CHAPTER 4.2.

POPULATION SUPPRESSION IN SUPPORT OF THE STERILE INSECT TECHNIQUE

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SUMMARY

Suppression or eradication of insect pest populations by the release of sterile insects is often dependent on supplementary methods of pest reduction to levels where the target pest population can be overflooded with sterile insects. Population suppression activities often take place in advance of, or coincide with, the production and release of sterile insects. Supplementary methods to remove breeding opportunities, or management methods that prevent access of pests or vectors to the hosts, may reduce the population or prevent damage or disease transmission. Insecticides have been used widely in direct applications or applied as baits, in traps, or on specific sites where the pest makes contact or reproduces, although they are increasingly being replaced by biopesticides. As sterile insect release does not kill the pest, adult biting pests or fertile mated females of the pests will continue to attack hosts after the release of sterile insects. Thus supplementary pest suppression programmes and quarantine measures are essential to prevent damage or the spread of disease. Eradication or effective pest management requires that the entire population of the pest be treated, or that the programme apply immigration barriers. It also requires taking into account interactions among control methods; they can be additive, synergistic or antagonistic. When supplementary pest control activities directly benefit the human population in areas being treated, such as in mosquito or screwworm control programmes, these area-wide suppression activities are usually acceptable to the public, but when the public receives no direct benefit from supplementary control activities such as in crop pest programmes, social resistance may develop unless public information is managed properly.

1. INTRODUCTION

The sterile insect technique (SIT) is highly species-specific and non-polluting; the target is the reproductive system of sexually reproducing pests. Supplemental systems to reduce pest populations are often required, prior to the release of sterile insects, to reduce the target pest population to the degree that the sterile insects have an advantageous numerical ratio to induce sterility. Most of the successful programmes releasing sterile insects were applied when field populations were at low densities, either after a natural population decrease (such as winters in subtropical or temperate climates) or after the application of area-wide suppression activities.

The decision to use suppression before the release of sterile insects may also be for economic reasons. Quarantine decisions, on market access of commodities attacked by pest outbreaks, are frequently based on adult trapping data. Reducing the adult population close to the detection level with adulticide sprays and/or other means adds the benefit of meeting quarantine protocols and reopening markets sooner than when the sterile insects have eliminated the population.

In other cases, the action of released sterile insects on the pest population is indirectly associated with reduction in pest damage. Mosquitoes and tsetse flies can continue to bite and spread disease after they are mated to sterile flies. Fertile-mated screwworms can, for the rest of their lives, continue to destroy livestock. These activities are not reduced by the release of sterile flies. Decisions to use pesticides or other methods to protect hosts will, in these cases, for example in the case of an epidemic, be largely independent of the success of the sterile insects.

In eradication programmes, multiple suppression methods may be combined, but interactions among them must be considered, particularly when they interact with the dynamics of the pests' Allee threshold (Suckling et al. 2012). Combinations of methods can thus be considered to have synergistic (greater efficiency from the combination in achieving extinction), additive (no improvement over single methods alone), or antagonistic (reduced efficiency from the combination) effects on Allee dynamics. When planning the integration of methods it is crucial to take these effects into account.

In this chapter the various pest control techniques that are used to suppress pest populations, in conjunction with the application of the SIT, are reviewed. Suppression activities applied as precursors, or in tandem with sterile insect release, will be emphasized. Quarantine treatments are not considered.

2. OVERVIEW OF PEST CONTROL TECHNIQUES

Major benefits of the SIT are species specificity and the possibility of eradication. Knipling (1979) outlined the techniques for reducing insect pest populations with respect to the species specificity (Table 1), and to their effectiveness with respect to pest density levels (Table 2). Table 2 is of particular relevance to the SIT as its effectiveness relates to the density of the pest population. He followed this overview with a discussion on integrating these techniques with the SIT.

Table 1. Classification of degrees of selectivity of various methods of insect control (adapted from Knipling 1979)

Highly selective	Moderately selective	Non-selective
Insect attractants (specific)	Attractants (baits)	Conventional insecticides
Insect pathogens (specific)	Biopesticides (specific)	Biopesticides (general)
Insect parasitoids (specific)	Parasitoids (general)	Mechanical control
Insect predators (specific)	Predators (general)	Cultural measures
Insect-resistant plant varieties	Insect entomopathogenic fungi (specific)	Insect entomopathogenic fungi (general)
Genetic techniques	Autoinoculation devices	
Mating disruption	Light traps	

Knipling (1979) also discussed a series of exceptions and modifications to this classification, and recent research has greatly extended the number of available suppression methods. The method of application was also recognized as being of crucial importance in selectivity. For example, aerial application of broad-spectrum insecticides will have a greater impact on non-target organisms than application of the same insecticide as a bait or to a specific location on a plant or animal that is to be protected from a pest.

Natural biological control is inevitably a part of any area-wide integrated pest management (AW-IPM) programme, but specific releases and manipulation of parasitoids and predators are being used as part of AW-IPM systems that include the SIT (Knipling 1992, 1998, 1999; Wong et al. 1992; Bloem et al. 1998; Vargas et al. 2004; Montoya et al. 2007). Marec et al. (this volume) describe the synergism between inherited sterility (IS) and natural enemies (Bloem et al., 1998; Carpenter et al. 2004). In New Zealand, irradiated male painted apple moths *Teia anartoides* Walker were released, and *Bacillus thuringiensis* Berliner variety *kurstaki* (*Btk*) was simultaneously applied to suppress the pest population (O'Callagahan et al. 2003; Suckling 2003; Simmons et al., this volume).

Knipling (1979) followed this table with an introduction to the concept of IPM, including descriptions of the purposes of pest management: to slow population growth, suppress and maintain populations below a certain level, or eliminate populations. Since then, there has been a number of recorded eradication successes using different IPM strategies combining various control methods, including insecticides, mating disruption, SIT, host removal, *Bt* plants, lure and kill, etc. (Table 3) (Suckling et al. 2014; Klassen and Vreysen, this volume).

Table 2. Classification of insect control techniques by efficacy at various pest densities (adapted from Knipling 1979)

Methods equally effective at all densities	Methods most effective at lowest densities	Methods most effective at highest densities
Conventional chemical insecticides[1]	Sterile insect and other genetic techniques	Host-specific pathogenic organisms
Chemical sterilants applied to natural populations	Sex- or aggregating-attractant traps	Host-specific parasitoids
Cultural and mechanical control methods	Sex-attractant diversion sources or mating disruption	Host-specific predators
Insect-resistant crop varieties	Sex-attractant vapours	
Genetically modified crops[2]		
Light traps		
Attractant baits		
Trap crops		
Synthetic non-pheromone attractants		
Sex pheromones that block responses		

[1]Some factors, e.g. spatial aggregation and partial protection by vegetation cover, can make their efficiency density-dependent

[2]Although leaving sufficient refugia with non-resistant plants to avoid rapid selection for insect resistance

3. CULTURAL, ENVIRONMENTAL, AND MECHANICAL CONTROL

Activities in agricultural production, property management or lifestyles can all influence insect pest densities, and a major advantage of cultural control is that it is pest density-independent. The disadvantage is that many cultural control activities reduce the population but do not protect the crops or animals being attacked. In cases where very low pest populations can have high economic or health impacts, cultural control through habitat manipulations alone probably will not provide the desired level of suppression.

Development of the SIT technique for control of the New World screwworm *Cochliomyia hominivorax* (Coquerel) relied heavily on activities that prevented infestation of livestock. The pest was subjected to considerable cultural control because of the value of livestock and the critical damage from infestations to animal and humans. Programmes for treating wounds, and preventing reinfestations of individual animals, were the primary actions taken to control screwworm damage (FAO 1992; Vargas-Terán et al., this volume). Dove (1938) proposed a combination of livestock management measures such as special care with wound protection, protection of females and offspring following pregnancy, curing tick bites, castrating and branding animals only during winter, protecting castrated and branded animals, and other management activities. Protecting animals from infestation, and wound treatment, are still the key suppression activities in screwworm programmes where this pest has not been eradicated.

Table 3. Examples where multiple suppression methods have been combined during successful eradication programmes (modified from Suckling et al. 2012, 2014)

Number of suppression methods	Combinations and their assumed density-dependence[1]	Insect scientific name	Insect common name	References
3	Mating disruption (DD) +*Bt*-cotton (DI) +SIT (DD)	*Pectinophora gossypiella* (Saunders)	Pink bollworm	Tabashnik et al. 2010; Simmons et al., this volume
5	Ground insecticides (DI) +Aerial *Btk* sprays (DI) +Mass-trapping (DD) +Host-plant removal (DI) +SIT (DD)	*Teia anartoides*	Painted apple moth	Suckling et al. 2007; Simmons et al., this volume
3	Pour-on (DD) + Insecticide targets (DD) + SIT (DD)	*Glossina austeni* Newstead	Tsetse fly	Vreysen at al. 2000; Feldmann et al., this volume
3	Pour-on (DD) + Insecticide targets (DD) + SIT (DD)	*Glossina palpalis gambiensis* Vanderplank	Tsetse fly	Dicko et al. 2014; Feldmann et al., this volume
3	Wound treatment (DD) + Cultural controls[2] (DD) + SIT (DD)	*Cochliomyia hominivorax*	New World screwworm	FAO 1992; Vargas-Terán et al., this volume

[1]Density-independent (DI) indicates a control method that removes a proportion of the population, independent of density (e.g. broad-spectrum insecticides). Density-dependent (DD) methods work better on bigger populations (e.g. pour-on applied on cattle will work better at high tsetse densities if they mainly feed on cattle but will not kill the small part of the population feeding on alternative hosts) or on the contrary on smaller populations, accelerating the extirpation towards the end (e.g. SIT works better because the overflooding ratio of sterile to wild individuals favours sterile individuals).
[2]Example of cultural control: dehorning, branding or castration during cold months.

Cultural control methods for crop pests can include area-wide destruction of crop residues, general orchard sanitation and removal of infested fruit, and enforcement of planting and harvesting dates.

Cultural control of the pink bollworm (Nobel 1969) in the USA was developed in the early 1950s as part of an area-wide approach as the pest spread across Texas, New Mexico, and Arizona. Activities included evaluation of stalk-shredding machines for killing the potential overwintering insects and incorporating the use of shredders. Devices were developed that killed bollworm larvae in cotton gin trash. In contrast to the screwworm programme, the impact of these activities was to decrease the pink bollworm population, rather than directly protecting the crop.

Early reviews of fruit fly pest control focused on environmental modifications to reduce reproduction and the survival of immature stages, and chemical control to kill adults. Back and Pemberton (1918) described covering of immature fruit with a bag or cloth material to prevent infestation. They also described a system used in Australia of bagging the canopy of trees with mosquito netting, but considered the method too expensive for large-scale use. Individual bagging of fruit was successful, but the bag had to be impermeable to oviposition, and problems with scale insects on the protected fruit developed. More recently, this concept has been revived to protect cabbage crops in Africa (Martin et al. 2013).

Another cultural control approach to fruit fly pests was described as "clean culture" (Back and Pemberton 1918). This method is based on removing all hosts from the infested area. Crawford (1927) reviewed clean-culture methods used in Mexico and determined that the approach was effective for the Mexican fruit fly *Anastrepha ludens* (Loew), but extreme measures such as the destruction of trees were not practical or effective (although see Kovaleski and Mumford (2007) for successful *Cydia pomonella* (L.) eradication in Brazil). He compared ranches that cleaned up fallen oranges once a week, and found the approach ineffective for complete control but more effective when coordinated with the application of poison bait. Crawford also recognized the value of trap crops in controlling fruit fly damage; he suggested that a few grapefruit trees (a preferred citrus species) could be used for this. He also recognized that the trap-crop trees could be sprayed.

The application of "clean culture" to fruit fly management programmes has been widely practiced in AW-IPM programmes integrating the SIT in the USA and the joint programmes in Mexico and Guatemala. Sanitation and the destruction of host material is widely carried out in the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann) eradication programme (Moscamed) in Mexico and Guatemala. During a series of outbreaks in the Palenque district of northern Chiapas, from 8332 hectares treated (e.g. bait sprays), 33 978 kg of host material were collected and destroyed (Moscamed data sheets for 2002). In Guatemala, from 411 739 hectares treated, 345 633 kg of host fruit were destroyed (USDA/APHIS/IS 2002). As an immediate response in 2003 to a large infestation (106 hectares) of Mexican fruit flies in Valley Center, California, the California Department of Food and Agriculture removed and buried host fruit. A total of 2 941 070 kg of fruit (mostly citrus) was collected from the ground and stripped from trees at sites ranging from 0.26 to 36 hectares. The removal and destruction of host material is a logical complementary suppression activity because it destroys immature stages of the pest that cannot be controlled by other methods. However, there is a possibility that the removal of host material induces adult females to migrate in search of hosts, and actually causes an outbreak to spread.

Where the primary purpose of the SIT is to eliminate or prevent diseases through eliminating or suppressing the vectors, cultural and mechanical controls have been applied widely. In addition to pesticide application as a supplementary treatment incorporated into programmes that also release sterile insects for mosquito control, Musil (2002) outlined improvements in integrated activities that reduce the vector populations, and in health care supplemental activities:

- Habitat management that interferes with the mosquito life cycle, including physical barriers, use of beneficial organisms, and removal of breeding sites,
- Community education and participation to improve public understanding of the mode of disease transmission,
- Public health strategies that integrate detection, diagnosis, and prompt treatment of the disease to prevent spread.

In the case of mosquito control, active source reduction, together with larviciding, adulticiding, and public education through door-to-door campaigns (source reduction through education) could achieve up to 75% reduction of adult densities in the case of *Aedes albopictus* (Skuse) (Fonseca et al. 2013). Such integrated strategies will be crucial when integrating the SIT, thus facilitating the overflooding of wild populations and inducing more than 50% sterility in females to reduce adult populations further (Bellini et al. 2013).

4. CHEMICAL CONTROL

4.1. Direct Insecticide Application for Population Suppression

Broadcasting insecticides has often been done in conjunction with AW-IPM programmes that integrate the SIT. However, public acceptance of insecticide application in this context has usually been limited to situations where the treated properties are owned by persons who receive some benefit. Eradication experiments, and programmes with medically important pests such as mosquitoes and tsetse flies, have frequently used applications of persistent insecticides. Programmes for pests such as the pink bollworm, with a distribution largely restricted to certain hosts, were also implemented with insecticides but with little publicity, although more recent supplementary suppression activities were based on attractants (Walters et al. 2000a). Suppression of the codling moth in Canada required initial insecticide treatments to reduce the pest population (Bloem and Bloem 2000). If an insecticide is applied at the same time that sterile insects are being released, the chemical may kill some of the sterile insects; however, as long as the ratio of sterile:wild insects remains the same, this would not impair the efficacy of the SIT.

In *C. capitata*, models demonstrated that it is crucial to determine optimal spraying schedules to ensure an efficient suppression of target populations in preparation of SIT application (Barclay et al. 2019). The most important biotic parameters to be considered were the relative length of the larval period, the fertility rate, and the age to first oviposition. The stage targeted by sprays, and the percent mortality caused by each spray, were also found to be important in determining the required number of sprays.

Mangan (2014) reviewed adulticidal insecticide bait sprays for fruit flies, and summarized the development of organic baits that replaced organophosphate baits.

In the 1960s when the first attempts to use the SIT, or other genetic modifications of released mosquitoes, were made, broadcasting insecticides to suppress mosquitoes was widespread. Patterson et al. (1980) described a field trial to control the stable fly

Stomoxys calcitrans (L.) with the SIT as an adjunct to insecticidal and physical methods. Insecticides were also applied for the control of tsetse flies in Africa; applying insecticides against these species was a component of the programmes as they developed.

According to Douthwaite (1992), the first area-wide attempts to control tsetse flies with insecticide sprays began in 1945 in South Africa using organochlorine insecticides. This programme resulted in the successful elimination of *Glossina pallidipes* Austen from 11 000 km^2 through the aerial application of DDT or lindane, and supported by game destruction, habitat clearing and massive trapping operations (Du Toit 1954). Although the negative effect of these treatments on beneficial insects was recognized, and an impact on bird populations was reported by Graham (1964), persistence and bioaccumulation of residues was not understood at the time.

The first tsetse programme using sterile mass-reared insects was carried out against *Glossina morsitans morsitans* Westwood in Tanzania (Dame et al. 1980; Williamson et al. 1983). The strategy of this test was to suppress the tsetse population with two aerial applications of endosulfan (28-day interval), and then control the population with sequential releases of sterile males. A 195-km^2 area was surveyed for 14 months using various trapping methods, and the reproductive status and density of the population were assessed. A 105-km^2 area was selected for treatments. A 1-km barrier was cleared and treated with manual backpack spray applications of DDT in a 300-m-wide swath to prevent the migration of flies into the treated area. Fly surveys showed that, after the first endosulfan application, there was nearly 100% reduction in *G. m. morsitans* and 91.5% reduction in *G. pallidipes*. Following the first spray, sterile *G. m. morsitans* males were released twice per week at a rate of 135 males per km^2, resulting in an average male sterile:wild ratio of 1.12:1. A comparison of the female reproductive status between control and treated areas showed that, following the second spray, the sterile males were highly effective. Over the 15-month sterile-treatment period, Williamson et al. (1983) reported an 81% reduction in *G. m. morsitans*. The population of *G. pallidipes*, which received only the insecticide treatment, recovered to pre-spray levels within 5 months.

The sequential aerosol technique (SAT) involves spraying ultra-low-volume formulations of insecticides from the ground (fogging) or air (fixed-wing aircraft or helicopter) with limited environmental impact. The goal is to kill adult tsetse flies in the first spraying cycle by direct contact, and kill emerging flies in subsequent cycles. Recently, the SAT has been used against *Glossina palpalis gambiensis* and *Glossina tachinoides* Westwood, and achieved reduction levels higher than 98% (Adam et al. 2013). Against savannah species in an open environment, it is even more efficient, and achieved complete elimination of *Glossina morsitans centralis* Machado (Kgori et al. 2006). The SAT might represent a rapid solution to reduce tsetse populations before releasing sterile males, provided that habitat specificities and individual insecticides sensitivities are taken into account (De Deken and Bouyer 2018).

The need for innovative tools in managing mosquitoes was recently pointed out by the Global Vector Control Response 2017–2030 (WHO 2017). This includes suppression tools in the case of *Aedes aegypti* (L.) and *Ae. Albopictus*; at present there are only limited possibilities because of their disseminated larval microhabitats. For species living in large water habitats, spraying *Bacillus thuringiensis* var. *israelensis* (*Bti*) is considered to be the most efficient larvicide strategy to control mosquito populations with negligible environmental impact. For example, it is used widely in French Atlantic and Mediterranean coastal wetlands (Lagadic et al. 2014).

Pal and LaChance (1974) reviewed early trials of genetic control during the late 1960s and 1970s. They cite the need for supplemental suppression activities to reduce the number of released sterile insects that are required. They suggested that, if insecticide-based control methods are to be applied concurrently with the release programme, the best chemical control would be a larvicidal programme that killed target insects without affecting released insects. If a pre-release suppression programme is used, then an adulticide treatment would be preferable.

Weidhaas et al. (1962), Morlan et al. (1962), and Patterson et al. (1970) performed field trials with sterilized mosquitoes in Florida, USA. In these tests DDT applications were made in perimeter areas to prevent the immigration of pests or as treatments to reduce populations. Patterson et al. (1970) concluded that:

> Obviously, other population suppressants such as insecticides, reduction in breeding sources, and biological control will have to be used to decrease a total population in a large area to a level commensurate with the mass-rearing capabilities.

Trials of genetic control of *Culex pipiens fatigans* Wiedemann in villages near Delhi, India, in a programme developed with the World Health Organization (WHO), were among the first to apply insecticides as part of an integrated supplemental population suppression experimental approach. After several attempts to introduce sterility into the populations (reported from 1971 and 1972 tests with negative results), tests were designed to distinguish the effects of rearing, chemosterilization and strain genetics from the effects of strain contamination with females and immigration (Pal 1974; Pal and LaChance 1974). Yasuno et al. (1976) reported the results of a 5-month sterile insect release (February to July 1973) of chemosterilized males into an area with mosquito fish *Gambusia affinis* (Baird and Girard) or larvicide-treated (temephos) breeding sites in buffer zones. A second treatment of an adulticide, pyrethrum, was applied to one set of villages. Although the Delhi programmes, summarized by Pal (1974), Yasuno et al. (1976) and Curtis (1977), were not permitted to continue to the stage of measuring population suppression, the programmes proposed in these tests included population monitoring and integration of adult and larval chemical control. Curtis and Andreasen (2000) cited the importance of insecticide-based barriers to females immigrating into areas treated for mosquito control. Immigrant females not only serve to increase the target population and impede eradication, but may also reintroduce the disease and set back the ultimate goal of eradication.

SIT treatments for *Anopheles* spp. will need to consider the increased resistance to pesticides (Mattingly 1957; Pal and LaChance 1974; Asman et al. 1981; Whalen 2002; Ranson et al. 2011). Alternatives (to the general spray programmes applied in previous mosquito SIT trials to suppress adult populations) are required in any new control programme -- preferably classic alternate methods of population reduction (Ross 1902) such as habitat modification, and more recent alternative methods both to reduce mosquito populations and protect people from bites and disease.

4.2. Stationary Devices (Traps and Insecticide-Impregnated Targets)

The goal of stationary attractive devices such as traps and insecticide-impregnated targets is to impose a modest daily mortality on tsetse females by attracting them to a device that either kills the flies by contact with an insecticide or retains them in a non-return cage. Pyrethroid compounds were identified as the principal insecticides used but sterilizing compounds, and compounds that inhibit reproduction such as triflumuron, may also be effective (Oloo et al. 2000). A review of using insecticides in traps and targets against tsetse is found in Bouyer and Vreysen (2018).

The deployment of insecticide-impregnated targets, and the release of sterile males, successfully eliminated *G. palpalis gambiensis*, *G. tachinoides*, and *Glossina morsitans submorsitans* Newstead from 3500 km^2 of agropastoral land in Burkina Faso (Politzar and Cuisance 1984). Prior suppression of the native fly populations was achieved by placing insecticide-impregnated screens along 650 km of gallery forest at a density of 10 screens per linear km for 4 months during the dry season. Subsequent releases of sterile males, at the rate of 20–35 per linear km, were sufficient to obtain sterile:wild ratios of 10:1 and to eliminate the target populations.

A trial against *Glossina palpalis palpalis* Robineau-Desvoidy was carried out in central Nigeria. The population was first reduced by deploying insecticide-impregnated screens and by removal-trapping with traps (Oladunmade et al. 1985; Takken et al. 1986) that reduced the native fly population by 90–99% over a 6–12-week period. Extending the period of control, using traps and targets, did not achieve eradication. A further major concern was the loss of the screens due to theft, flooding, and fire (Takken et al. 1986). Nevertheless, the target population was eventually eliminated over the entire 1500-km^2 area by weekly releases of sterile male flies from the ground (Oladunmade et al. 1990).

Recently, in Burkina Faso, insecticide-impregnated targets, in combination with pour-on treatments of livestock and ULV spraying of the gallery forests, enabled a reduction of 83% for *G. palpalis gambiensis* and a 92% reduction for *G. tachinoides* (Percoma et al. 2018). Also, recently in Senegal, the use of insecticide-impregnated targets set in suitable landscapes at a density of 1–3.4 per km^2 reduced populations of *G. p. gambiensis* by more than 95%; this was followed by releasing sterile males to reach population elimination (Dicko et al. 2014).

For fruit flies, because broadcast insecticides were not acceptable, Mangan and Moreno (2007) tested various baits in stations to suppress *Anastrepha ludens* populations. Besides a toxicant, baits contained attractants, feeding stimulants and other materials to help preserve the effectiveness of the bait over time.

Regarding mass-trapping for pest suppression, to be effective trap densities must be very high. The deployment and maintenance of large numbers of trapping devices is costly and logistically complex, and thus mass-trapping is generally not practicable or economically viable over large areas, and may be applicable only in special areas where other suppression approaches are not possible (Navarro-Llopis and Vacas 2014). Furthermore, two issues must be addressed when deploying traps at high densities for population suppression: (1) direct effects on non-target animals, and (2) indirect environmental effects related to trap placement and servicing (Nagel and Peveling, this volume).

4.3. Pour-Ons — Insecticide Applied to Moving Baits

Live-bait technology (pour-ons) is an efficient technology for tsetse flies, stable flies, and other nuisance pests or disease-transmitting vectors in infested areas with a high density of cattle, but the disadvantages are the high frequency of treatment, the high cost of insecticides, and the impact on the dung fauna (Vale et al. 2004).

A programme to control tsetse flies or trypanosomosis by treating livestock with insecticides can be effective by killing the flies as they attack animals. Leak (1999) noted that three conditions are required to achieve optimum control of tsetse populations through pour-on treatments: (1) a large proportion of feedings are taken from domestic rather than wild animals, (2) a large proportion of the livestock are treated, and (3) the level of fly reinvasion is relatively low. Leak also reviewed the use of artificial odours, colours, or targets attached to workers. Targets on workers were a component of the eradication of tsetse in Principe in 1910 (Hendrichs, Enkerlin et al., this volume; Klassen et al., this volume), and a tsetse-control technique using odour attractants and traps was proposed by Balfour (Balfour 1913).

Initially, pour-on insecticides consisted of DDT mixed with resins (Leak 1999). Other tests were done feeding lindane to cattle. Although applying these pesticides to cattle was terminated because of environmental concerns, the development of synthetic pyrethroids revived this treatment method (Bauer et al. 1992). These insecticides have the advantages of low human toxicity, high insect toxicity (especially to tsetse flies), and rapid movement through the epidermis. Ivermectin compounds were also discussed, but the effective dose is very close to the limit for toxic effects on the hosts, and cost is prohibitive (Pooda et al. 2013).

The eradication programme against *G. austeni* on Unguja Island (Zanzibar) was specifically planned to meet environmental concerns for supplementary population control (Vreysen et al. 2000). It was found that the pour-on treatment alone was not sufficient to eradicate the tsetse population in the island. Maybe this was due to flies feeding on hosts other than cattle, such as bush pigs, which enabled some flies to be unaffected by the cattle treatment. The programme relied on the use of live-bait technology (in areas of high cattle density), and the deployment of insecticide-impregnated screens (in the forested areas), to reduce the native tsetse population before releasing sterile males (Vreysen et al. 2000). The fly densities in the primary forest habitats were reduced 80–98% by using insecticide-impregnated screens, deployed at densities of 40–70 per km^2 for a period of 18 months (Vreysen et al. 1999). The same strategy was applied recently in Senegal (Vreysen et al. 2013).

In Burkina Faso, the application of deltamethrin to cattle failed to eradicate *G. tachinoides* because the preferred hosts, monitor lizards, were available for feeding by tsetse (Bauer et al. 1999). Apparently pour-on insecticides can reduce tsetse fly populations drastically, but untreated wild animals may serve as alternate food sources for the sustenance of the population (Bouyer et al. 2013).

4.4. House, Bednet, and Other Treatments

The use of insecticide-impregnated bednets has proven to be a successful treatment to reduce malaria morbidity. The development of pyrethroid insecticides, that are safe for human contact, has provided a substitute (for DDT, organophosphate and carbamate insecticide treatments) that gives more direct protection than outdoor sprays to control populations. According to Curtis (2002), treated nets can irritate, drive away or kill biting mosquitoes. Numerous tests have shown that this treatment greatly reduces both populations of mosquitoes and rates of disease. The use of insecticide-treated bednets, as well as treatment of curtains, wall hangings and clothing, have also been tested, but bednets, which act as a trap baited with the sleeping person, have proven more effective.

More than 20 tests of bednets have demonstrated a reduction of 20–63% in malaria disease rates. Tests carried out in The Gambia, Kenya, and Ghana showed a significant (25–39%) reduction in mortality of children. Mathenge et al. (2001) found that bednets reduced the rate that some mosquitoes (but not others) entered houses, and the action of bednets against mosquitoes was also species-specific. Slight shifts in feeding times were also noted for one species (but not the other). The success of bednets is reduced for mosquito species, such as *Aedes* spp., that bite earlier in the day. Treatment of other things in a household, and indoor spraying, may help control disease transmission by these species. However, it must be noted that the efficiency of these strategies tends to decrease with the spread of resistance in malaria vectors (Ranson et al. 2011). They are also challenged by the development of behavioural resistance, like outdoor feeding (Russell et al. 2011), hence the necessity of developing alternative methods (WHO 2017).

4.5. Chemical Treatments to Protect Hosts from Biting Adults or Immature Stages

Wound treatments have been an important and consistent part of the New World screwworm programme in North America (Graham 1979). In addition to reducing overall screwworm populations and protecting livestock from larval damage, the research programme to develop wound dressings had direct effects on the programme. The early development of a treatment called “Smear 62” (Knipling 1939) led to research methods that included rearing larvae on artificial diets. Not only are wound treatments an essential supplementary component of this programme that releases sterile insects, but research in developing these treatments also led to the implementation of the programme.

The use of small packets of coumaphos, chlorfenvinphos or similar insecticides, applied either as a spray on cattle or as an individual treatment to infested wounds, was an essential part of the screwworm eradication programme in Florida, southern Texas and Latin America. Unlike attempts to trap out or reduce adult screwworm populations by applying insecticides area-wide, larvicidal applications of insecticide directly saved livestock, and producers could easily observe the application’s benefit. During the breakdown of the programme in 1972, larvicide treatments were the main mechanism that saved livestock and slowed the spread of cases. During the late 1970s, when the programme was stalled in northern Mexico (Coppedge et al. 1980a), the lack of progress was attributed to both ineffective sterile flies and the lack of animal protection by livestock producers.

The efforts of the Mexican-American programme to use the coumaphos packets in conjunction with releasing sterile insects were very successful. Through grower education and publicity, producers were informed that these packets were provided by the inspectors of the programme. The ability to provide producers with an effective and free treatment for infested cattle was surely a major factor in gaining access to ranches in Mexico and Central America. Historically and culturally, ranches in these regions were not open to outsiders.

4.6. Insecticide Baits

An area-wide insecticide-bait treatment to control screwworm adults was developed in the 1970s, in conjunction with activities improving baits for monitoring populations. Mackley and Brown (1985) reviewed the development of swormlure, an attractant, and SWASS (Screwworm Adult Suppression System) pellets. In Texas, screwworms were believed to migrate hundreds of kilometres, so extremely large plots were needed to avoid the confounding effects of flies migrating into the treated areas.

SWASS pellets were tested, through "before and after treatment" observations, in Curaçao, Texas (Coppedge et al. 1980b), Colima (Tannahill et al. 1982), and Veracruz (Spencer and Garcia 1983). The bait swormlure was used to attract and sample adult screwworm flies. Wounded animals were used to collect eggs, and thus sample the reproductive capacity of the fly population. The general pattern in the experiments was a reduction in populations trapped and in reproduction. It was concluded that swormlure and SWASS were attractive and toxic, respectively. However, since the experiments were not replicated, no statistical conclusions about the effects of the SWASS treatments can be drawn. Although the baits reduced the total population, they may not have reduced the reproductive potential of localized populations. Another consideration is that, in wet areas such as Veracruz, the formulation of the SWASS pellet was such that it dissolved when wet (Mackley and Brown 1987), and the pellets may not have persisted long enough to reduce the populations.

Moreno and Mangan (1995, 2002) and Piñero et al. (2014) reviewed the development of improved insecticide baits for fruit flies. At the beginning of the 20th century entomologists discovered that fruit flies would feed on toxic chemicals contained in baits composed of various sugars. In search of an insecticide programme for the control of the recently established Mediterranean fruit fly in Hawaii, Back and Pemberton (1918) reviewed the research status of edible baits for use with arsenic poisons. The principal baits were carbohydrates and fermenting substances such as sugars, molasses, syrups, and fruit juices. McPhail (1937) found that sugar-yeast solutions attracted several species of *Anastrepha* and, in 1939, found that protein lures were attractive to these species. In 1952 Steiner demonstrated the use of hydrolysed proteins and partially hydrolysed yeast in combination with organophosphate insecticides to control fruit flies, leading to the attracticides currently used. The first protein-hydrolysate baits contained protein hydrolysate, sugar, and parathion (Steiner 1952). The early fruit fly eradication programmes in the USA relied on attracticide baits using DDT or organophospate pesticides. Flies responding to the attracticide needed only fume exposure, or to contact, taste, or ingest the mixture, whereupon in a short time they died.

Bait formulations that meet both the attraction and gustatory requirements of the pest permit the use of a wide range of contact and stomach insecticides (Moreno and Mangan 1995, 2002). The concentration of the active ingredient in bait can be reduced more than 90%. To be active, the formulations require consumption, either because the toxicant cannot penetrate, or the concentration is not sufficient to penetrate, the insect cuticle. Other important components include conditioners such as oils, humectants, and adjuvants. These components protect the spray drops from evaporation and running off vegetation, help keep the drops wet for fly ingestion, and enhance the toxicity of the insecticide. Mangan and Moreno (2001) showed that a series of commercial adjuvants varied widely in their interaction with dyes and fruit fly mortality, and under field conditions adjuvants could significantly increase bait effectiveness by about 30%.

A series of insecticides was tested in the laboratory with SolBait formulated for tropical fruit fly control (Moreno and Mangan 2002). In that study, 16 insecticides, with mammalian toxicity values at least 40x lower than malathion, were identified. As part of this study, Moreno and Mangan developed, and adopted for commercial use, spinosad for fruit fly control. This spinosad-based toxic bait, currently marketed as GF120, was formulated with proprietary modifications by Dow Agrosciences to optimize attraction, edibility, and stability. In addition, since spinosad is derived from naturally occurring soil bacteria, *Saccharopolyspora spinosa* Mertz and Yao, after being combined with a selected series of bait components, the product was eligible for organic registration, and is now used widely.

Benavente-Sánchez et al. (2021) indicated that drones could be used to apply bait sprays against fruit flies in “hot spots” and larvicides against mosquito breeding sites.

4.7. Autodissemination Techniques

A founder trial by Devine et al. (2009) against *Ae. aegypti* in an Amazon city (Iquitos, Peru) showed that adult mosquitoes might be used, as vehicles for insecticide transfer by harnessing their fundamental behaviours, to disseminate a juvenile hormone analogue (JHA) between resting and oviposition sites. Setting up JHA dissemination stations, in 3–5% of the available resting area, resulted in increased larval mortality in 95–100% of the larval cohorts developing at those sites. During these trials, overall reductions in adult emergence of 42–98% were achieved. The method has since been validated against various *Aedes* species, but to reach a good level of suppression, it is quite expensive; due to low attractiveness, a high density of dissemination stations is needed.

It has been suggested that released sterile male mosquitoes could be used as vehicles of JHA or other biocides (Bouyer and Lefrançois 2014); this was tested successfully on a small scale in Kentucky (Mains et al. 2015).

The autodissemination of entomopathogenic fungi in fruit flies is under study (section 7); this might represent an effective suppression technique compatible with the SIT (Dimbi et al. 2009; Flores et al. 2013; Toledo et al. 2017).

5. BEHAVIOURAL MODIFICATION WITH CHEMICALS

The use of pheromones for the detection and management of lepidopterous pests has become a standard procedure. Tamaki (1985) summarized the chemistry and application of pheromone technology for pest management. The chemical structures of pheromone compounds are known for 160 lepidopterous species in 20 families. Pheromone technology could be applied in three ways (Tamaki 1985):

- Monitoring and surveying for early detection of introduced exotic insects, forecasting pest outbreaks, and estimating population density,
- Mass-trapping for population suppression and detailed monitoring,
- Communication disruption to inhibit mate-finding and suppress the population.

Cardé and Minks (1995) reviewed the use of pheromones for mating disruption as a pest control strategy. Success with this strategy has been restricted to moths that have a mating behaviour that involves males following a pheromone plume as the principal means to locate females. Cardé and Minks described a series of modes of action that results in mating disruption, including effects on the sensory mechanisms of the target males, and control of behaviour and orientation. They described programmes for 9 pest moth species that have successfully used mating disruption, and 14 additional species that, at that time, had formulations available. An example of combining mating disruption with the SIT is the use of gossyplure in the pink bollworm control programme in the south-western United States (Walters et al. 2000a; Staten and Walters 2021; Simmons et al., this volume).

Gossyplure is a mixture of two isomers of 7,11-hexadecadienyl acetate (Hummel et al. 1973). This mixture was shown to be the effective attractant, with more than 56 times the attraction to males than hexalure (cis-7-hexadecenyl acetate) or than the less effective propylure mixtures reported to be sex pheromones (Jones et al. 1966; Jones and Jacobson 1968; Keller et al. 1969). Flint et al. (1974) used gossyplure for monitoring early season populations. The delta trap, previously used to control the gypsy moth *Lymantria dispar* (L.), was shown by Foster et al. (1977) to be a superior *P. gossypiella* monitoring tool. The first registered use of a pheromone to control the pink bollworm through mating disruption was developed by Gaston et al. (1977) in tests carried out in Arizona and California, USA.

Jenkins (2002) discussed current commercial formulations of gossyplure and modes of action of disrupting pink bollworm mating. Formulations exist as three types: (1) reservoir type such as the PB-ROPE L, which is containerized into a plastic tube or band, has a long field life (60–90 days), and is applied at 250–1000 units per hectare, (2) a low-rate, female equivalent, sprayable product has a field life of 7–21 days, contains an insecticide additive, and is contained in a paste, flake, or hollow fibre at 750–32 000 units per hectare, and (3) a low-rate, microdispersible system that can be applied as a fog or in a capsulated form, and has a field life of 7–28 days.

In addition to the application of insecticides against the codling moth, one of the pest suppression methods used in the Okanagan-Kootenay Sterile Insect Release (OKSIR) Program in British Columbia, Canada, was mating disruption (Judd et al. 1992; Dyck et al. 1993; Bloem et al. 2001; Nelson et al. 2021; Simmons et al., this volume). The integration of mating disruption and the SIT has also been successfully implemented against the codling moth in Washington State, USA, and south of the Canadian/USA border (Calkins et al. 2000). In organic orchards in British Columbia, Judd and Gardiner (2005) showed that within several years these two measures, coupled with removing overwintering larvae using cardboard tree bands (mechanical control), suppressed the codling moth population to non-detectable levels. These findings, as well as the integration of mating disruption as part of the successful pink bollworm eradication, point to a favourable interaction of mating disruption with the SIT, but precisely how these two approaches complement one another remains to be determined (Suckling 2011; Cardé 2021).

Parapheromones or synthetic lures, such as trimedlure, ceralure, cuelure, and in particular methyl eugenol, are effective attractants for fruit fly males (Cunningham 1989), and can be deployed in traps, panels or blocks from the ground by placing on host trees, or nailing to posts. Alternatively, insecticide-treated baited blocks (wood chips) or wicks can be released from aircraft for area-wide population suppression (Vargas et al. 2014). Such male annihilation technique (MAT) campaigns can be applied alone, prior to the release of sterile males, or more effectively simultaneous with the release of the males (Barclay et al. 2014).

More recently, it was proposed that sterile male fruit flies, e.g. Mediterranean fruit flies, could be used as pheromone sources to implement mobile mating disruption against moths, e.g. light brown apple moths (Suckling et al. 2011), a strategy called "ménage-à-trois" (Suckling et al. 2007b).

6. RESISTANT PLANTS

The development of cotton cultivars resistant to the pink bollworm has been a long-term component of the pest management programme. Nobel (1969) reviewed the characteristics of the components of resistance used in breeding programmes initiated in the 1950s. The cultivars screened, *Gossypium thurberi* Todaro and *G. thurberi* x *Gossypium hirsutum* L.*,* were recognized as the least attractive for oviposition. Pink bollworm larvae attacking these varieties experienced reduced larval survival and lengthened development time, apparently due to a protective response by the seeds.

Characters of varieties that induced oviposition away from the bolls exposed larvae to increased contact with pesticides and increased predation or parasitism. Boll, stem, and leaf morphologies that reduced oviposition were developed, and also nectariless cultivars to reduce the supply of food for adults. Although these characters appeared to reduce survival or oviposition, field trials did not show an increase in protection from attack. Increases in gossypol in the plant, though reducing pink bollworm survival, rendered the seed unusable for animal feed and the seed oil unusable for human food. Wilson et al. (1992) reported a 36% reduction in seed damage in a breeding line with a combination of nectariless, okra leaf, and early maturity; nevertheless, it still required insecticide treatment to control the pink bollworm.

Transgenic cotton varieties were developed by Monsanto, and released in the early 1990s. Tests in Arizona by Wilson et al. (1992) established that the pink bollworm adult populations were greatly reduced in transgenic cotton plots. The number of pests per 100 bolls was 87.5 for control varieties, and only 0.2 for transgenic varieties. Seed damage was similarly reduced in transgenic plots (0.14%) compared with 4.83% damage in control varieties. In summary, Wilson et al. reported that, in transgenic compared with susceptible lines, there was a reduction of 95–99% in rosetted blooms, pink bollworm populations in the bolls, and seed damage.

In China, the widespread adoption of *Bt*-cotton resulted in reduced insecticide sprays in this crop, leading to a marked increase in abundance of three types of generalist arthropod predators (ladybirds, lacewings, and spiders), and a decreased abundance of aphid pests in cotton fields and also in neighbouring crops (maize, peanut, and soybean) (Lu et al. 2012).

In the areas applying the SIT against the pink bollworm, the use of transgenic cotton has positively affected programme execution (Walters et al. 2000a, b). Already in 1997, 81% of the plantings in the Imperial Valley were genetically engineered cotton. As a result, Walters et al. (2000a) evaluated the possibility of moving from the containment to an eradication programme by integrating engineered cotton with the SIT and other control methods. They divided the components of eradication into five treatments — sterile insect release, genetically engineered cotton, high-rate pheromone release, mid-season pheromone application, and monitoring. Eradication was only possible by including all adjacent cotton growing areas in California, Arizona, and New Mexico in the USA, and in Baja California Norte, Chihuahua, and Sonora in Mexico (NAPPO 2004; Staten and Walters 2021).

By targeting the larval stages of the pest, this strategy is highly compatible with the SIT. A good example of using genetically modified crop plants that express a toxin is the area-wide programme against the pink bollworm in south-western USA and north-western Mexico. It demonstrated that planting *Bt*-cotton could effectively suppress the native moth population to a level where SIT application became very cost-effective, and enabled progress towards an eradication programme (Tabashnik et al. 2010). At the same time, releasing sterile pink bollworm moths was a viable alternative to the official refuge strategy for preventing the development of resistance to *Bt*-cotton; the sterile moths mated with the rare resistant insects, leaving no offspring, thereby delaying the evolution of *Bt* resistance (Wu 2010). As a result, susceptibility to *Bt*-cotton did not decrease in the target pink bollworm population, insecticide sprays against this pest were completely eliminated, and the density declined dramatically, leading eventually to regional pink bollworm eradication (Staten and Walters 2021).

7. BIOLOGICAL CONTROL

If natural enemies targeting the immature stages of a pest are released, the efficacy of sterile insects is enhanced because the number of pest insects reaching the adult stage is reduced; this increases the sterile:fertile overflooding ratio. Therefore, associating the SIT with biological control can result in synergistic associations (Suckling et al. 2012).

The integration of augmentative parasitoid releases and inherited sterility is especially synergistic (Carpenter et al. 2004; Carpenter 2013). When parasitoids develop normally on F_1 eggs, larvae, and pupae that result from the release of substerile moths (Marec et al., this volume), the increased number of hosts available will permit an increase in the parasitoid population. As most of the F_1 generation will not reach the adult stage, any parasitoids completing their development in these hosts will increase the efficacy of an area-wide programme. Most importantly, F_1 hosts can enable natural enemies to survive during critical times of low pest population, thereby increasing natural enemy populations prior to the time when the target pest reaches its economic threshold (Carpenter 2013).

Laboratory and field evaluations of *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metschnikoff) Sorokin (Hypocreales) have shown that these entomopathogenic fungi have the potential to suppress fruit fly populations (Ekesi et al. 2002; FAO/IAEA 2019; Abd-Alla et al., this volume). In recent large field trials on the Mediterranean fruit fly, sterile males, inoculated with *B. bassiana* as vectors to spread the fungus into the target pest population, were released (Toledo et al. 2017). By the end of the release period, the wild population had been reduced by more than 90% when compared with non-treated areas. If infected sterile males live long enough, even if sexual encounters do not result in matings, there might be horizontal transmission at leks (male aggregations visited by receptive females) that will result in the death of wild males and females; the fungus will also prevent infected wild females from remating and reproducing with wild males. Since *B. bassiana* is a generalist fungus, potentially infecting a wide range of arthropods, the environmental impact of such releases will need to be assessed further. Nevertheless, Flores et al. (2013) showed that the release of sterile flies as vectors is highly specific, and did not cause infection in bees or coffee berry borers *Hypothenemus hampei* (Ferrari); only trace quantities of conidia are required to inoculate sterile flies (0.0001 g per fly). The combined methods would be particularly useful for fruit fly population suppression during the rainy season in the tropics, when ground and aerial insecticidal sprays become largely ineffective (Toledo et al. 2017).

A similar strategy, coating sterile male *Aedes* mosquitoes with specific Densovirus, is presently under study (Bouyer et al. 2016). Also, *Bt* can be applied during the release of sterile insects to suppress a target population of a moth (Suckling et al. 2007a).

8. SUPPLEMENTARY TREATMENTS IN STERILE INSECT RELEASE PROJECTS

Releasing sterile insects in an area-wide pest control programme requires that the target population be isolated from adjoining populations, and that the target population is sufficiently reduced so that a high enough ratio of sterile to fertile matings inhibits reproduction. Current programmes achieve isolation by relying on combinations of quarantine barriers, geographic barriers, or treatment of buffers or barriers at the target population's margins (Hendrichs, Vreysen et al., this volume). To achieve the needed overflooding ratio, suppression/eradication programmes usually also require sufficient sterile insect production in conjunction with pest population suppression.

In addition to a lack of immigration and sufficiently high sterile:fertile ratios, other factors are required to achieve success in suppression or eradication programmes using the SIT. A key component of successfully applying pest management techniques is the effectiveness of the application in preventing pest damage. Of course, reducing pest populations by reducing their reproductive potential eventually reduces damage. However, sterile matings with the pests reviewed above do not kill the pest. Therefore, economic losses continue -- arising from reproduction by wild females mated before sterile insect release, and the continued biting and disease-transmission by infected blood-feeding females, independent of their sterile or fertile mating status.

The major supplementary treatments reviewed above provide direct and immediate reduction of crop damage by the pest or disease transmission by the vector, and are particularly needed before and during the first generation of sterile insect releases. Protection from damage by pests is practiced whether the programme releases sterile insects or not, so these treatments are usually widely applied components of pest suppression programmes. However, when these treatments are practiced in areas where the recipients (environmental and human) receive no direct benefits, as frequently must be done in AW-IPM programmes that integrate the SIT, the programmes can face social and political opposition, unless public opinion is preventively managed (Dyck, Regidor Fernández et al., this volume).

Target population suppression activities supplemental to sterile insect releases tend to be methods that were developed to control the pest populations or prevent damage from the pests, independent of sterile insect releases. Public acceptance of pest management programmes is best related to the benefits derived directly and indirectly from the activities, but the success of suppression or eradication efforts is dependent on pest population reduction (Klassen and Vreysen, this volume).

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