A reaction–diffusion model for the control of Eldana saccharina Walker in sugarcane using the sterile insect technique

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\textbf{A B S T R A C T}

A reaction–diffusion model is formulated for the population dynamics of \textit{Eldana saccharina} Walker infestation of sugarcane under the influence of partially sterile released insects. The model describes the population growth of and interaction between normal and sterile \textit{E. saccharina} moths in a temporally variable and spatially heterogeneous environment. It consists of a discretized reaction–diffusion system with variable diffusion coefficients, subject to strictly positive initial data and zero-flux Neumann boundary conditions on a bounded spatial domain. The primary objectives are to establish a model which may be used within an area-wide integrated pest management programme for \textit{E. saccharina} in order to investigate the efficiency of different sterile moth release strategies without having to conduct formal field experiments, and to present guidelines according to which release ratios, release frequencies and spatial distributions of releases may be estimated which are expected to lead to suppression of the pest. Although many reaction–diffusion models have been formulated in the literature describing the sterile insect technique, few of these models describe the technique for Lepidopteran species with more than one life stage and where F1-sterility is relevant. In addition, none of these models consider the technique when fully sterile females and partially sterile males are released. The model formulated here is also the first reaction–diffusion model formulated describing \textit{E. saccharina} growth and migration, and the sterile insect technique applied specifically to \textit{E. saccharina}.

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1. Introduction

The South African sugar industry is recognized as one of the top 15 cost competitive sugar producers in the world. The industry makes an important contribution to employment, sustainable development and the national economy, with an estimated one million people depending on the industry for a living (SASA, 2010). A major threat to the industry’s profit margins is the African sugarcane stalk borer, \textit{Eldana saccharina} Walker (Lepidoptera: Pyralidae), which has been identified as a serious pest in sugarcane plantations in South Africa since 1971 (Carnegie, 1974). \textit{E. saccharina} is indigenous to Africa and occurs naturally in wetland sedges and indigenous grasses. The physiological development of \textit{E. saccharina} is typical of insects – its lifecycle consists of eggs, larvae, pupae and moths (Atkinson, 1980; Atkinson and Carnegie, 1989; Carnegie, 1974; Sampson and Kumar, 1985). Evidence suggests that \textit{E. saccharina} infestation of sugarcane is a result of its cryptic egg-laying sites, namely dead leaf material (Atkinson, 1979). Infestation not only affects the sucrose content of sugarcane, but also the final sugarcane biomass, resulting in serious losses in sucrose production (Goebel and Way, 2003; King, 1989; Way, 2001). Crop and sucrose losses incurred as a result of \textit{E. saccharina} infestation have been estimated at approximately 1% loss in recoverable sucrose for every 1% internodes bored (King, 1989). During the 2003/2004 milling season, losses were estimated at R153 million \textsuperscript{1} (Goebel and Way, 2007). The \textit{E. saccharina} problem is thus of major concern among South African sugarcane farmers, and a means of effectively managing the pest is the subject of a number of intensive research programmes at the South African Sugarcane Research Institute (SASRI).

One of the more recent research programmes is the Sterile Insect Technique (SIT), a birth control method implemented through the release of large numbers of sterile insects (Dyck et al., 2005) as part of SASRI’s area-wide integrated pest management program

\textsuperscript{1} The Rand (R) is the currency of South Africa. The typical Rand/US$ exchange rate for 2012 was between R7.50 and R8.50 for every 1 US$.
(AW-IPM). SIT was initiated in South Africa in 1996 to create fruit fly-free areas in the Western Cape from both the Mediterranean fruit fly Ceratitis capitata Wiedemann (Diptera: Tephritidae) and the Natal fruit fly Ceratitis rosa Karsch (Diptera: Tephritidae). In 2003 the International Atomic Energy Agency (IAEA) approved funding for an SIT project against the coding moth Cydia pomonella Linnaeus (Lepidoptera: Tortricidae), the false coding moth Thaumatostiola leucotreta Meyrick (Lepidoptera: Tortricidae) and the Natal fruit fly (Agricultural Research Council, 2010). An SIT programme was initiated against false coding moth and E. saccharina, the use of SIT against E. saccharina appeared feasible. In 2009 the IAEA approved further funding for an SIT project involving four Lepidoptera pests, one of which was the sugarcane borer E. saccharina, under the management of SASRI.

Extensive research is required before altering a natural system by external manipulation, such as SIT, in order to avoid wasting resources and possibly altering the system into an undesirable ecological stable state (Murray, 2002). Research projects on E. saccharina physiology and its behaviour after sterilization are currently underway at SASRI and at Stellenbosch University. Valuable insights into the mortality, levels of sterility (Walton, 2011) and competitiveness in matings of the sterile insects (Mudavanhu, 2010) for different radiation doses have been gained in these projects. However, in contrast to mathematical modelling, these research projects and trials take time to complete. In order to suppress or eradicate a pest in its native environment, typical SIT questions raised are what the necessary numbers of sterile insects to release are, how frequent releases should be, what the best spatial distribution is for sterile releases and whether it is an economically viable control measure. The purpose of a previous study by the current authors (Potgieter et al., 2012) was to aid the current South African SIT effort through the use of a mathematical model by finding suitable parameters in terms of which E. saccharina population growth and interaction may be quantified, and according to which E. saccharina infestation levels and the associated sugarcane damage may be measured, and finally to validate the mathematical description. The study provided insight into optimal release ratios, release frequencies and the best timing for releases. However, in that study the model did not include the crucial effects of spatial variation of the environment and insect dispersal, but rather assumed averaged conditions across space. The primary objective in this follow-up study is to provide further aid to the SIT effort with the use of a reaction–diffusion model with parameters as defined in Potgieter et al. (2012) in order to investigate the possible effects of spatial variation and heterogeneous moth dispersal, and to identify the best spatial distribution for sterile releases.

The model in this paper builds on previous work by Hearne et al. (1991), Horton et al. (2002) and Potgieter et al. (2012) and describes the population growth and migration of a wild E. saccharina population under the influence of a release of fully sterile females and semi-sterile males in a spatially heterogeneous environment. The model comprises a reaction–diffusion system with variable diffusion coefficients, subject to strictly positive initial data and zero-flux Neumann boundary conditions on a bounded spatial domain. Eleven subpopulations are modelled, namely the fertile egg population, the inherited sterile egg population, the newly hatched fertile larvae population outside the stalk, the newly hatched inherited sterile larvae population outside the stalk, the fertile larvae population inside the stalk, the inherited sterile larvae population inside the stalk, the fertile pupae population, the inherited sterile pupae population, the fertile moth population, the inherited sterile moth population and the released sterile moth population. Promotions from stages occur at certain temperature-dependent rates (Potgieter et al., 2012).

2. Modelling approach

An E. saccharina population growth model for a spatially and temporally variable environment is derived in this section in order to describe the spatial dynamics of a set of interacting E. saccharina subpopulations under the influence of a release of fully sterile females and semi-sterile males on an isolated and bounded spatial domain. In the context of this study, the spatial domain is assumed to be an isolated set of adjacent sugarcane fields with heterogeneous cane age and cane variety, surrounded by land uses not corresponding to possible habitats for E. saccharina.

The temporal model developed by Potgieter et al. (2012) is not realistic in the context of a sugarcane farm comprising a heterogeneous environment. More specifically, it is also not realistic to assume an average abundance of sterile insects across space in the context of sterile insect releases as homogeneous, being driven along the edges of the sugarcane fields. The distribution of E. saccharina in a heterogeneous environment can therefore not be described by the mean-field approximation – a spatially explicit model is required.

The set of sugarcane fields is divided into discrete patches of sugarcane, each patch having the same number of sugarcane stalks and being small enough to allow for the adoption of the mean-field approximation within a single patch. This patchy environment is modelled as a two-dimensional arena in which E. saccharina populations are distributed amongst a grid of square patches with populations connected by dispersing individuals. The dynamics of each population are modelled by assuming the mean-field model described in Potgieter et al. (2012) as reaction terms, whereas the dynamics among populations (dispersal of individuals between neighbouring patches) are modelled by assuming the discretized Laplacian operator for the purpose of diffusion. During each day, a certain proportion of adult moths are assumed to leave the patch in which they emerged or from where they have been released, so as to colonize neighbouring patches within their flight range. Dispersal will only occur within the spatial domain, and not outside the domain as a result of the assumed land uses surrounding the set of sugarcane fields.

2.1. The model

The spatio-temporal model presented in this paper assumes that individual moths follow a pure random walk. During each time-step, a proportion of moths disperse randomly to neighbouring habitat sites. Consider the eleven subpopulations of an E. saccharina population within a closed, simply connected, two-dimensional spatial domain $S$. Let $E_1(\xi,t)$, $E_2(\xi,t)$, $E_3(\xi,t)$, $E_4(\xi,t)$, $E_5(\xi,t)$, $E_6(\xi,t)$, $E_7(\xi,t)$, $E_8(\xi,t)$, $E_9(\xi,t)$, $E_{10}(\xi,t)$, and $E_{11}(\xi,t)$ denote the densities (measured in $\text{e}/100s$, which is the number of members of the subpopulation per 100 stalks) of the eleven subpopulations at position $\xi = [\xi_1, \xi_2]^T \in S$ and at time $t \in [0, \infty)$, in the order in which they were mentioned at the end of Section 1. Furthermore, assume that the change of the population density of the 1th moth subpopulation (that is, for $i=9, 10, 11$) per time unit is equal to the dispersal of the ith subpopulation to and from adjacent habitat sites together with the amount of the ith subpopulation created per time unit within the site. Changes in the densities of all other subpopulations per time unit at a certain position are assumed equal to the amount created per time unit, with no dispersal occurring. The diffusion matrix, $D(\xi)$, therefore has zero entries corresponding to all types of subpopulations, except for moths. That is, $D(\xi) = \text{diag}(d_1(\xi), d_2(\xi), d_3(\xi), d_4(\xi), d_5(\xi), d_6(\xi), d_7(\xi), d_8(\xi), d_9(\xi), d_{10}(\xi), d_{11}(\xi))$. 


shown reaction–diffusion the mortality constant therefore, diffusion where the effect is effectively and these scenarios, without any assumption, the non-dimensional form of (1) is
\[
\frac{\partial E_i(x, t)}{\partial t} = f_i(x, t, \frac{E_i(x, 0)}{E_0(x, 0)}) + \frac{1}{l^2} \nabla \cdot [\mathbf{D}(x) \nabla E_i(x, t)]
\]
and at time \( t = 0 \), then the non-dimensional form of (1) is
\[
\frac{\partial E_i(x, t)}{\partial t} = f_i(x, t, \frac{E_i(x, 0)}{E_0(x, 0)}) + \frac{1}{l^2} \nabla \cdot [\mathbf{D}(x) \nabla E_i(x, t)]
\]
for \( i = 1, 3, 5, 7, 9 \) and \( j = 1, 3, 5, 7, 9 \), and
\[
\frac{\partial E_i(x, t)}{\partial t} = \frac{f_i(x, t, \frac{E_i(x, 0)}{E_0(x, 0)}) + \frac{1}{l^2} \nabla \cdot [\mathbf{D}(x) \nabla E_i(x, t)]}{k}
\]
is a finite-difference approximation to (3). In the equation above, \( \nabla G(x, t) \), given by
\[
\left( \frac{1}{2h}(G(x_1 + h, x_2, t) - G(x_1 - h, x_2, t)),
\frac{1}{2h}(G(x_1, x_2 + h, t) - G(x_1, x_2 - h, t)) \right),
\]
is the central-difference approximation and
\[
\nabla^2 G(x, t) = \frac{1}{h^2}(G(x_1 + h, x_2, t) + G(x_1 - h, x_2, t) + G(x_1, x_2 + h, t) + G(x_1, x_2 - h, t)) - 4G(x_1, x_2, t)
\]
is known as the discretized Laplacian operator for diffusion, with both spatial approximations having a leading error of order \( h^2 \) (Smith, 1985). Under the realistic assumption that dispersal only occurs during the night, a discrete time model for diffusion is appropriate. If \( t \) is measured in days and \( k = 1 \), a discrete time model for population growth [similar to the mean-field model described in Potgieter et al. (2012)] and diffusion is obtained, with diffusion being continuous in space. Since no approximation is required in terms of time, the discretized model therefore only exhibits approximating errors with respect to space, which gives a leading error of order \( h^2 \). As \( h \) tends to zero, the finite-difference approximation tends to the true solution of (3) with appropriate initial and boundary conditions (Smith, 1985).

2.2. Boundary conditions

The flux at the boundary is assumed constant. Therefore, Neumann boundary conditions of the form
\[
\frac{\partial E_i(x_1, x_2, t)}{\partial x_1} \bigg|_{x_1 = \eta} = \xi_i \frac{\partial E_i(x_1, x_2, t)}{\partial x_2} \bigg|_{x_2 = \eta} = \eta
\]
are assumed, where \( \partial S \) is the boundary of \( S \). Assuming the boundary is not part of \( S \), and letting the boundary nodes be situated at positions \( x_1 = x_1^1 \) and \( x_2 = x_2^m \) for \( x_2 = x_2^m \) and \( x_2 = x_2^m+1 \) for all \( x_1 \), the value of \( \xi \) for \( x_1^1 < x_1 < x_1^{m+1} \) and
\( x^2 < x < x^{n+1} \) is known since it is in the model domain. The Taylor expansion of \( \xi \) around \( x^1 \) is given by

\[
\begin{align*}
\xi(x^1 + h, x_2, t) &= \xi(x^1, x_2, t) + \frac{\partial}{\partial x_1} \xi(x^1, x_2, t) h + \frac{h^2}{2} \frac{\partial^2}{\partial x_1^2} \xi(x^1, x_2, t) + \mathcal{O}(h^3), \\
\xi(x^1 + 2h, x_2, t) &= \xi(x^1, x_2, t) + 2h \frac{\partial}{\partial x_1} \xi(x^1, x_2, t) + \mathcal{O}(h^3).
\end{align*}
\]

Similar expansions of \( \xi \) around \( x^{n+1}, x^1 \) and \( x^{n+1} \) may be obtained. By imposing the boundary conditions (4), and substituting the known values for \( \xi(x^{n+1}, x_2, t), \xi(x^1, x_2, t), \xi(x_1, x_0, t), \xi(x_1, x_2, t), \xi(x_1, x_2, t), \xi(x_1, x_{n+1}, t), \xi(x_1, x_{n+1}, t), \xi(x_1, x_2, t) \) and \( \xi(x_1, x_{n+1}, t) \), the boundary values

\[
\begin{align*}
\xi(x^1, x_2, t) &= \frac{4}{3} \xi(x^0, x_2, t) - \xi(x^1, x_2, t) - 2h\eta, \\
\xi(x_1, x^2, t) &= \frac{4}{3} \xi(x_1, x_0, t) - \xi(x_1, x_1, t) - 2h\eta, \\
\xi(x^{n+1}, x_2, t) &= \frac{4}{3} \xi(x^n, x_2, t) - \xi(x^{n+1}, x_2, t) - 2h\eta \\
\xi(x_1, x^{n+1}, t) &= \frac{4}{3} \xi(x_1, x^n, t) - \xi(x_1, x^{n+1}, t) - 2h\eta
\end{align*}
\]

are obtained. Since the spatial domain is assumed to be isolated and surrounded by land uses not corresponding to possible habitats for \( E. \) saccharina, zero-flux Neumann boundary conditions are appropriate \((\eta = 0)\), which results in migrants on the edge of the domain being prevented from crossing the boundary by \( \xi \). If migrants are prevented from leaving the domain, then \( \sum_{x} \mathbf{V} \mathbf{D}(x) \cdot \nabla \xi(x, t) + \mathbf{D}(x) \nabla^2 \xi(x, t) = 0 \). In order to calculate \( \mathbf{V} \mathbf{D} \) boundary conditions for \( \mathbf{D} \) must also be specified. From the Taylor expansion of \( \mathbf{D} \) around \( x^1 \), and ignoring the higher order terms, it follows that

\[
\frac{\partial}{\partial x_1} \mathbf{D}(x^1, x_2) + \frac{h^2}{2} \frac{\partial^2}{\partial x_1^2} \mathbf{D}(x^1, x_2) = \frac{1}{2}(1 - k) \mathbf{D}(x^1, x_2) + 2h_2 \mathbf{D}(x^1, x_2)
\]

for some constant \( k \). Substituting (5) into the Taylor expansion (for all similar boundary expansions) and simplifying, yields the boundary values

\[
\begin{align*}
\mathbf{D}(x^1, x_2) &= 2 - \frac{k}{2 - k} \mathbf{D}(x^0, x_2) - \frac{1 - k}{2 - k} \mathbf{D}(x^1, x_2), \\
\mathbf{D}(x_1, x^1) &= 2 - \frac{k}{2 - k} \mathbf{D}(x_1, x^0) - \frac{1 - k}{2 - k} \mathbf{D}(x_1, x^1), \\
\mathbf{D}(x^1, x_2) &= 2 - \frac{k}{2 - k} \mathbf{D}(x^0, x_2) - \frac{1 - k}{2 - k} \mathbf{D}(x^1, x_2) \\
\mathbf{D}(x^1, x_2) &= 2 - \frac{k}{2 - k} \mathbf{D}(x^1, x_2) - \frac{1 - k}{2 - k} \mathbf{D}(x^{n+1}, x_2) \\
\mathbf{D}(x^1, x_2) &= 2 - \frac{k}{2 - k} \mathbf{D}(x^1, x_2) - \frac{1 - k}{2 - k} \mathbf{D}(x_2, x_2).
\end{align*}
\]

The constant \( k \) may be chosen such that \( \sum_{x} \mathbf{V} \mathbf{D}(x) \cdot \nabla \xi(x, t) + \mathbf{D}(x) \nabla^2 \xi(x, t) = 0 \). For constant diffusion coefficients across the domain, \( k = -1 \), and all boundary values for \( \mathbf{D}(x) \) are zero.

2.3. Initial values

The initial population densities before applying SIT are assumed to be in a stable equilibrium state. Therefore, initial values of fertile egg, larval, pupal and moth population densities are computed according to the ratios

\[
\frac{\lambda_f}{\mu_E + \alpha_E} : \frac{\lambda_f \alpha_E}{(\mu_E + \alpha_E)(\mu_1 + \alpha_1)} : \frac{\mu_M \mu_P + \alpha_P}{\alpha_E \alpha_P} : \frac{\mu_M}{\alpha_P} : 1
\]

between the equilibrium population densities of the \( E. \) saccharina mean-field model with no sterile releases.

2.4. Diffusion coefficients

As mentioned, the use of a pure diffusion process with constant diffusion coefficients is based on the assumption that individual moths follow a pure random walk. This assumption is only realistic if individual moths have no long-term memory or large-scale knowledge of the landscape (Ovaskainen, 2008). At the time of this study, not much was known about the dispersal patterns of individual \( E. \) saccharina moths, and variable coefficients were therefore not assumed. In this paper the diffusion coefficient is defined as the number of moths that diffuse (disperse) across a unit area of 25 m² per day at a certain position \( x = [x_1, x_1] \) in the cane field under the influence of a spatial gradient of one moth. An appropriate range of 0.005 < \( |\mathbf{D}(x)| < 0.03 \) was obtained from simulations performed on a 1 ha field with initial infestation occurring only at one node in the middle of the field. For diffusion coefficients outside this range, infestation seemed either too concentrated around the initial patch, or too widespread to correspond to a field observation that \( E. \) saccharina was able to colonize most of a 0.65 ha field during the crop cycle with invasions both from nearby fields and internal spread within the field (Berry et al., 2010).

2.5. Release rate

It is assumed that moths are released from an all terrain vehicle (ATV) driven alongside the edge of each sugarcane field (in release lanes). At the time of this study, aircraft releases were not considered an economically viable option for sterile releases in South Africa due to the relatively small areas covered. SIT releases by means of ATVs driven alongside the edge of a sugarcane field may result in a uniform distribution of sterile moths along the release lanes if mechanical release devices are used to release moths. However, if releases are performed manually, a discrete distribution of sterile moths along the release lanes at specific release points is applicable (see Fig. 1). The release rate \( r(x, t) \) at position \( x = [x_1, x_1] \) is therefore obtained by distributing the required number of released sterile moths uniformly across all patches within the release lanes (or at discrete points), with \( r(x, t) = 0 \) in all other patches. The release lanes of the different sugarcane fields are defined according to the assumed field layout within the spatial domain.

2.6. Probability of fertilization

Releasing both sterile females and males into a native \( E. \) saccharina population may result in nine different mating combinations. Furthermore, if it is assumed that males and females mate more than once, the nine different mating combinations may be expressed by

\[
(P_{m}(t) + P_f(t) + P_{mf}(t))^n (P_{pm}(t) + P_{pm}(t) + P_{pm}(t))^n = 1,
\]

where \( P_m(t), P_f(t), P_{mf}(t), P_{pm}(t), P_{pm}(t) \) and \( P_{pm}(t) \) denote the probabilities of mating with a wild fertile female, an inherited sterile female, a released sterile female, a wild fertile male, an inherited sterile male and a released sterile male at time \( t \), respectively, and \( n \) denotes the total number of matings possible per insect.
In the study by Potgieter et al. (2012) it was shown that by expanding the above distribution, one may obtain the probabilities of a fertile egg being fertilized by a fertile or semi-sterile sperm as

\[
\gamma(t, x) = \sum_{n=1}^{B} \frac{M_n}{\sum_{k=1}^{n} \binom{n}{k} (-1)^{k+1} P_{\beta}(t, x)^k}
\]

and

\[
\rho(t, x) = \sum_{n=1}^{B} \frac{M_n}{\sum_{k=1}^{n} \binom{n}{k} (-1)^{k+1} P_{\gamma}(t, x)^k}
\]

respectively, where \(M_n\) denotes the proportion of males mating \(n\) times and where \(B\) denotes the maximum number of matings per male. Furthermore,

\[
P_{\beta}(t, x) = \sum_{n=1}^{A} F_n [1 - P_{\beta}(t, x) + (P_{\beta}(t, x) + c_s P_{\beta}(t, x) - c_b P_{\beta}(t, x))]
\]

and

\[
P_{\gamma}(t, x) = \sum_{n=1}^{A} F_n [P_{\gamma}(t, x) + c_s P_{\gamma}(t, x) - c_b P_{\gamma}(t, x)].
\]

where \(F_n\) denotes the proportion of females mating \(n\) times, where \(A\) denotes the maximum number of matings per female at time \(t\) and position \(x\), and where \(c_s\) denotes the competitiveness factor of released sterile sperm compared to other sperm.

2.7. The growth, mortality and maturation parameters

The number \(\lambda_t\) of viable eggs (e/100s) laid per day per female \(E.\ saccharina\) moth mated with a fertile male is assumed to be 4.725 (Hearne et al., 1991; Horton et al., 2002), whereas \(\lambda_s\) is only 23% of that associated with a normal fertile mating (Walton, 2011); therefore \(\lambda_s\) is assumed to be 1.08675 in this case. Each life stage of \(E.\ saccharina\) has a unique maturation and mortality rate which depends also on the daily average temperature.

The Entomology Department at SASRI has, through a number of research experiments, obtained stage-specific mortality and mortality rates of \(E.\ saccharina\) and how changes in temperature affect these rates (Horton et al., 2002; Way, 1995). The stage-specific mortality rates per day at a temperature of 26 °C are given in Table 1. Table 2 illustrates the change in mortality rate (in relation to mortality rates at a temperature of 26 °C) for each of the specified temperatures.

Crop varieties have different resistance levels with respect to \(E.\ saccharina\) infestation. The larval mortality rate is therefore multiplied by a resistance rating function \(v(\omega)\) to incorporate the increase/decrease in mortality for different crop varieties, where \(\omega\) denotes the resistance rating index of the crop variety (Horton et al., 2002; Potgieter et al., 2012). The mortality rate of each life stage at time \(t\) is \(\mu(t, \tau) = \mu(t, \tau) v(\omega)\), \(\mu(t, \tau) = \mu(t, \tau) v(\omega)\), \(\mu(t, \tau) = \mu(t, \tau) v(\omega)\), and \(\mu(t, \tau) = \mu(t, \tau) v(\omega)\), respectively, where the temperature functions \(k(t, \tau), k(t, \tau), k(t, \tau)\) and \(k(t, \tau)\) are determined by finding the lowest degree polynomial which achieves a satisfactory fit to the corresponding stage mortality data (Potgieter et al., 2012).

The maturation rates of the various life stages are \(\alpha(t, \tau) = g(t, \tau), \alpha(t, \tau) = g(t, \tau), \alpha(t, \tau) = g(t, \tau)\), and \(\alpha(t, \tau) = g(t, \tau)\), respectively.

Table 1
Stage-specific mortality rates for \(E.\ saccharina\) at a temperature of 26 °C (Hearne et al., 1991).

<table>
<thead>
<tr>
<th>Mortality rate (/day)</th>
<th>Eggs ((\mu_t))</th>
<th>Larvae (outside stalk) ((\mu_l))</th>
<th>Larvae (inside stalk) ((\mu_l))</th>
<th>Pupae ((\mu_p))</th>
<th>Moths ((\mu_m))</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.03</td>
<td>0.115</td>
<td>0.009</td>
<td>0.007</td>
<td>0.2</td>
<td></td>
</tr>
</tbody>
</table>

Table 2
Collocation points for the temperature functions used to adjust mortality rates (Hearne et al., 1991).

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Eggs</th>
<th>Larvae</th>
<th>Pupae</th>
<th>Moths</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>0.00</td>
<td>0.64</td>
<td>0.78</td>
<td>1.00</td>
</tr>
<tr>
<td>19</td>
<td>0.00</td>
<td>0.58</td>
<td>0.78</td>
<td>1.00</td>
</tr>
<tr>
<td>22</td>
<td>0.00</td>
<td>0.44</td>
<td>0.54</td>
<td>1.00</td>
</tr>
<tr>
<td>26</td>
<td>0.00</td>
<td>0.56</td>
<td>0.71</td>
<td>1.00</td>
</tr>
<tr>
<td>30</td>
<td>0.00</td>
<td>0.64</td>
<td>0.78</td>
<td>1.00</td>
</tr>
</tbody>
</table>

![Image](image.png)

**Fig. 1.** (a) Mechanical release devices release moths at a constant rate from an ATV, resulting in a uniform distribution along the release lanes. (b) If moths are released by hand, releases occur at specific release points along the release lanes.
Table 3
Average development time (in days) per life stage measured at different temperatures (Way, 1995). The maturation rate is approximated by the reciprocal of the average development time spent in each stage.

<table>
<thead>
<tr>
<th>°C</th>
<th>Eggs (Days)</th>
<th>Eggs (Rate)</th>
<th>Larvae (outside stalk) (Days)</th>
<th>Larvae (outside stalk) (Rate)</th>
<th>Larvae (inside stalk) (Days)</th>
<th>Larvae (inside stalk) (Rate)</th>
<th>Pupae (Days)</th>
<th>Pupae (Rate)</th>
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</thead>
<tbody>
<tr>
<td>13</td>
<td>16.8</td>
<td>0.06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>13.2</td>
<td>0.076</td>
<td>85.1</td>
<td>0.0117</td>
<td>97</td>
<td>0.01031</td>
<td>38</td>
<td>0.026</td>
</tr>
<tr>
<td>20</td>
<td>8.6</td>
<td>0.116</td>
<td>36.32</td>
<td>0.02753</td>
<td>50.5</td>
<td>0.0198</td>
<td>19.6</td>
<td>0.051</td>
</tr>
<tr>
<td>25</td>
<td>6.1</td>
<td>0.164</td>
<td>19.4</td>
<td>0.05155</td>
<td>30.3</td>
<td>0.033</td>
<td>9.8</td>
<td>0.102</td>
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<tr>
<td>30</td>
<td>4.8</td>
<td>0.208</td>
<td>12.7</td>
<td>0.07874</td>
<td>22.9</td>
<td>0.04367</td>
<td>8</td>
<td>0.125</td>
</tr>
<tr>
<td>35</td>
<td>4.6</td>
<td>0.217</td>
<td>14.88</td>
<td>0.0672</td>
<td>19.9</td>
<td>0.05025</td>
<td>6.1</td>
<td>0.164</td>
</tr>
</tbody>
</table>

where the temperature functions \( g_{\sigma}(\tau) \), \( g_{\delta}(\tau) \), \( g_{\gamma}(\tau) \) and \( g_{\theta}(\tau) \) are again determined by finding the lowest degree polynomial that achieves a satisfactory fit to the corresponding stage maturation data (see Table 3) (Potgieter et al., 2012).

2.8. Variability in \( S \)
Homogenous patches are assumed within each subset (a single field) of \( S \). As a result of the uniform environment, mortality and diffusion parameters are assumed to be spatially homogenous within a subset. The different subsets of the spatial domain \( S \) are assumed heterogeneous with respect to sugarcane variety and age which, in turn, results in mortality parameters being spatially heterogeneous across \( S \). As a result of crop varieties having different resistance levels with respect to \( E. saccharina \) infestation, the larval mortality parameter in each subset of \( S \) varies according to the crop variety in the field. Also, for differently aged crops, the larval mortality in each subset of \( S \) is increased by a density-dependent mortality parameter according to the age of the crop within the specific subset. The density-dependent parameter decreases with age, resulting in a larger carrying capacity for older crops because of higher nutrition levels for \( E. saccharina \). The value of the density-dependent parameter \( b(t) \) is determined by assuming a decreasing s-shaped function of the form

\[
b(t) = \frac{y}{d^2 + 1},
\]

where \( y > 0 \) and \( z > 1 \). In (7), \( d = (3/365)a \) for a one-year growth cycle, or \( d = (3/730)a \) in the case of a two-year growth cycle, where \( a \) denotes the age of the crop in days at time \( t \). The factor \( d \) is employed in (7) in order to scale the horizontal axis between 0 and 3 to days.

For the purposes of this study, region- and farm-specific factors, such as climate, soil type and farming practices, are assumed to be incorporated into the model by adjusting the values for \( y \) and \( z \) in (7) according to previous infestation data for the specific region or farm.

2.9. Crop damage index
A damage index \( \delta(x, t) \) is defined as the cumulative total of larval feeding up to day \( t \) at position \( x \) since the crop was planted, measured as a percentage of the total stalk length on day \( t \), and is given by

\[
\delta(x, t) = \sum_{j=0}^{t} \sigma(j)(\xi_5(x, j) + \xi_6(x, j)),
\]

where \( \sigma(j) \) denotes the amount of larval feeding per larva on day \( j \) and where \( \ell(x, t) \) denotes the average stalk length on day \( t \) at position \( x \). The total average length of stalk bored per larva assumed in this study is 42.525 mm (Potgieter et al., 2012). The daily feeding rate is approximated by the reciprocal of the average development time spent (\( a_{t_{j}}(t, \tau) \)) in each stage multiplied by 42.525. Furthermore, \( \ell(x, t) \) is an estimation (measured in mm) of the average stalk length on day \( t \) at position \( x \), given recursively by

\[
\ell(x, t + 1) = \ell(x, t) + 0.16(24)(-1.77 + 0.176(\tau - 10) + 0.45)
\]

for a two-year crop cycle, according to the CANEGRO model (Bezuidenhout, 2000), where \( \ell(x, 0) \) denotes the average stalk length at position \( x = [x_1, x_2]^T \) at time \( t = 0 \).

3. Model analysis
Release strategies for different release scenarios were obtained by means of simulations of the finite-difference approximation (4) implemented in Matlab (MathWorks, 2011). Twice a week and weekly releases were previously found to be the best release frequency in terms of suppression and the cost of applying SIT (Potgieter et al., 2012). Simulations were performed for a homogenous 1 ha field over a time period of 24 months for cane planted in November, with a homogenous initial infestation of 0.1 e/100s. The fertile proportion of the \( F_1 \) generation of released sterile males was taken as 0.1, the residual fertility in released moths was taken as 0, the male and female competitiveness were set at 1 and 0.1, respectively, sperm competitiveness was taken as 1, and sterile releases included both males and females. Also, the density-dependent

![Fig. 2. Simulation results of E. saccharina infestation and corresponding percentage internode damage for a susceptible cane variety (w = 8) and a resistant cane variety (w = 5).](image-url)
Table 4
Comparison between release lane distances (in metres), release ratios and infestation levels at the end of the sugarcane cycle (manual all terrain vehicle releases).

<table>
<thead>
<tr>
<th>Cane variety</th>
<th>Frequency</th>
<th>$d(x)$</th>
<th>Distance</th>
<th>Release ratio</th>
<th>$e/100s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resistant</td>
<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>10:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>43:1</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>35</td>
<td>107:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>40</td>
<td>150:1</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>25</td>
<td>146:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>150:1</td>
<td>9.6</td>
</tr>
<tr>
<td>Susceptible</td>
<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>21:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>105:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>35</td>
<td>150:1</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>20</td>
<td>150:1</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>25</td>
<td>150:1</td>
<td>6.6</td>
</tr>
</tbody>
</table>

mortality function $b(t) = (4/(d^{2.5} + 1))$ was assumed. The diffusion coefficient, $d(x)$, was assumed to be either 0.01 or 0.025. Simulations were performed for both a resistant ($\omega = 5$) and susceptible ($\omega = 8$) variety of sugarcane. Infestation and damage profiles for both types of varieties are shown in Fig. 2.

Larger release ratios were required for suppression in the susceptible variety compared to the more resistant variety with a higher mortality rate. Larger release ratios are therefore required for insect populations with a low mortality rate (or a higher growth rate). Suppression below 5 $e/100s$ was either difficult to obtain, or impossible to obtain for both the resistant and susceptible variety when release lanes were more than 40 m apart for both $d(x) = 0.01$ and $d(x) = 0.025$, with releases either twice a week or weekly. Suppression was achieved in most cases when release lanes were between 25 and 30 m apart. Smaller release ratios were required for suppression via mechanical releases than via manual releases, and with release lanes for mechanical releases further apart (see Tables 4 and 5).

The results indicated that suppression of E. saccharina below 5 $e/100s$ was highly dependent upon the distance between the

<table>
<thead>
<tr>
<th>Cane variety</th>
<th>Frequency</th>
<th>$d(x)$</th>
<th>Distance</th>
<th>Release ratio</th>
<th>$e/100s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resistant</td>
<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>4:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>10:1</td>
<td>0.2</td>
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<td></td>
<td></td>
<td></td>
<td>35</td>
<td>16:1</td>
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<td></td>
<td></td>
<td></td>
<td>40</td>
<td>40:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>45</td>
<td>109:1</td>
<td>0.1</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>50</td>
<td>150:1</td>
<td>4.5</td>
</tr>
<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>25</td>
<td>15:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>100:1</td>
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<td></td>
<td></td>
<td>35</td>
<td>150:1</td>
<td>1</td>
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<tr>
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<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>7:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>22:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>35</td>
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<td></td>
<td></td>
<td></td>
<td>40</td>
<td>115:1</td>
<td>0.1</td>
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<td></td>
<td></td>
<td></td>
<td>45</td>
<td>150:1</td>
<td>6.6</td>
</tr>
<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>25</td>
<td>35:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>150:1</td>
<td>4.7</td>
</tr>
<tr>
<td>Susceptible</td>
<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>10:1</td>
<td>0.05</td>
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<tr>
<td></td>
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<td>30</td>
<td>33:1</td>
<td>0.1</td>
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<td></td>
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<td>35</td>
<td>55:1</td>
<td>0.1</td>
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<td>40</td>
<td>150:1</td>
<td>4.25</td>
</tr>
<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>25</td>
<td>48:1</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
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<td>30</td>
<td>150:1</td>
<td>24.6</td>
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<tr>
<td>Susceptible</td>
<td>Twice a week</td>
<td>0.025</td>
<td>25</td>
<td>23:1</td>
<td>0.1</td>
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<td>30</td>
<td>77:1</td>
<td>0.1</td>
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<td>0.1</td>
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<td>40</td>
<td>150:1</td>
<td>36.3</td>
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<tr>
<td></td>
<td>Weekly</td>
<td>0.025</td>
<td>25</td>
<td>111:1</td>
<td>0.1</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td>150:1</td>
<td>46.7</td>
</tr>
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</table>
release lanes which, in turn, depended on the release method and dispersal capability of the insect – the larger the diffusion coefficient, the further apart release lanes may be. The chosen distribution for releases of any type of insect with a certain dispersal capability is therefore important in ensuring the success of the SIT. Furthermore, release ratios required for suppression were larger for \( d(x) = 0.01 \) than for \( d(x) = 0.025 \) at the different distances between the release lanes, emphasizing the importance of a strong dispersal capability of the released sterile insect in SIT.

Before considering SIT releases in the *E. saccharina* context, more research on the dispersal capability of *E. saccharina* moths within a sugarcane field is required in order to establish the maximum distances between release lanes at which suppression may be achieved. If these maximum distances are smaller than the average sugarcane field, ATV releases may not be viable within the sugarcane context and aerial releases may be the best method in terms of suppression since the method is independent of the sugarcane field layout. However, the cost of applying SIT by means of an aircraft may cause SIT not to be economically viable. Also, weekly releases required larger ratios and smaller distances between release lanes compared to twice a week releases – suppression is easier to achieve with more frequent releases and smaller ratios; the corresponding cost of applying SIT, however, may be higher. It is important to note that achieving suppression is not the only objective in a pest control programme, but rather both achieving suppression (or minimizing the risk of not obtaining suppression) and minimizing the cost of achieving suppression. Cost-benefit analyses are therefore necessary in deciding the best frequency, distribution and method of release in terms of both suppression and cost, and whether or not it is economically viable to proceed with SIT within the given context. The economic viability of the SIT will be considered in a further study by the authors.

4. Model application

The workability of the spatio-temporal model is demonstrated in this section by means of a simulation of the model applied to a pilot site near Eston, in KwaZulu-Natal (see Fig. 3). GIS shapefiles representing the field layout of the pilot site (Group IP, 2010) were implemented in MATLAB using its MAPPING TOOLBOX.

The pilot site was assumed to be a closed domain with zero-flux Neumann boundaries; therefore no dispersal of moths was allowed across the boundary (from outside or from inside the domain). The paths separating the fields from each other were either ignored, or in areas where the fields were more than 30 m apart, to be boundaries across which no dispersal of moths occurs between fields at these points. An edge patch was defined as a patch which contains the boundary line of a certain field. A section of each edge
patch may contain non-sugarcane areas (for example a section of a separating path) – these areas were nevertheless assumed to contain sugarcane, forming part of the nearest field. The total area of the implemented domain was therefore slightly larger than the actual size of the domain. Some of the edge patches were shared between two different fields, in which case the specific edge patch was assigned to only one of the fields. The different fields in the domain were assumed to be heterogeneous in terms of crop age, with homogenous crop resistance – this assumption corresponds to the 2009 data contained in the shapefiles (Group IP, 2010). The initial crop ages contained in the shapefiles were rounded to the nearest month. In cases where fields were too far apart, these isolated fields were considered separate spatial domains with no dispersal of moths occurring between different spatial domains.

At time \( t = 0 \), when the simulation was started, heterogeneous cane ages of 0, 1, 2, 6, 13, 14 and 17 months were assumed for the various fields, as indicated in Fig. 3. Harvesting occurred at times \( t = 215, t = 305, t = 336, t = 550, t = 701 \) and \( t = 731 \) for fields aged 17, 14, 13, 6, 2, 1 and 0 months, respectively. Weekly sterile releases commenced at time \( t = 0 \) only in fields with an age not exceeding 6 months. For fields older than 6 months, sterile releases commenced after harvesting. At time \( t = 336 \), all the fields aged 13 months were harvested, resulting in a sudden decrease in average infestation levels for the domain. For \( t > 336 \), sterile moths were released across the entire domain. At a release ratio of 40:1 in each respective field, sterile releases resulted in suppressed average \( E. \) saccharina infestation levels (below 5 e/100s) across the entire domain (see Fig. 4).

Closer examination revealed that, although the average infestation levels for the entire domain were suppressed below 5 e/100s, some fields did not experience suppression – release lanes were too far apart, resulting in higher infestation levels in the middle of the corresponding fields where sterile moth population densities were too low. Suppression in smaller fields was easily achieved – release ratios less than 40:1 may also have been effective in these fields. Fig. 5 contains a spatial overview of the percentage damage at each field’s respective harvest time.

In order to achieve suppression within all the fields, the field layout may be adjusted such that the release lanes are not more than 30 m apart (according to the numerical results obtained in Section 3). However, adjusting the field layout may not always be feasible. Moths may also be released inside the fields on foot where suppression is difficult to obtain if releases are only along the edges. However, this will be much more labour intensive than releasing only by ATVs, and as a result may increase the application cost of SIT. Aerial releases may be more effective in the sugarcane context, especially when large sugarcane fields are involved, since then release distributions do not depend on field layouts.

![Fig. 4. Average larval infestation simulated for the pilot site near Eston with weekly sterile releases commencing only in fields with age at most 6 months.](image)

However, the application cost involved in aerial releases is much higher compared to that of ATV releases.

5. Conclusion

Extending the temporal model by Potgieter et al. (2012) to a spatially explicit model, a discretized reaction–diffusion system with zero-flux Neumann boundary conditions was derived in order to describe \( E. \) saccharina growth and dispersal in a spatially and temporally variable environment and to investigate the effect of dispersal on SIT. Although constant diffusion coefficients were assumed in simulations, the spatio-temporal model was derived for variable diffusion coefficients. The numerical solution to the system of partial differential equations was approximated by means of the finite difference method, whereby the best release method and distribution were obtained for which suppression was possible.

Numerical results indicated that the best release distribution and release ratio are highly dependent upon the dispersal capability of the insect, the method of release, the frequency of releases and the growth or mortality rate of the insect population. Furthermore, it is important to not only consider achieving suppression, but also the cost of obtaining suppression. The economic viability
of SIT within a given context should be investigated before applying SIT.

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