CHAPTER 7.3.

IMPACT OF MOTH SUPPRESSION/ERADICATION PROGRAMMES USING THE STERILE INSECT TECHNIQUE OR INHERITED STERILITY

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SUMMARY

More than 22 lepidopteran species have been investigated as candidates for control using the sterile insect technique (SIT) or inherited sterility (IS). However, to date only three programmes have been operationalized on a large-scale. The pink bollworm programme was successful at eradication across a broad swath of the cotton production area in south-western USA and northern Mexico by operating an area-wide control programme across this region using a combination of *Bt*-cotton, mating disruption, sanitation, and the SIT. The codling moth suppression programme in British Columbia, Canada, and the false codling moth in South Africa, have both been successful at effective suppression of the pest populations, reducing insecticide use, and improving interactions between growers and the general public. Other smaller-scale programmes against outbreaks of gypsy moth, cactus moth, and painted apple moth have also been successful, contributing to local eradications of invasive populations. New programmes are being investigated for managing a range of other target pests, including European grapevine moth in Chile, sugar cane borer in South Africa, tomato leafminer (for glasshouse populations in Europe), carob or date moth in North Africa, and navel orangeworm in California. Methods to further reduce the cost of lepidopteran programmes might include combining the SIT/IS with other environment-friendly pest control tactics such as mating disruption or the release of natural enemies, the development of genetic sexing strains, or the application of molecular technologies to develop genetic markers, genetic sexing, and genetic sterility. In the future, the greatest potential for impact of lepidopteran SIT/IS programmes may be in combating key invasive threats, with examples such as the eradication of an outbreak of the painted apple moth in New Zealand and the cactus moth in Mexico, or by adding an additional tool to pest control programmes where the use of insecticides may be limited by the development of resistance or the objection by residents in urban areas to ongoing treatments.

1. INTRODUCTION

Lepidopterans are among the most devastating agricultural and forest pests in the world. In the United States of America (USA) seven of the eight most serious insect pests of agricultural crops are lepidopterans (Peters 1987). According to a list of the 37 worst invasive insect pest threats to US agriculture and plant resources, 19 are lepidopteran species (ESA 2001). A review of global eradications revealed 144 eradication efforts against 28 species of Lepidoptera (Suckling et al. 2017). Control of these pests relies largely on insecticides, and the development of resistance is becoming a serious problem for many species, e.g. codling moth (Varela et al. 1993), diamondback moth (Tabashnick et al. 1990; Shelton et al. 1993), navel orangeworm (Demkovich et al. 2015), and pink bollworm (Bagla 2010; Tabashnik and Carrière 2010). In addition, the indiscriminate use of pesticides has had a significant negative

impact on the environment. Of particular importance to agriculture is the destruction of crop pollinators and natural enemies that keep secondary pests in check (Edwards 2000; Zaller and Brühl 2019). Therefore, it is probably not surprising that more lepidopterans than any other group of insects have been investigated as potential candidates for integrated control using the sterile insect technique (SIT) or inherited sterility (IS) (a variation of the SIT that involves the release of partially sterile insects) (North 1975; LaChance 1985; Bloem and Carpenter 2001; Marec et al., this volume). At least 22 moth species have been investigated for their potential as SIT targets -- including those with completed radiation biology studies, with field tests, and with either pilot or operational programmes (Vreysen et al. 2016; Suckling et al. 2017).

In spite of the tremendous impact that area-wide control of key lepidopteran species could have, and that many species have been investigated in laboratory and field-cage studies for their suitability as candidates for SIT/IS programmes, field trials have been performed on only a limited number of species (Suckling et al. 2017). Of the 16 lepidopteran species that have been investigated in the field (Table 1), only three area-wide SIT/IS programmes have progressed to the operational stage. These are programmes against the pink bollworm in the southern USA and northern Mexico, the codling moth in British Columbia, Canada, and the false codling moth in South Africa. In these cases, partially sterile or sterile moths have been routinely released in the context of area-wide integrated pest management (AW-IPM) programmes that use a combination of pest control tactics.

Table 1. Main moth pest species that have been investigated as SIT/IT candidates

Successful operational moth SIT/IS programmes	Past efforts to develop and apply moth SIT/IS	Ongoing methods development of moth SIT/IS
Pink bollworm <i>Pectinophora gossypiella</i> (Saunders)	Tobacco budworm <i>Heliothis virescens</i> (F.)	European grapevine moth <i>Lobesia botrana</i> (Denis and Schiffmüller)
Codling moth <i>Cydia pomonella</i> (L.)	Corn earworm <i>Helicoverpa zea</i> (Boddie)	African sugar cane borer ¹ <i>Eldana saccharina</i> Walker
False codling moth <i>Thaumatotibia leucotreta</i> (Meyrick)	Light brown apple moth <i>Epiphyas postvittana</i> (Walker)	Navel orangeworm <i>Amyelois transitella</i> (Walker)
Painted apple moth <i>Teia anartoides</i> Walker	Oriental fruit moth <i>Grapholita molesta</i> (Busck)	Tomato leafminer ¹ <i>Tuta absoluta</i> (Meyrick)
Cactus moth <i>Cactoblastis cactorum</i> (Berg)	European corn borer <i>Ostrinia nubilalis</i> (Hübner)	Carob/date moth <i>Ectomyelois ceratoniae</i> (Zeller)
Gypsy moth ² <i>Lymantria dispar</i> (L.)	Asian corn borer <i>Ostrinia furnacalis</i> (Guenée)	
	Diamondback moth <i>Plutella xylostella</i> (L.)	

¹ The SIT/IS has not been field-tested against these moth species.

² Even though successfully applied to eradicate gypsy moth outbreaks, the SIT/IS for this pest was discontinued eventually because more economic alternatives were developed (see section 3.1.).

In addition, the release of partially sterilized male painted apple moths was successfully added to an eradication effort in Auckland, New Zealand, with aerial applications of *Bacillus thuringiensis* var. *kurstaki* (*Btk*) and an intensive trapping programme for this introduced pest, using virgin female moths (Suckling et al. 2007). The same approach was used to eradicate outbreaks of the invasive cactus moth in Mexico (Bello-Rivera et al. 2021).

Although studies on *G. molesta*, *O. nubilalis*, *O. furnacalis*, and *P. xylostella* generally reported positive results from releasing sterilized insects (Rosca and Barbulescu 1996; Apu 2002; Genchev 2002; Maung 2002; Wang et al. 2002; Yang et al. 2002), not enough detailed information concerning the size of treatment areas, release rates, release methods, and methods for evaluating efficacy of releases was provided. The programme against *L. dispar*, even though successfully applied to eradicate outbreaks, was eventually discontinued because more economic alternatives were developed. Also, programmes for *H. virescens* and *H. zea* were deemed uneconomic following a number of large-scale field studies.

2. SUCCESSFUL OPERATIONAL MOTH SIT/IS PROGRAMMES

The primary impact of successful lepidopteran SIT/IS programmes that has been reported is the degree of pest suppression or eradication, or the extent to which establishment of an invasive pest has been prevented in the treatment area. Quantification of other benefits, e.g. lower commodity-production costs, access to new markets, and fewer farm-worker health and safety problems or decreased ground-water contamination as a result of reduced insecticide use, has for the most part not taken place. Therefore, rather than limit this discussion to the little information available on accrued benefits from lepidopteran operational programmes, the major achievements of lepidopteran field programmes that have been undertaken are more broadly discussed to include their impact on the target pest population, the stakeholders involved, and the advancement of the SIT/IS as a tactic for lepidopteran control.

2.1. *Pink Bollworm*

2.1.1. *Development of the Programme*

The pink bollworm *P. gossypiella* was first reported in North America from Mexico in 1911, probably entering on cotton seed shipped from Egypt (Noble 1969). The first reported infestation in the USA was in 1917 in Robertson County, Texas (Scholl 1919). By 1926, this highly invasive insect had spread from Texas through New Mexico and into eastern Arizona, and then quickly established itself as one of the major pests of cotton in the south-western USA and north-western Mexico (Burrows et al. 1984). It is considered to be among the most damaging cotton pests worldwide due to feeding while protected within the cotton boll, high reproductive capacity, high mobility, and frequent development of resistance (Henneberry 2007). Past management of the pink bollworm relied on the extensive use of broad-spectrum insecticides, and growers experienced significantly increased production costs and

reduced yields (Watson and Fullerton 1969; Burrows et al. 1982, 1984). Ingram (1994) provided a worldwide perspective on the pest status and management of the pink bollworm, and Henneberry and Naranjo (1998) and Henneberry (2007) reviewed its status and the various integrated management approaches used for its control in the south-western USA.

Development of IPM strategies significantly improved the prospects for management of the pink bollworm in the south-western cotton belt which included the use of area-wide management with cultural controls, pheromone monitoring, coordinated insecticide applications, resistance monitoring, the widespread use of mating disruption, and the application of the SIT (Chu et al. 2006; Henneberry 2007; Lance et al. 2016). The work to integrate the use of the SIT into other AW-IPM tactics was based on research including mass-rearing and irradiation biology, extensive small-scale testing in field cages, several large-scale field trials, and demonstration projects (Staten et al. 1993; Henneberry 2007; Walters et al. 2009; Naranjo and Ellsworth 2010; Lance et al. 2016).

Stewart (1984) described the mass-rearing of the pink bollworm. Staten et al. (1993) and Walters et al. (2009) summarized the history and operational details of the programme. Miller et al. (2001) reviewed the efforts to enlarge the rearing facility in Phoenix, Arizona, developments like the twin-screw extruder technology to make high-volume and high-quality diet, and mechanization of the rearing process. These changes dramatically increased sterile-insect production capabilities at reduced costs, and opened up the possibility that sterile moths could be integrated into other AW-IPM programmes in the cotton belts of south-western USA and north-western Mexico.

Other developmental work included several field-cage studies and open-field trials to evaluate the potential of the SIT to control the pink bollworm. While the field-cage studies showed positive results, many of the early open-field trials failed or were only partially successful. These early failures were attributed to a lack of isolation from migrating moths, and the low competitiveness of mass-reared sterilized male moths that necessitated high (more than 60) sterile to wild overflooding ratios (Bartlett 1978). Henneberry and Keaveny (1985) provided detailed information on a large-scale SIT field trial in St. Croix, US Virgin Islands. Henneberry (1994) made a thorough review of all sterile-moth release trials for pink bollworm control, including the St. Croix project and the San Joaquin Valley programme.

2.1.2. Containment in the San Joaquin Valley

The history of development of the SIT for the pink bollworm included a long-term area-wide preventive sterile-moth release programme in the San Joaquin Valley, which was the only cotton-growing area in the south-western USA not infested with the pink bollworm. The long-term prevention of pink bollworm establishment in that valley was attributed to an ongoing area-wide monitoring and SIT containment programme that had been in continuous operation since 1967 (Staten et al. 1993; Henneberry 1994; Walters et al. 2009). The objective of this programme was containment rather than suppression or eradication (Henneberry 1994; Hendrichs et al. 2007; Lance et al. 2016; Hendrichs, Vreysen et al., this volume). This was achieved by operating an area-wide monitoring and coordinated sanitation programme, and included the release of large numbers of sterile moths each year relative to the number

of immigrating wild moths (Walters et al. 2009). The fact that the pink bollworm did not become established in the San Joaquin Valley, despite the annual immigration of moths from infested cotton-growing valleys to the south (Staten et al. 1993), and the demonstrated ability of the moth to successfully overwinter in the area (Henneberry and Keaveny 1985; Venette and Hutchison 1999), showed that the programme had been effective. The programme was financed by a self-imposed grower levy on cotton bale assessment, and USDA support for sterile moth release (Walters et al. 2009; CDFA 2019). Compared with cotton-production areas where the pink bollworm was established and not suppressed, growers saved an estimated USD 248–371/ha (CDFA 2019).

2.1.3. Area-Wide Integrated Pest Management

The success of the San Joaquin Valley containment programme, coupled with the development of other biorational tools such as pheromone mating disruption and later *Bt*-cotton, created the opportunity to test the feasibility of using combinations of these tools for the integrated management of established pink bollworm populations on an area-wide basis. The first test was conducted in 1986–1989 involving 30 cotton fields in the Coachella Valley, California, using a high-rate pheromone disruption system and sterile insects. During the 4-year project, pink bollworm populations were maintained at low densities, and major reductions in conventional insecticide use were achieved (average of 7.3 insecticide applications per field per y decreased to 1.2) (Staten et al. 1993; Henneberry 1994).

A second area-wide pest suppression trial, combining the SIT with mating disruption, *Bt*-cotton, and cultural controls, was conducted in the Imperial Valley, California, from 1994 to 2000. Walters et al. (2000) reviewed the strategic objectives and results of this integrated management trial for the period 1994–1998. During 1994–1996, sterile moths were released on 6 d/wk in all fields at variable rates (70–560 moths per ha per d) calculated to deliver an overflooding ratio of at least 60:1 as measured by trap captures. Sterile moth releases were supplemented with mating disruption if a 60:1 sterile to wild moth ratio was not maintained. In 1997 the cotton planted in the Imperial Valley consisted of 81% *Bt*-cotton, 17.5% conventional or non-*Bt*-cotton protected with mating disruption, and 1.5% conventional untreated cotton as a refuge. Releases were reduced to 40 sterile moths per ha per d, 3 d/wk, throughout the Valley. The trial was expanded in 1998 to include the Blythe and Palo Verde Valleys, California, where there also was widespread use of *Bt*-cotton. The trial was terminated in 2000 after having achieved a high degree of suppression of established pink bollworm populations in all areas using essentially no insecticides.

2.1.4. Area-Wide Eradication

Based on the success of these trials, a large area-wide eradication was launched to eradicate the pink bollworm from all cotton-producing areas of the USA and adjacent areas of northern Mexico (NCCA 2001, 2009; El-Lissy et al. 2002; Antilla and Liesner 2008; Tabashnik et al. 2010; Staten and Walters 2021). This large programme used a combination of tactics including mating disruption, regional widespread planting of genetically modified cotton expressing the *Bt* toxin, cultural control

methods and the SIT (Grefenstette et al. 2009; Tabashnik et al. 2010; Liesner et al. 2014). Each of the programme areas used grower-planted *Bt*-cotton, and pheromone applications for mating disruption, for 1 or 2 y to lower the pest population levels. Then, in the following 2 or 3 y, sterile-insect releases were to be included to complete the eradication process. In 2001, the programme was initiated in Texas and Chihuahua, Mexico, and moved to New Mexico in 2002, south-western USA, and north-western Mexico; in 2006 the programme proceeded into Arizona and the lower desert production area in southern California, bringing all programme areas under full eradication (Antilla and Liesner 2008; Lance et al. 2016).

Sterile pink bollworms were released at variable rates of up to 250–600 moths per ha per d on conventional cotton, and at a lower rate of 36 moths per ha per d on *Bt*-cotton (Antilla and Liesner 2008; Grefenstette et al. 2009). The data before and after the eradication programme in Arizona show a steep decline in larval infestation of bolls and moth captures (Fig. 1) and pesticide applications (Fig. 2).

For the Arizona programme, the release of sterile moths over *Bt*-cotton pioneered a new use of the SIT, enabling the planting of 100% *Bt*-cotton without using the EPA-mandated *Bt*-resistance management strategy, i.e. planting a refuge of 10% conventional cotton. Using sterile insects in this manner works as a form of resistance management by reducing the probability that a moth with a rare resistant recessive allele would encounter another moth of the same genotype (Wu 2010).

This was a novel use of the SIT, enabling eradication programme officials to obtain an EPA (Environmental Protection Agency) section 24C local-use variance that permitted the planting of 100% *Bt*-cotton in all programme areas. The area-wide (near 100%) planting of *Bt*-cotton was credited as a major factor in the success of the programme (Henneberry 2007; Tabashnik et al. 2010; Liesner et al. 2014).

After 2009 no larvae were observed in the field, and after 2012 no wild moths had been caught in any of the programme areas (Blake 2014; Liesner et al. 2014; Lance et al. 2016). Since 2014, all programme areas were under a four-year “Confirmation of Eradication” designation where the area-wide cultural practice of planting nearly 100% *Bt*-cotton continued in most areas, but all other control activities, including sterile-insect release, ceased (Liesner et al. 2014). Area-wide monitoring continued with pheromone traps, a mandatory “plough-down” host-free period, and a small maintenance level of production of the pink bollworm to support a response with sterile insects in the event of pink bollworm captures (Liesner et al. 2014; Lance et al. 2016). After completion of the 2018 cotton-growing season, pink bollworm eradication was declared for all USA programme areas (Fitchette 2018; USDA 2018; Staten and Walters 2021).

Even though the eradication campaign is a success, the pink bollworm remains a threat for reinvasion and a significant worldwide pest. The pink bollworm is still the primary cotton pest in all major cotton-producing areas of the world, and resistance to *Btk* in transgenic cottons has been reported in India (Bagla 2010; Tabashnik and Carrière 2010). In North America, there are some parts of eastern New Mexico and the Southern Plains region of Texas not included in the eradication programme; in these areas pink bollworm populations have been historically low, and the status is uncertain (Pierce et al. 2013). Outbreaks in 2009–2011 were confined to a small number of fields planted to non-*Bt*-cotton (Pierce et al. 2013). In 2012, these

populations were addressed by increased planting of *Bt*-cotton and releasing sterile insects; the area is considered eradicated (Pierce et al. 2013).

Figure 1. a) Pink bollworm larval infestation of non-*Bt*-cotton bolls from 1997 to 2009 in Arizona, USA. b) Wild male pink bollworm moths trapped in *Bt*-cotton fields from 1998 to 2009. Analysis of covariance shows that the number of moths caught per trap per week (log transformed) was significantly affected by year, treatment (before versus during the eradication programme), and a year-by-treatment interaction ($P < 0.0001$ for each factor and their interaction, $r^2 = 0.95$). Linear regression shows that the slope, which indicates the change in moths trapped per year, was significantly negative from 2006 to 2009 (-1.0 , $r^2 = 0.92$, $P = 0.04$), but did not differ significantly from 0 from 1998 to 2005 (0.017 , $r^2 = 0.071$, $P = 0.52$). (Figure adapted from Tabashnik et al. 2010.)

Figure 2. Decline in insecticide applications to cotton in Arizona, USA, by comparing sprays per year before and after the initiation of the pink bollworm eradication programme. (Figure adapted from Tabashnik et al. 2010.)

Other areas of concern include areas of central Mexico and the Caribbean where the pink bollworm remains a threat, and/or the status remains uncertain. Continued monitoring, mandatory “plough-down”, and quarantine enforcement will be needed in US cotton-production areas to ensure that the pink bollworm does not reinvade.

The economic impact of the pink bollworm to US cotton producers was estimated at more than USD 32 million per year for the entire infested area -- from yield losses and control costs related to the pink bollworm (El-Lissy et al. 2002; Frisvold 2006; Antilla and Liesner 2008). The removal of the pink bollworm from cotton-production systems, and reductions in the need to treat with insecticides, has enabled the development of better IPM programmes for other key cotton pests, e.g. *Lygus hesperus* Knight and *Bemisia tabaci* (Gennadius). Also, overall, it has reduced costs and insecticide use to record low levels, making cotton-production systems in the western USA more economical and environmentally sustainable (Henneberry 2007; Naranjo and Ellsworth 2010).

2.2. Codling Moth

The codling moth *C. pomonella* is the key pest of apples and pears in most regions of the world where pome fruit is grown (Vreysen et al. 2010). The larval stage burrows into the fruit, rendering it unmarketable and in breach of phytosanitary restrictions for trade. As a consequence, from the 1950s, organophosphate insecticides were applied to kill larvae as they emerge from eggs and before they can penetrate fruit. Control failures during the past 60 years, due to the development of insecticide resistance and

concerns about the impact of insecticides on the environment, have led researchers in different parts of the world to make numerous attempts to use the SIT/IS against the codling moth.

The Agriculture and Agri-Food Research Centre in Summerland (in southern British Columbia, Canada) provided the extensive initial investigations (Proverbs 1962, 1969, 1974, 1982; Proverbs et al. 1973, 1982) that led to the implementation of an operational AW-IPM programme that routinely releases irradiated moths (Dyck et al. 1993; Bloem and Bloem 2000). After the ground-breaking work of Proverbs, notable examples include the work of scientists at the USDA/ARS laboratory in Yakima, Washington, USA (Hutt et al. 1972; Butt et al. 1973; White et al. 1976a, b; Hutt and White 1979), and the research in Switzerland that used diapaused F₁ sterile larvae released into small pome-fruit orchards (Charmillot et al. 1973, 1976a, b; Charmillot 1977).

Research targeted gamma radiation (Proverbs and Newton 1962a, b, c), an inexpensive, agar-free meridic diet (Brinton et al. 1969), design of a rotating oviposition cage (Proverbs and Logan 1970), and ground-release devices to distribute chilled moths in the orchard (McMechan and Proverbs 1972). These components are currently in use in the OKSIR Program (Dyck et al. 1993; Bloem and Bloem 2000; Bloem et al. 2007a; Dyck 2010; OKSIR 2019).

2.2.1. Okanagan-Kootenay Sterile Insect Release Program

The Okanagan-Kootenay Sterile Insect Release (OKSIR) Program in Canada was launched in early 1992 (Dyck et al. 1993), more than a decade after Proverbs et al. (1982) had demonstrated in a 3-year (1976–1978) pilot project that local eradication of the codling moth was possible. Unfortunately, at that time, the cost of delivering this technology was about 2.4 times greater than the use of conventional insecticides (Proverbs et al. 1982). Between 1978 and 1992 several benefit/cost analyses were conducted at the request of growers to reassess the economics of the SIT (Holm 1985, 1986; Jeck and Hansen 1987). Following the more positive outcomes of these studies, an implementation plan was developed (DeBiasio 1988). A 2-year clean-up or sanitation phase (phase 1) was followed by 3 years of sterile moth releases (Phase 2) at an initial overflooding ratio of 40:1. Two zones, each containing about 4 000 ha, were treated sequentially, and urban trees were included in the programme. In addition, sterile codling moths were released along the USA-Canada border (phase 3 — containment) (Hendrichs et al. 2007; Hendrichs, Vreysen et al., this volume), which was (incorrectly) considered the only plausible route for reinfestation.

Construction of a mass-rearing facility at Osoyoos in the Okanagan Valley was completed in March 1993. Sterile moths were released into orchards for the first time in the spring of 1994. Unfortunately, clean-up activities during 1992 and 1993 were not entirely successful, and a higher-than-anticipated wild population resulted in poor overflooding ratios and poor control. In 1995, to help turn the programme around, reduce the wild population, and enable a 40:1 sterile:wild overflooding ratio to be achieved, growers received a one-time compliance grant of USD 115 per ha to support insecticide applications. Other strategic changes included tougher enforcement of codling moth control bylaws and an expanded communications campaign (Bloem and Bloem 2000; Bloem et al. 2007a).

As a result of these strategic changes, the average wild codling moth captures in pheromone traps in the Zone 1 treatment area were reduced from 13 moths per trap per week during the first generation, and 2.5 during the second generation (in 1995), to 0.08 moths per trap per week during both first and second generations (in 2000). The amount of codling moth fruit damage at harvest was significantly reduced; in 1995 42% of orchards in the treatment area had no detectable level of codling moth damage at harvest.

The programme for commercial orchards in Zones 2 and 3 commenced with the sanitation phase using a combination of mating disruption and insecticide sprays. Releases of sterile moths in these zones began in 2002 (Bloem et al. 2007a). It was expected that by the end of 2005 all zones would have achieved minimal codling moth population levels similar to those achieved in Zone 1, but the reduction in wild moth trap catch and fruit damage did not occur as rapidly as observed in Zone 1 (Bloem et al. 2007a). The reasons cited were the larger urban areas in these zones with untreated backyard trees, and the use of mating disruption in these zones which may not have been as effective as insecticide treatments in Zone 1. Despite this initial slow start, since 1999 moth captures and fruit damage decreased in all programme areas to below the treatment action threshold of 2 moths per trap per week (Fig. 3). Since 2015, the economic damage threshold was met, with less than 10% of programme areas having >0.2% fruit damage (Nelson et al. 2021).

During the life of the programme, insecticide use was reduced by 96% of pre-OKSIR Program amounts (Fig. 4) (Nelson et al. 2021). Although other factors have contributed, the decreased reliance on insecticides for codling moth control has resulted in local packing houses encouraging their apple growers to consider switching to certified organic production or following new “Growing with Care” production practices where no insecticides are applied in orchards between blossom and fruit harvest.

Finally, the Canadian OKSIR Program is a model of the development of support from the general public to implement more environment-friendly AW-IPM programmes. From its inception, home and business owners were encouraged to recognize the value that apple growers brought to the community — in terms of quality of life and economic benefits through agriculture and tourism (Dendy et al. 2001). As a result, area residents took responsibility for helping growers to implement a mutually beneficial AW-IPM programme by paying a portion of the annual budget and actively participating in activities such as the removal of unmanaged host plants.

Despite ongoing success, the operation of a long-term sustainable pest-suppression programme is threatened by that same success; reduced pest pressure may result in decreased funding support because the pest is no longer perceived to be a problem. Ironically, the unique public-funding model of this programme may contribute to this perception. An additional economic threat is the low profitability of pome-fruit production and the consequent conversion of some orchards to higher-value wine grapes and sweet cherries; this has led to a decrease in pome-fruit production areas and a decrease in the need for sterile moths (Carpenter et al. 2014; Nelson et al. 2021).

To provide additional support to maintain a sustainable programme, OKSIR has been working with researchers from other regions to supply sterile or fertile codling moths to develop further area-wide management of the codling moth with pheromone

mating disruption and sterile-insect releases (Carpenter et al. 2014; Horner et al. 2016; Nelson et al. 2021). Based on the successful pilot shipments from Canada to South Africa (Bloem et al. 2010), and using insects shipped “out-of-season” from Canada, since 2014 New Zealand researchers have been conducting a pilot programme in an isolated apple production area using mating disruption and regular sterile-moth releases (Horner et al. 2016).

Figure 3. Mean number of wild codling moths captured per trap per week for each zone managed by the OKSIR programme in Zone 1 (from 1995), in Zone 2 (from 1998), and in Zone 3 (from 1999). The dashed line indicates the recommended threshold (two codling moths per trap per week for two consecutive weeks) at which insecticide controls supplementary to the SIT would be required. (Figure from Nelson et al. 2021.)

Figure 4. Estimated insecticide active ingredient (kg or L) applied per ha per year for all zones managed by the SIR programme based on the estimated proportion of sales for the 15 products registered for use against the codling moth (note: some of these insecticides are also applied for other pests and/or crops). The estimates of active ingredients are divided by the area (ha) of planted pome fruit in the programme area to account for changes in sales due to the amount of pome fruit under cultivation. (Figure from Nelson et al. 2021.)

2.3. *False Codling Moth*

The false codling moth *T. leucotreta* is an indigenous pest in sub-Saharan Africa, and also in Atlantic Ocean islands off the African coast, islands in the Indian Ocean, and Israel (Newton 1998; Malan et al. 2018). It is a significant pest of several important crops, with citrus as one of its main hosts (Newton 1989; Hofmeyr et al. 2015; Malan et al. 2018). The larvae feed internally, causing fruit lesions (Malan et al. 2018). Until about 1969, it was unknown in the fruit-growing regions of the Western Cape province, South Africa, but by the end of the 1970s it had spread throughout all the important ones (Hofmeyr et al. 2015). The false codling moth can have 5–6 generations per year.

This moth is not present in North America, Europe and Asia -- this has phytosanitary implications for fruit exports to those regions (Hofmeyr et al. 2015; Malan et al. 2018; Boersma 2021). The South African citrus industry developed integrated pest management tactics to suppress the false codling moth, including sanitation, mating disruption, and chemical, microbial and augmentative biological controls (Newton 1998; Hofmeyr et al. 2015; Malan et al. 2018; Boersma 2021). However, the pest management programme was not adequate for effective moth control, insecticide resistance developed, and export markets increased in importance. Therefore, the citrus industry developed a more comprehensive area-wide control programme with the SIT as an additional method to suppress false codling moth populations (Bloem et al. 2003; Carpenter et al. 2007; Stotter et al. 2014; Hofmeyr et al. 2015; Boersma 2021).

A comprehensive research programme was organized by the industry, with support from the FAO/IAEA and USDA, to investigate the potential for applying the SIT against the false codling moth. There were several well-organized phases -- determine the radiation biology, evaluate mass-rearing technology, and conduct small-scale field-cage tests and subsequently a pilot project. The radiation biology experiments demonstrated that female moths were completely sterile at 200 Gy, but male moths were partially sterile with residual fertility of 5% at 350 Gy when crossed to fertile females (Bloem et al. 2003; Hofmeyr et al. 2015). Evaluating the fertility of the F₁ progeny showed that treatments of 150 Gy to male moths resulted in 100% sterility of their F₁ progeny, and demonstrated that an effective dose for an IS programme would be between 150–200 Gy. The field-cage test found that a dose of 150 Gy was effective for a mixed-sex release at a ratio of 10:1 sterile to fertile, and resulted in the highest percentage of uninfested fruit (Hofmeyr et al. 2005).

Based on these results, the pilot phase began with a treatment to 35 ha of citrus with a season-long release of moths treated at 150 Gy for a period of 29 weeks; the goal was to maintain an overflooding ratio of at least 10 to 1 over the course of the season. This trial resulted in a 95–97% reduction in fruit loss compared with the control plots (Fig. 5) (Hofmeyr et al. 2015).

Given the positive results of the first three phases of testing, and in support of a new operational SIT programme, the South African citrus industry constructed a mass-rearing facility (1900 m²); the goal was to produce 21 million moths per week (Hofmeyr et al. 2015). The facility incorporated many new improvements to the rearing system and infrastructure, including a new mass-rearing diet, improved oviposition cages, a new moth-collection system, an irradiation source, and new

release systems using ground-based and aerial release vehicles. Operational releases started in the 2007–2008 citrus-production season (Hofmeyr and Pretorius 2010; Hofmeyr et al. 2015).

During this period there was significant programme success, but also there were obstacles to overcome -- leading to a change to an extruded-diet production, a change in the release systems (using helicopters for sterile-moth release), and increasing the irradiation dose to 200 Gy (Xsit 2018, 2019). Over the next decade, the operational programme steadily continued to expand, reducing wild moth populations and fruit damage to low levels -- 95% or more below pre-programme levels, and reducing export-fruit damage-rejection levels (Fig. 6) (Hofmeyr et al. 2015; IAEA 2016; Boersma 2021).

Figure 5. Fruit drop due to *T. leucotreta* infestation in non-SIT and SIT-treated citrus orchards (35 ha) as part of an SIT pilot project conducted in the Citrusdal region during the 2005–2006 season. (Figure from Boersma 2021.)

Figure 6. Reduction in the number of wild *T. leucotreta* males and infested fruit in the Sundays River Valley, Eastern Cape Province, South Africa, as a result of sterile insect releases (data obtained from Xsit). (Figure from Boersma 2021.)

The programme has gained additional participation, increasing operations to encompass nearly 20 000 ha of the programme's three main operational treatment areas in citrus of the Western Cape and the Eastern Cape provinces (Boersma 2021). The programme attributes its success to focussing on a single crop industry, with broad support from growers to focus on the demands of the export market, integrating the SIT with other area-wide control tactics, and making the necessary investments in research and methods development to improve rearing, handling, and release procedures to maintain high moth quality and competitiveness (Boersma 2021).

2.4. *Cactus Moth*

The cactus moth *C. cactorum* is famous as a very successful biological control agent of invasive cacti (*Opuntia* spp.) in Australia, South Africa, and other regions, but it has proved to be a “two-edged sword” (Suckling and Sforza 2014). Following its accidental introduction into Florida, and subsequent spread along the coast of the Gulf of Mexico, and subsequent detections in Mexico (Fig. 7), the threat posed to native *Opuntia* ecosystems and agricultural production led to the launch of a binational emergency response against this invasive pest (Bloem et al. 2007b; Hernández et al. 2007; Bello-Rivera et al. 2021).

Figure 7. Location of Isla Contoy and Isla Mujeres near Cancun, Quintana Roo, in the Caribbean Sea, where infestations of *Cactoblastis cactorum* occurred but were later eradicated. (Map from Bello-Rivera et al. 2021.)

To address this threat, an area-wide control programme, with containment and eradication as the main goals, was implemented (Bloem et al. 2007b; Hernández et al. 2007; Bello-Rivera et al. 2021). This was a challenge because few control or surveillance tools were available (Stiling 2002; Bloem et al. 2005). The main methods

of cactus moth control consisted of insecticide treatments and hand-removal of infested cladodes and egg sticks. No pheromone was available for use in a detection system or for mating disruption (Bloem et al. 2003). Manual removal methods are effective but labour intensive (Hight et al. 2005), and insecticide treatments cannot be applied over large natural areas (Leibee and Osborne 2001; Zimmermann et al. 2004).

To address the limited number of tools available, research was initiated to improve monitoring methods, and to develop the SIT for eradication, barrier establishment, and as a resource to increase hosts for natural-enemy establishment (Carpenter et al. 2001a, b; Bloem et al. 2003; Hight et al. 2005; Heath et al. 2006). An artificial diet and mass-rearing system were developed (Carpenter and Hight 2012). A dose of 200 Gy was selected for implementation of an IS release programme where females were 100% sterile and male moths had residual fertility of between 40–50% (Carpenter et al. 2001; Hight et al. 2005).

The operational programme used surveillance, removal of host plants, sanitation efforts, and releases of sterile moths to contain and reduce cactus moth populations along the US Gulf Coast, and to eradicate this invasive pest in Isla Mujeres and Isla Contoy, preventing an invasion into the mainland of Mexico (Fig. 8) (Carpenter et al. 2008; NAPPO 2009; Hight and Carpenter 2016; Bello-Rivera et al. 2021).

Figure 8. Wild *C. cactorum* male moths caught per week in pheromone-baited traps from October 2006 to March 2007 in Isla Mujeres, Mexico (66 traps were deployed, except 115 in the last month). (Figure modified from Bello-Rivera et al. 2021.)

2.5. Painted Apple Moth

The painted apple moth *T. anartoides* is an Australian tussock moth species with flightless females (Fig. 9). There was concern that larvae would feed on many different plants of importance to horticulture in New Zealand, e.g. apple, forestry, e.g. plantation pine, and native ecosystems (Stephens et al. 2007). In fact, it has since been shown that the potential host range was wider in male than in female moths (Suckling et al. 2014); this has not been recorded previously in insects. This invasive pest was estimated to have a potential total cost to New Zealand of USD 52–203 million.

An eradication programme was approved, with a budget of up to USD 52 million (including communications and human-health monitoring costs). Operations began in January 2002, initially applying aerial sprays of *Btk*. In February 2003, releases of partially sterile males irradiated as pupae at 100 Gy (Suckling et al. 2002; Wee et al. 2005) were initiated at three sites with known or suspected painted apple moth

breeding populations. Regular quality assessments of males were made in a wind tunnel (Fig. 9). By May 2003, 45 000 males had been released. In virgin female-baited traps, recapture ratios of sterile to wild males averaged ca. 100:1.

Outbreaks of this invasive pest in Auckland, New Zealand, were eradicated in 2007 (Suckling et al. 2007).

Earlier modelling of the impact of the aerial *Btk* spray programme on the insect pest population suggested that a protracted programme would be needed to achieve eradication using this tactic alone. The addition of IS to eradication efforts was welcomed by public factions that opposed the spray applications. However, an assessment of the full benefit of the addition of IS to the successful eradication of the painted apple moth is not possible because of confounding among several techniques used together. Nevertheless, because reared virgin females were being used a lot as lures in a trapping grid across Auckland, the additional cost of rearing, sterilizing, and releasing males was rather minor (less than USD 145 000 per year). All indications from the IS programme were positive, including a highly favourable benefit/cost analysis (Brockerhoff et al. 2010) and little public resistance (Gamble et al. 2010).

Figure 9. Male painted apple moth attracted to a caged calling virgin-female moth -- part of a quality assurance bioassay conducted weekly on a subsample of irradiated male moths released during the successful eradication in urban Auckland. (Photo from D. M. Suckling.)

3. PAST EFFORTS TO DEVELOP AND APPLY MOTH SIT/IS

3.1. *Gypsy Moth*

The gypsy moth *L. dispar* was accidentally introduced into the USA in 1869 near Boston, Massachusetts, from where it has been gradually expanding its distribution. The area infested by the gypsy moth in North America is confined to the eastern USA (behind an advancing front slowly moving in a south-westerly direction) and the eastern provinces of Canada (Sharov et al. 2002a; Liebhold et al. 2021). It remains an important forest defoliator that periodically builds to outbreak levels resulting in serious economic, environmental, and public nuisance problems (Liebhold et al. 2000; Thorpe et al. 2006). Since 1924 more than 32.8 million ha of US forests have been defoliated by the gypsy moth (USDA Forest Service 2001).

The potential of using the SIT to contain and manage gypsy moth leading-edge populations, and to eliminate isolated outbreak areas resulting from the accidental transportation of egg masses and other life stages through commerce and recreation, led to the initiation in 1957 of radiation biology studies (Godwin et al. 1964). Based on several criteria, the gypsy moth appeared to be well suited for population management with the SIT — females do not fly, males may mate several times, and females typically mate only once, producing an egg mass in the fall from which larvae hatch the following spring (Reardon and Mastro 1993).

Mastro et al. (1981) and Reardon and Mastro (1993) provided good reviews of the considerable amount of research that was conducted throughout the 1960s, 1970s, and 1980s. This research defined the sterility effects of various doses of radiation when applied to different gypsy moth developmental stages, assessed and developed methods to optimize competitiveness of sterile gypsy moths, and quantified the impact of releasing sterile and partially sterile insects. Three different release strategies were investigated (Reardon and Mastro 1993): (1) field-placement (from the ground) of male pupae (sexed visually by size and form) treated with at least 150 Gy that emerged as fully sterile adults, (2) deployment (from the ground) of substerilized male pupae treated with 100 Gy, and (3) broadcast release (from the ground or air) of diapausing F_1 sterile eggs produced from untreated females mated with males treated with 100 Gy. Schwalbe et al. (1991) discussed the gypsy moth problem in North America and the rationale for focusing on the use of F_1 sterile eggs to eradicate isolated infestations. Unfortunately, the programmatic details of the various field trials that were conducted are lacking, with the exception of a few key pilot tests (Berrien County, Michigan, 1980–1982, using fully sterile male pupae; Horry County, South Carolina, 1982, using partially sterile male pupae; and Bellingham, Washington, 1984–1985, using sterile F_1 egg masses) (Mastro and Schwalbe 1988; Mastro et al. 1989; Schwalbe et al. 1991; Reardon and Mastro 1993).

What little additional information exists on gypsy moth SIT is contained principally in a series of unpublished annual progress reports by the United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) Laboratory, at Buzzards Bay, Massachusetts. However, in a report to the USDA, Agricultural Research Service (ARS), National Technical Advisory Board, LaChance (1976) provided some information on early gypsy moth field tests.

Small SIT field trials to suppress the gypsy moth also were conducted in Yugoslavia in 1969–1971 (Maksimović 1971, 1972, 1974). Even though it was concluded that the release of sterile males reduced wild population levels, an assessment of the actual impact of these releases is difficult given the experimental design that was used (LaChance 1976).

3.1.1. Release of Irradiated Pupae and F_1 Sterile Egg Masses

In general, the release of irradiated pupae was effective in eradicating isolated infestations and in suppressing low-density populations along the leading edges of spreading infestations. However, despite the technique's effectiveness, several operational difficulties were identified, and the technique was judged to be impractical for large-scale use (Mastro et al. 1989). Some of the problems were: (1) pupae were fragile and required special care in packaging and shipping (Reardon and Mastro 1993), (2) pupae had to be released in emergence cages that were expensive to deploy and maintain (Reardon and Mastro 1993), (3) pupae and newly emerged adults were sometimes subject to intense predation, (4) overcrowding in emergence cages resulted in poor-quality adults (LaChance 1976), and (5) since released males lived only 2 or 3 d, frequent releases were necessary to maintain high ratios of released to wild insects (Schwalbe et al. 1991; Reardon and Mastro 1993). In addition, since male flight activity lasts only about 4 wk, a mass-rearing facility would be underutilized for most of the year (except potentially for producing the gypsy moth nuclear polyhedrosis virus) (Mastro 1993; Reardon and Mastro 1993).

As a result of the difficulties in releasing pupae, research efforts were refocused on the release of F_1 sterile egg masses. Male pupae were irradiated with 100 Gy, and then these males were mated to fertile females; the F_1 egg masses were stored in diapause until needed for release the following spring. In this way, in theory, some F_1 sterile larvae would emerge and develop in the field in synchrony with the wild population. This technique had the advantages that the F_1 sterile egg masses were easier than pupae to handle and ship, could easily be produced and stockpiled in diapause throughout the year using a relatively small rearing facility, and required only a single release per season (Schwalbe et al. 1991; Reardon and Mastro 1993). In spite of these advantages, the additional population suppression that IS offers (suppression by the release of partially sterile males followed by the field production of their F_1 sterile progeny) could not be taken advantage of when this approach was used. Also, some larvae (the feeding stage) resulting from the released F_1 eggs might cause some plant damage (although it was never actually observed) (Mastro et al. 1989; Mastro 1993).

Although the early use of gypsy moth F_1 sterile egg masses was successful in eradicating an isolated population in Bellingham, Washington (Mastro and Schwalbe 1988; Mastro et al. 1989; Schwalbe et al. 1991; Reardon and Mastro 1993), similar results were not consistently obtained in subsequent trials against isolated outbreak populations, and the technique proved inadequate for managing gypsy moth populations along invading fronts of established infestations (Reardon and Mastro 1993). Apparently, the low efficacy and inconsistent results of releasing F_1 sterile egg masses were due to the fact that the resulting sterile adults that developed in the field were less competitive than the wild population, and were actually less competitive than laboratory-reared males irradiated and released as pupae. Part of the poor

competitiveness was due to developmental asynchrony with wild moths, which was likely exacerbated by variably delayed development that was subsequently shown to be caused by low bioavailability of iron in the diet of the maternal parent (Keena et al. 1998). Nevertheless, between 1988 and 1992, eight isolated populations of the gypsy moth were treated with F₁ sterile egg masses with apparently “generally positive results” (Reardon and Mastro 1993). Between 1980 and 1992, infestations covering a total of 2385 ha were eradicated using sterile gypsy moth releases of all types (USDA Forest Service 2001). However, after nearly 35 years of study and application, it was determined that the SIT/IS was not sufficiently cost-effective relative to other less-expensive options. After 1993, this technology was no longer employed against the gypsy moth.

Current programmes for gypsy moth suppression rely on the use of *Btk*, a gypsy moth nuclear polyhedrosis virus, and the synthetic sex pheromone disparlure (Sharov et al. 2002b; Lance et al. 2016). In recent years, sterile gypsy moths have been used only for such purposes as calibrating trapping grids to confirm that phenological models are giving reasonably accurate estimates of the timing of egg hatch, and determining parasitoid host preferences. Nevertheless, the investigations associated with the development of the SIT for this pest led to a better understanding of its biology and behaviour that is being utilized in ongoing management activities (Mastro et al. 1989).

In Europe, more recent investigations have been conducted on the release of F₁ sterile egg masses in advance of imminent gypsy moth outbreaks; the objective is to enable natural enemy populations to build-up early, and thus reduce the magnitude of an outbreak (Zúbrik and Novotný 2009).

3.2. Tobacco Budworm

The tobacco budworm *H. virescens* is a key pest of cotton and tobacco, and has been developing resistance to most insecticides used for its control (Harris et al. 1972; Elzen et al. 1992). In an attempt to develop an alternative control strategy for the tobacco budworm, Laster (1972) discovered hybrid sterility in F₁ male moths when male *H. virescens* were hybridized with female *Heliothis subflexa* (Guenée). The F₁ (hybrid) females produced from this cross, when backcrossed to *H. virescens* males, produced sterile male and fertile female progeny. This male sterility persisted in all subsequent backcross generations. Genetic studies of tobacco budworm backcross sterility discovered abnormalities in the sperm of hybrid and backcross males (Richard et al. 1975; Goodpasture et al. 1980). LaChance (1985) and Laster et al. (1988) reviewed in detail the different biological mechanisms responsible for sterility in the hybrid, including the early backcross and subsequent backcross generations. The potential use of backcross sterility was examined using population models (Makela and Huettel 1979; Levins and Parker 1983) that predicted a decline in a natural population of tobacco budworm following the release of backcross insects. Following encouraging results from many studies of host-plant preference, mating preference, and mating competitiveness (Laster et al. 1988), a pilot release programme was planned for the island of St. Croix, US Virgin Islands.

The objectives of the pilot programme on St. Croix during 1977–1981 were to introduce a measurable amount of backcross sterility into the natural population of tobacco budworm, and to evaluate the population suppression and the level of backcross sterility in subsequent generations. This project was a cooperative effort between the USDA and the Mississippi Agricultural and Forestry Experiment Station. During 1979 and 1980, four separate releases were made (Proshold et al. 1983). Male sterility in tobacco budworm wild populations continued to increase as long as backcross insects continued to be released. During the last 6 weeks of 1981, 94% of wild tobacco budworm males were sterile (Proshold 1983). However, as the backcross frequency declined following the last release, tobacco budworm populations returned to pre-release levels. Proshold and Smith (1990) were not able to detect the backcross phenotype five years after the last release, presumably because of genetic drift and selection.

Following the pilot release programme on St. Croix, in 1991–1993 a pilot test was conducted in the central delta of Mississippi, USA, to study the effects of released backcross insects on natural tobacco budworm populations in a typical agricultural production area (where it overwinters and from where it annually undergoes long-distance dispersal to northern states and Canada (Laster et al. 1993, 1996; Hardee and Laster 1996). Backcrossed moths were released by placing pupae in emergence boxes at the test location, a 16.7-km² area in Washington and Sunflower Counties, Mississippi, in 1992, and in Bolivar County, Mississippi, in 1993. Control areas of the same size were used for each year. In 1992, the backcross to budworm overflooding ratio achieved was 3:1. After releases had ceased, this ratio declined to 1.3:1 during June, and to 1:2.3 during July. In 1993 the backcross:budworm ratio in the same area was 1:2.2 (29.9% sterility) for the overwintering generation. Releases in Bolivar County during 1993 achieved a backcross:budworm ratio of 2.6:1. After releases had ceased, this ratio declined in June to 1:1.6, in July to 1:3.6, and in August to 1:4, producing in 1994 a 12.1% sterility carry over. Hardee and Laster (1996) concluded that backcross release results were favourable. However, considering the survival and migration potential of the tobacco budworm, higher overflooding ratios of released to wild insects would be needed on an area-wide basis in overwintering areas of the budworm to achieve more sustainable results.

3.3. *Corn Earworm*

The corn earworm *H. zea* is a major pest of maize, cotton, and many other field crops in the Western Hemisphere. Due to the importance of this pest, a method to mass-rear the corn earworm was developed (Burton 1969), and several attempts to eradicate this pest using the SIT in St. Croix, US Virgin Islands, were made (Snow et al. 1971; Laster et al. 1988). The first eradication trials were conducted for 3 months in 1968, and 6 months in 1969, with a second campaign being conducted from 1972 to early 1974.

Many problems were encountered during the 1968 trial, including an unexpected increase in the area planted to maize, inconsistent releases of irradiated insects, and poor and inconsistent insect production resulting from disease contaminants in the laboratory colony. Shipping and disease problems were reduced in 1969, but still

caused periodic slumps in the supply of sterile corn earworms. Nevertheless, when there was no slump in the insect supply, releases of corn earworm males (treated with 320 Gy) resulted in sterile to wild overflooding ratios of 10:1–15:1. As a result of the 1969 programme, there was a reduction in the field in the number of fertile corn earworm eggs, rather than an increase in the number of sterile eggs. It was concluded that this reduction in oviposition was caused by a high incidence (50%) of locking (failure of mating pairs to disengage upon completion of copulation) between released and wild adults (Snow et al. 1971; Laster et al. 1988).

For the 1972–1974 eradication campaign, changes were made in the rearing system to improve the insect quality and reliability of supply of insects for release. In general, only males were released, and the radiation dose used to sterilize males was reduced from 320 to 225 Gy (Hamm et al. 1971; Young et al. 1976). However, several times during the course of the campaign, changes were made in the radiation dose actually used, and in the sex (males alone or mixed sex) of the insects actually released. Local eradication of the corn earworm population was not achieved during either campaign, but much knowledge and experience were gained concerning the operation of an area-wide programme against a lepidopteran pest. Laster et al. (1988) concluded that improved rearing techniques and more competitive insects were critical, and suggested that using a lower radiation dose would improve the efficacy of future AW-IPM programmes against the corn earworm.

To assess the influence of released males treated with a substerilizing dose of radiation (100 Gy), and to measure the level of IS induced in wild populations of the corn earworm, Carpenter and Gross (1993) conducted a pilot test in small mountain valleys in western North Carolina, USA, from 1986–1990. They found that the number of wild males captured per ha was positively correlated with the distance from the release site of the substerilized moths. Analyses of seasonal population levels of wild corn earworms, estimated from mark-recapture data, indicated that seasonal increases of wild males were significantly delayed or reduced (or both) in mountain valleys where substerile males had been released. The incidence of corn earworm larvae with chromosome aberrations (indicating they were progeny of irradiated, released males) collected from the test sites during the growing seasons demonstrated that substerile males were competitive with wild males in mating with wild females, and were successful in producing sterile F_1 progeny that further reduced the wild population. These significant reductions (73.5%) in populations of the corn earworm resulted even though the average overflooding ratio of irradiated to wild males (5.3:1) was low compared with that of other programmes that release sterile insects.

The use of the SIT has not been implemented into operational programmes for the control of either *H. virescens* or *H. zea*. Although hybrid backcross sterility and F_1 sterility suppressed pest populations in the field, the cost of rearing the insects, the highly mobile nature of these species, and in particular the development and adoption of effective *Bt* transgenic crop varieties, make it economically impractical at the present time to use the SIT to control these pests. However, preventive releases of sterile moths at overwintering sites, when wild populations are concentrated and are present in naturally low populations, would be an opportunity to apply IS to minimize the moth populations migrating north in the spring (Hardee et al. 1999).

3.4. *Light Brown Apple Moth*

The light brown apple moth *E. postvittana*, a native to Australia, was first detected in California in 2007 (Brown et al. 2010). As a pest, the light brown apple moth is best known from tree fruits (e.g. apples, pears, citrus, peaches, nectarines, and apricots), vines, berry fruit, and to a lesser extent from forestry, and vegetable and flower crops (Wearing et al. 1991). The suspected-host list is estimated at about 500 species (Brockerhoff et al. 2010; Suckling and Brockerhoff 2010). The potential for harm from this pest triggered a major response from the USDA and the State of California agricultural authorities (Suckling and Brockerhoff 2010). Infested areas in the core California coastal areas were quarantined, and regulatory and control measures were put in place (including a large-scale effort to apply aerial pheromones in an attempt at eradication). As the programme progressed, with both public opposition leading to some challenges to the State's authority to implement a pheromone-based control programme (Lance et al. 2016), and the realization that more control tools were needed to contain this pest, a research and pilot project to develop the SIT was launched. It developed mass-rearing technology, examined both pupal (Soopaya et al. 2011) and adult irradiation biology (Jang et al. 2012), and conducted field trials in New Zealand and California (Suckling et al. 2011; USDA/APHIS 2011; Stringer et al. 2013). Modelling the overflooding ratios showed that, at 300 Gy, the population extinction was 95% probable when the ratio of released to wild males in monitoring traps exceeds 6.4 (Kean et al. 2011). Higher overflooding rates would achieve eradication more rapidly. There was an advantage to using IS over full sterility early in such a programme (due to the superior fitness of males at lower doses) (Kean et al. 2011; Suckling et al. 2011). A male-biased sex ratio was shown (Soopaya et al. 2011), adding to the multiplier effect of matings by sterile F₁ offspring.

In 2011, a pilot SIT project was initiated in California; it included sterility testing of adult moths, confirming the dose of 300 Gy for full sterility (shown by Soopaya et al. 2011). The mass-rearing and adult-collection systems were adapted from methods used in the pink bollworm and codling moth, and a sterile-insect field release trial followed in a 2.6-km² residential area in a coastal city in southern California. Twice-weekly releases of sterile moths (60 000–70 000 sterile moths per week) were made by hand on a grid system for 11 weeks, with a total release of 650 000 sterile moths. Due to the high population of wild moths in the area, satisfactory overflooding ratios were not achieved. However, moth quality appeared to be high, with moth recaptures of about 0.1% in the widely spread trap grid, with dispersal distances of up to 0.5 km, and field longevity of released adult moths observed for greater than 2 wk after release. At the end of 2011, the project was stopped -- due to financial constraints, and the evolution of the project away from a control programme towards a regulatory programme designed to limit further spread out of the quarantine areas.

4. ONGOING METHODS DEVELOPMENT OF MOTH SIT/IS

4.1. *European Grapevine Moth*

Historically the European grapevine moth *L. botrana* has been a pest of the Mediterranean regions of Europe, North Africa, and Asia. Recently, it was introduced into the Americas region, with first detections in Chile in 2008, California, USA, in 2009, and Argentina in 2010 (Varela et al. 2010; Gilligan et al. 2011; Ioriatti et al. 2011, 2012). A successful eradication campaign was completed in the USA in 2016 (Schartel et al. 2019; Simmons et al. 2021), but there is increasing pest pressure in the South America region. Infestations in urban areas are difficult to treat, and market-access problems affect the trade of other hosts, e.g. blueberries. Increasing problems for grape production in the Mediterranean regions are related to the development of insecticide resistance, warmer growing seasons with climate change, and the high cost of mating-disruption treatments (Martin-Vertedor et al. 2010; Ioriatti et al. 2011; Gutierrez et al. 2018). These factors have increased interest in the development of the sterile insect technique for *L. botrana* (Mansour 2014; Saour 2014, 2016).

Saour (2014) found complete female sterility when irradiating adults at 150 Gy, but a much higher dose of 400 Gy was needed to achieve near 100% sterility in males. A dose of 150 Gy was recommended for use in an IS strategy, a trade-off between high field competitiveness, as measured by flight ability, and higher residual male fertility (Saour 2016). (Higher irradiation doses significantly impacted the flight ability of male moths compared with a dose of 150 Gy.) At 150 Gy, the frequency of F₁ male progeny increased, and these had high sterility levels (Saour 2014).

In Chile, *L. botrana* was first detected in Santiago in urban grapes, and is now present in grape production areas in the central region of the country (Ioriatti et al. 2012; SAG 2019), and has also caused problems for the export of the large and valuable blueberry (*Vaccinium* spp.) crop. In urban areas (that are near grape and fruit production areas) many Chileans grow wine grapes in their gardens; this is a significant problem for the control programme because urban treatments can be very expensive and logistically challenging (residents can refuse treatments). The government's national control programme strategy for urban areas includes the use of mating disruption. A pilot project to test releases of sterile moths and parasitoids has been initiated (SAG 2018, 2019; H. Donoso, personal communication).

For the development and evaluation of the SIT as a control tool, the Chilean government and the fruit industry have formed a partnership to develop *L. botrana* mass-rearing systems, determine the radiation biology, and in 2016 began field-cage and pilot-scale field releases (H. Donoso and S. Izquierdo, personal communication). These trials were designed to measure the field-performance traits of irradiated males (e.g. dispersal, longevity, and mating with wild moths), determine release rates and frequency, and identify any needed changes in the rearing and handling of moths to improve performance.

The programme developed a sterile-insect laboratory in Arica with a capacity to produce >100 000 mass-reared moths per week to support a larger programme; currently it is producing 50 000–75 000 per week. This project has access to the gamma irradiator (Bakri et al., this volume) used for Chile's Mediterranean fruit fly

programme. The work in Arica has focused on optimizing the adult diet, developing quality-control procedures, and developing methods to collect and irradiate adult moths. The programme is also working with its fruit-industry partner Fundación para el Desarrollo Frutícola (FDF) to develop mass-rearing procedures, verify previous radiation-biology studies, and begin pilot-scale releases of sterile moths. Production capacity at the FDF mass-rearing laboratory in Santiago exceeds 100 000 pupae per week. The FDF programme is focused on methods of pupal collection and irradiation. Even though it is challenging to collect and irradiate pupae for large-scale moth SIT programmes, there are advantages to using pupae, e.g. a decrease in the impact on moth quality compared with handling and storage of adults. Early results from the programme suggest that it is having success – good insect dispersal performance and recapture rates. However, while a system of using irradiated pupae may be suitable for a small-scale programme targeting residential areas (Sucking et al. 2007) and selected vineyards (Stringer et al. 2013), a larger production effort for the area-wide release of sterile moths over a region will likely require the collection and irradiation of adult moths.

In 2018, the programme initiated several larger pilot-release evaluations in residential areas measuring 12.5 to 25 ha, and for a longer period of time releasing up to 16 700 sterile moths per week (FAO/IAEA 2018; SAG 2018; H. Donoso and S. Izquierdo, personal communication). This programme was expanded in 2019 to release 50 000 moths per week for a season-long project in a 25-ha residential area next to commercial vineyard and agricultural production areas. The goals of this larger phase of testing are to evaluate dispersal, field longevity, overflooding ratios, and suppression of wild populations, and also to develop the operational procedures needed to conduct an SIT programme. While it remains to be seen whether this pilot project will succeed and lead to operational releases, the first results are promising. The Chilean programme is making substantial progress, and may be the only solution available to reduce the extent of *L. botrana* movement from residential into production areas.

4.2. African Sugar Cane Borer

The African sugar cane borer *E. saccharina* is a native pest in several regions of Africa. It infests sugar cane, maize, and sorghum, as well as other grain crops of the grass family, and several native grasses and sedges (Walton and Conlong 2016a, b). The larvae's boring activity causes crop loss and reduced yields in sugar cane (Conlong 1994). After its spread into South Africa, the sugar cane industry launched a large effort to understand its biology, use of other hosts, methods of biological control, and prospects for area-wide management using various habitat management strategies. Efforts to determine if the SIT could be incorporated into the current area-wide programme were launched with work on mass-rearing, radiation biology, mating competitiveness, and modelling (Barnes et al. 2015; Mudavanhu et al. 2016; Walton and Conlong 2016a, b; Conlong and Rutherford 2017).

Work by Walton and Conlong (2016b) showed complete sterility of females at 200 Gy and residual male fertility of 20%, and suggested the potential of an IS approach for this species using 200 Gy. Mudavanhu et al. (2016) found that reared males,

irradiated at a dose of 200 Gy, were as competitive as wild fertile males, and have a high mating compatibility with wild females, suggesting that the effects of colonization, mass-rearing, and irradiation would not greatly affect the competitiveness of mass-reared irradiated moths.

4.3. Navel Orangeworm

The navel orangeworm *A. transitella* is the key pest of California tree nuts: almonds, pistachios, and walnuts. It causes feeding damage on kernels that can also lead to the introduction of aflatoxin producing the *Aspergilli* fungus. The insect has a wide host range that includes other tree and fruit crops such as oranges, figs, pomegranates, pecans, and ornamental species (Bentley et al. 2016; Ferguson and Haviland 2016). These crops are planted on more than 768 900 ha, and valued at more than USD 6200 million per year. For all of these crops, tolerance to pest damage by the navel orangeworm is extremely low, especially for pistachios (because of the difficulty of sorting out damaged nuts while still in the shell). Contamination by aflatoxin can impact quality and marketability. Levels of navel orangeworm damage are directly correlated with those of aflatoxin contamination. Standards of aflatoxin and insect damage for export markets are very demanding; this is a prominent concern (Bentley et al. 2016; Ferguson and Haviland 2016).

In view of concerns about the long-term sustainability of the current navel orangeworm management methods, there is interest in developing the SIT as an additional tool for navel orangeworm control; also, there is support to develop an area-wide control programme (Northcutt 2015). Work on radiation biology by USDA scientists in California (Light et al. 2015), and strong support shown by the tree-nut industry, has led to a pilot project to develop mass-rearing and to field-test sterile navel orangeworms (Wilson and Burks 2019). The USDA-APHIS-PPQ pink bollworm sterile-insect mass-rearing facility in Phoenix, Arizona, may be used to rear navel orangeworms (Blake 2015). An earlier demonstration project developed and evaluated navel orangeworm area-wide control measures (mating disruption, sanitation, and coordinated applications of insecticides), and showed that navel orangeworm control could be improved by using area-wide tactics. Since the use of the SIT is complementary with area-wide control, development of the SIT as a new tool would be especially useful for the long-term sustainability of navel orangeworm management in California.

Development of mass-rearing (focusing on evaluations of diet, rearing trays, and adult collection at the USDA-APHIS-PPQ facility) shows that there is a potential to produce several million navel orangeworm per week. That this was accomplished (without making significant changes to a system optimized for the pink bollworm) demonstrates that much higher numbers of navel orangeworm could be produced if the entire facility was committed to rear navel orangeworm on a much larger scale. Current production levels are being maintained to support the pilot-project field testing needed to develop an SIT system. Field trials were initiated in 2018, and are ongoing in 2019.

4.4. *Tomato Leafminer*

The tomato leafminer *T. absoluta* is an emerging pest of solanaceous crops from the neotropics that has expanded into North America, Europe, the Middle East, Africa, and parts of South-East Asia (Biondi et al. 2018; Biondi and Desneux 2019; Han et al. 2019). Internal feeding damage to fruit, leaves, and stems may cause losses as high as 100%; such damage increases the need for insecticide applications, but they disrupt the integrated management programmes of other tomato pests. Given its rapid range expansion and adaptability to diverse climatic conditions, this pest is predicted to have a high impact on tomato growers throughout these regions (Biondi et al. 2018).

Current control practices often rely on insecticide applications, but more sustainable control practices are needed (there are several reports in several regions of the development of insecticide resistance) (Biondi and Desneux 2019; Guedes et al. 2019; Silva et al. 2019). Furthermore, augmentative biological control using Neotropical parasitoids may not be available in other regions due to increased biosecurity that is increasingly excluding non-native natural enemies. Thus, there is interest in developing the SIT for the tomato leafminer for use in greenhouses (as an alternate tool to insecticide treatments) which would be compatible with biological control-based tactics (FAO/IAEA 2016, 2019).

Recent work includes completion of radiation-biology studies, field-cage testing showing pest suppression on infested tomatoes, and incorporation of predator releases with sterile-moth releases in glasshouse tomato production (Cagnotti et al. 2016; Kuyulu and Hanife 2016; Vreysen et al. 2016; FAO/IAEA 2019). Radiation-biology data for *T. absoluta* suggest that doses of 200–250 Gy could be used to induce IS in males (Cagnotti et al. 2016; Carabajal Paladino et al. 2016).

4.5. *Carob/Date Moth*

The carob or date moth *E. ceratoniae* is a major pest of dates in North Africa. The use of *Btk*, parasitoids, and postharvest fumigation does not provide sufficient pest control to enable the industry to reap the potential economic benefits from increased exports of dates.

Laboratory and field studies have been carried out in Tunisia and Algeria, with a view to integrating the SIT into AW-IPM programmes for date and pomegranate plantations. A mass-rearing system was established, and some small-scale releases of partially sterile moths were made (Dhouibi et al. 2000; Mediouni and Dhouibi 2007; Chakroun et al. 2017).

5. IMPACT, CHALLENGES, AND FUTURE DIRECTIONS

The long list of pestiferous lepidopterans (with increasing development of resistance to insecticides, and their tremendous impact on agriculture and forestry) necessitates an ongoing search for more efficient, economical, and environment-friendly ways of dealing with these pests. The SIT/IS is a species-specific technique that is highly compatible to integration with other pest management tactics, including the use of ground or aerial spraying of selective or biorational insecticides, mass-trapping,

cultural controls, sanitation, host removal, host-plant resistance, and biological control (Carpenter et al. 2007; Vreysen et al. 2016; Suckling et al. 2017; Mangan and Bouyer, this volume). It is likely to be especially effective when combined with other inversely density-dependent tactics such as mating disruption (Suckling et al. 2012).

5.1. Effectiveness and Impact

The overall effectiveness of the SIT/IS has been demonstrated to reduce lepidopteran pest populations in several operational programmes, resulting in the successful eradication of the pink bollworm in four states in the south-western cotton belt in the USA and in northern Mexico, and the eradication of outbreaks of the gypsy moth in the USA, painted apple moth in New Zealand, and cactus moth in Mexico. The application of the SIT/IS continues (in suppression programmes) to manage moth pests in the OKSIR programme against the codling moth in Canada, and now New Zealand, by reducing fruit-damage levels and reliance on insecticides. Within a comparatively short timespan of about 15 years, a programme targeting the false codling moth was developed in South Africa; it is effectively expanding the SIT-based area-wide control to additional citrus-production areas to reduce fruit-damage levels below demanding export thresholds.

At the same time, efforts started in recent years are continuing to develop the SIT against several emerging pests: the programme in Chile on European grapevine moth has moved into pilot-phase testing, with interest from several other countries; progress has been made towards the SIT for the African sugar cane borer in South Africa for a potential addition to a programme of comprehensive AW-IPM; and radiation-biology studies, and the development of mass-rearing systems, to develop the SIT are targeting the navel orangeworm. Also, research is underway to enhance the potential for the SIT to manage the carob moth in date production for export from North Africa, as well as the tomato leafminer in greenhouses (an emerging pest of solanaceous crops that has expanded into new regions).

5.2. Challenges

Despite these successes, there remain serious challenges to be met to make the SIT/IS for Lepidoptera more cost-effective relative to other pest-management tactics (Simmons et al. 2010; Vreysen et al. 2016; Suckling et al. 2017). Development of lepidopteran mass-rearing systems are complex endeavours, cost-effective meridic diets are difficult to develop, insect developmental times are long, larvae are often cannibalistic, sanitation measures must be stringent to prevent pathogen contamination (fungi, viruses, microsporidia) (Abd-Alla et al., this volume), and the insects, especially adult moths, are fragile.

Unlike in dipteran SIT programmes, methods to collect and irradiate the more robust pupae have not been widely developed for operational programmes. Using pupae in moth SIT programmes could reduce costs related to handling, storage, irradiation, and transport. However, the collection, handling, and irradiation procedures for current operational programmes are based on adult moths, which require optimized protocols to maintain high quality and low mortality rates of sterile

insects for release. This is in part because, for many moth-rearing systems, larvae pupate within the diet, and are difficult to separate out easily. Also, compared with dipteran mass-rearing systems, collections of pupae from lepidopteran rearing systems are of a less uniform physiological age, ranging from young pupae several days from emergence to pharate pupae (G. S. Simmons, personal observations). There are significant reductions in moth quality and emergence rates when irradiating pupae that are less developed than the pharate state. While there are some examples of small-scale programmes based on pupal irradiation and releases, there are significant obstacles for a larger programme to adopt these methods.

Another challenge, unlike dipteran SIT programmes (e.g. tephritid fruit flies and the New World screwworm), is that until recently relatively little attention had been given to development of procedures to maintain quality, fitness, and competitiveness traits in mass-rearing colonies of Lepidoptera (Simmons et al. 2010). While there have been no documented failures of Lepidoptera SIT programmes based on colony strain or mass-reared quality defects, in the past ten years there has been significant emphasis devoted to the importance of maintaining high quality in Lepidoptera to obtain mass-reared insects that are highly competitive (Simmons et al. 2010; Vreysen et al. 2016). This includes the idea of building rearing systems that can resist the negative effects of genetic drift and natural selection that can either result in the loss of important genetic variability associated with high performance in the field or selection for high reproduction and fitness in the rearing system that comes at the expense of high field performance (Woodworth et al. 2002; Simmons et al. 2010).

Important components to maintain in a mass-rearing system are the capacity to fly (e.g. using moths from an adult collection system in oviposition cages because they have to fly to reproduce) and the capacity for male moths to respond to a sex pheromone (Simmons et al. 2010). There is a general idea in many SIT programmes that high performance of an SIT release strain can be maintained by adding to or replacing on a regular basis the colony strain with new wild individuals. As Woodworth et al. (2002) and others show there is very strong selection for performance in captive populations, and the “wild” traits introduced with the field-collected individuals are quickly lost in a rearing system containing “captive” selected individuals. This process can occur in just a few generations, which will easily swamp the effect of new beneficial traits introduced into a mass-rearing colony, and will not improve SIT performance unless specific rearing procedures are in place to maintain competitive characteristics in the colony (Nunney 2001; Simmons et al. 2010; Hendrichs and Robinson, this volume).

Rearing large numbers of lepidopterans produces potent allergens due to the presence of scales and setae (Davis and Jenkins 1995; Parker, Mamai et al., this volume), requiring specialized equipment and air-filtration systems to reduce/mitigate allergic reactions suffered by workers. The fact that only a limited number of SIT/IS programmes for Lepidoptera have become operational has unfortunately also meant that they have not been able to take advantage of shared learning experiences in the way that the many fruit fly programmes have, and the beneficial impacts of such programmes are less well documented and accepted.

Methods to reduce the cost of lepidopteran programmes might also include combining the SIT/IS with other suppression tactics such as the release of natural

enemies. In this instance, the cost of rearing might be reduced by using the same facility to rear both insect species, while the efficiency and effectiveness of a combined programme can help meet objectives in a more timely fashion through synergistic action of both tactics. Especially in the case of implementation of an IS strategy, the residual fertility in the parental release generation can generate some field reproduction to produce a completely sterile F_1 generation that can provide a significant additional resource for the build-up of natural enemy populations (Barclay 1987; Knipling 1992; Carpenter 1993; Vreysen et al. 2016; Mangan and Bouyer, this volume).

As it has for dipteran programmes, the development of genetic sexing strains (Marec et al. 2005) would greatly reduce the costs of rearing and release in lepidopteran programmes. Marec et al. (2005) demonstrated genetic sexing in the Mediterranean flour moth *Ephestia kuehniella* Zeller, using a mutant-male strain that is trans-heterozygous for two lethal genes (Marec et al., this volume). However, there is not universal agreement that having the ability to develop single-sex male release strains is necessary for increased effectiveness of the SIT in Lepidoptera; a large number of female sterile moths released in the field can distract (through sex pheromone release) fertile wild male moths, thereby assisting with mating disruption (Stringer et al. 2013).

5.3. Future Directions

The application of molecular technologies might be used to develop genetic sterility, sexing systems, and reliable genetic markers for the released moths (Peloquin et al. 2000; Miller et al. 2001; Marec et al. 2005, 2007; Simmons et al. 2007; Simmons et al. 2011; Morrison et al. 2012; Bolton et al. 2019; Häcker et al., this volume). Since about 2007 there has been significant progress to develop and evaluate transgenic technology for two of the most difficult moth pests, the pink bollworm and the diamondback moth. In the pink bollworm, there were two efforts to introduce a sterile release moth into an operational programme. Genetically marked strains with fluorescent proteins could provide more reliable monitoring methods for standard sterile release programmes; they could also provide a heritable marker enabling implementation of IS systems. Field production of highly sterile F_1 progeny (Simmons et al. 2007, 2011), and production of a genetically sterile strain, could avoid radiation treatments and enable the production of male-only release strains (Simmons et al. 2007; Morrison et al. 2012; Jin et al. 2013). Work on the diamondback moth has progressed to the stage of field-testing genetically sterile or self-limiting strains to determine their field performance and competitiveness compared with wild strains (Bolton et al. 2019). It remains to be seen whether these technologies will be applied in new or existing operational programmes, but with further development these technologies could enable the operation of more cost-effective programmes.

The SIT/IS has special attributes that make it a desirable and unique insect pest management tool. However, because this technique requires a large start-up investment and a management-intensive support system, candidate pest species to be controlled with the SIT/IS should be selected carefully. A decision process to evaluate the suitability of the SIT/IS for controlling a pest lepidopteran should consider many

factors including: (1) key pest status, (2) economic importance, (3) mass-rearing costs and technical feasibility, (4) favourable radiation biology, (5) migration ability, (6) potential for an area-wide approach to minimize the treatment area becoming reinfested, (7) host specificity, (8) availability of monitoring tools, (9) stakeholder and customer support, and (10) the availability and effectiveness of other compatible control options for the target pest (Simmons et al. 2010; Vreysen et al. 2010, 2016; Suckling et al. 2017).

In addition to selecting carefully the most appropriate candidate species to be controlled with the SIT/IS, the strategic objective and type of programme should also be evaluated (Hendrichs, Vreysen et al., this volume). Since prevention is far more cost-effective and environmentally desirable than long-term measures that would be required once a non-native invasive species has become established, future considerations for selecting target lepidopterans should emphasize key invasive threats, similar to the SIT preparedness model that was developed for use in Australia for the Old World screwworm *Chrysomya bezziana* (Villeneuve) (IAEA 1998; Tweddle 2002; Hendrichs, Enkerlin et al., this volume; Vargas-Terán et al., this volume). For example, the false codling moth, the leek moth *Acrolepiopsis assectella* (Zeller), the European grapevine moth, and the Central American potato moth *Tecia solanivora* (Povolny) are all serious invasive threats to the USA and other countries such as Australia and New Zealand (Suckling 2003). The proactive development of the SIT/IS technologies offshore at the point of origin offers the following advantages:

- Capitalization on contributions by foreign counterparts due to their interest in controlling the same pest,
- Reduction in pest pressure at the point of origin (offshore risk mitigation) and thereby the risk of the pest being accidentally introduced elsewhere, and
- Availability of the SIT/IS for invasive moth pests, allowing significant reduction in response time to implement an SIT/IS eradication programme should such pests become established in a new location while pest populations are still restricted geographically and at low densities.

Rapid responses to incursions rely on the ability of scientists to make use of existing knowledge, and quickly provide decision-makers with ready-response capabilities (Bloem et al. 2014). Market drivers for reducing insecticide use for IPM also provide grounds for optimism for the future of SIT/IS implementation, particularly against high-value pests of export horticulture, where the absence of insecticide residues on fruit increasingly creates market value (Walker et al. 2017). These technologies are versatile, and can be used for pest management as well as for eradication goals.

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