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Use of a temperature-sensitive lethal mutation strain of medfly (*Ceratitis capitata*) for the suppression of pest populations

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Abstract Before the Sterile Insect Technique can be applied successfully, the size of the target population has to be reduced to a manageable level. At present this reduction is achieved by the use of insecticides. Computer simulations have been performed to examine the possibility of achieving this initial population suppression by genetic control strategies; in particular, the effect of releasing fertile males carrying a recessive temperature-sensitive lethal mutation and a Y-autosome translocation has been simulated. The results show that the release of such males is most effective when applied under permissive conditions, i.e. those which allow flies homozygous for the temperature-sensitive lethal mutation to survive and spread the mutation through the population. However, combining this population replacement with a population-suppression strategy is even more effective. If the released males are partially sterile, e.g. due to the presence of a Y-autosome translocation, the population size is reduced before the restrictive conditions for the temperature-sensitive lethal mutation are reached, i.e. before the increase of temperatures in the target area eliminates all flies homozygous for this mutation. By combining these two strategies the resulting population should be low enough to apply the Sterile Insect Technique for eradication.

Key words Computer simulation · *Ceratitis capitata* · Sterile insect technique · Translocations Temperature-sensitive mutation

Introduction

The Sterile Insect Technique (SIT) is an environmentally safe method to control or eradicate insect pests. It has been applied successfully on several occasions (for a review see Klassen et al. 1994). Mass-reared, sterile males are the primary active agent in SIT. Consequently, the development of sex separation systems for the large-scale elimination of females would not only reduce the cost of SIT programmes significantly, but would also make this strategy clearly more efficient. However, it is still necessary to reduce the wild population before the release of sterile flies can be effective; this is usually accomplished through the application of insecticides. We investigated the possibilities of achieving this initial suppression through the application of genetic control strategies. The Mediterranean fruit fly, *Ceratitis capitata*, was used as model.

The size of medfly populations is seldom constant, being greatly affected by the climatic conditions and the availability of food and host plants. In the Mediterranean region the fly population is generally low during winter and spring due to the relatively cold climate and the lack of host plants. However, during the main fruit-growing season of the respective host plants, populations increase dramatically.

LaChance and Knipling (1962) proposed that the control of insect pest populations could be achieved by introducing conditional lethal mutations into the population. We simulated the effects of introducing a recessive temperature-sensitive lethal mutation (*tsl*) into a wild population. If this mutation were introduced during the colder periods of the year (i.e. low population size, but more or less constant) it would kill homozygous individuals when the temperature rose. However, compared with the introduction of sterile males (SIT), the release of *tsl* flies would not provide any immediate population suppression at low temperatures. To achieve optimal suppression, the mutation must spread throughout the target population, thereby increasing the number of homozygous, temperature-sensitive flies.

The strategy involves releasing only males in order to avoid increasing the reproductive potential of the population. This implies that a Y-autosome translocation would be introduced along with *tsl* mutation, as this is at

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present the only possible way to obtain large-scale sex separation in medfly. These translocations result in semi-sterility; this is a potential additional strategy to reduce the population size, even when the temperature is low. Many reports have documented the use of chromosomal aberrations to introduce a genetic load into wild populations (for review see Robinson 1976). In addition to the mutation and translocation, the genetic background of the laboratory-reared strain could be introduced into the native population. This could make the target population more compatible with the sterile males released during the SIT phase and, consequently, would increase the efficiency of SIT releases.

In the simulations presented in this article, we combined a Y-autosome translocation with a *tsl* mutation to show how several parameters interacted and contributed to the suppression of a native population. The release of flies containing a translocation with reduced fertility together with a *tsl* mutation was apparently more effective than the release of flies with only a translocation or with only a *tsl* mutation. The optimal genotype to release was a heterozygous *tsl* male; this genotype appeared to be more efficient than SIT under certain environmental conditions. However, the optimal suppression strategy was first to release fertile *tsl* males and, once sufficient suppression had been attained, continue with classic SIT release.

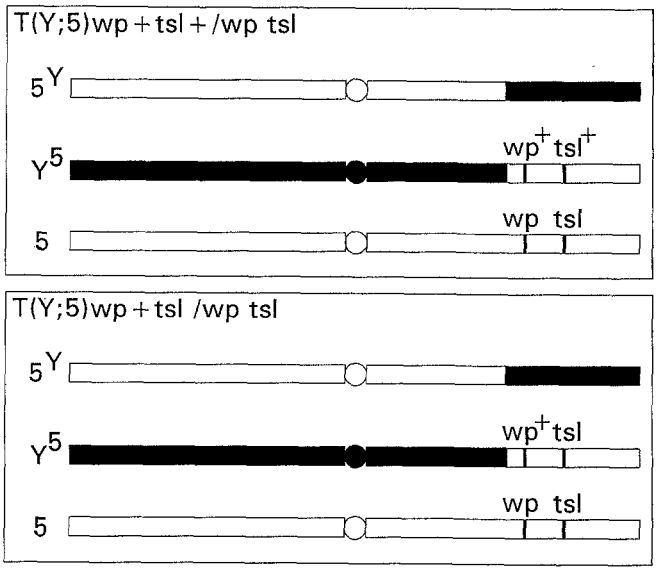


Fig. 1 The two genotypes most used in the simulations are *T(Y;5)wp + tsl + /wp tsl* or *T(Y:5)wp + tsl/wp tsl*. Both mutations, *wp* and *tsl*, are located on the right arm of chromosome 5 (Kerremans and Franz 1994). The other chromosomes (X, 2, 3, 4, and 6) are not shown

Materials and methods

The simulation programme Sim Tsl2

General description

A computer programme for the simulation of the population dynamics of the release of laboratory-reared flies into a native population was developed (Sim Tsl2). A deterministic model with discrete generations was used.

Genotypes of the released males that were used in most of the simulations are shown in Fig. 1. Released and native flies contain a maximum of two closely linked mutations [i.e. *wp* (white pupa) and *tsl*] and a Y-autosome translocation. When a translocation is used, the two mutations are sex-linked, i.e. located on the autosome involved in the translocation. Parameters of the genotypes such as fertility and mating competitiveness can be specified for released and native flies separately. An equal sex ratio of the native population is assumed in all simulations.

Fertility

For the model, fertility is defined as the total offspring from a cross between a male/female, for which the fertility has to be determind, with a wild-type male/female divided by the offspring of a cross between wild-type males and females. The fertility can be specified for each genotype or is calculated from the entered fertility of the translocation or mutations. A multiplicative model was used.

Mating competitiveness

Mating competitiveness is defined as the relative probability of mating success. As with fertility, mating competitiveness can by entered for each genotype or for the translocation and mutations. Complete fertilization of all females is always assumed, independent of the sex ratio after release of the flies. Therefore, differences in mating competitiveness and sex ratio do not influence the population size.

Temperature and temperature sensitivity

The percentage of wild-type and *tsl* flies killed at a given temperature can be specified. For the *tsl* mutation available in the medfly, the eggs are treated at 33 °C to kill all of the homozygous *tsl* genotypes. However, a proportion of the *tsl* homozygotes does not survive lower temperatures (Franz, in preparation), and a small proportion of the wild-type eggs do not survive the 33 °C temperature treatment.

For each generation the environmental temperature is given.

Environmental conditions

The rate of increase is defined as the average offspring produced by a female, irrespective of the genotype. A rate of increase of 1.0 means that there would be no population increase. Simulations were performed with or without density regulation. If simulations were done with density regulation, another parameter, the carrying capacity of the environment (or the density at which the population stays at an equilibrium), was specified. The formula for calculating the rate of increase reported by Foster et al. (1988) was used.

Programme structure

The initial conditions can be entered for each run or else retrieved from a file. After each generation the programme stops, and some parameters can be changed. The results are shown on screen in tabular and graphical from and can be written on an ASCII file for further analyses.

Several routines determine the population structure of the next generation: Environment, Fitness, Gametes, Zygotes and Release. The Environment routine calculates the rate of increase each generation. The Fitness routine calculates the fitness of each genotype. The Gamete routine calculates gametic frequencies depending on zygote frequencies and their fitness. The Zygote routine determines the

zygotic frequencies of the next generation depending on gametic frequencies and temperature sensitivity (*tsl* mutation). If during this generation, laboratory flies are released they are then added to the native population in routine Release.

The programme is written in Turbo Pascal for Windows 1.0 and is available on request.

Simulations

All simulations were done with an initial population size of 1 million native flies of equal sex ratio. Only males were released, 0.5 million per generation, if not stated otherwise. Several genotypes were released, but males containing a Y-autosome translocation and heterozygous for two mutations, *wp* and *tsl*, represented the most common genotype used (Fig. 1). The fertility of the translocation males is 50% from wild-type males. The other parameters are stated in the figure legends.

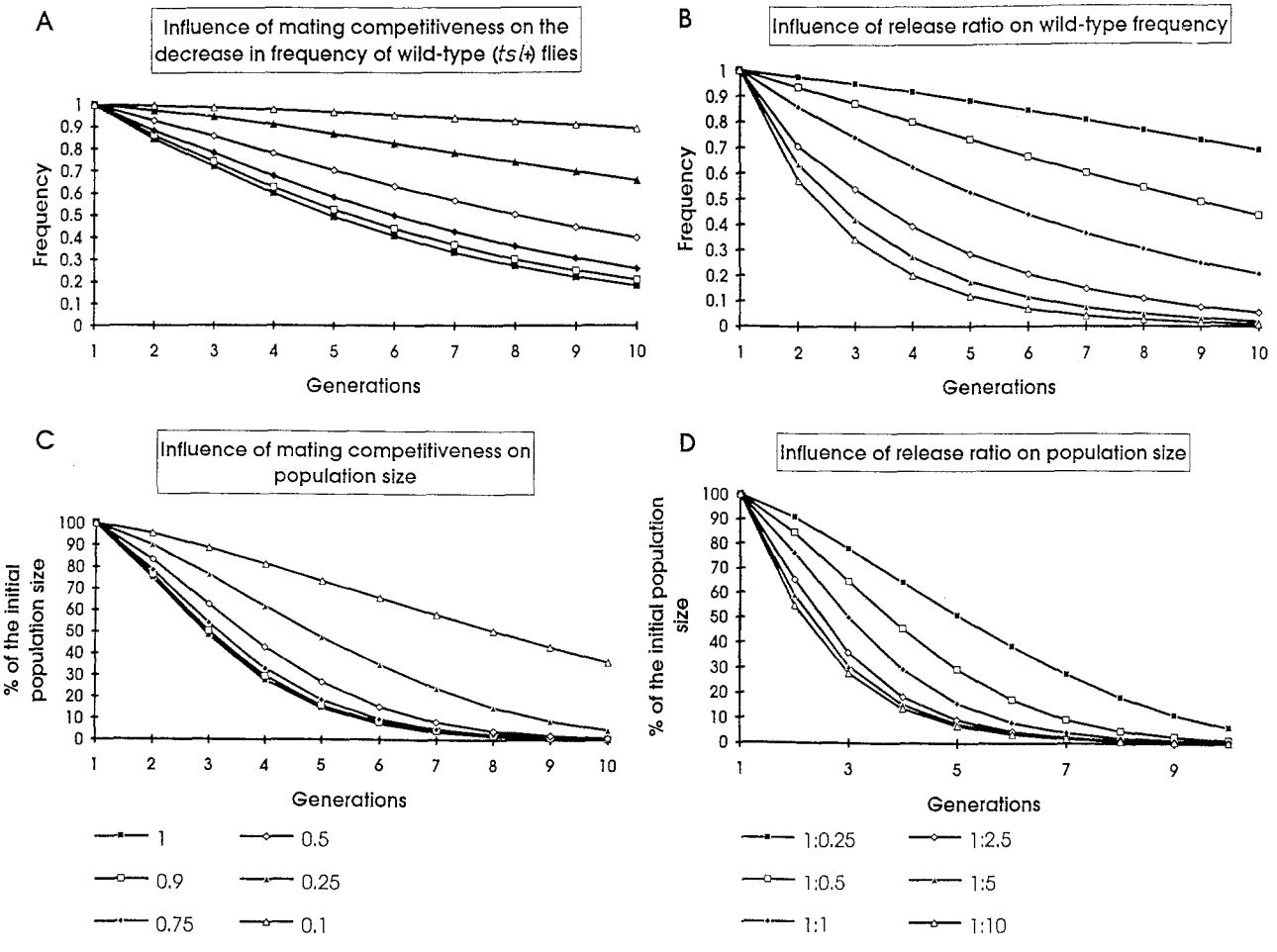
Results

Influence of releasing males containing a *tsl* mutation or a translocation on population suppression

In Fig. 2A and B the introduction of a *tsl* mutation into a native population is simulated. Figure 2A shows the frequency of flies with a *tsl*+ phenotype (i.e. homozygous and heterozygous for the wild-type allele). Male populations with a *tsl* phenotype and varying mating competitiveness were released. It is assumed that the resulting heterozygotes or homozygotes in the native population have the same competitiveness as wild-type flies. The population size remains constant during the simulation and the environmental parameters allow the survival of individuals homozygous for the *tsl* mutation. In Fig. 2B the same parameters are used, but with a constant competitiveness of 0.9 and varying release ratios.

After 10 generations more than a 90% replacement of the *tsl*+ flies with *tsl* flies is attained when the number of

Fig. 2 **A** Males were released that are homozygous for the *tsl* mutation. The mating competitiveness of the released males varied between 1 (the same as the native flies) and 0.1. The intrinsic rate of population increase is 1.0 (no increase) and was not density-regulated. A permissive environmental temperature was used. The decrease in frequency of flies with wild-type phenotype (*tsl*+) is shown for 10 generations. **B** The simulation conditions were the same as those for 2A. In this figure the release ratio varied between 1: 0.25 and 1: 10 (native males: released males). The mating competitiveness of the released males is 0.9. **C, D** The same conditions were used in these simulations, however, this time, males were released that contain a translocation causing a 50% reduction in fertility compared to wild-type flies. This time the population size is shown. The legends indicate the release ratio (native to released) in **2B** and **2D** and mating competitiveness in **2A** and **2C**



released flies is larger than the number of flies in the native population. To replace the native population by more than 99%, a release ratio higher than 10:1 is required, and mating competitiveness has to be high.

In Fig. 2C and D the effect of introducing a chromosome aberration, in this case a Y-autosome translocation causing 50% sterility, into a native population is simulated. The other parameters are as in the first simulation. This time an actual decrease in population size is observed. If the results illustrated in Fig. 2A, B are compared with those in Fig. 2C, D the overall effectiveness of the translocation release is clearly superior. If *tsl* males are released with a mating competitiveness of 0.9 and a 1:1 release ratio, 79% of the native flies will die if a restrictive temperature is applied in generation 10. However, if males that are 50% sterile are released, 99.5% of the original native population will have been eradicated after 10 generations.

In the above comparison the effect on population size after generation 11, when *tsl* release cease, is not included. If temperature increases in generation 10 only 79% of the population is eliminated, but still 96% of the surviving flies are heterozygotes. This means that in the next generation, without further releases, 80% of all flies will become homozygous for the *tsl* mutation and will also die. No additional decrease in population size will occur in the simulation indicated in Fig. 2C and D from generation 11 onwards if no new translocation males are released. A second factor makes it difficult to compare the two simulations; we have simulated a population that is not density-regulated. If a density-regulated population is simulated, the release of translocation-containing flies becomes less efficient under certain conditions than the release of flies containing a *tsl* mutation (data not shown).

Releasing males that contain a Y-autosome translocation and are heterozygous for the *tsl* mutation

In the third set of simulations both strategies are combined, i.e. released males carry a Y-autosome translocation and are heterozygous for the *tsl* mutation. In this case, a restrictive temperature was used during the last 2 generations, i.e. generation 9 and 10. The results are shown in Fig. 3. For example, assuming a mating competitiveness of 0.5 and a 1:1 release ratio, the native population is reduced to 0.6% of its original size after 10 generations of fly releases. Under the same conditions, the release of *tsl* males results in a 73% potential reduction and the release of males containing a translocation results in a 97% reduction after 10 generations. From these simulations it appears that the combined use of translocations and *tsl* mutation would be more effective than using either of the two components alone. The use of translocation-bearing males has a positive effect on suppression. There is a direct effect on population size due to the inherited sterility and an indirect effect through an increase, under certain conditions, in the spread of the *tsl* mutation (data not shown).

The fertility of a strain containing a translocation has no major effect on the rate of replacement of native males by translocation males when a 1:1 ratio of released to native males is simulated (data not shown). After 5 generations almost all native males are replaced by translocation males. However, there is a large effect of fertility on the rate of decrease of the population. When the translocation produces 50% sterility, the population will be ten times smaller after 5 generations, while with a 10% sterility the population size is only 25% smaller than the initial population.

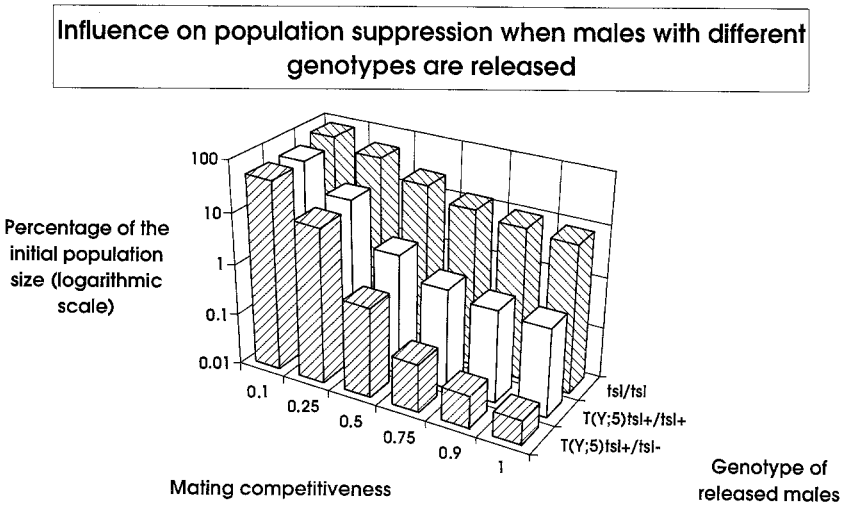
Comparison between the release of homozygous and heterozygous males

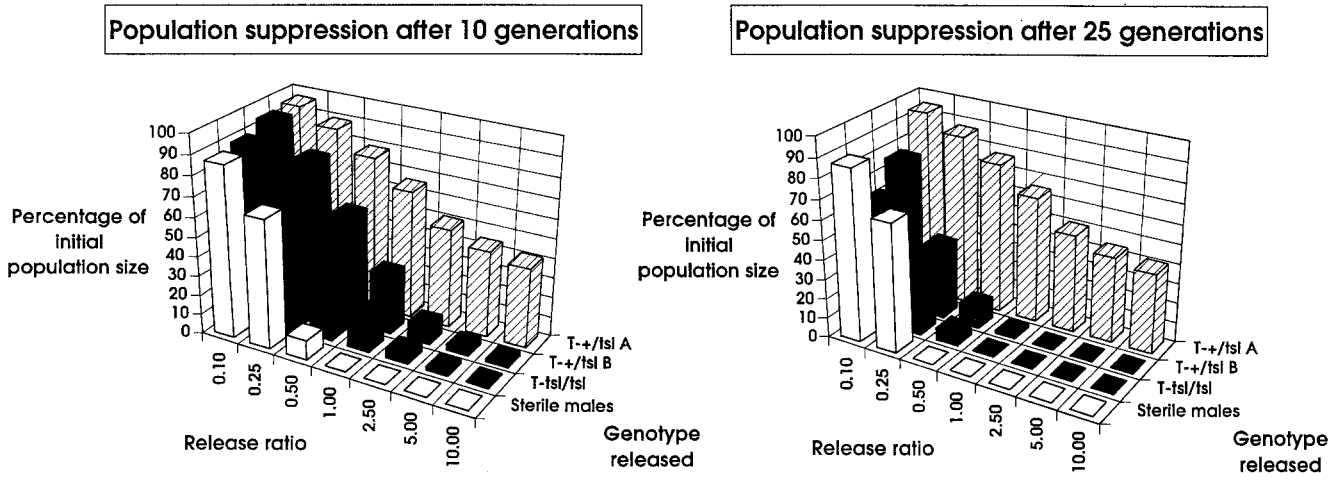
There will be a higher frequency of *tsl* genes in the total population if males homozygous for the *tsl* mutation are released rather than those that are heterozygous for the mutation. However, the simulations shown in Fig. 4 indicate that there is no major effect on population suppression between the release of heterozygous males ($T(Y;5)wp + tsl + /wptsl$) and homozygous males ($T(Y;5)wp + tsl/wptsl$). This is due to the fact that the number of females determines the population size of the next generation, irrespective of the number of males (assuming that all females are fertilized). Because homozygous and heterozygous males both pass the same amount *tsl*-bearing chromosomes on to their female offspring, there is consequently no major difference in suppression between the release of these two genotypes.

Depending on the developmental stage at which the *tsl* mutation causes lethality, *tsl/tsl* males could be released during the hot season. If the released flies are not affected by the high temperature this can be a more efficient pest control strategy under certain environmental conditions (depending on native population size, influence of density regulation etc.).

Efficiency of SIT and *tsl* releases under different environmental conditions

Simulations were done to compare the efficiency of the release of *tsl* males with that of sterile males under different conditions. Figure 5 shows the influence of the ratio between the number of released males and the native population size. Under certain conditions, releasing *tsl* males can be more efficient than releasing fully sterile males. These results are similar to those reported by Foster et al. (1988). The release of *tsl* males is more efficient than the sterile males under specific conditions, e.g. translocation fertility of the *tsl* males, intrinsic rate of increase and equilibrium population density. Furthermore, efficiency depends on the release ratio. In the example shown in Fig. 5, for a 0.3:1 ratio of released to





native males, the release of *tsl* males is more efficient than SIT; however, for a release ratio of 0.4:1 SIT is more efficient.

In these simulations a continuous restrictive temperature was used. When a restrictive temperature is simulated in the last generation, the release of *tsl* males is more efficient than SIT under a larger set of conditions (see also Fig. 4).

Fig. 4 The influence of releasing different genotypes for 10 or 25 generations on population suppression. The genotypes (sterile flies = $T(Y;5)wp + tsl + wp\,tsl$; $T\text{-}tsl/tsl = T(Y;5)wp + tsl/wp\,tsl$; $T- + /tsl = T(Y;5)wp + tsl + /wp\,tsl$) are released at different ratios (released males: native males). Males of genotype $T- + /tsl$ are released under restrictive ($T- + /tsl\,A$) or permissive ($T- + /tsl\,B$) temperatures. When a release under permissive conditions is simulated, high temperatures start in the last 2 generations (generations 9 and 10 in the left chart, generation 24 and 25 in the *right* chart). The native population is density-regulated. The carrying capacity is 1 million flies and the maximum rate of population increase is 10

Influence of mating competitiveness

Irradiation of males lowers mating competitiveness. Because the *tsl* males are not irradiated they should have a higher mating competitiveness value then the sterilized flies. Carpenter (1991) found that irradiation reduces the mating competitiveness of medfly by 67–75%. Figure 6 shows the influence of this reduced mating competitiveness on the efficiency of sterile males releases (SIT) with respect to *tsl* male releases. SIT will always be more effective than *tsl* releases for a 0.5:1 release ratio under the environmental conditions specified in Fig. 6. However, once the sterile males have a mating competitiveness lower than 0.8, releases of *tsl* males are more efficient, depending on the fertility of the translocation. For a higher release ratio, e.g. 0.75:1, the mating competitiveness of the sterile males has to be higher than 0.5 before SIT is more efficient than *tsl* releases.

Consecutive releases of *tsl* males and sterile males

To eradicate a native population we can compute the number of generations of *tsl* male releases before the

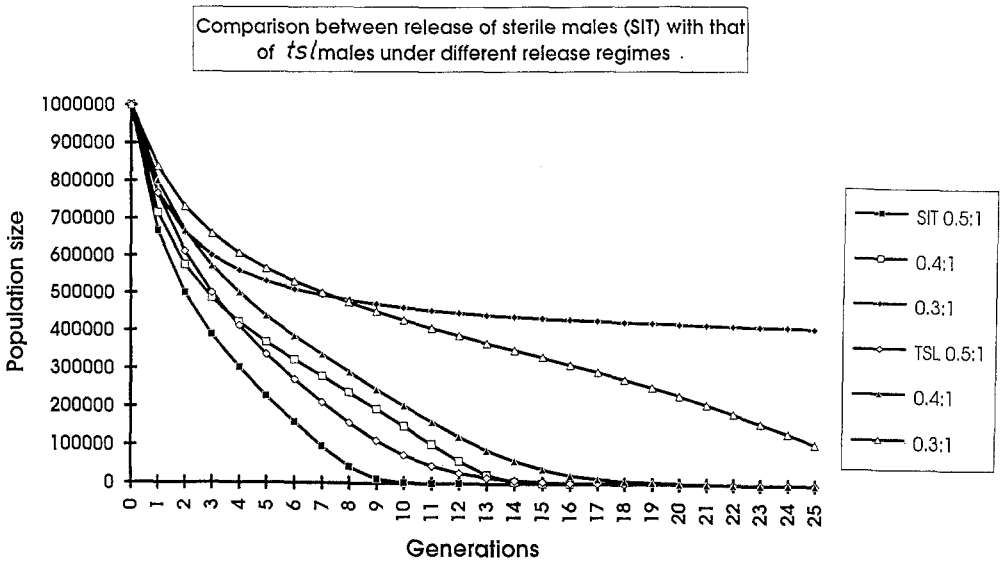


Fig. 5 Under certain conditions the release of *tsl* males can be more efficient in suppressing a population than the release of sterile males. These simulations were done with a density-regulated population with an equilibrium density of 1 million flies. The rate of increase is 3.5. The translocation fertility of the *tsl* males is 0.3. Different ratios of released to native males were simulated (e.g. 0.5: 1). A restrictive temperature was simulated during all generations

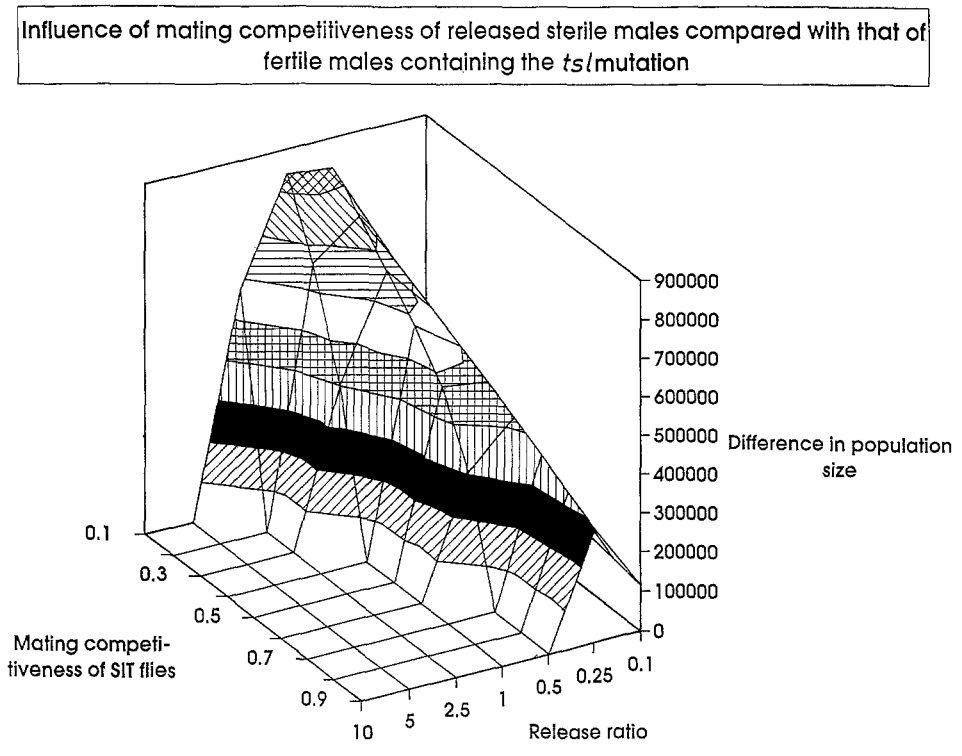


Fig. 6 The influence of mating competitiveness on population suppression. The effect of reduced mating competitiveness of irradiated, sterile flies is compared to releasing non-irradiated, *tsl* flies. Releases were simulated for 30 generations, and the results are expressed as relative efficiency of the two methods (difference in resulting population size), i.e. a difference in population size of zero or lower means that under the given conditions the release of sterile males (SIT) is more efficient than the release of *tsl* flies. At lower release ratios, the release of *tsl* flies is more efficient than sterile fly releases. The simulations were done with a density-regulated native population with an equilibrium density of 1 million flies and a rate of increase of 3.5. For the *tsl* releases a restrictive temperature was simulated in the last 2 generations. There was no reduced translocation fertility

release of sterile males begins. Figure 7 shows the optimal generation to start the release of sterile males based on the ratio of released flies to the native population size and the fertility of the translocation. The parameters used for this simulation are given in Fig. 7. For low release ratios, long releases of *tsl* males are more efficient. However, the higher the number of released *tsl* males, the sooner SIT releases should start. The fertility of the translocation also influences the generation when sterile male releases should start, but this parameter is not so crucial as the release ratio.

Discussion

The computer simulations presented here indicate that the use of conditional lethal mutations in combination with a Y-autosome translocation can be an effective strategy to suppress pest populations. We show that the use of a conditional lethal mutation alone is not very effective in comparison to other control strategies (see Figs. 2, 3 and Klassen and Creech 1973).

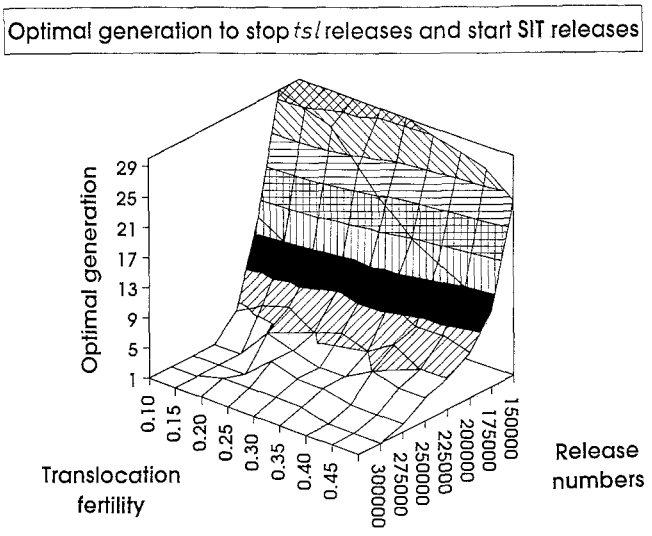


Fig. 7 The optimal generation to stop releasing *tsl* males and to start releasing sterile males was determined under various conditions, i.e. translocation fertility of *tsl* males and the ratio of released to native flies. These simulations were done with a density-regulated population with an equilibrium density of 1 million flies, a rate of increase of 5.0 and a duration 30 generations

If the native population is below the carrying capacity of the environment, the release of males and fertile females will accelerate the increase of the native population under permissive conditions. This effect can be avoided by releasing only males; this requires using a genetic sexing strain, which in medfly is based on Y-autosome translocations, to separate males and females before the releases. If the fertilization rate in the target population is already at a maximum, a release of fertile males would not lead to an additional increase in the native population.

The semisterility caused by the translocation is another feature that can be used for pest control. The use of translocations for population replacement (Curtis 1968; Robinson 1977) or population suppression (Whitten 1971; Foster et al. 1972; Curtis and Robinson 1971; Curtis and Hill 1971) is well-documented. Translocations introduce a genetic load into the population through the production of unbalanced gametes. Most reports describe the use of autosomal translocations that are fertile in homozygous conditions but exhibit a reduced fertility in heterozygous conditions. Furthermore, all models and experiments describe the consequences of a single release of males carrying a translocation. In our simulations we release males for several generations. Moreover, we intend to use translocations to keep the population at a low level, not to eradicate the native population.

We have constructed genetic sexing strains for the medfly that contain a reciprocal translocation between the Y-chromosome and chromosome 5 (Franz et al. 1994). On chromosome 5, two mutations, white pupa (*wp*) and temperature-sensitive lethal (*tsl*), are located (see Fig. 1). The presence of the *wp* mutation allows males to be separated from females in the pupal stage and, consequently, the release of only males. The males used in the simulations are heterozygous for the *wp* mutation and either heterozygous or homozygous for the *tsl* mutation. The latter males survive at a temperature below 33 °C, but die at higher temperatures (data not shown). For the simulations presented here, males that are heterozygous for the *tsl* mutation are assumed to have the same sensitivity to temperature as wild-type males.

We have determined the fertility of several translocation strains (Franz and Kerremans 1993). Translocation fertility was found to be 10–60% of that of wild-type males, the fertility depending mainly on the complexity of the translocation. Whereas releasing males with a low fertility increases the suppression efficiency, it has several disadvantages. Firstly, it will lower the fly production and, consequently, increase the cost of rearing. Secondly, releasing males with a low fertility will reduce the spread of *tsl* in the native population because this is inversely related to the fertility of the released males under many conditions. It will therefore be necessary to select a translocation that provides an optimum between efficiency and cost.

Only a few reports exist on the combined use of chromosomal rearrangements and conditional lethal mutations (Fitz-Earle et al. 1975; Foster and Smith 1991; Foster et al. 1988). The principles of population replacement and eradication with a *tsl* mutation have been demonstrated successfully with *Drosophila melanogaster* under laboratory conditions (Fitz-Earle and Suzuki 1975). However, in this study a compound chromosome, not a translocation, was used.

A similar method has been used to control the sheep blowfly, *Lucila cuprina*, in Australia (Foster et al. 1988). There are, however, several qualitative differences between the use of this field-female killing (FFK) system and the release of males carrying a *tsl* mutation. Firstly, both sexes are released in the FFK system. Males carry a translocation and are heterozygous for an eye mutation that renders homozygous flies non-viable under field conditions (Whitten et al. 1977). The females are homozygous for the eye mutation and thus non-viable in the field. Secondly, at low temperatures, homozygous *tsl* flies are not killed and can accumulate in the population. When the eye mutation is used, homozygous mutant flies are always non-viable. Simulations of this field-female killing system (Foster et al. 1988; Foster and Smith 1991; Foster 1992) can be compared with the release of *tsl* males at high (restrictive) temperatures, i.e. all homozygous *tsl* individuals are killed immediately. If these simulations are compared with simulations in which males are released under low temperature conditions, the latter strategy is more efficient in density-regulated populations. As is shown in Fig. 4, eradication is possible, under certain conditions, when the temperature is low during the releases but this is not possible when the temperature is high.

There are two possible genotypes to release (see Fig. 1): males that are homozygous for the *tsl* mutation or heterozygous males. Several simulations showed that there is no major difference in efficiency between the release of these two genotypes (Fig. 4). If the releases are performed at low temperatures, there is a small advantage in the use of homozygous males, but this advantage depends mainly on the intrinsic rate of natural increase (data not shown).

The *tsl* mutation that has been isolated in medfly causes temperature-dependent lethality during the complete life cycle of the fly; this restricts the release of homozygous *tsl* males to the cold season. But when the *small* advantage of using homozygous *tsl* males is considered, it seems to be more advantageous to release heterozygous males. This has the advantage that temperature does not need to be considered; temperatures might well fluctuate during the release period between permissive and restrictive. Another advantage of using heterozygous *tsl* males for *tsl* releases is that the same males can be used for SIT releases. Thus, only one genotype needs be reared for both types of release strategies.

Foster et al. (1988) showed that SIT is less efficient than the field-female killing system when low numbers of flies are released relative to the size of the native population. The same results were found in this simulation study when SIT was compared with *tsl* releases. *Tsl* releases can be more efficient when low release rates are used, the native population is density-regulated and the translocation fertility of the released flies is rather low (20–60%). The *tsl* releases at high temperatures are only more efficient under very restrictive conditions, and the same is true for the field-female killing strategy. However, if *tsl* males are released at low temperatures, a broader range of conditions exists where this strategy is more efficient than the release of sterile males.

Nevertheless, SIT remains the most efficient option when the native population can be overflooded with released flies. The best strategy will therefore be to start with releases of *tsl* males until a certain level of suppression is attained and then proceed with the release of sterile flies. The optimal time to stop *tsl* releases and to start the release of sterile males is environmentally dependent and can be calculated. The combined use of *tsl* and sterile male releases can therefore be more efficient than the use of only one of the strategies. However, the main reason why the release of *tsl* might be more efficient under a given set of conditions is that the males used in a SIT programme are sterilized through irradiation. Since the mating competitiveness of irradiated males seems to be 25–33% of that of non-irradiated males (Carpenter 1991), our simulations show that the release of *tsl* males is a more beneficial strategy for medfly eradication/control under a wide range of conditions.

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