the SIT is now officially considered as one type of biological control, and it is ideally suited for incorporation into AW-IPM programmes.

The scientific underpinning of SIT programmes has broadened as new areas of science have developed, e.g. insect mass production and quality, geographic information systems and data management systems, genetics and molecular biology, insect behaviour, aerial release of sterile insects, and modelling of AW-IPM. The practical success of a programme incorporating the SIT requires a holistic and multidisciplinary approach, and effective management, since in the last analysis programmes must produce substantial economic benefits. This is clearly evident in the major successes using the SIT against screwworms, fruit flies, and moths.

In spite of documented successes, many colleagues in the scientific community are partially or inadequately informed on the application and importance of this powerful addition to the biological weapons that can be used against insect pests that are economically important or a threat to human health. The credibility and impact of the technology needs to be described in an objective, comprehensive, and balanced fashion, and in an accessible format. New insect pest problems, new restrictive legislation, as well as older problems such as insecticide resistance and minimum residue levels, require new solutions. There is a real need, and an increasing demand, for information on the SIT so that its potential for addressing some of these problems can be assessed.

The chapters have been written by well-known experts on the SIT and other technologies that are integrated into IPM systems. A “first” in its field and worldwide in scope, this book will provide an in-depth resource for the whole range of documented scientific information about the SIT. The target audience of the book is the scientific community worldwide. It will assist animal health and plant protection practitioners, as well as students, teachers, and researchers, in understanding and applying the SIT. It is anticipated that the book will have a considerable impact on the science and practice of pest control systems.

Research workers new to this field have difficulty accessing the literature — it tends to be widely scattered in multiple publications (some with very limited distribution), in conference proceedings, and in unpublished programme reports. To further the science and application of the SIT, the accumulated knowledge and experience needs to be integrated and synthesized from a generic standpoint. The consolidation of comprehensive information into one volume, with references to the large amount of previous work, is long overdue. Such a consolidation will facilitate the application of the SIT to those pest problems for which it is appropriate. It will also lay the groundwork for future applications. The present book is uniquely designed to fill this gap. The strengths and weaknesses, and successes and failures, of the SIT have rarely been evaluated openly and fairly from a scientific perspective.

This is just the beginning. This book will help develop further the use of the SIT for pest suppression, and where advisable, eradication. It will be a gold mine for graduate students who want to learn about the history, accomplishments, problems, and promises of the SIT. As an “autocidal” biological control method, it fits into present-day concerns regarding human health and the environment. There is great potential for significant advances that will make the SIT more effective and economically viable, such as commercializing the different components, developing genetic sexing strains that permit the release of only males, treating sterile insects hormonally and semiochemically to increase their quality and competitiveness, releasing insects from improved aerial systems, and using modern biotechnology.

It is an honour to have been asked to write these introductory remarks. The developments in this technology are exciting, and I will always remain a part of them.

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PART I

INTRODUCTION

CHAPTER 1.1.

HISTORY OF THE STERILE INSECT TECHNIQUE

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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 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 tropical fruit flies, some species of tsetse flies *Glossina* spp., the pink bollworm *Pectinophora gossypiella* (Saunders), and the codling moth *Cydia pomonella* (L.). 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 now appears to be reviving. Development of the SIT for use against the boll weevil *Anthonomus grandis grandis* Boheman 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 false codling moth *Cryptophlebia leucotreta* (Meyrick), the carob moth *Ectomyelois ceratoniae* (Zeller), the cactus moth *Cactoblastis cactorum* (Berg), the Old World screwworm *Chrysomya bezziana* (Villeneuve), additional *Glossina* spp., other *Anastrepha* spp. and *Bactrocera* spp. fruit flies, and other pest insects.

1. PROLOGUE

When using the sterile insect technique (SIT), it is applied usually as a component of area-wide integrated pest management (AW-IPM) (Klassen, this volume). The density of the target insect pest population is reduced, eliminating already mated females, with auxiliary control methods (Mangan, this volume). Then the SIT imposes birth control on the population to further reduce its numbers (Klassen, this volume). The SIT involves rearing large numbers of the target species, exposing them to gamma rays to induce sexual sterility (Robinson, this volume), and then releasing them into the target population. The released sterile males mate with wild females to prevent them from reproducing.

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. However, only after 1950, when Muller made a special effort to publicize the biological effects of radiation, did economic entomologists become aware that, through irradiation, sexual sterility in male insects was quite easily achieved (Bakri et al., this volume).

Nevertheless, already in the 1930s and 1940s, the idea of releasing pest insects to introduce sterility into wild populations, and thus control them, had been conceived independently 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). 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).

The debut of the most successful AW-IPM programme integrating the SIT to date occurred in the 1950s. It was started to rid the south-eastern USA of the New World screwworm *Cochliomyia hominivorax* (Coquerel), a deadly parasite of livestock. During the next 43 years the technique was used to eradicate this screwworm from the USA, Mexico, and Central America to Panama (Vargas-Terán et al., this volume).

Currently, the SIT is most widely applied against tephritid fruit flies (Enkerlin, this volume). Following extensive Research and Development since the late 1950s (Klassen et al. 1994), the first large-scale programme, established in the 1970s, stopped the invasion of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) 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 *Bactrocera cucurbitae* (Coquillett) 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 country of the Mediterranean fruit fly. 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 in huge volumes have entered the US market 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 recently 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 applied with the objective to reduce losses and pesticide use rather than fruit fly eradication, with effective suppression programmes ongoing in Israel, South Africa, and Thailand, and in preparation in Brazil, Portugal, Spain, and Tunisia. To prevent Mediterranean fruit fly establishment in the continental USA through infested imported (smuggled) fruit, sterile males are being released regularly 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 pest outbreaks.

Since 1967, sterile pink bollworm moths *Pectinophora gossypiella* (Saunders) have been released over cotton fields in the San Joaquin Valley of California to prevent the establishment of this pest by moths immigrating from southern California. The SIT is also being used to suppress the codling moth *Cydia pomonella* (L.), an economic pest of apples and pears, in the Okanagan region of British Columbia, Canada (Bloem et al., this volume).

Tsetse flies, which in sub-Saharan Africa transmit the disease trypanosomosis [trypanosomiasis] to humans (sleeping sickness) and livestock (nagana), are regarded as a major cause of rural poverty because they prevent mixed farming. Crops are produced with hoes because nagana kills draught animals. The existing 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 (Feldmann et al., this volume). The eradication in 1997 of the tsetse fly *Glossina austeni* Newstead in Zanzibar, Tanzania, confirmed the feasibility of integrating releases of sterile males with other suppression methods to create sustainable tsetse-free areas (Vreysen et al. 2000). As a result, 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 and sleeping sickness will require many decades of concerted effort. Currently there is a debate about the desirability of using the SIT to eradicate major tsetse populations from large areas of the African mainland (DFID 2002, Hargrove 2003), and the perceived high cost of applying the technique.

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. 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. 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).

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. Khruschev and of Lysenko (whom Khruschev 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 released emerging flies in a 26-km^2 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* G. swynnertoni *habitat on the density of these two species and of the interspecific hybrids (*G. morsitans *released into a 26-km^2 habitat in Tanzania 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	*G. morsitans* released (number)	Average catch of old males (per 5 hours of catching)		
		G. morsitans	*G. swynnertoni*	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			

[1] In 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

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 managed 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. 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 entomologist C. Coquerel, who published an accurate description of the New World screwworm in the Annals of the Entomological Society of France. 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 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 carcasses, 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* 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 km^2 (Lindquist 1955, Meyer and Simpson 1995).

4.1.2. Studies on Reared Screwworms in 1930s, and Conception of 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 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 of insecticides on the dynamics of screwworm populations (Barclay, this volume; Klassen, this volume).

The idea of the SIT may well have been triggered in part by the observation of monogamy in female screwworms. However, Bushland (1960) asserted that, in instances in which irradiation induces dominant lethal mutations in sperm which can still penetrate eggs, female monogamy is not a requirement of the SIT, and this view was accepted by Knipling (1959, 1979) (Lance and McInnis, this volume; Whitten and Mahon, this volume).

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, H. J. Muller was awarded the Nobel Prize in Medicine for his discovery of induced mutagenesis, and this gave him the 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.

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. 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 km^2), 4 km from the coast of Florida, was selected for a release-recapture experiment (Bushland 1960; Itô and Yamamura, this volume) using ^{32}P-labelled flies. In addition, the ratio of radioactive egg masses to non-radioactive masses was assessed. The release of approximately 39 sterile male flies per km^2 per week for several weeks resulted in up to 100% sterility of the egg masses from 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 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 km^2. 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 km^2 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 km^2 per week, whereupon egg sterility increased to 69%, and then to 100% by the time two generations had elapsed. Subsequently 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 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 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 km^2 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 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, this schedule could be accelerated 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 infestation to the border with Georgia using 10 aircraft. The programme 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 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 km^2 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. Lopez Mateos) agreed to a feasibility study to eradicate the New World screwworm in Mexico.

The strategy for dealing with the 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 built in Mission, TX, 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 et al., this volume).

4.1.8. Managing Screwworm Population Along US-Mexico Border

Both US and Mexican cattle producers were anxious to push the screwworm population south to the Isthmus of Tehuantepec, where a barrier of only 360 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 AW-IPM programme in 1972 were the unusually favourable conditions for winter survival of screwworms, the abandonment of 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 genetic selection, making wild adults prone to avoid matings with the released strain, and the existence of cryptic species (Richardson et al. 1982). However no data were generated to support these views (Krafsur 1998; Krafsur, this volume), and they 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, 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, TX, 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 screwworm 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 the Isthmus of Tehuantepec (Peneda-Vargas 1985). 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 1995, Honduras 1996, Nicaragua 1999, Costa Rica 2000, and Panama 2001, where a permanent sterile-fly barrier is being maintained in the Darien Gap along the border with Colombia (Wyss 2000; Vargas-Terán et al., this volume). A rearing facility is being constructed at Pacora, Panama, and eventually the facility at Tuxtla Gutiérrez will be closed.

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 km^2. 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. On the other hand, all of the conditions for successful overwintering and dispersal existed in a 15–25-km-wide zone along the Mediterranean coast (Krafsur and Lindquist 1996). 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).

4.1.11. Screwworm Programmes in the Caribbean

By 1975 the screwworm had been eradicated from Puerto Rico and the Virgin Islands. In 1999, the Government of Jamaica initiated a programme to eradicate the screwworm (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 *C. hominivorax* could easily be reintroduced into areas that have been cleared of this pest (Hendrichs 2000; Vargas-Terán et al., this volume).

4.2. Tephritid Fruit Flies

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
- The capacity to exploit a large number of host plants
- 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 (Hendrichs 1996, 2001; Klassen et al. 1994; Enkerlin, this volume).

The mating behaviours of tropical fruit flies are very different from the aggressive behaviour of male screwworms and involve complex courtship behaviours including female mate choice (Robinson et al. 2002). Thus, close attention 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).

Investigations into the possibility of using the SIT to eradicate populations of the Mediterranean fruit fly, melon fly, and oriental fruit fly *Bactrocera dorsalis* Hendel were initiated in 1955 in Hawaii (Steiner and Christenson 1956). 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).

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 quarantine 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. Nevertheless, since the mid-1990s, an SIT containment programme protects a “Fruit Fly Exclusion Zone” comprising major fruit production areas in New South Wales, Victoria, and South Australia. In 1990, use of the SIT resulted in the eradication of this pest from an incipient infestation in 125 km^2 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). By 1976 the pest had expanded its range into Honduras, El Salvador, and Guatemala, and in a few years occupied 15 000 km^2 in southern Mexico. 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 1978. Pest eradication in the infested area of Mexico was achieved in 1982 (Hendrichs et al. 1983), and a barrier was created through Guatemala (Villaseñor et al. 2000; Enkerlin, this volume). For over 25 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 to the USA. According to The Economist (2004), the Mexican horticulture export earnings since 1994 have tripled to over USD 3500 million per year, with exports of fresh vegetables rising by 80% and fresh fruit by 90%. In the meantime, the production capacity of the Moscamed programme has increased to over 3500 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 South-Western Islands of Japan

Between 1919 and 1970, the melon fly was discovered to have invaded various 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 km^2) 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, Hendrichs 1996). Evidently bisexual releases of sterile flies could not be used for this programme because sexually sterile female Mediterranean fruit flies sting fruit with their ovipositors. 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. Therefore, 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 sorted at the FAO/IAEA Seibersdorf laboratory in Austria, and performed very well in large-scale tests in Israel (Nitzan et al. 1990; Franz, this volume). Subsequently the Seibersdorf laboratory developed a genetic sexing strain in which a segment of an autosome bearing the dominant wild type allele of a temperature-sensitive lethal (*tsl*) mutant was translocated to the Y chromosome (Franz and Kerremans 1994, Caceres et al. 2004). In addition, this laboratory developed a "filter rearing system" to maintain stability in the mass-rearing of genetic sexing strains (Fisher and Caceres 2000; Franz, this volume; Parker, 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 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 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 (Dowell et al. 2000, Barry et al. 2004). The same preventive approach was also followed in 1998 in three high-risk Florida counties. Sterile males of the *tsl* sexing strain VIENNA 7, mainly produced by the Moscamed programme in Guatemala, are used for these preventive release programmes. Sexing strains are now used in most Mediterranean fruit fly suppression, containment, or eradication programmes (Caceres et al. 2004; Enkerlin, this volume; Franz, this volume; Hendrichs et al., this volume).

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. Consequently, the various governments and the Palestinian Authority met in Vienna, agreed to develop a cooperative area-wide programme with the support of the FAO/IAEA, and asked these organizations to conduct an economic analysis of three area-wide programme alternatives (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, 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 almost USD 30 million per year (Cayol et al. 2004; Enkerlin, this volume). The sterile pupae for this programme have been shipped from the Moscamed facility in El Pino, Guatemala, although the largest producer of biological control agents in Israel is currently constructing a commercial mass-rearing facility, with the goal of expanding suppression to the area north of the West Bank, including northern Jordan.

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

For technical and economic reasons, including difficulties in maintaining effective quarantines (even with large capital investments in facilities), today most fruit fly AW-IPM programmes that integrate the SIT aim to suppress the pest populations (Mumford 2004; Enkerlin, this volume; Hendrichs et al., this volume; Mumford, this volume). Examples of suppression programmes are:

- Mediterranean fruit fly
  - Cap Bon, Tunisia (Ortiz Moreno 2001)
  - Costa Rica (Reyes Flores 2004)
  - Hex River Valley, South Africa (Barnes et al. 2004; Enkerlin, this volume)
  - Madeira, Portugal (Dantas et al. 2004)
  - San Francisco Valley, Bahia, Brazil
  - Valencia, Spain (Generalitat Valenciana 2003)
- Mexican fruit fly
  - North-east Mexico (SAGAR/IICA 2001)
- Oriental fruit fly
  - Ratchaburi Province, Thailand (Sutantawong et al. 2004)

4.3. Onion Maggot

Since 1981, the SIT has been applied by a private firm (De Groene Vlieg) in The Netherlands to control the onion maggot *Delia antiqua* (Meigen) on an aggregate area of 2600 hectares (Loosjes 2000). The flies are reared year-round, and stockpiled in diapause for release during the onion-growing season. Individual farmers contract for the SIT independently of their neighbours, many of whom use chemical control. Much efficiency is lost since 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 refuse to contribute to the programme (free-riders). The programme has not been able to expand beyond 16% of the onion production area.

4.4. Tsetse Flies

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 et al., this volume). However, rearing tsetse flies is relatively laborious and expensive because both sexes require frequent blood feeding (Parker, this volume).

Table 2 summarizes the SIT trials and operations that have been conducted on tsetse flies. (Data from the trial by Vanderplank is shown in Table 1.) In a trial on *G. m. morsitans* Westwood in 1969 on an island (5 km^2) 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 km^2) trial in Tanzania using factory-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 the recently developed attractant traps and insecticide-treated targets. Three tsetse species were eradicated simultaneously in 3000 km^2 in Burkina Faso (Politzar and Cuisance 1984), and one species in 1500 km^2 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.

Traps were also used on a small island (12 km^2) 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.

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

Species, habitat, and location	Method	Outcome and objectives	References
Glossina swynnnertoni, savannah, north-western Tanzania	Release of *G. morsitans*, which mated with *G. swynnertoni*	99% suppression in 256 km^2, permitted development of the area for agricultural production	Vanderplank 1947, and hitherto unpublished data shown in Table 1
G. morsitans morsitans, 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
G. tachinoides Westwood, riverine, Chad	Radiation-sterilized, transport from France, ground release sterile ♂	Feasibility study, sterilization, transport, release	Cuisance and Itard 1973
G. palpalis gambiensis 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
G. palpalis palpalis Robineau-Desvoidy with *G. tachinoides* as a control, riverine, Lafia, Nigeria	Suppression with traps and targets followed by ground release of radiation-sterilized adults	Eradication of *G. p. palpalis* in 1500 km^2	Takken et al. 1986, Oladunmade et al. 1990
G. morsitans morsitans, 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
G. morsitans morsitans, and *G. pallidipes* Austen*,* savannah, Lake Kariba, Zimbabwe	Autosterilization of wild flies with pyriproxyfen	Suppression (12 km^2), feasibility study	Hargrove and Langley 1990
G. morsitans submorsitans Newstead*, G. palpalis gambiensis, G. palpalis palpalis, G. tachinoides*, 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
G. austeni, 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
G. fuscipes fuscipes 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