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PERSPECTIVES AND PARADIGMS

Global range expansion of pest Lepidoptera requires socially acceptable solutions

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Abstract Caterpillars of key moth pests can cause significant losses in cropping systems worldwide, and globalization is spreading such pests. Failure to control some species can jeopardise the economics of food production. A Global Eradication and Response Database (http://b3.net.nz/gerda) was reviewed on known government-level incursion response programs specific to invasive Lepidoptera. Geographic range expansion of Lepidoptera was evident from 144 incursion response programs targeting 28 species in 10 families. The countries involved in responses to Lepidoptera were USA (104), Australia (8), Canada (7), New Zealand (6), Italy (3), Mexico (2), with the remainder with one programme each (Brazil, Czech Republic, France, Hungary, and Spain). Most programs have been undertaken since the 1990's. Control options exist for the long-term management of Lepidoptera, but most have issues of cost, efficacy or non-target impacts that reduce their acceptance. Pheromone-based technologies are increasingly available and are generally highly compatible with other tactics. The development of tactics for new targets is a major undertaking, although previous programs can be invaluable. New and improved

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socially-acceptable technologies are needed to counteract range expansion in Lepidoptera, and usually need to be used in combinations to achieve eradication. The sterile insect technique, which involves mass-rearing and release of sterile insects to reduce wild populations of the pest, has been used successfully against a number of lepidopteran species. Several sterile moth programs are under development. New technologies must have a social license to operate in urban areas, where new incursions are frequently detected. This factor is likely to reduce tactical flexibility and increase the complexity of insect eradication.

Keywords Lepidoptera · IPM · Eradication · Suppression · Tactic · Sterile · Pheromone

Introduction

In the past decade, numerous invasive insect pest species have emerged and continue to emerge as a threat to food production and ecosystem health as a consequence of global trade and climate change (Levine and D'Antonio 2003; Liebhold et al. 2016). Lepidoptera include key insect pests that require control to avoid significant losses in many cropping systems in temperate, sub-tropical and tropical regions of the world (Vreysen et al. 2016). Failure to control these species can have serious consequences for the economics of production, including failure of the crop worldwide (Vreysen et al. 2007). Like other arthropod pests, many Lepidoptera are undergoing geographical range expansion (Lopez-Vaamonde et al. 2010). Some pests, such as diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) have already become ubiquitous global pests. Many moth pests are still undergoing geographic range expansion. A recent European review reported that 97 non-native Lepidoptera species in 20 families have established so far in Europe and 88 European species in 25 families have expanded their range within Europe, with 74% established during the 20th century (Lopez-Vaamonde et al. 2010). As part of a project identifying factors affecting outcomes from arthropod eradication efforts (Liebhold et al. 2016; Tobin et al. 2014), a global eradication database called "GERDA" (Kean et al. 2016) has recorded 28 lepidopteran species that were the target of 144 known government-led incursion responses (Table 1; Fig. 1), with effort spread across 12 moth families, dominated by the Lymantriinae and Tortricidae. The data, scope and definitions used in the database are available (www.b3nz.org/gerda), reviewed here for Lepidoptera. Government-led incursion response programs, usually targeting eradication, represent a high decision threshold for entry due to cost, and normally mean that a risk analysis has been conducted to assess whether the establishment of the unwanted organism is likely to exceed an economic, environmental or social impact threshold (Tobin et al. 2014). Assembly of the developing data set of responses to invasive Lepidoptera is therefore proposed as a guide to trends in this key threat group, since such response programs are typically multi-million dollar in size (range US$ 2–94 M in non *Lymantria* programs, normalised to 2012).

For European gypsy moth *Lymantria dispar dispar* (L), there is a large history of government responses (particularly since 1980), comprising 66% of entries in GERDA which can be analysed separately (Fig. 1). It is evident that a recent expansion of responses has occurred for other species (10 cases from 1900 to 1990, and 33 responses arising since 1990, Fig. 1). The countries involved in responses to all Lepidoptera incursions were USA (104), Australia (8), Canada (7), New Zealand (6), Italy (3), Mexico (2), with the remainder with one programme each (Brazil, Czech Republic, France, Hungary and Spain).

A total of 42 non-lymantriin eradication programs recorded in GERDA include species such as the tomato leafminer, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), a key and expanding threat to tomato production in the Mediterranean, reported in 2016 by EPPO as detected or transient and under eradication (UK, Austria, Czech Republic, https://gd.eppo.int/taxon/GNORAB/distribution). Likewise, the old world bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), a severe pest of cotton, has recently been detected in South American and Caribbean countries (EPPO Global Database, https://gd.eppo.int). The European grapevine moth, *Lobesia botrana* Denis & Schiffermüller (Lepidoptera: Tortricidae) has been detected in the USA and Chile (Gilligan et al. 2011) and affects grapevine production in many Mediterranean countries. The light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Torticidae), a polyphagous horticultural leafroller pest

Table 1 Cases of 144 incursion responses against 28 species in 12 families of Lepidoptera, recorded in the global Eradication Database (GERDA, http://b3.net.nz/gerda, with indications of dose response or sterile insect field release (seven species))

Moth species	Common name	Family	No. of reported incursions
Lymantria dispar dispar[a,b]	European gypsy moth	Lymantriinae	78
Lymantria dispar asiatica[a]	Asian gypsy moth	Lymantriinae	18
Cydia pomonella[a,b]	Codling moth	Tortricidae	9
Paysandisia archon	Palm moth	Castniidae	4
Epiphyas postvittana[a,b]	Light brown apple moth	Tortricidae	4
Duponchelia fovealis	European pepper moth	Pyralidae	3
Tuta absoluta[a]	Tomato leafminer	Gelechiidae	2
Euproctis chrysorrhoea	Brown-tail moth	Lymantriinae	2
Helicoverpa armigera[a]	Old world bollworm	Noctuidae	2
Thaumetopoea pityocampa[a]	Pine processionary moth	Notodontidae	2
Thaumetopoea processionea[a]	Oak processionary moth	Notodontidae	2
Cactoblastis cactorum[a,b]	Cactus moth	Pyralidae	2
Lobesia botrana[a, b]	European grapevine moth	Tortricidae	2
Hyphantria cunea[a]	Fall webworm	Arctiidae	1
Ostrinia nubilalis[b]	European corn borer	Crambidae	1
Pectinophora gossypiella[a,b]	Pink bollworm	Gelechiidae	1
Conopomorpha cramerella	Cocoa pod borer, cocoa moth	Gracillariidae	1
Spulerina isonoma	Mango stem miner	Gracillariidae	1
Dendrolimus pini	Pine tree lappet moth	Lasiocampidae	1
Lymantria umbrosa	Hokkaido gypsy moth, dosanko gypsy moth	Lymantriinae	1
Orgyia thyellina	White spotted tussock moth	Lymantriinae	1
Teia anartoides[a,b]	Painted apple moth	Lymantriinae	1
Spodoptera litura[a]	Tropical armyworm	Noctuidae	1
Uraba lugens	Gum-leaf skeletoniser	Noctuidae	1
Pieris brassicae[a]	Large white cabbage butterfly	Pieridae	1
Citripestis eutraphera	Mango fruit borer	Pyralidae	1
Opogona sacchari	Banana moth	Tineidae	1
Grapholita molesta[a]	Oriental fruit moth	Tortricidae	1
Total			144

[a] Dosimetry recorded by the Joint FAO/IAEA Programme of Nuclear Techniques in Food and Agriculture (http://nucleus.iaea.org/ididas/TaxonomicTree.aspx)

[b] Field releases have been undertaken on these species [15]

has recently spread in California (Suckling et al. 2014a), while the cactus moth, *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae) is spreading in the southern USA towards Mexico (Hight et al. 2002), where it threatens endemic and valued cacti (Bloem et al. 2007a). The spotted sugarcane borer, *Chilo sacchariphagus* Bojer (Lepidoptera: Crambidae) is locally spreading along the eastern coast of Africa in Mozambique, and is present in the Indian Ocean islands of La Réunion, Madagascar and Mauritius (Conlong and Way 2015). The African sugarcane stalk borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae) is reported as difficult to control in maize in West African countries, and in sugarcane in South Africa, Zimbabwe, Tanzania and Uganda (Assefa et al. 2006; Conlong and Way 2015). These cases are a mixture of introductions and regional spread, and illustrate global and regional scales of range expansion and do not always involve eradication responses which depend on the jurisdiction and geolocation.

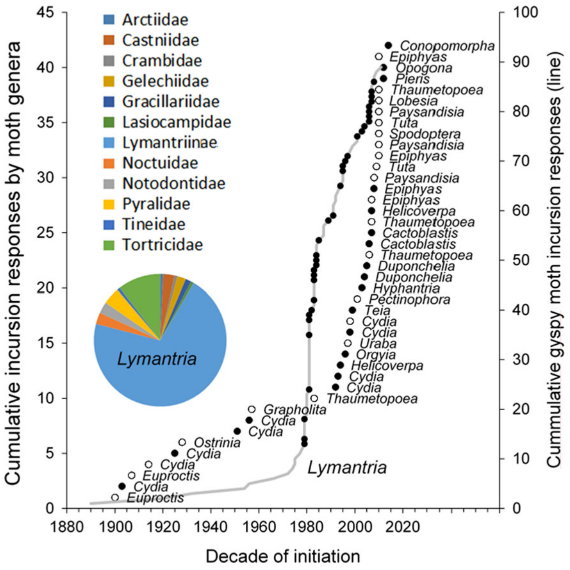

Fig. 1 Commencement dates of government incursion responses to Lepidoptera by decade, for gypsy moths (*Lymantria, grey line*), compared with other genera of Lepidoptera (*filled circles* indicate successful eradications, *opened circles* are failures or ongoing). *Pie chart* shows distribution by family

Analysis of control options for Lepidoptera

There is broad international consensus that the management of these key pests is ideally based on the concept of area-wide integrated pest management (AW-IPM) (Klassen 2005), i.e., control tactics should be integrated based on their suitability for a given pest and local ecological characteristics, and the control tactics should be targeting an entire insect population (total population control). Lepidopteran pests have been predominantly managed for decades by application of broad-spectrum and often persistent insecticides, but a wider range of classes of insecticides is potentially available today for use in eradication (Bloem et al. 2014). This management approach has enormous direct and indirect economic, social and environmental consequences and is considered unsustainable in the long term as many lepidopteran pest species have developed resistance to insecticides, including more benign low hazard materials, although this risk may be overstated (Sparks et al. 2012). Many effective but older broad-spectrum insecticides are being phased out in use, due to increased recognition of the long-term effects of their excessive use on human health and the environment. Finally, there is increasing market pressure to reduce insecticide residues on food.

Each suppression tactic that can be used to manage these lepidopteran pests has advantages but also limitations, e.g. some have issues of cost or efficacy, justifying a search for alternatives. Others may be inversely-density dependent and require a population knockdown before they are practical. In addition, usage during an eradication programme in urban environments may also face different acceptability from agriculture (Suckling et al. 2014b). For example, while insecticides are widely used in agriculture, their aerial use during an eradication or even suppression campaign in urban areas can be problematic.

The use of sex pheromones remains an ideal tactic for the management of invasive Lepidoptera, more than for any other group of insects, as there are so many leads already developed in the pest management literature, and the same targets are often invasive (Suckling 2015). Mass trapping and lure and kill options rely on a supply of the attractant (El-Sayed et al. 2006), which is more likely for known pests than novel invasives. Mating disruption can be effective where the technology has been developed, but is comparatively expensive, labor intensive, has issues with edge effects/topography in relation to efficacy, and is most widely adopted in horticulture in developed countries (Witzgall et al. 2010). However, mating disruption has been used in eradication programs against five species/subspecies of Lepidoptera (Lance et al. 2016; Suckling 2015). There are emerging versatile semiochemical technologies with formulations for aerial or ground application, enabling rapid development in future (Brockerhoff et al. 2012; Lance et al. 2016; Mafra-Neto et al. 2014).

Classical biological control using egg or larval parasitoids has been widely investigated for the management of many invasive insect pests (Gurr and Wratten 2000), but is usually inadequate alone in suppressing the pest below the economic threshold. The host species specificity of natural enemies on Lepidoptera needs to be demonstrated before release to avoid possible negative impacts on non-target arthropod species, or to avoid establishment of the parasitoid becoming a pest themselves (Munro and Henderson 2002). Biopesticides such as *Bacillus thuringiensis* kurstaki and baculoviruses can be made effective for some pests, although commercial availability, cost, efficacy and the evolution of resistance can be problematic (Glare and O'Callaghan 2000; Tabashnik et al. 2012). Cultural controls such as sanitation can also be used as part of integrated pest management approaches where intensive field surveys may occur (Stephens et al. 2007), although sanitation or host removal is only considered effective when integrated with other control tactics.

The sterile insect technique (SIT) has been used successfully against moth pests by mass-rearing and release of sterile insects to overflood the wild population (Vreysen et al. 2016). The ongoing area-wide suppression of codling moth in apple and pear orchards of the Okanagan Valley of British Columbia, Canada has used the SIT along with other tactics (Bloem et al. 2007b) and there is potential to expand this approach for pest management in Canada, Europe, New Zealand, South Africa, and South America. Field trials commenced in New Zealand in 2014 involving the release of sterile Canadian codling moths in combination with mating disruption (Horner et al. 2016), where the target is market access, in a pilot program testing the potential for local eradication.

An AW-IPM suppression approach that integrates the SIT has also been successful in the private sector management of the false codling moth, *Thaumatotibia* (*Cryptophlebia*) *leucotreta* (Meyrick) (Lepidoptera: Tortricidae) in South African citrus orchards (Carpenter et al. 2007; Hofmeyr et al. 2015) (http://www.xsit.co.za). Small scale releases of sterile *Lobesia botrana* were planned by the government in Santiago, Chile in September 2016 (H. Donoso pers. comm.) and were also conducted in Los Angeles by USDA APHIS with sterile *E. postvittana* (G. Simmons pers. comm).

While concepts and technologies of SIT for one species can often provide a basis for developing methods for another species, technology development and adaptation is needed each time a new species is targeted. Even within a species, scaling up from pilot to operational, or simply moving into a new rearing facility, can generate problems that have to be solved. The SIT acts with inverse density dependence, and becomes therefore more efficient with lower densities of the target population. The most effective approach therefore, is to combine the SIT with control tactics that are more effective at high population densities–the ideal efficiency pattern in AW-IPM strategies. In addition, the SIT combines well with other control tactics such as parasitoids and the combination can even be synergistic where tactics interact positively (Suckling et al. 2012). Bi-sex sterile moth releases and egg parasitoid inundation may exhibit greater complementarity than other combinations of methods, since their optimal action is at opposite ends of the host density spectrum and they do not in any way interfere with each other unless adult hosts are parasitized (Barclay 1987). Genetic modification can target marking or sterility of Lepidoptera, which could accelerate response and eradication outcomes (Simmons et al. 2007; Thomas et al. 2000).

Combinations of tactics

The integration of area wide tactics has been successfully used for the suppression, containment and eradication of moth pest populations (Bloem et al. 2005), but the small number of moth eradication programs means that information gained from long term pest management programs should not be overlooked. Strategies for integration of tactics vary between insect orders (Suckling et al. 2014b), although there are several socially-acceptable tactical options for Lepidoptera under development, which have been combined in various ways to target suppression of either gypsy moth or other moth species. Many different combinations have been used against gypsy moth and other pests, sometimes successful but other times not, but with an improving success rate over time if the ongoing cases are removed (Fig. 1). The use of more tactics has generally produced more success (Fig. 2), according to a two way ANOVA for success in *Lymantria* and non-*Lymantria* cases ($F_{3,1,3} = 9.62$ and $P < 0.05$ for number of tools and $F_{3,1,3} = 7.19$ and $P = 0.08$ for

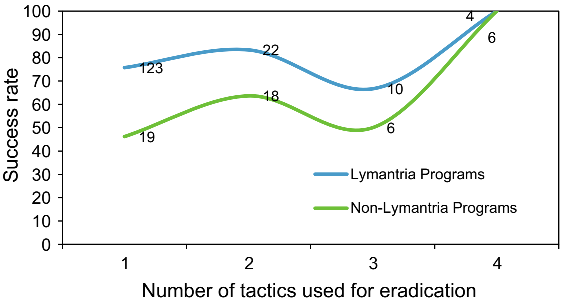

Fig. 2 Effect of tactical combinations on eradication success in *Lymantria* and other Lepidoptera (numbers are the sample size of known programs). *Source* www.b3nz.org/gerda

moth type). The main tactics identified in previous programs against Lepidoptera include pesticides and biopesticides, host removal, sterile insect release and pheromone-based tactics (mating disruption, lure and kill and mass trapping). However, an additional component to consider is the time taken for the development of each tactic and the steps needed for implementation (Fig. 3), which may need to take place during an emergency response. A ranking and comparison of what is involved in the development of these tactics for new targets is generalised from the example of the painted apple moth eradication in Auckland (Suckling et al. 2007). For codling moth, most of the recorded eradications were in Western Australia, and generally involved host destruction, requiring several years.

Undoubtedly, the most impressive example of the integrated approach is the eradication of the pink bollworm, *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) from the southern USA and northern Mexico using an AW-IPM approach that combined Bt cotton, sterile insect release and mating disruption (Tabashnik et al. 2012). Other examples of successful AW-IPM programs that included a SIT/IS component include the eradication of the Australian painted apple moth, *Teia anartoides* Walker (Lepidoptera: Lymantriinae) from urban Auckland, New Zealand (Suckling et al. 2007) and *C. cactorum* from Isla Mujeres and Isla Contoy in Mexico (Bloem et al. 2007a). Clearly, despite several successful cases, the technology is contributing below its potential in an area with an expanding challenge for global food security. A diagram illustrates a simplified decision tree for use of SIT based on essential components (Fig. 4). The remainder of this article will focus on sterility in Lepidoptera, as this technology has much potential for use in suppression or eradication strategies, especially in combination with sex pheromones, biopesticides and other tactics (Carpenter et al. 2005).

Sterile with competitive field performance

Despite the successes of operational field programs and the availability of generally encouraging results from pilot field releases of a range of moth pest species (Table 1), there are remaining issues pertaining to the competitiveness of the released insects that require further investigation to increase the efficacy and cost efficiency of the SIT against lepidopteran pests. Some

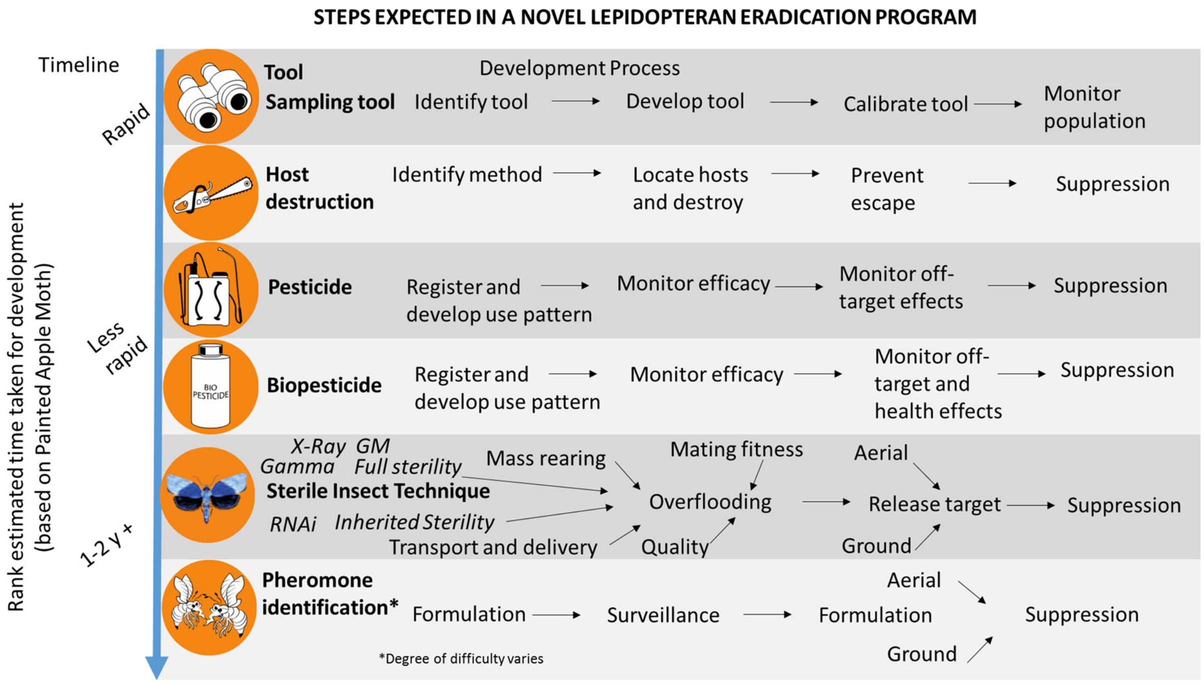

Fig. 3 Schematic diagram of generic steps expected in the potential development of eradication tools for Lepidoptera, based on painted apple moth (Suckling et al. 2007)

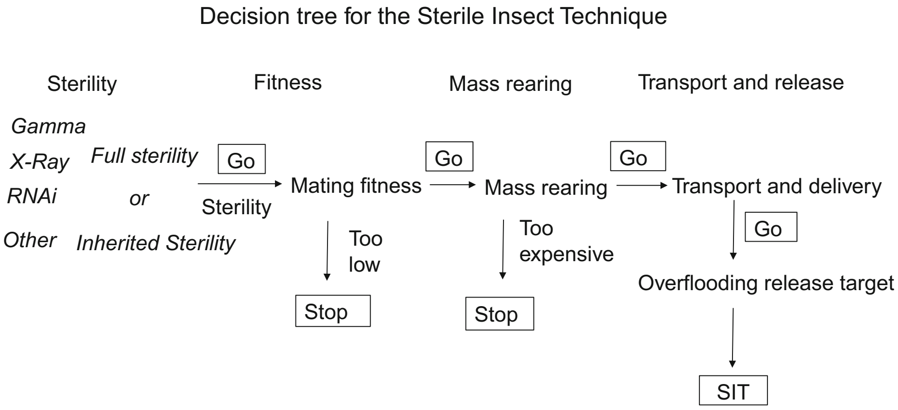

Fig. 4 Decision tree on the suitability of the Sterile Insect Technique for use in an eradication or population reduction program

of these critical aspects were addressed in an FAO/IAEA coordinated research project entitled "Increasing the efficiency of Lepidoptera SIT by enhanced quality control" which was implemented between 2008 and 2014, and reported in a special issue of the Florida Entomologist (Vreysen et al. 2016). The use of the SIT has been limited to only a few operational programs against Lepidoptera for long term pest suppression (codling moth in Canadian apples and false codling moth in South African citrus) or eradication (pink bollworm in US cotton, Australian painted apple moth in urban New Zealand and cactus moth on islands in Mexico) (Bloem et al. 2005) but assessment of moth quality was investigated on a wider range of species (Simmons et al. 2010; Vreysen et al. 2016). The SIT requires mass-rearing and release of sterile insects with competitive field performance, which creates a major threshold for entry through the need for a specialised factory, which is a capital cost hurdle that in part explains the small number of cases (Fig. 4). While there is pre-requisite information on irradiation dose–response effects for many moth pest species, the overall effects are not necessarily sufficiently understood for practical purposes at the program level. There are key factors and variables in the rearing and release processes that affect the quality of the moths and their field performance that need further research and development (Simmons et al. 2010).

Other factors affecting the outcome

SIT may not be appropriate when there is no artificial diet and rearing system, sterility has too great an impact on fitness or other logistical factors limit the application (Fig. 4). Thus factors other than irradiation can influence the outcome of a programme with a SIT component. Mass-rearing, handling and transport methods all have critical impacts on the quality and performance of insects (Fig. 4), and these are major practical issues requiring more research (Simmons et al. 2010). Insect quality can be gradually degraded during all these processes up to a point where the sterile insects are no longer competitive with wild insects. There are many quality measures showing reduced competitiveness of irradiated insects, which can be used to determine the over-flooding ratio of sterile to wild insects needed. These factors would be just as important for programs using other sources of marking and sterility, from transgenic (Simmons et al. 2011) to RNAi (Schetelig et al. 2012), although this has not always been acknowledged or perhaps understood by proponents of these technologies (Alphey 2000; Knipple 2013). Hence there is a need to link production, handling and transport more closely with behavioral traits, and to select for traits that might improve field performance, such as mating or flight propensity at particular times or temperatures (Sørensen et al. 2012). This can be achieved by introducing selection for desirable traits into rearing procedures, similar to those for maintaining other traits (Fisher and Caceres 2000). Although this can be complex and management intensive to implement in an operational programme, it is likely to increase the probability of technical and financial success, as has been shown with programmes against the Mediterranean fruit fly (McInnis et al. 2002). New genetic methods could be developed to mark fitness traits easily, and maintain appropriate genetic diversity in colonies.

In Lepidoptera, adult irradiation may give better field performance of sterile males, but can potentially be less practical and more damaging than transport of pupae, which can offer more flexibility for programs (Blomefield et al. 2011; Soopaya et al. 2011; Suckling et al. 2005). Irradiation and shipment of pupae may have logistical and other advantages over shipment of adults depending often on the distance between the mass-rearing site and the target release area, but most programs against Lepidoptera have used adult irradiation to date (Bloem et al. 2005). Some of these programs faced issues of stockpiling insects, synchrony, losses during extended storage, and other tradeoffs. Placement of irradiated pupae to emerge in the field has been done experimentally, but requires adequate protection from predation (Stringer et al. 2013). The Australian painted apple moth program in New Zealand was an operational example using pupal irradiation (Suckling et al. 2007) and this approach was also explored for gypsy moth (Reardon and Mastro 1993). Although not implemented anywhere, adult moths could also be irradiated at satellite emergence and release facilities after pupal shipment (assuming appropriate diets and rearing systems are developed), possibly by X-ray.

Operational strategies

Despite attempts to model the effects of bi-sex or male-only releases of moths that suggested little benefit from females (Kean et al. 2011), there is evidence for a background contribution of the female moths through communication disruption of males from calling virgin females, despite their irradiation-reduced attractiveness and pheromone titre (Stringer et al. 2013; Suckling et al. 2006). Further, it has been suggested that there may be a benefit from sterile females acting as a “sperm sink” for wild males thereby reducing wild male fertility, which could contribute to part of the observed effect of population suppression. Although it remains unclear whether bi-sex releases are superior to male-only releases of moths, there is no risk of commodity damage from oviposition by sterile female moths, as unlike fruit flies, these species do not pierce the fruit. In fact, oviposition and the production of F_1 sterile adults is a key component of inherited sterility, and offers several benefits over releases of fully sterile parental individuals (Bloem et al. 2005). In particular, successful sterile males mating a wild female produce a large number of offspring biased towards males (depending on dose) and sterile at F_2. It may be necessary to take crop damage from F_1 larvae into account (LaChance 1985), although during an eradication this should be of short duration. In addition, a synergistic benefit of the combination of two tactics has been demonstrated to occur, for example where sterile eggs oviposited by released sterile females have been shown to enhance the numerical response of egg parasitoids (Bloem et al. 1998; Cossentine and Jensen 2000).

As with fruit flies, male-only release of moths might reduce costs, including rearing, handling, shipping and release costs. Currently, the lack of any effective genetic sexing strain in Lepidoptera for production of males alone presents a limitation, although sorting of the sexes at pupal or adult stages might enable release of separate sexes, offering similar benefits. Females can be used for baiting traps, as was done in the painted apple moth eradication program in New Zealand, which used sterile male-only release after manual sorting of larvae (Suckling et al. 2007). Collection of pupae and sorting by sex if possible would reduce or avoid mating before adult collection and release, which represents a source of inefficiency. Sorting options with less than complete separation of sexes might still be practical if significantly skewed sex ratios provided sufficient benefit from male dominant release. Anoxia and other treatments during irradiation could decrease the somatic damage and hence improve sterile moth quality and their field performance. Moths are often irradiated under chilled conditions, and this process needs to be optimized. The impact of temperature shocks during rearing warrants investigation for some species (Chidawanyika and Terblanche 2011). There is also an upper limit to the practical duration of shipping before release (60–80 h in the case of irradiated codling moth adults at 0.5 °C) (Blomefield et al. 2011; Horner et al. 2016).

Transport and release methods that avoid degradation by physical damage can significantly improve the performance of sterile insects in the field. Ground release of chilled moths that take some time to warm up and fly could lead to significant losses from predation or other sources (Stotter and Terblanche 2009). Negative effects of ground release of chilled moths on their quality might be mitigated by aerial release, allowing the insects to warm up, become active and settle into the canopy before reaching the ground.

It remains a challenge to have suitable unbiased standard methods for measuring moth quality at the factory and after transport and handling. This is important for the interpretation of field performance, to understand measures like trap catch. For example, Judd and Gardiner (2006) found that non-irradiated mass-reared codling moths were recaptured about four-fold less often than non-irradiated wild moths released under identical conditions. Potential differences in responses between wild and diet-reared insects could provide a misleading source of feedback on sterile moth performance to program managers, leading to potentially expensive and suboptimal decisions. Laboratory, semi-field and open field methods need to be aligned to help ensure overflooding ratios are adequate, or there is a risk of unwanted population growth despite assumed adequate insect release densities. Other new methods could be used to support field programs, including direct assessment of the frequency of F_1 sterile progeny by histology (Carpenter et al. 2009) or other methods, although this may require living or freshly-dead insects (Wee et al. 2011). Female moth attractants are increasingly emerging as a population sampling and control tool (e.g. El-Sayed et al. 2013; Landolt et al. 2007; Light 2016).

Population modelling for decision support

Modelling approaches can help field programs with an SIT component by optimizing field deployment of the sterile insects (Barclay et al. 2011; Kean et al. 2011; Potgieter et al. 2013). Deployment strategies can have a large impact on the outcome of sterile insect release programs because of insect aggregation (Kean et al. 2007). Population models suggest that there is a risk of program failure unless over-flooding ratios remain above critical threshold values throughout the target area, including the hotspot, or areas of local high density (Kean et al. 2007). Variance in over-flooding ratios can be minimized by the identification and incorporation of information of the location and density of hotspots along with different crop ages (Potgieter et al. 2013). This problem is amenable to spatially-explicit modelling, to overcome naturally occurring aggregations, by directing releases appropriately to improve efficiency. Combinations of tactics such as the SIT and mating disruption, Bt crops, a heterogeneous agricultural crop landscape (Potgieter et al. 2014) or a range of alternatives, can theoretically lead to more efficient outcomes if the tactics can be made to work together synergistically (Suckling et al. 2012). These approaches can also be modeled to investigate interactions (Blackwood et al. 2012; Kean et al. 2011) and male calling and lek behavior (van Vuuren et al. 2015). Variance in overflooding ratios could potentially be minimized by the identification and incorporation of information of the location and density of hotspots. Other tactical combinations also warrant investigation where eradication is sought, since all methods can help to reduce populations and enable Allee effects to operate best (Liebhold et al. 2016). The use of global positioning and global information systems (GPS/GIS) has introduced considerable improvements in control tactics of fruit flies due to the feasibility of mapping movement of pests, hotspots, reservoirs as well as phenological and physical barriers so its deployment should be a must for Lepidoptera control programs. Additionally, the economic implications of different SIT deployment approaches can be compared taking into account aggregation (Potgieter et al. 2013; Wee et al. 2011).

Conclusions

Global range expansion is evident in pest Lepidoptera from data (which are undoubtedly incomplete) available so far in GERDA. For gypsy moth, there was an increase in the US response programs to slow-the-spread from the 1980s onwards (Sharov et al. 2002). For other Lepidoptera, an increase occurred from the 1990s, with 75% of the government response programs established since then (a tenfold increase per decade). Expansion of effort in pest management has no doubt also occurred against aggressive species such as *T. absoluta* (Desneux et al. 2010), where ranges expansion in Europe has occurred without government response programs targeting eradication.

Eradication and/or effective suppression of Lepidoptera is likely to be more successful when more tactics are available, including pheromone-based tactics, the SIT, biopesticides and other alternative options. The development of a range of socially-acceptable control tactics is much needed to combat the spread of invasive Lepidoptera, including many known pests with potential for increased impacts on food production if established more widely.

However, maintaining the highest quality of insects mass-reared, sterilized and transported for release is crucial to success with counterattacks based on sterile insects, independent of source of sterility. Key areas for further development include determining the relative effectiveness of different methods for quality assessment and performance comparison of sterile and wild moths. This can be done by determining the impact that different rearing performance parameters, rearing practices and behavioral traits have on competitiveness of sterile moths, through correlation of laboratory and semi- and open-field performance (Suckling et al. 2011; Woods et al. 2016). Knowledge is needed on the impact of timing of adult and pupal collection and irradiation on field competitiveness, as well as the role of sterile females on population suppression. Further needs include the development of best practice methods of handling, transporting and releasing sterile moths to maintain field competitiveness, in particular considering the option of long distance shipment. In addition, it would be valuable to develop best practice deployment of sterile insects in relation to hotspots (Kean et al. 2007), taking into account insect quality and performance and spatial variation in density (i.e., determine appropriate and dynamic sterile: wild release ratios for population suppression). It would also be valuable to know more about the type and role of microorganisms/symbionts in Lepidoptera egg and larval development, to improve rearing and handling practices, and potentially lead to new complementary control tactics. Workers in all these fields are encouraged to contribute their knowledge to the development of the SIT and other tactics for invasive species such as those discussed here.

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