Research Article

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Exploration of the potential of a boosted sterile insect technique to control fruit flies in mango orchards

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Abstract

BACKGROUND: An innovative version of the sterile insect technique (SIT) for pest control, called boosted SIT, relies on the use of sterile males coated with a biocide to control a target wild pest population of the same species. The objective of the present study was to assess the relevance of such technology to control the fruit fly *Bactrocera dorsalis* and fruit losses in mango orchards using. An agent-based simulation model named BOOSTIT was used to explore the reduction of fruit losses thank to sterile male fruit flies control and economic benefits according to different strategies of sterile male release. The simulation considered a landscape of 30.25 ha made up of four mango orchards.

RESULTS: The SIT and the boosted SIT reduced fruit losses when releases were made before the mango fruiting period. According to model simulations, releases should be performed at least seven times at 2-week intervals and with a sterile/wild male ratio of at least 10:1. Considering the benefit/cost ratio (BCR), few releases should be done with a late start date. The BCR showed economic gains from the two control methods, the number of saved fruits and BCR being higher for SIT.

CONCLUSION: Our simulations showed that SIT would have better results than the boosted SIT to contribute to an effective control of *Bactrocera dorsalis* at the scale of a small landscape. We highlight the need for laboratory studies of other types of pathogen to find a suitable one with higher incubation time and lower cost.

Keywords: biological control; *Bactrocera dorsalis*; SIT; boosted SIT; *Metarhizium anisopliae*

1 INTRODUCTION

The sterile insect technique (SIT) is a species specific, preventive, and environmentally-safe method for the areawide management of insect pest populations through the release of sterile males leading to a decrease of reproduction.[1] The SIT successfully eradicated the New World screwworm *Cochliomyia hominivorax* (Coquerel) in 1954 in Curaçao, North America.[2] Since then, several insect pests such as fruit flies [e.g., *Ceratitis capitata* (Wiedmann,1824) in Mexico and Guatemala,[3] *Bactrocera cucurbitae* (Coquillett, 1899) in Okinawa, Japan,[4] *Bactrocera* spp. in Thailand[5]], mosquitoes [e.g., *Culex quinquefasciatus* (Say, 1823) in Florida,[6] *Aedes albopictus* (Skuse, 1894) in La Réunion[7]] or lepidopterans [e.g., *Cydia pomonella* (Linnaeus, 1758) in British Columbia[8]] have been targeted. An innovative way of using sterile insects has been called boosted SIT.[9] It relies on the use of sterile males as vectors of biocides into the wild target pest population of the same species.[9,10] They would contaminate wild females during mating, but can also contaminate wild males during lekking, adding a 'boost' to the SIT that just relies on sterility conferred to wild flies.

Upstream research efforts on the life system of target pests are needed to optimize the implementation and performance of the SIT or boosted SIT. Research goals include better knowledge of the (i) population dynamics of the target pest, which generally fluctuates both in time and space in relation to the changing environment, (ii) mating system and breeding areas, and (iii) dispersal patterns.[11] In this context, the development and analysis of simulation models are very useful to shed light on critical implementation issues such as when, where, how often, and how many sterile males should be released. Modelling is a relevant tool as it can generate scenarios that can reduce uncertainty and guide field experiments. Many mathematical models have been proposed to explore the performance of release strategies.[12–15] In these

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models, a focus was generally placed on biophysical factors such as quantity and mating competitiveness of sterile males *versus* wild males,[16,17] dispersal of sterile males,[18,19] environmental context,[20,21] technical factors for the integration of SIT with other pest control methods[22,23] or economical ones in cost and benefit analyses.[24] Until now, few studies have been devoted to the boosted SIT. Pleydell and Bouyer[25] used mathematical modelling to analyse the efficacy of SIT, boosted SIT and auto-dissemination for controlling *Aedes* vectors and *Aedes* borne diseases. They showed that boosting SIT with pyriproxifen as the killing agent could reduce by over 95% the number of sterile males required for *Aedes* elimination but could also reduce time for elimination. Using another mathematical model, Haramboure *et al.*[26] found that the release of sterile males coated with pyriproxifen was more effective than SIT to control *A. albopictus* (Skuse 1894) mosquitoes in La Réunion when sterile males are poorly competitive, and that the optimal window to start the control period could be extented. Using an agent-based model, Diouf *et al.*[27] showed that SIT and boosted SIT relying on the used of entomopathogenic fungal spores could successfully reduce fruit fly populations of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel 1912) and fruit infestation in mango orchards. However, more explorations of the performance and economical returns of the boosted SIT are still needed.

The present study deals on the use of an agent-based modelling approach to assess the performance of the boosted SIT to control *Bactrocera dorsalis*, a major pest of mango in Africa. Originally from Asia and first reported in Kenya in 2003,[28] the Oriental fruit fly rapidly spread throughout the African continent. This invasive species has become a serious agricultural pest causing direct losses to a range of fruits and threatening mango exports due to quarantine restrictions.[29,30] Many control methods have been deployed, from the widespread use of insecticides to more environmentally-friendly methods such as mass-trapping, male annihilation technique (MAT), food baits, and auto-dissemination of entomopathogenic fungi using pheromone-based devices.[31–34] In Thailand, integrated pest management including SIT effectively reduced fruit damage caused by *Bactrocera dorsalis* from over 80% to an average of less than 4% in the Ratchaburi Province (2000–2004) and from 43% to 16% in the Pichit Province where the control programme had been carried out for only 2 years (2003–2004).[5,31] The SIT or boosted SIT for the control of *Bactrocera dorsalis* has not yet been implemented in Africa. Some studies showed, however, that entomopathogenic fungi such as *Metarhizium anisopliae* could be used in auto-dissemination strategies to control *Bactrocera dorsalis* in orchards.[35,36]

The objectives of the present study were to determine (i) the potential of the boosted SIT as a control method of fruit flies in mango orchards, (ii) the optimal male release strategy (when, how often, how many males) and (iii) the economical returns of the boosted SIT. For this purpose, we used the agent-based model BOOSTIT (*Bactrocera dorsalis* boosted SIT) developed by Diouf *et al.*[27] We first explored scenarios of SIT and boosted SIT under different release conditions (start date, frequency of sterile male releases, and sterile/wild male ratio) to identify combinations that best limit fly populations and fruit infestation and that increase the benefit/cost ratio (BCR).

2 MATERIALS AND METHODS

2.1 Model description

The BOOSTIT model described in Diouf *et al.*[27] is an agent-based model implemented and simulated in the NetLogo 6.1.1 platform (https://ccl.northwestern.edu/netlogo/6.1.1/). The model simulates the spatio-temporal dynamics of a *Bactrocera dorsalis* wild population, releases of sterile males contaminated or not with spores of the entomopathogenic fungus, *M. anisopliae*, transmission of spores through fly interactions during mating, and availability of oviposition sites (mainly mangoes and citrus fruits) in different types of orchards in the Niayes area in Senegal. It uses time series of mean daily temperature and fruiting periods of different mango cultivars and citrus that create a landscape dynamic and influence the development and the survival of *Bactrocera dorsalis* (Fig. 1).

BOOSTIT represents two types of entities: the cell and the fly. The cell is units of a given landscape that can be a fruit tree, bare soil, shrubs, other non-host tree species or a clear cell. If the cell represents mango trees, it offers methyl-eugenol that increases the mating competitiveness of males. Some can also be a 'lekking' area where males gather for mating. Trees produce fruits with a given carrying capacity (maximum sum of eggs laid by fruit fly females) over a period of time. Once fruits are at a 'susceptible' stage (i.e., they can be stung by female fruit flies), laid eggs are counted until fruits cannot host more eggs or are considered harvested. Females cannot lay more eggs when the carrying capacity of the cell is filled or after fruits are harvested. For each cell with a mango tree, the number of fruits that are considered stung by females (sf) is computed using the following equation:

$$sf = \left(9.1108 \times \ln\left(np_{egg}\right) + 32.685\right) \times \frac{np_{fruit}}{100}$$

where np_{egg} is the number of eggs laid in the cell, and np_{fruit} a parameter giving a mean number of mango fruits per cell. Parameters were established based on data from Rwomushana *et al.*[37] The number of eggs we considered here is the number of eggs that will hatch, thus resulting from mating with wild males.

The model can be initialized with cell assemblage (11 × 11 cells of 50 m × 50 m each) that can form different landscape types with four orchards. In the present study, we made our simulations with a landscape composed with four monocultivar orchards of the mango cultivar 'Kent', given its economic importance in fruit exports from Senegal.

The 'fly' entity can be at an immature (egg, larva, pupa, immature adult) or at a mature adult stage (mature male or female) of *Bactrocera dorsalis*. The mature adult male can be 'wild' as opposed to 'released'. Each fruit fly stage evolves according to a developmental function depending on the daily temperature. A development level accumulates each day and when it becomes equal or more than 1, the fly moves to the next life stage. Two mortality rates were considered: (i) daily mortality depending on the temperatures and (ii) establishment mortality when individuals pass from one development stage to another. Males first seek plants containing methyl-eugenol to increase their mating competitiveness.[38,39] Then, they can join a close lekking area where competition with other males for mating occurs.[29,40] Adult females also visit lekking areas and mate with one competitive male.[41,42] Males can mate every day whereas 52% of females remate after a mean refractory period of 20 days.[42,43] Mated females that can lay eggs search for fruit to lay their eggs. When they find a suitable fruit, they lay a number of eggs (tolay) calculated as follows:

$$tolay = -0.08 \times T^2 + 4.17 \times T - 48.60$$

where T is the daily temperature expressed in Celsius degree with 24 °C ≤ T ≤ 29.9 °C and the parameters originate from Yang

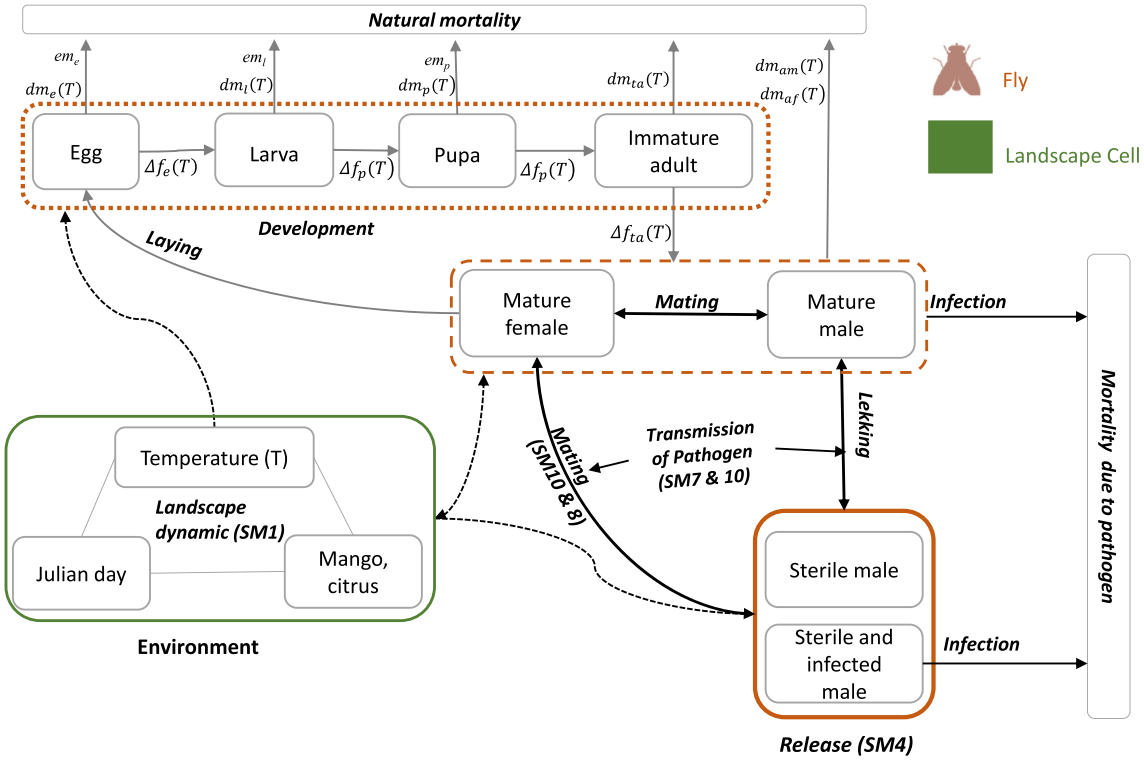

FIGURE 1. Conceptual diagram of main processes simulated in the BOOSTIT model. Dotted rectangle: immature stages of fruit flies. Dashed rectangle: adult flies. Bold rectangle: released sterile flies. The colours represent the entities involved in the processes: The fly's processes are in brown and the landscape cell's ones are in green. Grey arrows: demographic parameters. Bold arrows: interactions between sterile and wild flies. Dotted arrows: interactions between flies and the environment.

et al.[44] When females have mated with sterile males, eggs are not viable. Thus, the number of eggs that will hatch ($tolay_{final}$) depends on the number of matings with wild *versus* sterile males:

$$tolay_{final} = \frac{tolay \times mat_{wild}}{(mat_{wild} + mat_{sterile})}$$

where mat_{wild} and $mat_{sterile}$ are counters of the number of matings with wild and sterile males, respectively.

After release, sterile males inoculated with entomopathogenic spores transmit spores to wild males and females during lek or mating interactions. When wild healthy males interact with inoculated males in leks, these can receive entomopathogenic spores. The number of spores collected by the recipient male (sp_r) is calculated as follows:

$$sp_r = sp_c \times sp_d$$

where sp_c is the proportion of spores transmitted during male interactions in leks and sp_d the number of spores from the donor male. Similarly, an inoculated male can transmit a number of spores to females during mating (sp_f) calculated as follows:

$$sp_f = sp_m \times sp_d$$

where sp_m is the percentage of spores transmitted during mating and sp_d the number of spores of the donor male.

All wild flies that receive spores could in turn transmit spores to other wild flies during behavioural interactions. The remaining number of spores from the donor fly become the difference between its initial spore load and the number of spores transmitted to the recipient fly. The adult males and females that carry spores will be infected as soon as they will have received the minimal lethal dose. We have adjusted this minimum quantity of lethal spores to 300 spores based on unpublished work carried out by B. Diouf and A. Chailleux (unpublished data) who showed that the minimum lethal dose was very low. After being contaminated, adult go through an incubation time of 2 days and then, a proportion of them die every day. The mortality rate due to the entomopathogen is different between males and females and does not occur at the same time for all infected adults. The contaminated females have a daily probability of mortality due to pathogen $F_{mort} = 0.0235\%$ while contaminated males (sterile and wild) have a daily probability of mortality due to pathogen $M_{mort} = 0.05\%$ (A. Chailleux and F. Dosso, unpublished data).

2.2 Simulations

We simulated scenarios of SIT and boosted SIT to identify combinations of release parameter values that most save fruit from fruit fly damage. We then compared the best case of boosted SIT with the best case of SIT. We finally determined, for the scenarios of SIT and boosted SIT, the parameter combination that had the best BCR, and the BCR for the parameter combination that most saved the fruits from fruit fly damage. Release parameters included the date of first release, number of releases, time between releases, and ratio of sterile *versus* wild males. Values of these parameters are given in Table 1 while other parameters were set as in Diouf *et al.*[27] Simulations started on 1 March (Julian Day 60) and ended

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on 31 December. A total of 20 replicates leading to 2160 simulations per scenario were performed. At the end of a simulation, the total number of released males was recorded while the proportion of 'saved fruits' (pf_{saved}) was calculated as follows:

$$pf_{saved} = \frac{(psf_{nc} \times mp \times fpn - sf_t)}{mp \times fpn}$$

where psf_{nc} is the proportion of stung fruit in the absence of any control method; sf_t the number of stung fruits under SIT or boosted SIT scenarios; mp the number of cells with mango trees; fpn the number of fruits per cell. The number of cells with mango trees (mp) and the number of stung fruit (sf_t) were recorded at each simulation. The number of fruits per cell (fpn) was equal to the mean number of fruits per mango tree in the mango-producing area (152; E. Faye, unpublished data) multiplied by 100, which was the number of mango trees per cell. The maximum proportion of fruit that could be stung in the absence of any control (psf_{nc}) was:

$$psf_{nc} = \left(9.1108 \times \ln\left(max_{egg}\right) + 32.685\right) \div 100$$

where $max_{egg} = 180$ is the carrying capacity of a cell and the parameters were adjusted with data from Rwomushana *et al.*[37]

The quantity of fruit saved by the SIT and the boosted SIT and the number of released sterile males were expressed into monetary terms to calculate the cost–benefit balance. The benefit is considered here as the sale of fruits. It is calculated as follows using the farm gate price of a kilogram of mango in Senegal ($kg_{mango} = 250$ FCFA (USD 0.43), https://www.asepex.sn/la-mangue-made-in-senegal/):

$$benefit = pf_{saved} \times kg_{mango}$$

where pf_{saved} is the proportion of saved fruit calculated earlier in this section. To calculate the cost of the SIT, we multiplied the production cost of sterile flies ($prod_{sfly}$ = USD 500 for 1 000 000 flies,[24]) by the number of released sterile males ($released_{sm}$):

$$cost_{SIT} = released_{sm} \times prod_{sfly}$$

For the boosted SIT, cost was higher due to the use of fungal spores (1 kg = USD 4000, Real IPM, personal communication). Estimation of the quantity of spores needed to inoculate a fly was based on laboratory experiments (A. Chailleux and B. Diouf, unpublished data). In this experiment, an inoculation device of 8 cm × 6 cm contaminated with 0.32 g of *M. anisopliae* spores resulted in 100% mortality of the 30 fruit flies introduced. Considering results of this experiment, we approximated the quantity of spores to inoculate a fly as equivalent to the weight of an adult fly, as 0.32 g of *M. anisopliae* were necessary for 30 flies of about 0.011 g.[45] Therefore, the cost of *M. anisopliae* spores for a sterile male could be computed ($cost_{masm} = 4\$ \times (0.32 \div 30) = 0.043\$$) where USD 4 are the cost of a gramme of *M. anisopliae*. The cost of the boosted SIT is then equal to:

$$cost_{bSIT} = released_{sm} \times \left(prod_{sfly} + cost_{masm}\right)$$

From these cost and benefit analyses, the BCR was calculated respectively for the SIT and the boosted SIT, as follow:

$$BCR_{SIT} = \frac{benefit}{cost_{SIT}} \text{ and } BCR_{bSIT} = \frac{benefit}{cost_{bSIT}}.$$

The calculation of the BCR for the SIT and boosted SIT was done conservatively. Between the range of values of the *M. anisopliae* cost and the mango sale price that we found in Senegal, we chose the maximal cost and the minimal sale price.

3 RESULTS

The highest proportion of saved fruits under the boosted SIT was obtained with a first release at day 91 (1 April), with a total of seven releases performed every 15 day-intervals and a sterile/wild male ratio of 10:1 (Fig. 2). The day to start releases, the sterile/wild male ratio and the release number were the most influential parameters (Table 1). Mangoes became susceptible to fly stings from day 159 (8 June). The fruit fly population progressively increased from that date. Days of the first release that better protected the fruits were before the increase of fly population density (91, 121, 152) for all combinations of number of releases and sterile/wild ratio (Fig. 2). However, the optimal date of first release depended on the release interval, the number of release and the sterile/wild ratio. In these conditions, the amount of saved fruit increased when the sterile/wild male ratio and the number of releases increased.

The highest number of saved fruits under SIT was also obtained with a first release at day 91 (1 April), seven releases at 15 day-interval and a sterile/wild male ratio of 10:1 (see Appendix, Fig. A1). The release start date and the sterile/wild

TABLE 1. List of the explored parameters, their values and part of the variance of the 'saved fruit' variable explained by each parameter in the two scenarios (SIT or boosted SIT)

		SIT		Boosted SIT	
Parameters	Short name	Values	Percentage of variance to saved fruit (%)	Values	Percentage of variance to saved fruit (%)
Day of first release (Julian Day)	rt	91, 121, 152, 182	46	91, 121, 152, 182	37
Number of releases	rn	3, 5, 7	7	3, 5, 7	25
Release intervals (days)	ri	7, 15, 30	3	7, 15, 30	3
Sterile/wild male ratio	swr	1, 5, 10	44	1, 5, 10	34

Abbreviation: SIT, sterile insect technique.

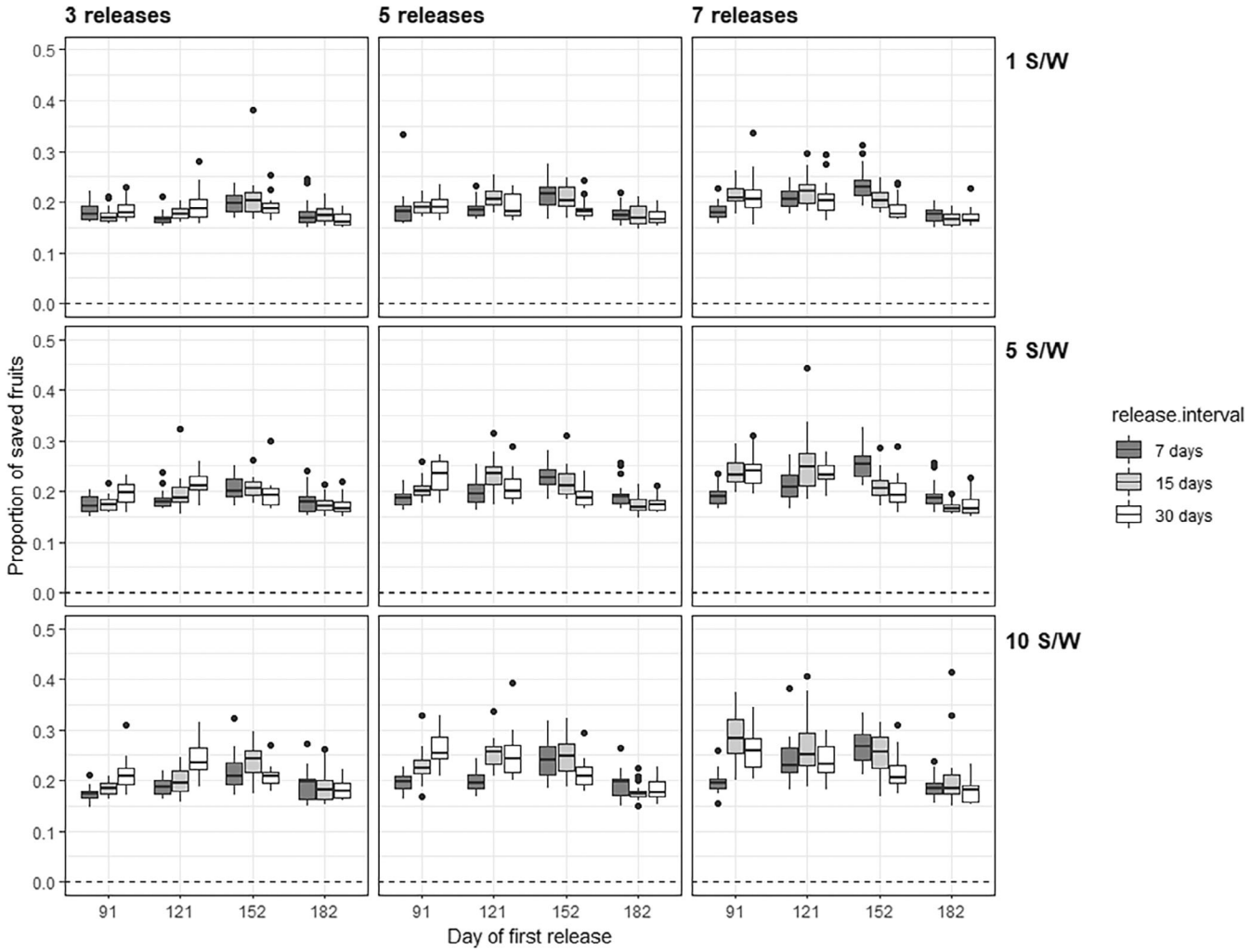

FIGURE 2. Proportion of mango fruits saved by the boosted SIT according to the day of first release (*x* axis), number of releases (columns), release interval (box shade), and the sterile/wild ratio (rows).

male ratio were the most influential parameters (Table 1). The comparison of saved fruits between the two scenarios showed that, generally, SIT performed better than boosted SIT (Fig. 3).

The release parameter values that offered the best fruit protection under SIT and boosted SIT scenarios were not the ones that made the best BCR (Fig. 4). BCR was beyond 1 whatever the control method, and SIT had always a better BCR than boosted SIT. The parameter combinations that gave the best BCR were (rt = 121, rn = 3, ri = 15, swr = 1) and (rt = 152, rn = 3, ri = 15, swr = 1) for SIT and boosted SIT, respectively (see Figs A2 and A3). These scenarios correspond to release strategies with the fewest released males (lowest rn and lowest swr). Hence, releasing as many sterile males as possible provided good fruit protection but did not maximize the benefit.

4 DISCUSSION

We used the BOOSTIT model to address the performance of the boosted SIT under different release strategies including when, how many and how often should sterile males be released for optimal fruit protection and BCR. The best fruit protection with the boosted SIT requires an early implementation, before the susceptible stage of mangoes and increase of the fly population. The boosted SIT also requires many releases at a sterile/wild male ratio of 10:1 and a small release interval (15 days) to be the most effective. The best release strategy was not the same when the BCR was considered. In this case, late start date and releases of less males were key (the fewest release number and sterile/wild male ratio). Overall, we observed that the boosted SIT was less efficient than the classical SIT, both in terms of fruit protection and BCR. In the following, we will first discuss the key processes of the boosted SIT regarding our results. Second, we will discuss the practical and economic implications of our findings.

4.1 Boosted SIT processes to consider

The success of boosted SIT was optimal when sterile males overflooded wild males at low population density. This result suggests that boosted SIT releases should target periods with low fly abundance, especially in refuge habitats (reservoirs) during the off-season when resources are scarce. In the case of *A. albopictus* mosquitoes, the best date to start releases of sterile males was when the mosquito population started to increase.[26] This difference could be explained by the mating system of *Bactrocera*

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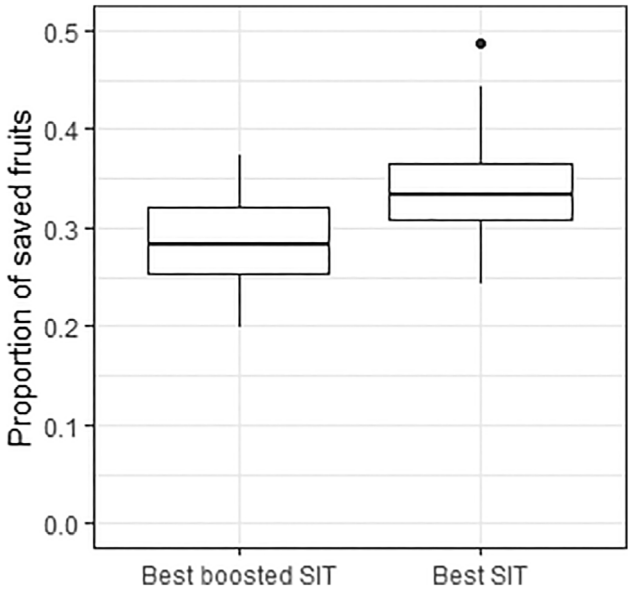

FIGURE 3. Proportion of saved fruits under the best boosted SIT and SIT scenarios. Best boosted SIT corresponds to the parameter value combination that allowed the best fruit protection in the boosted SIT scenario (rt = 91, rn = 7, ri = 15, swr = 10, see Fig. 2). Best SIT corresponds to the parameter value combination that allowed the best fruit protection in the SIT scenario (rt = 91, rn = 7, ri = 15, swr = 10; see Appendix, Fig. A1).

dorsalis in the form of leks[46] where males meet and compete to mate with females. Under a low population level, the lek mating system should enhance the chance of horizontal transmission of the pathogen. The pyriproxyfen considered in the model of Haramboure *et al.*[26] is a juvenile hormone analogue inhibiting metamorphosis to adult. When contaminated, females deposit the biopesticide in breeding sites while laying eggs, which enables further transmission to larvae. Thus, elevated mortality at the pupal stage and reduction of the pest density are observed.[47] Moreover, the pyriproxyfen spreads easily in water, so it can persist in breeding sites and inhibits the development of other larvae. For the boosted SIT, this vertical transmission is very advantageous. In the case of fruit flies, the vertical transmission of *M. anisopliae*, that is the transmission of a pathogen from an infected individual to its offspring has not been evidenced. According to Hedström and Monge-Nájera,[48] the transmission of pathogens is increased when there is high levels of contact between females and males, which is more likely when the insect population is high. In our case, we observe in the model that transmission is higher during peak of population size (results not shown). However, this does not maximize fruit protection since a high fruit fly population size causes high losses.

In our model, fruit protection by the use of sterile males as vectors worked primarily through overflooding of wild males by sterile males, and not through pathogen dissemination. Indeed, the parameters regulating the releases (day to start, number of releases, release interval and sterile/wild male ratio) were identical for SIT and boosted SIT. In this case, SIT reduced more fruit losses than the boosted SIT did, and was less expensive. As sterile males survived longer than boosted sterile males, they experienced more matings with females, so that the proportion of non-viable eggs increased. In addition to male mortality, low transmission of entomopathogenic spores did not reduce enough the female population. The most important parameters to be considered for the success of the two techniques are the day to start releases that should be early before the peak of abundance of fruit flies, and the ratio of sterile males to wild males that should be the highest. For the boosted SIT, the number of releases is also critical. Numerous releases could maintain the pathogen pressure until the triggering of an epizootic.

Despite the high transmission rate of fungal spores during lek and mating, and subsequent mortality of wild males and females, the boosted SIT simulated by our model would need to be improved to be acceptable by the stakeholders. The incubation period, as time elapsed between pathogen exposure and when symptoms or signs of disease appear, is probably too low and does not give the flies enough time to transmit it to a lot of congeners. Increasing the incubation period would increase the number of contaminated flies and therefore improve the performance of the boosted SIT. Hence, it would be relevant to explore other types or strains of entomopathogens with different traits including longer incubation period. This could be the case with *Purpureocillium lilacinum* (Thom 1910) whose incubation period was shown to be longer than that of *M. anisopliae* or *Beauveria*

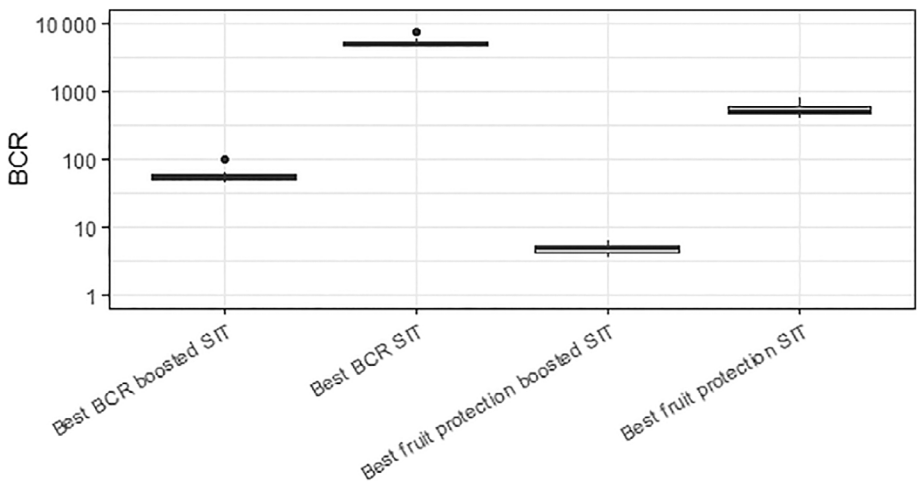

FIGURE 4. Benefit/cost ratio (BCR) of the parameter combination that gave (on the right) the best fruit protection under boosted SIT and SIT (with rt = 91, rn = 7, ri = 15, swr = 10) and (on the left) the best BCR under boosted SIT and SIT (with rt = 152 and 121, respectively, rn = 3, ri = 15, swr = 1).

bassiana for the Mexican fruit fly.[49] This pathogen would likely be more epizootic because of a possible higher rate of transmission. Further explorations of our model on the incubation period and transmission rates of the pathogen could help to find the characteristics of the best entomopathogen to be used in an effective boosted SIT strategy to control *Bactrocera dorsalis* in mango orchards.

Combining the boosted SIT with self-disseminating method could also enhance fruit protection. It was shown that the self-disseminating method, that uses auto-inoculation devices to attract and contaminate wild male flies, can successfully reduce fruit fly population in the field.[33,50] However, Toledo *et al.*[50] have shown for the Mediterranean fruit fly that this method does not allow a better transmission of the entomopathogen to wild population than the boosted SIT. Thus, the combination of the two techniques could help to trigger an epizootic and maintain it longer than when only boosted SIT is applied.

4.2 Practical and economic implications

The costs of *M. anisopliae* spores applied on released sterile males were estimated very conservatively. After being inoculated with *M. anisopliae*, sterile males often groom themselves to try to get rid of the fungus spores. This behaviour can decrease the initial spore load by a minimum of 30% or more depending on the time after inoculation (45). In our simulations, the load of spores of sterile males at the time of release corresponded to the load of spores after grooming. However, for the calculation of the cost of the *M. anisopliae* the amount of spore lost during the grooming behaviour of flies and the residual amount of spores in the tube after inoculation of sterile males are included. The fact that we considered the amount of spores lost during grooming and after inoculation for the cost estimate of the *M. anisopliae* is more realistic. Nevertheless, our estimates being based on laboratory experiment, it would be very useful to implement field release of sterile males inoculated with *M. anisopliae* to verify the amount of spores needed to inoculate flies and the benefit to cost ratio of the boosted SIT. Other experiments showed that disease was triggered with a low quantity of spores, about 1/150 of the initial spore load of inoculated males, and that incubation period decreased with initial load (B. Diouf, unpublished data).

Model simulations showed that the best strategy for sterile male releases under the boosted SIT was not necessarily the best from an economical point of view. The combination with other control methods could significantly improve fruit protection while reducing costs. For example, the attract-and-kill method that is cheaper than boosted SIT could already reduce the abundance of flies and therefore increase the efficiency of the SIT or boosted SIT without increasing costs. The implementation of such techniques on an area-wide basis could also be relevant to limit the re-infestation of orchards by fruit flies from other sources. Area-wide approaches consist in treatment of all habitats of the pest population in space and time so that none produces migrants to re-establish significant infestations in areas of concern.[51] This approach generally includes stakeholders and the public authority for the coordination of a collective effort. Moreover, according to Keenan and Burgener,[52] area-wide control of highly mobile pests is generally more environmentally friendly, efficient and cost-effective than control at the individual farm level. All costs related to the SIT and the boosted SIT implementation were not included. An estimation of the costs of monitoring (during and post-eradication), delivery of sterile pupae, survey of fruit fly abundance and release operations (ground or aerial) would help to make a better assessment.[24]

In our simulations, the effect of the release of sterile males was observed immediately on population growth. This was also the case in some of the works carried out in field conditions.[49] Gato *et al.*[53] released sterile males of the mosquito *Aedes aegypti* in urban areas of the Havana city from April to August 2020. The released sterile males were able to suppress the population of mosquitoes within less than 1 year in the target area. However, most of the SIT programmes aimed at eradication or suppression extend over many years.[4,54,55] It would be interesting to simulate the SIT and boosted SIT over several years and at a larger spatial scale to investigate the relevance of such methods for the sustainable control of fruit flies.

Another aspect to explore could be the relative success of the pathogen transmission *versus* the induction of sterility, and their synergy or complementarity. In their field trial, Flores *et al.*[56] used sterile males of *Ceratitis capitata* as vectors of fungal spores of *Beauveria bassiana* when the Mediterranean fruit fly populations were highest in Guatemala.[57] They observed a large dissemination of the pathogen within the wild fly population. However, this case is not an example of boosted SIT but an example of sterile insect being used as carriers of an entomopathogen to suppress medfly populations prior to the use of SIT. In such context, the pathogen transmission should be enhanced by high insect density whereas the SIT success relies more on the timing of a low insect density. Our model results did not show the results of Flores *et al.*,[57] mainly because the sterility had more influence on success than the pathogen transmission in our system. In this case, one could also question the name of 'boosted SIT' since the carrying of the pathogen by the sterile males did not boost the success of the SIT. This underlines the need for further research to optimize many parameters as timing and site of releases, number of released flies, and pathogen properties such as incubation period to accurately boost the SIT.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in CIRAD dataverse at https://dataverse.cirad.fr/dataset.xhtml?persistentId=doi:10.18167/DVN1/5WELPP.

REFERENCES

1 Knipling EF, Possibilities of insect control or eradication through the use of sexually sterile males. *J Econ Entomol* **48**:459–462 (1955). https://doi.org/10.1093/jee/48.4.459.
2 Baumhover AH, Graham AJ, Bitter BA, Hopkins DE, New WD, Dudley FH *et al.*, Screw-worm control through release of sterilized flies. *J Econ Entomol* **48**:462–466 (1955). https://doi.org/10.1093/jee/48.4.462.
3 Hendrichs J, Ortiz G, Liedo P and Schwarz A, Six years of successful medfly program in Mexico and Guatemala, in *Fruit Flies of Economic*

Importance. AA Balkema, Rotterdam, The Netherlands, pp.353–365 (1983).
4 Ito Y, Kakinohana H, Yamagishi M and Kohama T, Eradication of the melon fly, *Bactrocera cucurbitae*, from Okinawa, Japan, by means of the Sterile Insect Technique, with special emphasis on the role of basic studies. *J Asia Pac Entomol* **6**:119–129 (2003). https://doi.org/10.1016/S1226-8615(08)60177-6.
5 Orankanok W, Chinvinijkul S, Thanaphum S, Sitilob P and Enkerlin WR, *Area-Wide Integrated Control of Oriental Fruit Fly Bactrocera dorsalis and Guava Fruit Fly Bactrocera Correcta in Thailand*. Springer, Netherlands, pp. 517–526 (2007). https://doi.org/10.1007/978-1-4020-6059-5_48.
6 Patterson RS, Weidhaas DE, Ford HR and Lofgren CS, Suppression and elimination of an Island population of *Culex pipiens quinquefasciatus* with sterile males. *Science* **168**:1368–1369 (1970). https://doi.org/10.1126/science.168.3937.1368.
7 Oliva CF, Jacquet M, Gilles J, Lemperiere G, Maquart PO, Quilici S *et al*., The Sterile Insect Technique for controlling populations of *Aedes albopictus* (Diptera: Culicidae) on Reunion Island: mating vigour of sterilized males. *PLoS One* **7**:e49414 (2012). https://doi.org/10.1371/journal.pone.0049414.
8 Vreysen MJB, Robinson AS and Hendrichs J, *Area-Wide Control of Insect Pests. From Research to Field Implementation*. Springer, Netherlands (2007). https://doi.org/10.1007/978-1-4020-6059-5.
9 Bouyer J and Lefrançois T, Boosting the sterile insect technique to control mosquitoes. *Trends Parasitol* **30**:271–273 (2014). https://doi.org/10.1016/j.pt.2014.04.002.
10 Bouyer J, Chandre F, Gilles J and Baldet T, Alternative vector control methods to manage the Zika virus outbreak: more haste, less speed. *Lancet Glob Health* **4**:e364 (2016). https://doi.org/10.1016/s2214-109x(16)00082-6.
11 Vreysen M, Principles of area-wide integrated tsetse fly control using the sterile insect technique. *Médecine Trop Rev* **61**:397–411 (2001). https://pubmed.ncbi.nlm.nih.gov/11803833/.
12 Cai L, Ai S and Li J, Dynamics of mosquitoes populations with different strategies for releasing sterile mosquitoes. *SIAM J Appl Math* **74**:1786–1809 (2014). https://doi.org/10.1137/13094102X.
13 Li J and Yuan Z, Modelling releases of sterile mosquitoes with different strategies. *J Biol Dyn* **9**:1–14 (2015). https://doi.org/10.1080/17513758.2014.977971.
14 Multerer L, Smith T and Chitnis N, Modeling the impact of sterile males on an *Aedes aegypti* population with optimal control. *Math Biosci* **311**:91–102 (2019). https://doi.org/10.1016/j.mbs.2019.03.003.
15 Hui Y, Lin G, Yu J and Li J, A delayed differential equation model for mosquito population suppression with sterile mosquitoes. *Discrete Contin Dyn Syst-B* **25**:4659–4676 (2020). https://doi.org/10.3934/dcdsb.2020118.
16 Barclay HJ, The sterile release method with unequal male competitive ability. *Ecol Model* **15**:251–263 (1982). https://doi.org/10.1016/0304-3800(82)90029-1.
17 Vreysen MJB, Barclay HJ and Hendrichs J, Modeling of preferential mating in areawide control programs that integrate the release of strains of sterile males only or both sexes. *Ann Entomol Soc Am* **99**:607–616 (2006). https://doi.org/10.1603/0013-8746(2006)99[607:MOPMIA]2.0.CO;2.
18 Tyson R, Thistlewood H and Judd GJR, Modelling dispersal of sterile male codling moths, *Cydia pomonella*, across orchard boundaries. *Ecol Model* **205**:1–12 (2007).
19 Yang C, Zhang X and Li J, Dynamics of two-patch mosquito population models with sterile mosquitoes. *J Math Anal Appl* **483**:123660 (2020). https://doi.org/10.1016/j.jmaa.2019.123660.
20 Dufourd C and Dumont Y, Impact of environmental factors on mosquito dispersal in the prospect of sterile insect technique control. *Comput Math Appl* **66**:1695–1715 (2013). https://doi.org/10.1016/j.camwa.2013.03.024.
21 Rodríguez N, On an integro-differential model for pest control in a heterogeneous environment. *J Math Biol* **70**:1177–1206 (2015). https://doi.org/10.1007/s00285-014-0793-8.
22 Anguelov R, Dumont Y and Djeumen IVY, Sustainable vector/pest control using the permanent sterile insect technique. *Math Methods Appl Sci* **43**:10391–10412 (2020). https://doi.org/10.1002/mma.6385.
23 Douchet L, Haramboure M, Baldet T, L'Ambert G, Damiens D, Gouagna LC *et al*., Comparing sterile male releases and other methods for integrated control of the tiger mosquito in temperate and tropical climates. *Sci Rep* **11**:7354 (2021). https://doi.org/10.1038/s41598-021-86798-8.
24 Mumford JD, Design and economic evaluation of programmes integrating the sterile insect technique, in *Sterile Insect Technique Principles and Practice in Area-Wide Integrated Pest Management*, ed. by Dyck VA, Hendrichs J and Robinson AS. Springer, Netherlands, pp. 731–752 (2021). https://library.oapen.org/handle/20.500.12657/43144.
25 Pleydell DRJ and Bouyer J, Biopesticides improve efficiency of the sterile insect technique for controlling mosquito-driven dengue epidemics. *Commun Biol* **2**:1–11 (2019). https://doi.org/10.1038/s42003-019-0451-1.
26 Haramboure M, Labbé P, Baldet T, Damiens D, Gouagna LC, Bouyer J *et al*., Modelling the control of *Aedes albopictus* mosquitoes based on sterile males release techniques in a tropical environment. *Ecol Model* **424**:109002 (2020). https://doi.org/10.1016/j.ecolmodel.2020.109002.
27 Diouf EG, Brévault T, Ndiaye S, Faye E, Chailleux A, Diatta P *et al*., An agent-based model to simulate the boosted Sterile Insect Technique for fruit fly management. *Ecol Model* **468**:109951 (2022). https://doi.org/10.1016/j.ecolmodel.2022.109951.
28 Lux S, Copeland R, White I, Manrakhan A and Billah M, A new invasive fruit fly species from the *Bactrocera dorsalis* (Hendel) group detected in East Africa. *Int J Trop Insect Sci* **23**:355–361 (2003). https://doi.org/10.1017/S174275840001242X.
29 Clarke A, Armstrong KF, Carmichael AE, Milne JR, Raghu S, Roderick GK *et al*., Invasive phytophagous pests arising through a recent tropical evolutionary raditation: the *Bactrocera dorsalis* complex of fruit flies. *Annu Rev Entomol* **50**:293–319 (2005). https://doi.org/10.1146/annurev.ento.50.071803.130428.
30 Ekesi S, De Meyer M, Mohamed SA, Virgilio M and Borgemeister C, Taxonomy, ecology, and management of native and exotic fruit fly species in Africa. *Annu Rev Entomol* **61**:219–238 (2016). https://doi.org/10.1146/annurev-ento-010715-023603.
31 Sutantawong M, Orankanok W, Enkerlin WR, Wornoayporn V and Caceres C, The sterile insect technique for control of the oriental fruit fly, *Bactrocera dorsalis* (Hendel), in mango orchards in Ratchaburi Province, Thailand (2002). Proceedings, of the 6th International Symposium on Fruit Flies of Economic Importance, Isteg Scientific Publications, Irene, South Africa pp 223–232. https://api.semanticscholar.org/CorpusID:129598071.
32 Mwatawala MW, Mziray H, Malebo H and De Meyer M, Guiding farmers' choice for an integrated pest management program against the invasive *Bactrocera dorsalis* Hendel (Diptera: Tephritidae) in mango orchards in Tanzania. *Crop Prot* **76**:103–107 (2015). https://doi.org/10.1016/j.cropro.2015.07.001.
33 Faye PD, Bal AB, Ndiaye NM, Diop F, Sangaré YK, Haddad C *et al*., Field efficacy of *Metarhizium acridum* (Hypocreales: Clavicipitaceae) in the control of *Bactrocera dorsalis* (Diptera: Tephritidae) in citrus orchards in Senegal. *Int J Trop Insect Sci* **41**:1185–1195 (2020). https://doi.org/10.1007/s42690-020-00306-5.
34 Wangithi CM, Muriithi BW and Belmin R, Adoption and dis-adoption of sustainable agriculture: a case of farmers' innovations and integrated fruit fly management in Kenya. *Agri* **11**:338 (2021). https://doi.org/10.3390/agriculture11040338.
35 Maniania JNK and Ekesi S, Development and application of mycoinsecticides for the management of fruit flies in Africa, in *Fruit Fly Research and Development in Africa - Towards a Sustainable Management Strategy to Improve Horticulture*, ed. by Ekesi S, Mohamed SA and De Meyer M. Springer International Publishing, Berlin, pp. 307–324 (2016). https://doi.org/10.1007/978-3-319-43226-7_15.
36 Marri D, Gomez DAMA, Wilson DD, Billah M, Yeboah S and Osae M, Evaluation of the efficacy of a commercial formulation of *Beauveria bassiana* for the control of the invasive fruit fly *Bactrocera dorsalis* (Diptera: Tephritidae). *Biopestic Int* **12**:9–19 (2016).
37 Rwomushana I, Ekesi S, Gordon I and Ogol CKPO, Host plants and host plant preference studies for *Bactrocera invadens* (Diptera: Tephritidae) in Kenya, a new invasive fruit fly species in Africa. *Ann Entomol Soc Am* **101**:331–340 (2008). https://doi.org/10.1603/0013-8746(2008)101[331:HPAHPP]2.0.CO;2.
38 Metcalf RL, Chemical ecology of Dacinae fruit flies (Diptera: Tephritidae). *Ann Entomol Soc Am* **83**:1017–1030 (1990). https://doi.org/10.1093/aesa/83.6.1017.

39 Nishida R, Shelly TE and Kaneshiro KY, Acquisition of female-attracting fragrance by males of Oriental fruit fly from a hawaiian lei flower, *Fagraea berteriana*. *J Chem Ecol* **23**:2275–2285 (1997). https://doi.org/10.1023/B:JOEC.0000006673.27221.2e.

40 Shelly TE and Kaneshiro KY, Lek behavior of the Oriental fruit fly, *Dacus dorsalis*, in Hawaii (Diptera: Tephritidae). *J Insect Behav* **4**:235–241 (1991). https://doi.org/10.1007/BF01054615.

41 Fitt GP, Responses by female Dacinae to "male" lures and their relationship to patterns of mating behaviour and pheromone response. *Entomol Exp Appl* **29**:87–97 (1981). https://doi.org/10.1111/j.1570-7458.1981.tb03045.x.

42 Shelly TE, Fecundity of female Oriental fruit flies (Diptera: Tephritidae): effects of methyl eugenol-fed and multiple mates. *Ann Entomol Soc Am* **93**:559–564 (2000). https://doi.org/10.1603/0013-8746(2000)093[0559:FOFOFF]2.0.CO;2.

43 Wei D, Feng Y-C, Wei D-D, Yuan G-R, Dou W and Wang J-J, Female remating inhibition and fitness of *Bactrocera dorsalis* (Diptera: Tephritidae) associated with male accessory glands. *Fla Entomol* **98**:52–58 (2015). https://doi.org/10.1653/024.098.0110.

44 Yang P, Carey J and Dowell R, Temperature influences on the development and demography of *Bactrocera dorsalis* (Diptera: Tephritidae) in China. *Env Entomol* **23**:971–974 (1994). https://doi.org/10.1093/ee/23.4.971.

45 Liu H, Gao Z, Deng S-Z, Cao F-Q and Lu Y-Y, The photokinesis of Oriental fruit flies, *Bactrocera dorsalis*, to LED lights of various wavelengths. *Entomol Exp Appl* **166**:102–112 (2018). https://doi.org/10.1111/eea.12648.

46 Hendrichs J, Robinson AS, Cayol JP and Enkerlin W, Medfly areawide sterile insect technique programmes for prevention, suppression or eradication: the importance of mating behavior studies. *Fla Entomol* **85**:1–13 (2002). https://doi.org/10.1653/0015-4040(2002)085[0001:MASITP]2.0.CO;2.

47 Chandel K, Suman DS, Wang Y, Unlu Y, Williges E, Williams GM *et al.*, Targeting a hidden enemy: pyriproxyfen autodissemination strategy for the control of the container mosquito *Aedes albopictus* in cryptic habitats. *PLoS Negl Trop Dis* **10**:e0005235 (2016). https://doi.org/10.1371/journal.pntd.0005235.

48 Hedström I and Monge-Nájera J, Is sexually transmitted fungal infection evidence for size-related mating success in neotropical guava fruit flies? *Rev Biol Trop* **46**:1131–1134 (1998).

49 Toledo-Hernández RA, Toledo J, Valle-Mora J, Holguín-Meléndez F, Liedo P and Huerta-Palacios G, Pathogenicity and virulence of *Purpureocillium lilacinum* (Hypocreales: Ophiocordycipitaceae) on Mexican fruit fly adults. *Fla Entomol* **102**:309–314 (2019). www.jstor.org/stable/48562018.

50 Toledo J, Flores S, Campos S, Villaseñor A, Enkerlin W, Liedo P *et al.*, Pathogenicity of three formulations of *Beauveria bassiana* and efficacy of autoinoculation devices and sterile fruit fly males for dissemination of conidia for the control of *Ceratitis capitata*. *Entomol Exp Appl* **164**:340–349 (2017). https://doi.org/10.1111/eea.12608.

51 Klassen W and Vreysen MJB, Area-wide integrated pest management and the sterile insect technique, in *Sterile Insect Technique Principles and Practice in Area-Wide Integrated Pest Management*, ed. by Dyck VA, Hendrichs J and Robinson AS. CRC Press, London, pp. 75–112 (2021). https://doi.org/10.1201/9781003035572-3.

52 Keenan SP and Burgener PA, Social and economic aspects of areawide pest management, in *Areawide Pest Management: Theory and Implementation*, ed. by Koul O, Cuperus G and Elliott N. CABI Digital Library, Wallingford, UK, pp. 97–116 (2008). https://doi.org/10.1079/9781845933722.0097.

53 Gato R, Menéndez Z, Prieto E, Argilés R, Rodriguez M, Baldoquin W *et al.*, Sterile insect technique: successful suppression of an *Aedes aegypti* field population in Cuba. *Insects* **12**:469 (2021). https://doi.org/10.3390/insects12050469.

54 Gillman H, Nations F and A. O. of the U, *The New World Screwworm Eradication Programme: North Africa, 1988–1992*. Food & Agriculture Org, Rome (1992).

55 Vreysen MJB, Saleh KM, Ali MY, Abdulla AM, Zhu Z-R, Juma GJ *et al.*, *Glossina austeni* (Diptera: Glossinidae) eradicated on the Island of Unguja, Zanzibar, using the Sterile Insect Technique. *J Econ Entomol* **93**:123–135 (2000). https://doi.org/10.1603/0022-0493-93.1.123.

56 Flores S, Campos S, Villaseñor A, Valle A, Enkerlin W, Toledo J *et al.*, Sterile males of *Ceratitis capitata* (Diptera: Tephritidae) as disseminators of *Beauveria bassiana* conidia for IPM strategies. *Biocontrol Sci Technol* **23**:1186–1198 (2013). https://doi.org/10.1080/09583157.2013.822473.

57 Flores S, Montoya P, Ruiz-Montoya L, Villaseñor A, Valle A, Enkerlin W *et al.*, Population fluctuation of *Ceratitis capitata* (Diptera: Tephritidae) as a function of altitude in eastern Guatemala. *Environ Entomol* **45**:802–811 (2016). https://doi.org/10.1093/ee/nvw051.

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5 APPENDIX

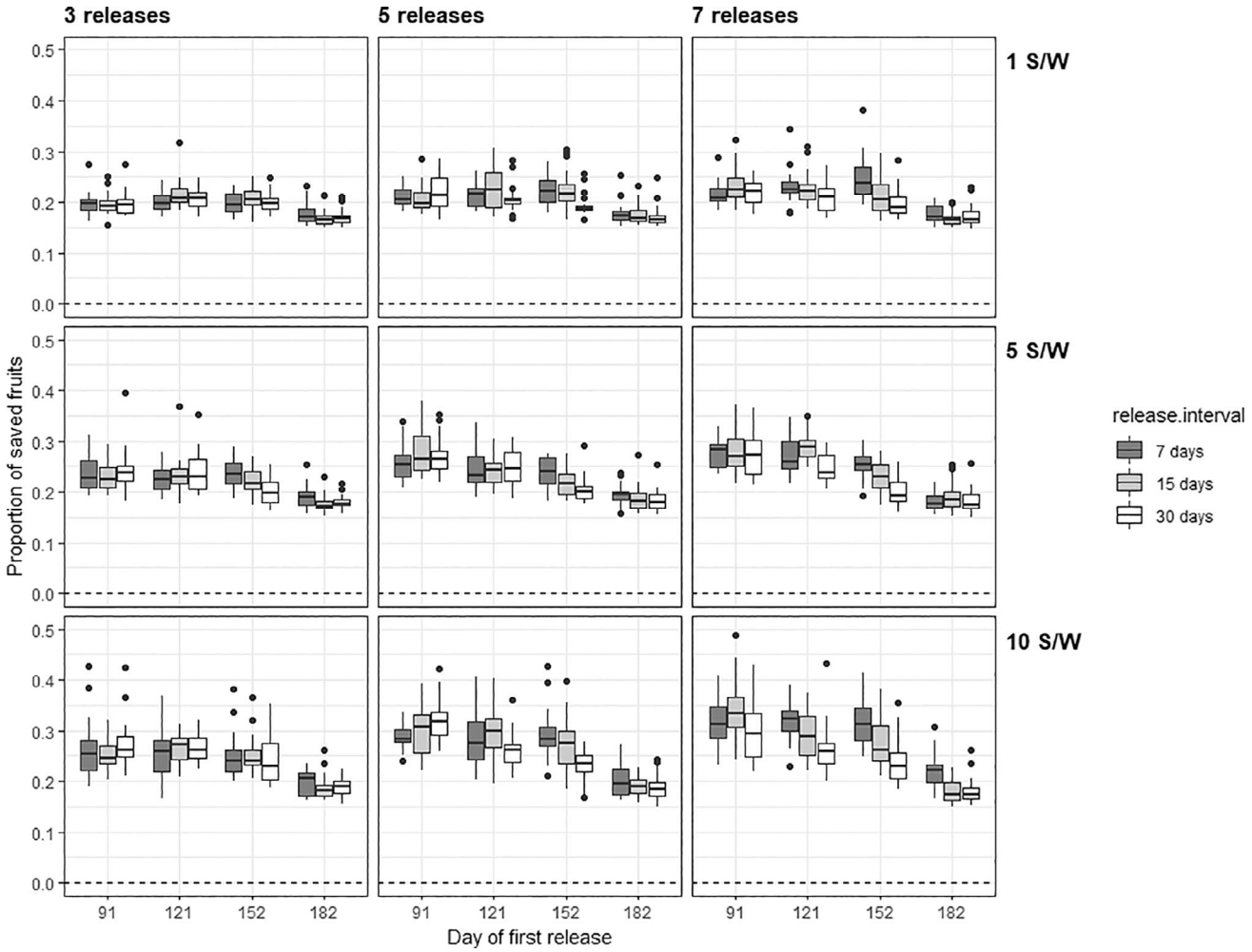

FIGURE A1. The number of fruit protected by the SIT according to the start of releases, the release intervals, the number of releases and the sterile/wild male ratio (S/W).

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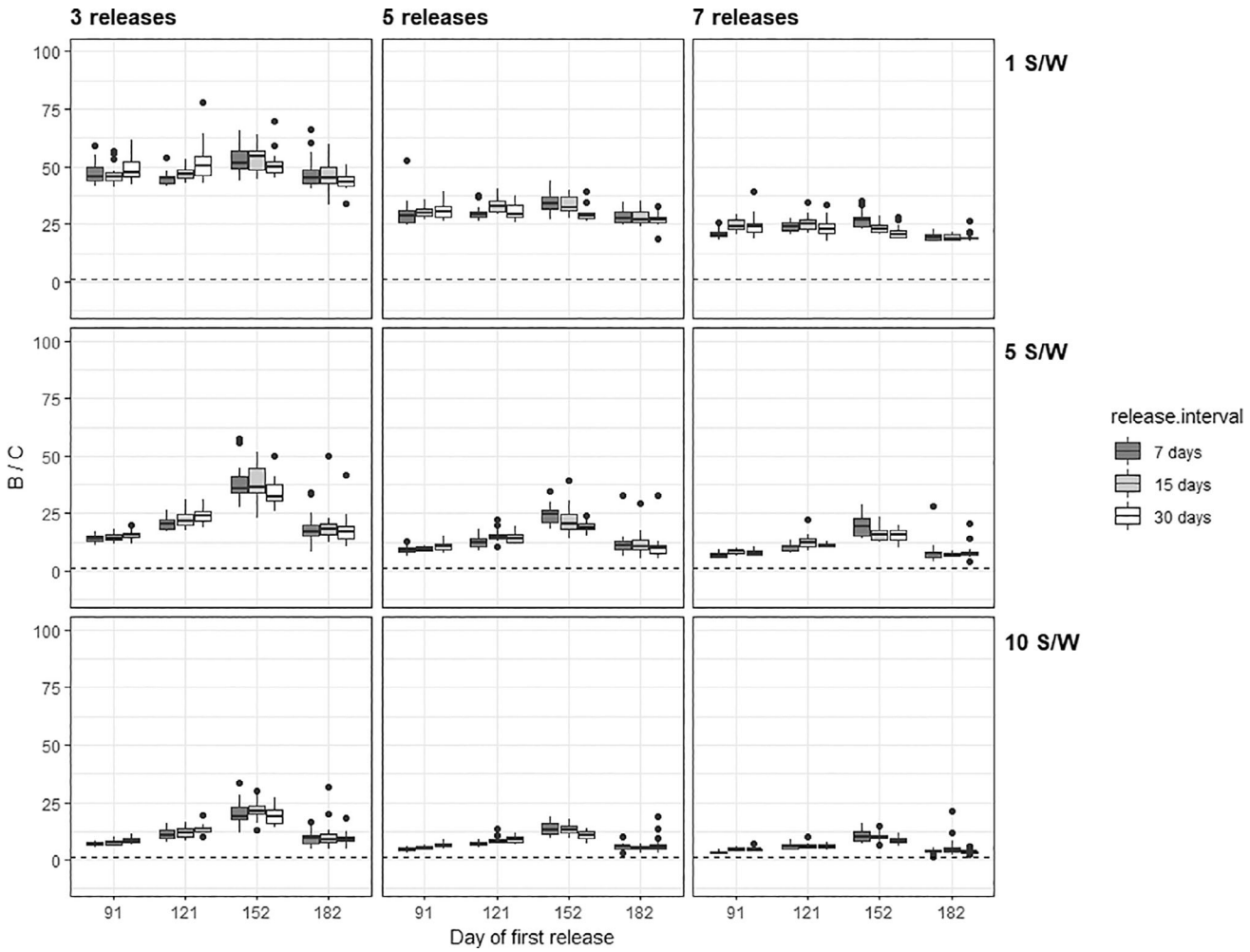

FIGURE A2. Benefit/cost ratio (B/C) of the boosted SIT scenario according to the start of releases, the release intervals, the number of releases and the sterile/wild male ratio (S/W).

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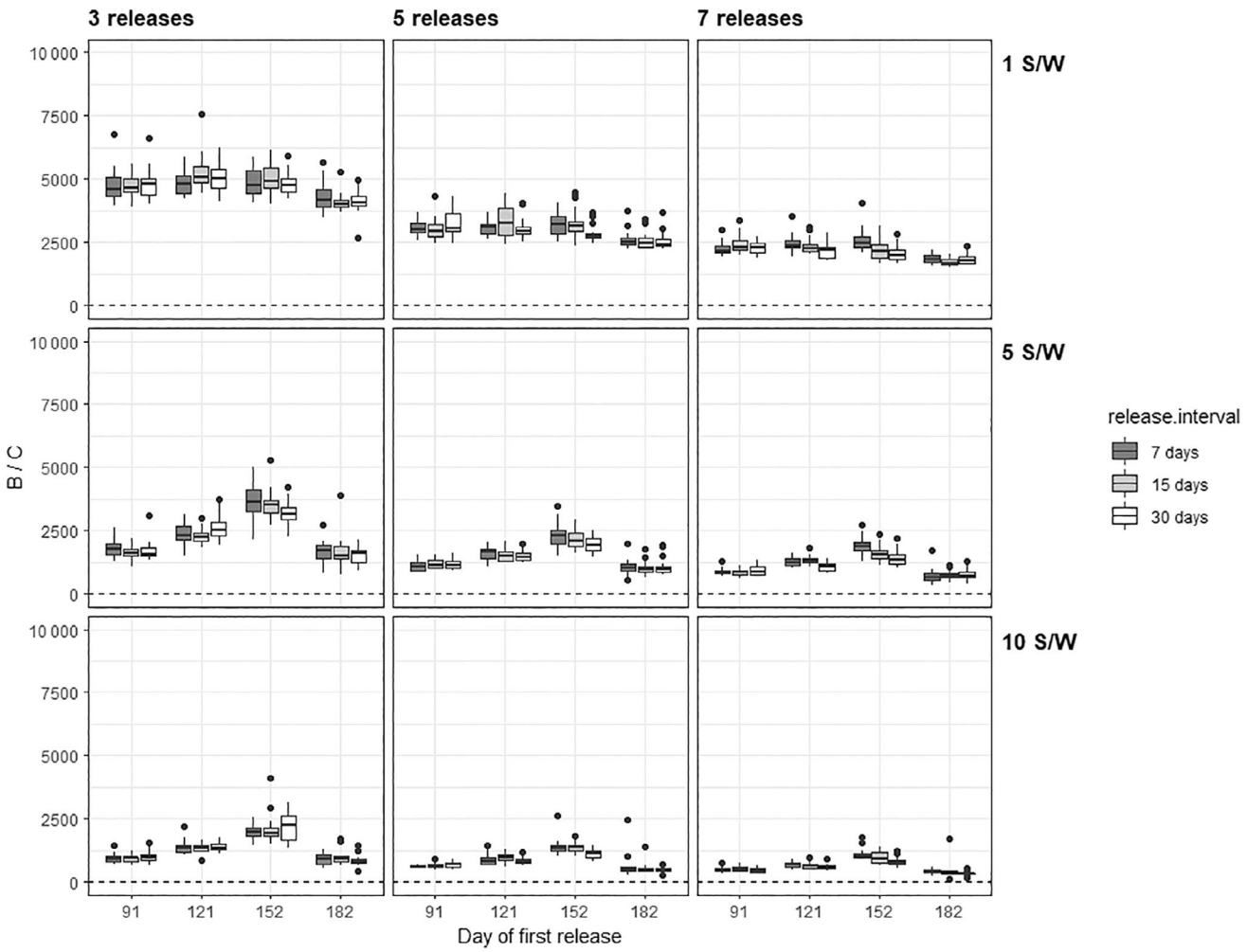

FIGURE A3. Benefit/cost ratio (B/C) of the SIT scenario according to the start of releases, the release intervals, the number of releases and the sterile/wild male ratio (S/W).

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