The role of heterogeneous agricultural landscapes in the suppression of pest species following random walk dispersal patterns

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ABSTRACT

The contribution of a heterogeneous agricultural landscape (in terms of field layouts of diversified crop ages) towards pest suppression is considered in this study. The population dynamics of a pest species is modelled for a number of different mosaic configurations of differently aged agricultural crops across a spatial domain, where the harvesting of these fields occurs at different points in time. A reaction–diffusion model (with constant diffusion coefficients) of the pest species' growth and dispersal within a temporally variable and spatially heterogeneous environment is utilised to perform simulations. The primary objective is to establish whether or not there exist certain field configurations of differently aged crops in which average infestation levels are a minimum. It is found that more diversified field configurations (in terms of crop age) with the total length of boundaries shared between differently aged crops at a minimum, yield lower average infestation levels.

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1. Introduction

It has long been recognised that the manipulation of planting and harvesting schedules may impact negatively on pest populations in agricultural crops (Anon., 1996). Mobile organisms are expected to adjust foraging decisions to the local distribution and quality of resources. In the case of pest insects, resource availability is often linked to changes during the life cycle of their host plants. The plant growth stage is directly related to its suitability as a host (quality of resources) and may, in turn, have an influence on infestation levels and movement patterns (Mazzi and Dorn, 2012). Infestation levels decrease to zero or almost zero in crop plants when harvested—the pests in immobile or semi-mobile life stages, such as pupae and larvae, are removed together with the harvested crop and those in mobile life stages adjust their foraging, mating and oviposition decisions to the local distribution and quality of remaining host plant resources. Due to harvesting being considered as such a large controlling factor of pest species in crop plants, the question has been raised whether there exist suitably diversified agricultural landscapes (with respect to crop age), in which the

harvesting of the different fields at different points in time impact negatively on pest populations. If this question can be answered in the affirmative, then a combination of such field layouts with other pest control methods may significantly reduce the cost of achieving suppression.

The primary objective of this paper is, therefore, to examine, using mathematical simulation models, whether or not there exist certain heterogeneous spatial configurations of agricultural landscapes (with respect to fields with differently aged crops), in which harvesting of these fields at different time points yield lower average infestation levels than in other spatial configurations. The population dynamics of the pest species *Eldana saccharina* Walker (Lepidoptera: Pyralidae) in sugarcane (*Saccharum officinarum* L.) is taken as application scenario in this study, with the model presented in this paper similar to the models discussed and validated by Potgieter et al. (2012, 2013), but excluding the effect of the sterile insect technique.

2. Description of host plant and pest species

Sugarcane is a tall perennial grass from the family Gramineae. To ensure the next year's crop, the sugarcane roots are left in the field to allow shoots to regrow for an additional year (a *ratoon*) when the stalks are harvested. When the fields are replanted, the roots are ploughed out and mature sugarcane stalks are cut into

sections (*setts*), laid horizontally in furrows and covered with soil. Because of the long harvesting season, sugarcane farmers often have fields of different ages on their farms. These are also made up of different varieties bred for specific agronomic conditions. The maturation time of sugarcane varies according to the location. In South Africa, the maturation time for sugarcane varies between 12 and 24 months. During this period various diseases and pests can damage sugarcane which, in turn, may result in yield losses.

One of the most serious pest species in sugarcane is the stalk borer *E. saccharina*. Various methods have been proposed for the control of *E. saccharina* in sugarcane (Carnegie, 1981; Heathcote, 1984; Conlong, 2001; Keeping and Rutherford, 2004; Webster et al., 2005). Although contributing towards suppression, none of these have proven successful in preventing *E. saccharina* infestations. Harvesting of sugarcane at an early age is still considered an important controlling factor for *E. saccharina* in sugarcane (Atkinson and Carnegie, 1989). The lifecycle of *E. saccharina* is typical of insects—consisting of eggs, larvae, pupae and moths. The time spent in each stage of the lifecycle is variable, depending as much on the quality of food as on the temperature experienced. As a result of individual variation in development time and the longevity of the crop, generations completely overlap with all stages present in the crop at all times (Atkinson and Carnegie, 1989). Adult females lay their eggs in hidden positions on the dead leaves and sheaths on the lower parts of the plant. Larvae hatching from eggs feed initially on organic matter under leaf sheaths. When the larvae are sufficiently robust, they start boring into the stalk, and feed on the internal tissues causing yield losses in sugarcane (Atkinson, 1979; Carnegie, 1974). *E. saccharina* seems to be a relatively weak flier (Atkinson and Carnegie, 1989). However, research results suggest that a small proportion of individuals may disperse over longer distances. The female, being larger and stronger than the male, is thought to be the more likely to migrate (Atkinson, 1981).

3. The model

An *E. saccharina* population is considered in its various stages within a closed spatial domain, which, in the context of this study, is assumed to be an isolated set of adjacent sugarcane fields with heterogeneous ages, surrounded by land uses not considered as possible habitats for *E. saccharina*. A population growth and dispersal model in a spatially and temporally variable environment is used to describe the spatial dynamics of the set of interacting subpopulations in this isolated and bounded spatial domain. Consider the various stages of an *E. saccharina* population within a closed, simply connected, two-dimensional spatial domain $\mathcal{S}$. Let $E_1(\underline{\xi}, t)$, $E_2(\underline{\xi}, t), E_3(\underline{\xi}, t), E_4(\underline{\xi}, t)$ and $E_5(\underline{\xi}, t)$ denote the densities (measured in $e/100s$, which denotes the number of members of the subpopulation per 100 stalks) of the five subpopulations of eggs, larvae outside the sugarcane stalks, larvae inside the sugarcane stalks, pupae, and moths, respectively, at position $\underline{\xi} = [\xi_1, \xi_2]^T \in \mathcal{S}$ and at time $t \in [0, \infty)$. Not much is known about the dispersal patterns of *E. saccharina* moths except that they are weak fliers. In this study, adult moths are assumed to have no spatial working memory; individual movement is rather represented by a pure random walk. If individual moths follow a pure random walk, population movement may be approximated by a pure diffusion process (Ovaskainen, 2008). Also, a diffusion process is a good approximation in the case of weak fliers. Larval dispersal is not considered applicable since the distances they cover are very small compared to the spatial scale of the model. The diffusion matrix, $\mathbf{D}$, therefore has zero entries corresponding to all subpopulations, except for moths. That is, $\mathbf{D} = $ diag $\{0, 0, 0, 0, d\}$, where the (constant) diffusion coefficient d is a measure of how effectively moths disperse between habitat sites.

The dynamics of the *E. saccharina* subpopulations in the various stages are described by the reaction–diffusion equation

$$\frac{\partial \underline{E}(\underline{\xi}, t)}{\partial t} = \underline{f}(\underline{\xi}, t, \underline{E}) + \mathbf{D}\nabla^2 \underline{E}(\underline{\xi}, t) \tag{1}$$

under these assumptions, where $\underline{E}(\underline{\xi}, t) = [E_1(\underline{\xi}, t), \ldots, E_5(\underline{\xi}, t)]^T$ and where $\underline{f}(\underline{\xi}, t, \underline{E}) = [f_1(\underline{\xi}, t, \underline{E}), \ldots, f_5(\underline{\xi}, t, \underline{E})]^T$ and $\nabla := (\partial/\partial\xi_1, \partial/\partial\xi_2)$. The i-th entry of $\underline{f}(\underline{\xi}, t, \underline{E})$ denotes the number of individuals of the i-th subpopulation created during time t. More specifically,

$$f_1(\underline{\xi}, t, \underline{E}) = 0.5\lambda E_5(\underline{\xi}, t) - (\mu_E(t, \tau) + \alpha_E(t, \tau))E_1(\underline{\xi}, t),$$

$$f_2(\underline{\xi}, t, \underline{E}) = \alpha_E(t, \tau)E_1(\underline{\xi}, t) - (\mu_{L_1}(\underline{\xi}, t, \tau) + \alpha_{L_1}(t, \tau))E_2(\underline{\xi}, t),$$

$$f_3(\underline{\xi}, t, \underline{E}) = \alpha_{L_1}(t, \tau)E_2(\underline{\xi}, t) - (\mu_{L_2}(\underline{\xi}, t, \tau)\left(1 + b(\underline{\xi}, t)((E_3)(\underline{\xi}, t))\right)$$
$$+ \alpha_{L_2}(t, \tau))E_3(\underline{\xi}, t),$$

$$f_4(\underline{\xi}, t, \underline{E}) = \alpha_{L_2}(t, \tau)E_3(\underline{\xi}, t) - (\mu_P(t, \tau) + \alpha_P(t, \tau))E_4(\underline{\xi}, t),$$

$$f_5(\underline{\xi}, t, \underline{E}) = \alpha_P(t, \tau)E_4(\underline{\xi}, t) - \mu_M(t, \tau)E_5(\underline{\xi}, t),$$

where λ denotes the egg laying rate of a female, $\mu_E(t, \tau)$, $\mu_P(t, \tau)$ and $\mu_M(t, \tau)$ denote the egg, pupal and moth stage-specific mortality rates at time t at a temperature of τ degrees, $\mu_{L_1}(\underline{\xi}, t, \tau)$ and $\mu_{L_2}(\underline{\xi}, t, \tau)$ denote the larval mortality rates outside and inside the stalks at position $\underline{\xi}$, at time t and at a temperature of τ degrees. Furthermore, $b(\underline{\xi}, t)$ denotes the density-dependent mortality parameter at position $\underline{\xi}$ and time t, and $\alpha_E(t, \tau)$, $\alpha_{L_1}(t, \tau)$, $\alpha_{L_2}(t, \tau)$ and $\alpha_P(t, \tau)$ denote the egg, external larval, internal larval and pupal maturation rates at time t and at a temperature of τ degrees, respectively. A finite difference approximation is used to solve Eq. (1) numerically.

3.1. Boundary conditions

Zero-flux Neumann boundary conditions of the form

$$\left.\frac{\partial \underline{E}(\xi_1, \xi_2, t)}{\partial \xi_1}\right|_{\partial\mathcal{S}} = 0 \text{ and } \left.\frac{\partial \underline{E}(\xi_1, \xi_2, t)}{\partial \xi_2}\right|_{\partial\mathcal{S}} = 0 \tag{2}$$

are assumed for Eq. (1), where $\partial\mathcal{S}$ is the boundary of $\mathcal{S}$. Assuming the boundary is not part of $\mathcal{S}$, boundary values for $\underline{E}$ and $\mathbf{D}$ on the discretized domain are similar to those described by Potgieter et al. (2013).

3.2. Initial values

Three possible initial infestations are assumed in this study, namely 0% across the entire newly harvested/planted area, low levels (0.1 e/100s) at a small percentage (1%) of randomly selected points (with 0 e/100s at the other points), and low levels (0.1 e/100s) uniformly spread across the entire (100%) harvested area. A newly planted field and a newly harvested field are assumed to have the same initial infestation. Assuming no initial infestation (0%) after harvesting (i.e. the *E. saccharina* individuals in all life stages are removed during harvesting) is similar to a scenario where infestation only occurs in the form of diffusion from neighbouring infested areas (*E. saccharina* gradually spreading from the edges inwards). Assuming that infestation occurs only at randomly selected points in a newly planted/harvested area, corresponds to a scenario where not all *E. saccharina* are removed at the time of harvest, where some of the planted seed cane is infested with *E. saccharina*, or where some moths not only spread gradually along the edges of fields, but also fly longer distances to infest neighbouring fields within-field. The initial infestation levels of older sugarcane fields at the start of simulations are estimated by the mean-field model of Potgieter et al. (2012).