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Transgenic crops and sterile insect releases are eco-friendly approaches for the management of major insect pests of crops

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Abstract: Transgenic crops, genetically engineered to express insecticidal crystal (Cry) proteins derived from the bacterium *Bacillus thuringiensis* (Bt), have revolutionised agricultural pest insect control and are now planted on more than a billion acres worldwide. The benefits of this method would be lost if resistance to the toxins spread to a significant proportion of the pest population. Classical biological control is a pest control tool involving the release of imported natural enemies. The sterile insect technique is a pest control strategy used to suppress or eliminate regional populations of insects that pose significant threats to agriculture or human health. The process involves mass-rearing, sterilization and release of male insects who fail to produce viable offspring when they mate with wild females, which leads to a population decline. The SIT has constantly proven its capacity to suppress, contain, prevent (re)introduction or even locally eradicate populations of selected key insect plant and livestock pests. However, there is also a continuous need to further refine and improve the efficiency as well as the cost-effectiveness.
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Introduction

Many insects in agro-ecosystems are considered to be major global pests causing significant economic harm. Arthropod pests cause an estimated >$470 billion in lost agricultural crops worldwide (Culliney, 2014). The main tool for controlling such pests is the use of insecticides, the global annual market value of which is projected to reach $16.44 billion by 2019. Insecticides will remain an important component of integrated pest management (IPM) programs but there are concerns about their off-target effects. Furthermore, resistance to insecticides is a growing problem, with 586 insect species known to be resistant to one or more insecticides (Sparks and Nauen, 2015; Zafar et al., 2020). Synthetic insecticides are widely used for control; however, potential off-target ecological damage, and the capacity of pest populations to develop resistance, has driven demand for alternative methods of pest control. Integrated pest management (IPM) approaches have been developed, utilizing multiple tools including biological insecticides (applied and expressed in transgenic crops), enhanced biological control, mating disruption, and the release of sterile insects (sterile insect technique, SIT) to sustainably manage insect pest populations. Other tactics will increasingly play a role in pest management in the future. Already the use of genetically engineered, insect-resistant crops (i.e., Bt crops expressing insecticidal proteins from the bacterium *Bacillus thuringiensis*) over the last two decades has played a major role in reducing the use of traditional insecticides in cotton, maize and other crops (James, 2017; Ren et al., 2019). As with traditional insecticides, however, the efficacy of Bt crops is threatened by the emergence of insects resistant to the Bt proteins expressed in them (Tabashnik and Carrière, 2017; Razzaq et al., 2021).

Genetic pest management goes beyond using genetically engineered pest-resistant crops and now includes genetic control of the pest itself. A predecessor of such methods is the sterile insect technique (SIT), in which sterile insects are released into wild populations of the same pest as a management intervention. This concept was independently conceived in the 1930s and 1940s by geneticist A. S. Serebrowskii in Moscow; tsetse field researcher F. L. Van der Planck in what is now Tanzania; and E. F. Knipling at the U.S. Department of Agriculture (USDA) (Klassen and Curtis, 2005; Kamber et al., 2022). Van der Planck and Serebrowskii focused on sterility resulting from hybrid crosses between different species or different genetic strains. Knipling pursued the use of ionizing radiation to induce dominant lethal mutations causing the effect of sterility in treated insects (Knipling, 1955). The most successful population control method in use today is the sterile insect technique. The SIT reduces target pest populations through sustained mass-releases of radiation-sterilized insects, thus reducing the frequency of mating between fertile insects. SIT relies on the mate-seeking and mating behavior of released insects, and is therefore species-specific and can be effective against pests that are difficult to control by other methods. SIT has been successful in area-wide eradication and suppression programs against numerous crop pests (Dyck et al., 2005; Qasim et al.,2022). Wider applicability of SIT is hindered by several challenges, including the negative effects on insect performance of sterilization by irradiation (Helinski et al., 2008; Rasheed et al., 2022) and difficulty in conducting large-scale sex-sorting for male-only releases (Haseeb et al., 2022). Sterilized insects are released into the wild where sterile males compete with wild males to mate with wild females. Since females of many pest insects only mate once in their lifetime, mating with a sterile male prevents successful reproduction. Sufficiently large releases of sterile insects can be used to eliminate wild populations or prevent their establishment in a new area. Also, SIT is considered safe to humans and the environment, as there are less off-target impacts compared to the application of chemical pesticides (Das et al., 2020). SIT programmes typically release both males and females, lacking a practical method to sort the sexes easily in large numbers. This is inefficient because the released sterile females and males tend to court and mate with each other rather than seeking out wild mates. Male‐only releases are generally more efficient than mixed sex releases, a large‐scale study of irradiated Medfly quantified this as being three‐ to five‐fold more efficient per male (Rendón *et al*., 2004). Early removal of females (eggs or early larval instars) in the generation destined for release also potentially saves on rearing costs as only the males need to be housed and fed.

Successful cases of SIT

As with other insects, the SIT/IS can be applied against Lepidoptera using different strategic approaches, e.g., suppression, local eradication, and containment strategies (Hendrichs et al., 2005).

Codling moth is the main pest affecting apples and pears worldwide. Most pest control strategies used against this insect have relied on the use of broad-spectrum insecticides which have led to non-desirable effects like pesticide resistance, residues in the environment, human health concerns and the reduction of access to international markets. Therefore, alternative pest control strategies that would result in sustainable fruit production systems while taking care of the environment are strongly promoted. The use of the sterile insect technique has proven to be a valuable pest control tactic within area-wide integrated pest management strategies, and its synergistic effect for Lepidoptera pests when combined with other biological control tactics such as parasitoids has been documented. The purposes of this research were to evaluate the response of an Argentinean codling moth strain to a sub-sterilizing radiation dose of 100 Gy and to assess the acceptability and suitability of sterile codling moth eggs by the egg parasitoids, Trichogramma cacoeciae (Marchal) and Trichogramma nerudai (Pintureau and Gerding). Irradiated female moths survived better than irradiated male moths and nonirradiated male and female moths. Also, the fecundity of irradiated female moths was reduced by more than 30% as compared to nonirradiated ones whereas their fertility was close to zero. The F1 generation was male biased with a lower fertility (inherited sterility) than the parental generation. Trichogramma cacoeciae and T. nerudai parasitized both fertile and sterile eggs. However, there was a significant reduction in acceptability for sterile eggs. Trichogramma nerudai parasitized more eggs than T. cacoeciae, but egg acceptability for this species was proportionally lower than for T. cacoeciae especially on eggs oviposited by irradiated females. Development to adult of both parasitoids species was not substantially affected by the origin of the eggs and the wasps had acceptable levels of adult emergence, survival and fecundity (Botto et al., 2010).

There are many successful examples of the integration of the SIT in AW-IPM programmes against Lepidoptera (Bloem et al. 2005; Carpenter et al. 2005). These include operational programmes for containment (pink bollworm Pectinophora gossypiella (Saunders) (USA)), suppression [codling moth Cydia pomonella (L.) (Canada) and false codling moth Thaumatotibia leucotreta (Meyrick) (South Africa)], or eradication [cactus moth Cactoblastis cactorum (Berg) (USA, Mexico), painted apple moth Teia anartoides Walker (New Zealand)] (Suckling et al. 2005; Carpenter et al. 2007; Hernandez et al. 2007). In addition, several pilot field projects have demonstrated the feasibility of using the SIT against the gypsy moth Lymantria dispar (L.), the tobacco budworm Heliothis virescens (F.), the corn earworm Helicoverpa zea (Boddie), the oriental fruit moth Grapholita molesta (Busck), the carob moth Ectomyelois ceratoniae (Zeller), and the Asian corn borer Ostrinia furnacalis (Guene´e) (Carpenter et al. 2005).

Tuta absoluta is one of the most devastating pests of Solanaceae crops in Africa. We previously demonstrated the efficacy of *Metarhizium anisopliae* isolates ICIPE 18, ICIPE 20 and ICIPE 665 against adult *T. absoluta*. However, adequate strain selection and accurate spatial prediction are fundamental to optimize their efficacy and formulations before field deployment. This study therefore assessed the thermotolerance, conidial yield and virulence (between 15 and 35 °C) of these potent isolates. Over 90% of conidia germinated at 20, 25 and 30 °C while no germination occurred at 15 °C. Growth of the three isolates occurred at all temperatures, but was slower at 15, 33 and 35 °C as compared to 20, 25 and 30 °C. Optimum temperatures for mycelial growth and spore production were 30 and 25 °C, respectively. Furthermore, ICIPE 18 produced higher amount of spores than ICIPE 20 and ICIPE 665. The highest mortality occurred at 30 °C for all the three isolates, while the LT_{50} values of ICIPE 18 and ICIPE 20 were significantly lower at 25 and 30 °C compared to those of ICIPE 665. Subsequently, several nonlinear equations were fitted to the mortality data to model the virulence of ICIPE 18 and ICIPE 20 against adult *T. absoluta* using the Entomopathogenic Fungi Application (EPFA) software. Spatial prediction revealed suitable locations for ICIPE 18 and ICIPE 20 deployment against *T. absoluta* in Kenya, Tanzania and Uganda. Our findings suggest that ICIPE 18 and ICIPE 20 could be considered as effective candidate biopesticides for an improved *T. absoluta* management based on temperature and location-specific approach (Agbessenou et al., 2021).

The OKSIR program is the longest-running, most successful, area-wide integrated pest program for the suppression of codling moth in the world, and its implementation is accompanied by continuing extensive research (Thistlewood et al., 2019). The SIT is integrated with orchard sanitation, surveillance, tree banding, and mating disruption. After more than 20 years of operation, the codling moth populations in the valley have been drastically reduced, and as a result, the growers, the industry, and the local community have significantly reduced fruit damage and costs associated with codling moth control. The program has achieved less than 0.2% damage in more than 90% of all commercial pome fruit acreage and reduced insecticide use to control codling moth by over 95% in the valley (from 50,000 kg of chemicals in 1991 to <3000 kg in 2015). In addition, the number of chemical sprays targeting codling moth has been reduced from 1.5–2.7 sprays/acre in the early 1990s to <0.3 sprays/acre in 2013 in the southern part of the valley. A recent cost–benefit analysis showed the economic efficiency of the program, i.e., a benefit to the producers from insecticide cost savings, monitoring cost savings and reduction in codling moth injury amounting to CAN $395/acre (versus CAN $377/acre for mating disruption). The economic benefits per acre of orchard were much higher using the OKSIR strategy as compared to using conventional insecticides: the overall cost–benefit ratio of the SIT program was 1.19 for the producer and 2.51 in total. The use of sterile moths against pink bollworm started as a containment program in 1968 to protect the cotton fields in the San Joaquin Valley of California. For more than 20 years, sterile moths were released every season, covering 0.4 million hectares of cotton that prevented the establishment of the pest (Staten et al., 1993).

There have also been a number of successful studies combining SIT and biological control for lepidopteran targets. The combined use of inheritedly sterile (sterile F1 adults) potato tuber moth, Phthorimaea operculella (Zeller) and Trichogramma spp. (oophagous parasitoids) in a laboratory trial was more effective in reducing fertile F1 P. operculella progeny than either technique used alone. Furthermore, the level of suppression attained by the combined releases was thought to be additive in effect (Saour, 2004). The authors predicted that because this reflected a single release, when multiple releases of sterile insects and Trichogramma occur, that synergism of treatment effects may be obtained and concluded that further work on the integration of these two control strategies was warranted. Field cage studies of sterile adult codling moth, Cydia pomonella (L.) along with the parasitoid Trichogramma platneri led to less apple damage than when either tactic was used alone (Bloem et al., 1998). In an earlier study, T. platneri were released in apple orchards using SIT against codling moth in British Columbia, Canada (Cossentine and Jensen, 2000). Combined use of parasitoids and SIT led to significantly lower codling moth damage compared with plots where T. platneri was not released. A further benefit of this integrated strategy was that the non-viable codling moth eggs produced by released steriles were suitable hosts for T. platneri and so contributed to persistence of the parasitoid population

Kumano et al. (2010), evaluated the effect of irradiation dose intensity on fertility, mating propensity, and mating competitiveness in sweetpotato weevil, Cylas formicarius elegantulus (Summers) (Coleoptera: Curculionidae), for 16 d after irradiation. Although the mating propensity of males irradiated with 200 Gy, the dose currently used to induce complete sterility of C. f. elegantulus in the SIT program in Okinawa Prefecture, was equal to that of nonirradiated weevils for the first 6 d, the mating propensity of males irradiated with doses between of 75 and 150 Gy was maintained for the first 12 d. The potential fertilization ability of weevils was highly depressed compared with the control weevils, even in those treated with 75 Gy. Mating performance was severely compromised in weevils that were irradiated with a dose of 100 Gy or more.

The success of area-wide pink bollworm management is highly dependent on participation by all segments of the agricultural community in the planning, site selection, implementation, and assessment phases of the programme. A highly effective extension-education communication programme is an essential component. The outstanding performance of *Bt*-cotton and pheromone behavioural control for pink bollworm, and the availability of historically-proven effective pink bollworm population suppression technologies (cultural controls, crop residue destruction, water management, planting dates, and sterile moth release), encouraged formulation of a multi-agency and transboundary pink bollworm eradication plan. The eradication programme was initiated in 2001-2002 in the El Paso/Trans Pecos area of Texas, in South Central New Mexico and in Chihuahua, Mexico. The results of area-wide suppression have been exceptionally encouraging and provide promising expectations for the other infested areas of the south-western USA and north-western Mexico. The pink bollworm population has been reduced to levels that can be targeted for sterile pink bollworm releases to pursue the goal of eradication (Henneberry et al., 2007). The sweet potato weevil (*Cyclas formicarius* Fabr.) remains a serious threat to sweet potato (*Ipomoea batatas* Poir.) production and is considered the most destructive pest of sweet potatoes in the field and storagein the Philippines. Chemical control of the weevil is seldom practiced by farmers because they find it too costly, it may increase the chance for pesticide resistance, and because of public concern of its effectson non-target organisms. The use of biological controls such as entomopathogenic nematodes (EPN) could offer an effective, economical, and environmentally-friendly alternative management of the weevil. This study determined the occurrence and distribution of entomopathogenic nematodes in selected sweet potato growing areas in the Philippines. Using soil from 13 sweet potato growing areas, EPNs were recovered using the insect baiting method. Morbid insect larvae were suspended in sterile water for 48 h, and the suspension was examined under a stereomicroscope for the presence of EPN. Out of 47 samples collected from the 13 sweet potato production areas, 39 (82%) were positive for the presence of EPNs. Preliminary identification of the EPNs through morphological characters showed that they belonged to Rhaditida: Heterorhabditidae and Steinernematidae.

Horrocks et al (2020) investigated the irradiation biology of *N. viridula* for the potential application of SIT against this pest. Male and female *N. viridula* were gamma-irradiated at doses between 4 and 28 Gy and mated with both irradiated and nonirradiated conspecifics. Sterility of the resulting eggs followed a dose-response in each case. Irradiated males crossed with untreated females showed higher F_1 egg sterility than crosses where the female was irradiated. The greatest F_1 egg sterility was observed when both parents were irradiated. There was no obvious dose-response for the longevity of irradiated males, and for the fecundity of nonirradiated females mated with irradiated males. The fecundity of irradiated females appeared to decrease with irradiation dose. These results can be applied to a potential future application of SIT against *N. viridula*, but predominantly supports the ongoing development of SIT for *Halyomorpha halys* Stål (Hemiptera: Pentatomidae) and hemipteran pests in general.

Populations maintained on *Bt* broccoli alone expanded rapidly after strong selection for *Bt* resistance. However, low rates of OX4319L male release in combination with *Bt* broccoli significantly reduced population growth, controlling the target populations well when each treatment on its own failed to do so. This apparent synergistic effect supports model predictions that introgression of susceptibility alleles into a target population by released transgenic males could prevent or reverse the spread of resistance, thereby preserving susceptibility to *Bt* toxins (Alphey et al., 2009). Introductions of MS-engineered P. xylostella males into wild-type populations led to rapid pest population decline, and then elimination. In a separate experiment on broccoli plants, the release of relatively low level of MS males in combination with broccoli expressing Cry1Ac (Bt broccoli) suppressed population growth and delayed the spread of Bt resistance (Harvey-Samuelet al., 2015).

Conclusions

To be sustainable, agriculture needs to adopt a broader IPM approach to reduce reliance on insecticides. The sterile insect release method and other autocidal control techniques are completely compatible with other types of insect control that might be used in IPM programs.

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