An agent-based simulation model of
_Eldana saccharina_ Walker

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Abstract

_ Eldana saccharina_ Walker (Lepidoptera: Pyralidae) is a stalk borer pest plaguing the sugar producing industry in South Africa. The pest feeds on the internal tissue of sugarcane stalks, causing yield losses in sucrose. Various control methods have been proposed in an attempt to suppress the pest. These control methods are, however, often difficult and costly to test, implement and develop further in an iterative manner. In an attempt to better understand the behaviour and population dynamics of _E. saccharina_, an agent-based simulation model is presented in this paper which simulates the stalk borer’s biology, feeding habits, mating behaviour, dispersal patterns and various other characteristics as accurately as possible. The flexibility and validity of the model are then ascertained by subjecting the model to expert opinion and parameter variation analysis. Finally, the model is implemented in a user-defined, decision support system aimed at assisting in understanding the behaviour of _E. saccharina_.

**Keywords:** Agent-based modelling, _Eldana saccharina_ Walker, simulation model, pest control, decision support system.

1 Introduction and background

In spite of an increasing negativity surrounding the adverse effects of excess sugar consumption on the human body, the sugar industry continues...
to thrive. Global consumption of sugar in 2015 topped 170 million metric tons, up to 15 million tons more than 5 years prior [1]. The South African sugar industry is one of the world’s leading cost competitive producers of high-quality sugar, generating an estimated average direct annual income of R12 billion [30]. The industry makes an immense contribution to sustainable development, the South African national economy and employment, particularly in rural areas. Approximately one million people, or more than 2% of South Africa’s population, depend on the sugar industry for a living.

_Eldana saccharina_ Walker is a stalk borer pest which infests sugarcane by virtue of its suitability for egg-laying sites in dead-leaf material [2]. The first record of the pest was in 1939 when a severe infestation occurred in the Umfolozi area in the province of KwaZulu-Natal. This infestation, however, did not spread and eventually died out in 1950 [15]. During the early 1970s, a second infestation resurfaced in the Hluhluwe area of the same province [7] and has since spread to much of the local producing areas, with the exception of inland crop areas where the cooler temperatures limit the development of the insect. _E. saccharina_ infestation results in decreased sugarcane quality (measured as a decrease in sucrose yield) when larvae penetrate and feed on the internal tissue of sugarcane stalks, resulting in negative impact on total plant biomass [12].

In light of this, _E. saccharina_ remains a topical concern in the sugar industry and the _South African Sugarcane Research Institute_ (SASRI) continues to spearhead research efforts towards finding a means of effectively controlling the pest. A number of pest control measures currently exist, achieving only limited success in most cases. These include sugarcane variety development [10, 19], chemical control [15] and biological control. Habitat management [9, 8, 10] and the sterile insect technique (SIT)\(^1\) [26] are in the research phase as part of the further development of SASRI’s _area-wide integrated pest management programme_ (AW-IPM)\(^2\).

IPM systems aim to combine a series of control methods in order to achieve better overall pest management whilst decreasing the use of pesticides, thereby decreasing associated environmental problems. As a result, IPM is considered more sustainable in the long run. Ideally, a number of existing techniques should be applied in conjunction with one another to a sugarcane crop in order to achieve improved control of _E. saccharina_.

\(^1\)SIT is a birth control method implemented by the release of a large number of sterile insects.

\(^2\)Currently employed IPM practices includes the use of resistant sugarcane varieties, pre-trashing, the removal of old stalks in the field, improved soil management, responsible use of insecticide and the use of uninfested seedcane [28].
When applied together, research shows that the existing *E. saccharina* control methods can endorse one another [28]. In view of this knowledge, it is important to identify the shortcomings in the individual control methods, as well as the role of possible interactions between them. Determining these intricacies on either individual or interacting control methods by in-field testing is both costly and labour-intensive, and there is not always sufficient time available to conduct large-scale in-field tests in order to observe these effects. Moreover, a means for practical evaluation of the relative impact of control strategies before they are actually applied to infested sugarcane is lacking.

The aim of this paper is to present an agent-based computer simulation model of *E. saccharina* which reflects current knowledge about its biological behaviour and dispersing patterns, both on an individual and population level. The simulation model is implemented as a user-defined system in order to afford flexible, diverse testing of different scenarios and parameter set selection. The manner in which such a simulation model is constructed, validated and visually presented is described in this paper.

The paper begins with a review of existing simulation models of *E. saccharina* in §3, followed by a description of the essence of agent-based modelling. The modelling approach followed to implement the behaviour of *E. saccharina* in a simulation environment is then detailed in §4, including the life-cycle, mating process and oviposition and dispersal process model building blocks, discussed in §4.2, §4.3 and §4.4 respectively. In §5, the manner in which the different building blocks were calibrated and the model as a whole was verified to be operating correctly is discussed, followed by two means of applied validation in §6. The paper then concludes in §7, with some acknowledgements made in §8.

## 2 Biological background of *E. saccharina*

The fundamental structure of *E. saccharina*’s life cycle are shown in Figure 1. This framework encapsulates the most notable life stages and activities of the pest which must be included in a simulation that aims to accurately mimic its behaviour and distribution. These attributes are discussed in finer details by van Vuuren et al. [33].

The life-cycle of *E. saccharina* is typical of that of insects. Eggs hatch into larvae, after which pupation occurs and, finally, adult moths emerge [4]. The amount of time spent in each stage depends both on the quality of food, as well as the temperature experienced [24]. Certain important activities oc-
Adult moths emerge
Eggs laid in batches
of approximately 20
Most eggs hatch
into larvae
3-6 Males form lek
Larvae pupate
Single female approaches lek
Female is impregnated
Adults mate and female is impregnated
Random migration of female between batches
Natural/ predator mortality
Female mortality post oviposition
Natural/ predator mortality
Natural/ predator mortality
Natural/ predator mortality
Male moths Female Moths
Male moths post mating
Natural mortality without mating
Possible migration before mating

Figure 1: Flow diagram of the general life cycle which must be emulated by agents in the agent-based simulation model of the growth and spread of an E. saccharina population.

cur in each stage which affect the pest’s development and future growth and spread as a population. Most notably, the lek mating process followed by E. saccharina. These aspects are introduced and explained in the appropriate sections which follow in the text.

3 Existing E. saccharina simulation models

A number of working simulations have been proposed in the literature for evaluating the estimated effect of particular pest control methods imposed on sugarcane fields and are discussed in [33].

Work of this nature began with Van Coller [31] and Hearne et al. [14] who employed a system of differential equations aimed at modelling the change in population growth in the various stages of the life cycle of E. saccharina. The primary insight provided by this model was concerned with the biological control of the pest through parasitoids, but the spatial spread of an E. saccharina population was not explicitly taken into account. More specifically, testing policies for the timing, frequency and magnitude of parasitoid releases were facilitated by the model in terms of their relative
effectiveness in the biological control of *E. saccharina*.

Later, a model was designed by Horton *et al.* [16] which aimed to investigate the effects of insecticides and early cane cutting as control measures for *E. saccharina*. The effects of temperature on the pest’s life cycle were explicitly included in this model, but it again assumed a homogeneous spread of the population over the spatial habitat. In order to assist in determining an ideal time for harvesting, this model’s function was to produce an index measuring the extent of sugarcane damage under different temperature patterns.

Most recently, Potgieter *et al.* [24, 23] developed a discretised reaction-diffusion model of the growth and spread of an *E. saccharina* population over time and space under the influence of SIT. This consisted of an accompanying SIT simulation tool whereby the effectiveness of SIT can be investigated in different scenarios. The model and accompanying tool can also be applied in the context of realistic sugarcane field layouts by importing geographic information system (GIS) maps. Although the current design of the SIT simulation tool includes only SIT as control measure, a framework for a computerised platform was developed which may be extended to a decision support system for use in an area-wide IPM programme.

Potgieter *et al.* [25] presented a high-level design of such a simulation tool for investigating different IPM strategies against a number of pest species in sugarcane. This design consisted of four interacting subsystems that simulate the population dynamics of different pest species, sugarcane growth, environmental dynamics and the cost of IPM strategies, respectively. One of the limitations highlighted in the study was the inflexibility of the population dynamics model for use in an IPM context — particularly the difficulties surrounding the inclusion of more than one pest control strategy in the model. Possible improvements to the simulation tool were suggested, including an agent-based approach for the pest species population dynamics subsystem.

Despite the advancement in understanding of *E. saccharina* population growth and the relative success achieved by the aforementioned models, the design of each model is founded upon approximations of the pest on a population level. Local interactions of individual moths are not simulated or incorporated explicitly into the population dynamics; instead, approximate changes are executed in simulations at discrete time steps. Furthermore, the models all focus on single control measures, limiting their development and flexibility in the context of IPM systems. The resulting analyses therefore yield conclusions that do not necessarily reflect the continuous, changing nature of *E. saccharina* on a localized level.
In an attempt to address the shortcomings of the existing simulation models described above, an approach was advocated by van Vuuren et al. [33] in which the individual members of a population of \textit{E. saccharina} are simulated, thereby incorporating the effects of local interactions between individual stalk borers.

Agent-based modelling is the computational study of social agents interacting in an autonomous manner as evolving systems. It allows for the study of complex adaptive systems and facilitates investigations into how macro-phenomena develop from micro-level behaviour among heterogeneous sets of interacting agents [18]. By simulating \textit{E. saccharina} moths as individual agents who are governed by their biological preferences and limitations as documented in literature, the resulting relationships between these agents can be used to predict population dynamics of the pest in a more realistic manner over space and time (based on local interactions) than is possible in the population-aggregated \textit{E. saccharina} models. Using such a detailed agent-based modelling approach, the proposal made by van Vuuren et al. in [33] is adopted to construct an individualised, non-aggregated population model of \textit{E. saccharina}.

4 Modelling approach

In this paper, a simulation model of \textit{E. saccharina} is put forward comprising four fundamental building blocks. These are the graphical user interface (GUI), the life cycle of \textit{E. saccharina} and the associated influence of temperature on the pest, the mating process of \textit{E. saccharina} and, finally, the oviposition and consequent in-field spatial distribution of the stalk borer within the simulated area. Each one of these building blocks is deemed to play a pivotal role in the reconstruction and simulation of the biological behaviour of \textit{E. saccharina}. The temporal interaction between the building blocks and the anticipated simulation user is shown in Figure 2.

The agent-based model was designed and developed in the \textsc{Anylogic University 7.1.2} [35] software suite. This software is a multi-method simulation modelling tool developed by \textit{The AnyLogic Company} and supports all major modelling approaches. \textsc{Anylogic} has a sophisticated suite of model building tools for different domain models, as well as a graphical modelling language which allows the user to extend simulation models by including Java code [35]. \textsc{AnyLogic} was found to be a suitable choice of software environment owing to its sophisticated facilitation of the modelling approach for a number of reasons. The model architecture supported in \textsc{AnyLogic}
allows for simple hierarchies to be defined and interconnectedness between agents is easily governed in the top-level agent tab. Furthermore, ANYLOGIC offers continuous, discrete and, importantly, GIS animation and mobility, which is useful for future work which may stem from this study. Agent communication and networks are also well defined and supported in ANYLOGIC, simplifying interaction instances involving a small group of agents selected from a large population, as is the case during the mating process of *E. saccharina*. Finally, the ability of an ANYLOGIC simulation model to dynamically create or remove agents facilitates the development of population dynamics through multiple generations of the pest.

The general structure of each agent’s life cycle was designed using a statechart-based approach in which each state represents a different point in the agent’s life cycle. Each state imposes specific behavioural aspects of the pest, as determined by a combination of the appropriate variables, parameters and functions. States are connected by transitions which can be executed by a number of different triggers. When a transition is triggered, an agent moves from its current state to the new state, as directed by the transition. In this manner, the agent moves through its life cycle and emulates *E. saccharina* in nature as proposed by van Vuuren *et al.* [33].

The general modelling approach followed to implement each of the building blocks of the simulation is explained in the following sections.

Figure 2: *Arrangement of the simulation model and proposed interaction with the user.*
4.1 The graphical user interface

In AnyLogic, the GUI is typically constructed in the ‘Main’ tab of the project and is the environment in which the default output of the simulation, as seen by an operator, is designed. Features which contribute to the functionality, flexibility and understanding of the model are incorporated on this level in the simulation model. A screenshot of the GUI for the simulation model of *E. saccharina* is shown in Figure 3.

The system being represented in this model is a population of *E. saccharina* moths infesting part of a sugarcane plantation. The model boundary was chosen to be one hectare (100 m × 100 m) of continuous simulation space. There are approximately 130 000 sugarcane stalks per hectare in a typical sugarcane plantation in South Africa [8]. This is deemed suitable to provide enough complexity for prevailing behaviour and population dynamics to become evident in the simulation, whilst still not cluttering the simulation space and over-complicating analysis and investigation. The model was chosen to make use of an hourly time unit (*i.e.* one second represents an hour of activity in the simulation). This time unit was chosen to accommodate control of time-specific activity of the agents, whilst still allowing the simulation to progress acceptably quickly.

Almost all events which occur in the simulation are *endogenous* owing to the specified system boundaries. A few instances where data or specific external events are incorporated by means of *exogenous* event triggers are also incorporated. Furthermore, in order to realistically simulate the given hectare as part of a larger sugarcane field, the possibility of moths entering and exiting the simulation space by means of an absorbing and emitting boundary condition was also incorporated as an *exogenous* event.

Three object classes are included in the simulation. The male and female moths are incorporated by their own independent object classes, whilst a third object class is incorporated to assist in simulating the mating behaviour of the pest, as discussed later in this section. A layer function was also incorporated into the GUI to show or hide specific life stages of the pest. In a simulation model containing 130 000 sugarcane stalks, there may be tens of thousands of agents present at a given time. Furthermore, these agents may exist across all four life stages of the pest. Using the layer function, a user can show or hide specific life stages and/or, in the case of adults, different sexes of the moth. This functionality can be used both whilst the simulation is static or operational, so as to allow for specific analyses of certain life stages or attributes of the pest.

In the simulation, temperatures are sampled from a linked EXCEL spread-
Figure 3: The model graphical user interface.
sheet which contains a historical temperature profile for the simulated region. In this case, monthly averages of data collected during the period January 2011–September 2015 at SASRI (Mount Edgecombe, KwaZulu-Natal, South Africa) are incorporated into the model. In order to facilitate analysis of abnormal scenarios, a temperature-adjustment slider bar is incorporated. This bar increases or decreases the daily temperature value by a set amount for the duration of the entire simulation run. This attribute of the simulation environment may be used to simulate ‘out of the ordinary’ warm or cold periods, facilitating investigations of the pest propagation into previously uninfested areas, linked to a global rise in mean temperature as a result of climate change. A temperature history chart is also incorporated to show a local history of the daily temperatures which have been incorporated into the simulation.

Two other charts exist in the GUI, tracking the number of adults of both sexes of the moth present within the simulation and the number of larvae which have penetrated sugarcane stalks. Adult moths are responsible for propagating and distributing a population within sugarcane, whilst the robust larval stage of \textit{E. saccharina} is primarily responsible for the damage caused to sugarcane when it bores into the stalk of the plant to feed on the inner nutrients, making these two attributes of each simulation run important to keep track of.

The literature suggests that the maturity of sugarcane might play a role in the female’s choice of where to oviposit eggs post-mating [11]. Furthermore, in order to mature sufficiently and progress to the pupal stage of its life cycle, \textit{E. saccharina} larvae require a certain amount of nutrients from the sugarcane stalk into which they bore. In order to facilitate realistic testing and analysis of these factors, the underlying simulated hectare was discretised to represent 129,600 (360 × 360) defined sugarcane stalk points. Each point could then be attributed a certain maturity value which may be discoverable and distinguishable by the agents in the simulation and prompt their behaviour. Furthermore, three different underlying sugarcane crop arrangements were incorporated which divide the simulation space into a preset arrangement of mature and immature sugarcane within which the moths can disperse owing to their biological propensity. In conjunction, sugarcane growth and carrying capacity of each stalk once it became infested was simulated using inputs derived from the well-known CANEGRO model [17].
4.2 The life cycle of *E. saccharina*

The logical progression through the life cycle of *E. saccharina* along with the associated activities, as implemented in the simulation model, are summarised in Figure 4.

The sex of an agent in the simulation is already defined in the egg life stage. The behaviour and life cycle of both male and female *E. saccharina* moths are, however, identical until they reach the adult life stages. In light of this, the description given in this section is appropriate for both sexes and, where appropriate, gender-specific activity is noted.

Eggs are laid in oviposition sites selected by females and agents enter the simulation as eggs. Naturally, not all eggs successfully hatch and progress to the next life stage. Furthermore, some eggs may be victims of predator mortality. If an agent’s parameter governing this condition exceeds a selected probability of occurrence, the egg perishes and the agent is removed from the model. No other activity occurs in this life stage and the egg simply matures as a result of the temperature experienced by the agent. Once the egg has matured sufficiently, it hatches and progresses to the next life stage.

Newly hatched larvae are also subject to random or predator mortality as in the egg life stage, but according to a different probability. Being without any form of protection, the young larval life stage is the most vulnerable and, as a result, its probability of mortality will most likely be higher than in any other life stage. Larvae that do not perish proceed to disperse among the sugarcane stalks. Conlong [8] describes a process whereby larvae move away from other neonates by moving up the stalk at the oviposition site to the top of the cane plant. From here, larvae ‘parachute’ from the green leaf tips to surrounding plants. They then move down the plants on which they land and bore into the more mature bottom parts of new stalks, through cracks in the rind of the stalk, or through buds at each internode. This results in early dispersion within the local area surrounding the site where eggs were oviposited. Thereafter, the larvae are assumed not to move significantly for the remainder of the period spent outside of the sugarcane stalk. Once sufficiently robust and mature, each larva progresses to the next part of the larval life stage where it begins boring into a selected sugarcane stalk.

This part of the larval life stage begins with the larva searching in its immediate vicinity for the closest sugarcane stalk into which to bore [8]. The larva then moves towards this selected stalk and attempts to burrow into

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3The probability thresholds for predator or random mortality in all states are incorporated into the model according to the best available measurements from in-field testing, but they are also changeable by the user of the simulation.
Figure 4: Flowchart of the general life cycle, including assumed associated activities, followed by E. saccharina agents in the simulation model.
it. If the carrying capacity of the stalk has not yet been exceeded, the larva will successfully enter the stalk and begin feeding. If, however, the stalk is densely occupied and there remains insufficient space and nutrients for another larva to feed on in that particular stalk, it perishes and is removed from the simulation. This was implemented according to the assumption that only a very small number of larvae can successfully change their choice of stalk as a result of exceeded carrying capacity. It has been observed that more larvae may feed on a stalk than can feasibly be accommodated and all may progress to pupation instead of perish as assumed in the model [8]. In such cases, however, the resulting adult moths have been observed to be very small, weak and uncompetitive in mating as a result of undernourishment and are, therefore, assumed not to have significant future impact on the growth and spread of the population.

Random and predator mortality is far less likely in this life stage and, as such, the probability of these forms of mortality is likely to be low. The quality of the selected stalk as a food source for larvae affects the strength and competitiveness of the moth when it becomes an adult. Once the larva has matured sufficiently, it progresses to the next life stage and becomes a pupa.

Very little happens in the pupal life stage apart from the possibility of natural or predator mortality. If a pupa does not perish and matures sufficiently, it progresses to the final life stage of the life cycle where it becomes an adult moth. The sex of the adult moth plays a determining role in its behaviour and decision making. The possibility of natural or predator mortality still exists in the adult life stage and is incorporated in the same manner as in the other life stages.

Once adults, male and female moths progress into the mating, oviposition and dispersal sub-cycles, as discussed later. All mating and dispersal activity of E. saccharina occurs at night, and natural mortality of the pest depends on maturity driven by temperature exposure experienced primarily during the day. For this reason, it is assumed that the final progression from the adult stage to that of mortality never occurs during the aforementioned sub-cycles. Mortality only takes place once the adult moth has both matured sufficiently and resides in the primary adult state post any adult activity.

4.3 The mating process of E. saccharina

E. saccharina moths follow a so-called lek mating process which has been documented thoroughly by Atkinson [3]. The mating process of E. sac-
charina is of notable importance as it is responsible for the spreading of the pest within sugarcane. Furthermore, pest control strategies, such as the sterile insect technique, affect the pest during mating [24] and it was therefore deemed vital to reconstruct the mating process in the simulation model with sufficient accuracy so as to mimic the in-field observations made by Atkinson [3] and Carnegie [7]. In all previous models of E. saccharina’s population growth and dispersal, an aggregation approach was followed which excluded small-scale intricacies such as the lek mating and mate selection processes. The facilitation of these processes may, however, significantly improve the accuracy of simulating E. saccharina’s population dynamics.

Males typically emerge from pupae slightly before females and climb up the stalks of their host plants to the canopy where, after approximately 30 minutes, they begin a display. This display consists of rapid wing flapping in bursts, pencil hairs extending from the abdomen into a round brush and the release of an attracting pheromone into the surrounding air. The aim of the display is to attract females for mating purposes [3].

Although males can display singly, they far more frequently display in groups of 3–6 males, called leks, on the same plant. During the mating process, a female approaches a lek of males upon being attracted by their display and the strength of the scent of the released pheromone. Once she has located the lek, one male is selected to mate with. It is generally understood that the most dominant male (that is, the male with the strongest pheromone or display) is selected by the female [8]. Once mating ensues between the female and the chosen male, the remaining males contributing to the lek may either continue to attract other females in a smaller lek, or disband the lek if there are too few males to make it competitive in attracting potential mates.

Almost all females mate only once during their lifetimes owing to the large size and durability of the spermatophore, as well as the relatively short lifespan of the adult moth [7]. About 24 hours after mating, a female will begin oviposition in preferred sites such as dead-leaf sheaths and areas between the plant and soil. A female typically lays approximately 450 eggs in batches of approximately 20 per oviposition site, only a small percentage of which survive and hatch [7, 8].

The logical progression followed and assumptions made to effectively implement E. saccharina’s mating process in the simulation model are summarised in Figure 5. This process is described in detail by van Vuuren et al. in [32].

Once a male has reached adulthood and the simulated time of day is appropriate for mating activity to commence, he attempts to form a lek
Figure 5: Flowchart of the general mating process, including assumptions, followed by *E. saccharina* adapted from [32].
with males in his immediate vicinity. This time window is assumed to be 18h00–23h00 [3]. If there are 3–6 males in close enough proximity, a lek will be formed and the mating process will progress to the next stage\(^4\). If a male is drawn into joining a lek which was initiated by another male nearby, he loses the ability to initiate his ‘own’ lek until such time as the lek to which he belongs is disbanded. This may occur due to a lack of sufficient males nearby, meaning that the lek never actually materialises, or it may materialise, but then dissipate once the female has chosen and approached her preferred partner from the lek. The motivation behind including leks as an independent object class is the superior control offered by incorporating a feasible entity to which males can belong. It also holds the advantage that the lek can possess position co-ordinates and a display/pheromone strength which female moths can discover. This object class is, however, hidden and only contributes to simulation execution on the ‘back-end’ of the model.

When a lek is successfully initiated and a group of males become members of it, its location is assumed to be specified as the centroid of the males included in the lek. That is, if \(n\) males with Cartesian co-ordinate positions \((x_1, y_1), \ldots, (x_n, y_n)\) participate in the lek (when viewed from above), the lek co-ordinates are \((L_x, L_y)\), where \(L_x = \frac{1}{n} \sum_{i=1}^{n} x_i\) and \(L_y = \frac{1}{n} \sum_{i=1}^{n} y_i\). Once the lek has been located at this point, it becomes discoverable to females which are ready to mate and may potentially be attracted to it.

In a full-scale simulation, several leks are likely to materialise in the vicinity of a female at a given point in time. It is assumed that the female is aware of and attracted to all leks in her vicinity, but the lek which has the strongest attraction, based on the total pheromone strength of all the males in the lek, as well as its distance from her, has the highest probability of being selected.

It is possible that two or more females in the simulation may be attracted to and begin to approach the same lek. In accordance with the standard assumptions of a Poisson arrival process [34], no two females will, however, arrive at a lek at precisely the same instant during the simulation. When a female arrives at a lek, she chooses a mate (assumed to be the most competitive male) with a certain probability\(^5\) and occupies this mate during the entire mating process. As a result, the male no longer participates in the lek [8]. As soon as the female has selected her mate, the other members of the lek are ‘freed’ and once again become available to participate in a remaining lek (provided that a sufficient number of unmated males remain).

\(^4\)This proximity is included in the model as a user-changeable parameter.

\(^5\)This probability is also included as a user-modifiable model parameter.
This weaker lek essentially functions as a continuation of the previous lek and its centroid is typically very close to that of the previous lek. As a result, other females already in the process of approaching the original lek continue their approach, but move to the new centroid, selecting a mate from the remaining males who participate in that lek. This may occur several times until fewer than three males remain as participants of the remaining lek, at which point, it dissipates — no longer attracting females [8, 22].

Mating ensues for two to three hours. Due to the limited time available per night for mating, it is assumed that males will only mate once per night. After mating, the female departs in order to prepare for oviposition. In line with assumptions made in the literature, the female only oviposits batches of eggs during the early hours of the night and, during the day, will remain relatively static, moving randomly on a very small scale (resembling walking), until such time as she can oviposit again. Once the female has laid all of her eggs, she typically does not partake in any further activity and perishes after a few days.

4.4 Oviposition and dispersal of E. saccharina

The largest propagator of E. saccharina infestation in sugarcane is considered to be the oviposition and dispersal flights of female moths. This may cause either a rapid population expansion in a certain area where localised oviposition occurs, or spread a population to previously unaffected areas. That said, there are many unanswered questions and unknown aspects with respect to the oviposition site selection process of E. saccharina, as well as the propensity of some females to fly longer distances [8]. It was therefore deemed crucial to implement the oviposition and dispersal flights of the females based on valid, sensible assumptions so as to facilitate testing of different possibilities of the decision making process followed by female moths during dispersal in order to progressively make sense of the manner in which the pest spreads throughout its habitat. Effective implementation of these aspects may significantly improve the accuracy of simulating E. saccharina’s population dynamics, as well as shed light on some of the unanswered questions surrounding their behaviour.

The logical progression followed and assumptions made to effectively implement the oviposition and dispersal cycles of E. saccharina in the simulation model are summarised in Figure 6.

Once a male and female moth have completed the mating process, the male returns to random localised movement for the remainder of that night. During subsequent nights, males may mate a second or even third time.
Figure 6: Flowchart of the general oviposition and dispersion processes, including assumptions, followed by E. saccharina post-mating in the simulation model.

Females only begin oviposition approximately 24 hours after mating [3]. For this reason, they wait close to the mating site, moving only on a very small scale, until they are ready to oviposit. Oviposition usually takes place over the next one to two nights.

Some females have the ability to fly considerable distances in search of oviposition sites [7]. In such cases, a female may attempt to fly to areas which theoretically exist outside of the simulated environment. This departure from the simulation space can occur at any stage between batches of eggs laid by the female. During departure from the simulation space, the female
moves toward the edge of the simulation environment and then exits the visible area and, in doing so, no longer exists in the simulation. If a female wishes to continue laying eggs in the visible simulation space, the process begins by assessing the time of day. Since females are understood to only oviposit during the early hours of the evening (the same time period during which mating is assumed to take place) [8], the oviposition process in the simulation begins by assessing whether or not this time period is currently being experienced. If not, the female remains in her current location, moving on a very localised scale (resembling walking) until the appropriate time for oviposition to ensue.

Once this time period is entered, the next step in the oviposition process involves the selection of a suitable location to lay eggs. Conlong [11] has suggested that females may have an inherent ability to seek out more mature sugarcane in which to oviposit, but at the same time, have been observed to oviposit in almost any cryptic site in the absence of suitable leaf sheaths. Furthermore, it has been speculated that males may even play a role in the selection of oviposition sites for females [8]. This notion is consistent with the research of Berry [6] who found, using in-field experimentation, that sugarcane stalks with a higher number of internodes are typically more heavily infested by *E. saccharina*. This suggests that shoots exhibiting the largest growth potential may attract the insect, possibly due to nitrogen content. In light of this, an *E. saccharina* population may inherently gravitate toward these regions and, as a result, male displays would be more heavily congested and, hence, stronger in these areas of more mature cane. This means that females may congregate in these areas to mate and, since most eggs are laid close to the emergence site, so the population would continue to grow in the region where the males are located. These assumptions and insights surrounding the selection of an oviposition location are intuitively included in the simulation model by two processes which incorporate the preference for more mature sugarcane in different manners.

In the first process, the route for oviposition is modelled by performing a search to find the direction in which the female should move from her current location in order to encounter the most mature sugarcane and, by extension, good oviposition sites. The search is confined to areas within a radius specified by the user. Once the most suitable direction has been found, the female moves off within a randomly generated ‘direction window’, centred around the primary ‘best’ direction discovered. Oviposition occurs at intervals, the distance between which are informed, in part, by the flight ambition of the female. Each time oviposition occurs, a new direction within the ‘direction window’ is chartered. The female consistently moves away
from the mating location until the final batch of eggs is oviposited within close proximity of the intersection point between the original direction in which the female set off and the maximum distance over which she was willing to fly, indicated by her flight ambition.

The second process is, in essence, the converse of the first. In this instance, the route for oviposition is modelled by setting the female off in a random direction from her current location, with the maximum flight distance specified by her flight ambition. Whilst flying, a search window of a user-defined length is established in which the female can assess the quality of the sugarcane stalks over which she flies. This approach was inspired by the agent-based model of mosquito foraging behaviour of Gu et al. [13]. Upon discovery of a stalk within a search window which meets the user-defined quality criteria threshold, the female diverts from her route in order to make use of this oviposition site, before continuing towards her original destination post oviposition. This process continues until six batches of eggs have been oviposited and the cycle is over, or until the female reaches the outer boundary of her flight ambition. At this point, if she has not yet oviposited all of the batches of eggs, she will oviposit the remaining batches in the vicinity of this location.

Both algorithms assume cognitive ability of *E. saccharina* in decision making processes. This assumption is based on expert opinion [8], as well as other research which has been conducted on similar insects [13, 27].

Upon arrival at an oviposition site in both search paradigms, the female assesses the surroundings in respect of how densely populated the oviposition sites in the area are. In line with Conlong’s suggestions [8, 11], if the oviposition sites in the current location are occupied by existing eggs, the female attempts to find an area nearby with more available sites (that is, where fewer eggs are present). Once located, the female then moves to this area to oviposit a batch of eggs. This attempt at finding a less congested site only occurs once and, even if the new site is also densely populated, oviposition occurs since *E. saccharina* has been observed to resort to almost any site (even against the sugarcane stalk stem base) when no cryptic sites are available [22].

Once the female has oviposited a batch of eggs, the cycle begins again with an assessment of whether or not the female must leave the simulation space. If not, the female continues using the specified means of oviposition site selection in order to find an appropriate location for the next batch of eggs, as described above. Once six batches of eggs have been oviposited, the female returns to random movement until mortality occurs.

The oviposition and dispersal processes also model the possibility of fe-
male moths entering the simulation environment from the hypothetical surrounding simulation space. Since males are not strong fliers, it is assumed in the simulation that no males enter the simulation space from the surrounding areas. When a female enters the visible environment, it is assumed that, for the most part, she does so in search of oviposition sites as a far flying female. There also exists a small possibility that the reason for dispersal is that the female remains unmated after the first few nights after emergence [3]. Female enterers who are in the process of oviposition immediately enter the oviposition cycle, whilst females coming in search of mates join the adult life stage to begin looking for leks at the appropriate time.

5 Model calibration and verification

The complete life cycles of both the male and female agents are shown in Figures 7 and 8. These cycles contain all of the possible states each of the two sexes of moths may encounter in mimicking the life cycle of *E. saccharina* moths in nature. An agent in the simulation may occupy any one of its respective states during the execution of the simulation, and its decisions, preferences and actions are governed thereby. The statecharts represent the combination of three of the building blocks discussed previously (the life cycle, the mating process and the oviposition and dispersion process) and agents reside in and are affected by the environment constructed within the GUI.

Each building block was tested independently by conducting specific experimental runs and, where necessary, recording the output data to determine whether or not it was functioning as intended. Visual inspections of agent action in specifically generated, simple, hypothetical scenarios were also conducted using the animation output facility in AnyLogic. Where possible, all possible outcomes and implemented actions of agents were tested. The GUI was also tested to ensure that the simulated underlying sugarcane stalks grew according to the CANEGRO model (as a function of time and temperature) as well as the other important factors which influence model execution. Once confidence in each building block had been ascertained, they were combined and executed in unison to form the complete model presented in this paper.

Verification of the simulation model was performed throughout the course its development, as well as once the final model implementation has been completed. Typical means suggested by Law [21] and Banks [5] were employed, such as the use of an *interactive run controller* (IRC) or debugger to
detect and locate code errors halting model execution, as well as a graphics terminal or animation feature, in order to visually detect any irregularities in the behaviour of the system. Traces in the code were also employed in order to evaluate each possible simulation path, as well as the simulation’s ability to deal with extreme conditions. This feature was comprehensively used during the verification process, specifically to evaluate parameter values during simulation runs, as well as to indicate progression of agents between states during sub-cycle execution.
6 Model validation

The most common and, often, insightful method of model validation involves recreating scenarios already recorded in real-life experiments, and comparing the output data of the simulation model to those which were gathered during the in-field experiments in order to determine the degree to which they agree. In the case of *E. saccharina*, data are limited and sporadic owing to a number of complications, both in conducting experiments and in the actual gathering of the relevant data. For this reason, various other suitable techniques of simulation model validation were employed.

6.1 Face validation

Law [20] suggests that a simulation model attains credibility when the relevant decision makers or key project personnel accept the model as “correct.” He suggests that, during face validation, an expert in the field should be made familiar with the assumptions and processes incorporated into the model. He or she should agree with them, view the animation output of the model and verify that it is similar to the real-life scenarios which are recreated. Ideally, he or she should also be assured that the model builders...
are reputable and professional, having involved the expert in the design and development of a simulation model in an iterative fashion.

Conlong [8] is affiliated with SASRI and is one of the leading experts in South Africa on *E. saccharina* behaviour and control. Conlong’s insight into the intricacies of *E. saccharina* behaviour, both as individuals and as a population, is amongst the best currently available and, as such, he was deemed a reliable, independent expert in terms of reviewing the simulation model, and providing commentary and feedback on its credibility. Conlong was consulted throughout the course of the development of the research and, once the appropriate point in the study had been reached, a meeting was conducted whereby assumptions, inclusions, exclusions and general approaches adopted in the model building process could be described and discussed in order to ascertain how realistically and appropriately these elements had been incorporated. This was done both in principle from a design perspective, as well as based on the visible animation output of the running model. More specifically, Conlong was asked to assist in adding validity to areas of the simulation model that are based on aspects of *E. saccharina* in which there exist little or no surety about the exact behaviour of the pest, or where no relevant, reliable data are available against which to test the output of a simulation model.

It is important to note that the face validation process conducted was simply an interim validation to evaluate the model’s accuracy and realism with which it mimics the behaviour of *E. saccharina*. This served as a progress point from which to depart with more intensive testing which was conducted using the model. A formal, comprehensive face validation is to be conducted consisting of experts from a variety of backgrounds, including entomologists, sugarcane experts and experts on other, similar pests. Such a validation is planned in the future development of this model.

During the validation with Conlong, it was affirmed that no conclusive evidence exists in respect of the manner in which female *E. saccharina* moths select oviposition sites in nature and, as such, the two available oviposition site selection algorithms served as fair approximations of the process. This was accompanied by a discussion on the underlying sugarcane simulated and the role played by the maturity of the stalks in governing the dispersion of females. Conlong agreed that the user-defined characteristics of the oviposition algorithms afforded sufficient flexibility to test a variety of possibilities pertaining to this role.

The manner in which the dispersion of newly hatched larvae (described in §4.2) and the subsequent carrying capacity of the sugarcane was implemented in the model was discussed with Conlong and several pointers were
given to simplify the modelling process, focusing only on what is definitively known to happen in nature. Finally, the absorbing and emitting boundary condition within the simulation model, whereby agents have the ability to enter and exit the simulated space during its execution, was presented and Conlong commented on it’s inclusion in the model at present, as well as the possibilities it presented for future model development.

6.2 Sensitivity analysis and parameter variation

Ultimately, the simulation model presented in this paper may serve as a tool within the investigation and planning process of establishing manners to control *E. saccharina* and, as such, should possess the ability to recreate any realistic behaviour or population dynamics desired by the operator. A pilot sensitivity analysis was, thus, conducted using the model to determine the parameters which alter the simulation behaviour most significantly. In doing so, the tools available to model users for manipulating the simulation (so as to mimic the specific scenario which they would like to investigate) were discovered. Sensitivity analysis consists of changing the values of the input and internal parameters of a simulation model and determining the resulting effect on the model behaviour or output [29].

Upon examination of the results generated during the sensitivity analysis, large ranges of output values resulted from the simulations when using identical parameter values and, as such, the analysis does not offer a definitive conclusion on the influence of each parameter. Some individual simulation runs yielded expected results, based on the parameter varied, but were countered by other runs with resulting statistics of, sometimes, an entirely different order of magnitude. This diversity and inconsistency of results may be attributed to the large number of assumptions and accompanying randomness incorporated into the model. In the numerous cases where insufficient knowledge of *E. saccharina* exists to inform an accurate construction process that mimics its real-life behaviour, an assumed or derived process was implemented which makes use, in most cases, of several random variables or samples from appropriate distributions as input parameter values which direct movement and behaviour. This results in a large range of possible behavioural outcomes for each agent in the simulation; a phenomenon which is intensified when thousands of such agents interact in the same space.

Coupled with the intention of the simulation model to serve as a diverse and flexible tool with the ability to mimic any realistic *E. saccharina* behaviour as desired by the user, a parameter variation analysis was conducted
to provide a general indication of the role of the most notable parameters in the simulation. This, it is hoped, will aid users of the simulation model in recreating their particular experimental conditions so as to more accurately mimic their in-field observations or situations upon which they would like to impose testing strategies.

Experiments were conducted over a 6-month period based on specifically selected starting conditions depending on the nature of the test being conducted. Figures 9 and 10 show that, by alternating the type of oviposition site selection algorithm used, as well as the parameters controlling the typical flight distance of females, the perception distance over which they can ‘sense’ or discover suitable egg-laying sites and the strictness with which their flightpaths are governed by the discovered sugarcane attributes, very different population dispersal dynamics may be achieved. Both experiments began with the initial infestation level of 0.1 e/100s\(^6\) focused in centre of simulated hectare of sugarcane.

Figure 9 shows a significantly clumped population in the centre of the simulated space surrounded by a few clusters of agents dispersed toward the outskirts of the hectare. These results correspond to those of diffusion-type models such as that employed by Potgieter et al. [24], whereas the results shown in Figure 10 employ a larger number of ‘far flying’ females, resulting in a flatter, more erratic distribution of the population. These results correspond with the observations of Berry et al. [6] who reported that, in experiments monitoring *E. saccharina* damage in sugarcane crops, the borders of the trial areas indicated infestation levels equal to those of the central areas. Berry also identified different levels of infestation between adjacent stalks, resulting in a clustered arrangement of high and low areas of infestation across the field, dissimilar to the ‘diffusion-like’ dispersal observed in the case of Figure 9.

In an experiment with the same initial conditions, the degree to which the maturity of the underlying sugarcane stalks in the simulation can influence the direction of dispersal was conducted. The simulated hectare of sugarcane stalks was partitioned into four congruent squares and arranged such that adjacent squares were of different maturity levels. In Figure 11, the oviposition site selection process chosen, along with an associated parameter selection, results in a lesser impact of the underlying sugarcane structure in terms of dispersal direction. As may be seen in the figure, the chosen simulation configuration also has the effect of slowing population propagation and the infestation level appears relatively low after the simulated 6-month period.

\(^{6}\) *Eldana* per 100 stalks. This is the typical measure of infestation levels.
experiment. In Figure 12, however, there is a large influence of the sugarcane maturity values owing to the selections employed. As may be seen, the population size is also far larger and a large percentage of the agents have dispersed toward the bottom-right, mature portion of the sugarcane field. The ability to simulate this feature is particularly useful to proposed users since much debate still exists surrounding the role of sugarcane stalk maturity in oviposition site selection and, as such, the simulation model may assist future research efforts in this respect.

Various other tests were conducted to demonstrate the flexibility of the simulation model and, in order to equip possible future users with a platform from which to execute simulations with their preferred configurations, the settings tab, coupled to the GUI, shown in Figure 13 was constructed for easy manipulation. Note that, in the figure, only one of the two available oviposition site selection algorithms has been selected in the tab and, as such, the modifiable parameters of the second algorithm are hidden.

7 Conclusion

An operational agent-based model simulating the population dynamics of *E. saccharina* interacting in a simulated sugarcane field was successfully designed and implemented. The model consists of four primary building
blocks necessary to mimic the pest’s behaviour accurately according to the literature and, where insufficient knowledge surrounding an attribute of its biology exists, valid assumptions. The model was verified and validated using standard techniques, and a face validation and parameter variation analysis were conducted. By establishing appropriate parameter values for particular configurations, the simulation model is capable of simulating a number of different scenarios, in particular, resulting in population dispersal similar in shape to those achieved by Potgieter [24] and those observed in the field by Berry [6]. The simulation model was then further equipped with a user-friendly settings tab in which potential users may easily modify parameters before executing a simulation run.

This model serves as a departure point for agent-based simulation modelling pertaining to this area of research. Future improvements, both in the fields of simulation modelling, as well as entomological research on the pest, may assist in refining the model, producing more accurate, reliable and consistent results. The input of data gathering during in-field experiments is also necessary in order to qualitatively compare the output of the model to that which is observed in nature and further serve as a manner of calibration and verification. This is also important in the investigation and refinement of the user-defined parameters to move toward smaller parameter value ranges and hone in on actual parameter values in an attempt to accurately mimic true in-field behaviour of the pest.
Figure 13: The settings tab of the simulation model where users may manipulate parameter values to influence the manner in which the population develops.
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