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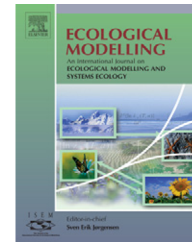

Modelling dispersal of sterile male codling moths, *Cydia pomonella*, across orchard boundaries

Rebecca Tyson[a,*], *Howard Thistlewood*[b], *Gary J.R. Judd*[b]

[a] *Barber School of Arts and Sciences, University of British Columbia Okanagan, 3333 University Way, Kelowna, BC V1V 1V7, Canada*

[b] *Pacific Agri-Food Research Centre, 4200 Hwy 97, Summerland, BC V0H 1Z0, Canada*

ARTICLE INFO

Article history:
Received 31 October 2005
Received in revised form
22 December 2006
Accepted 28 December 2006
Published on line 30 April 2007

Keywords:
Mathematical modelling
Sterile insect technique
Spatial heterogeneity
Reaction-diffusion model
Codling moth
Cydia pomonella

ABSTRACT

In this paper we present a simple diffusion model for sterile male codling moth dispersal, to investigate the effect of orchard boundaries on the pattern of spread of released sterile male codling moths. The codling moth is an important pest for apple and pear growers, with uncontrolled infestations causing significant damage to these crops. The model results are used to determine a possible control strategy. Analysis of the model reveals that release of sterile moths is most efficient if it can be done downwind of the orchard, and that control of moth damage might be enhanced by surrounding individual orchards with a row or two of non-pome fruit trees.

1. Introduction

The codling moth, *Cydia pomonella* (L.), is a pest of significant economic importance wherever pome fruits (mainly apples and pears) are grown throughout the temperate regions of the world (Geier, 1981). The moth larvae burrow into the fruit, creating a large, visible tunnel and filling it with brown frass (larval waste material). The damaged fruit is unmarketable, and will comprise most of the fruit in the orchard if the codling moth infestation is not controlled. Traditional control methods involve extensive use of chemical sprays. In an attempt to reduce fruit growers' reliance on neurotoxic insecticides, agricultural scientists have developed a tactic called sterile insect technique (SIT) (Knipling, 1979). In an operational SIT program, pest insects are mass-reared, sterilized, and then mass-released in target areas where it is hoped that they will mate with the wild insects, preventing egg fertilization and thus decreasing the wild population. In 1994, the Okanagan-Kootenay Sterile Insect Release Program was implemented in the Creston, Okanagan and Similkameen Valleys in the southern interior of British Columbia, Canada (Dyck and Gardiner, 1992). This was the world's first fully operational SIT program against *Cydia pomonella*, and the stated goal was to eliminate codling moth from the agricultural region. Since that time, while the wild population has decreased substantially, this SIT program has not been as successful as predicted (Judd et al., 2004; Myers et al., 2000). Consequently, the goal of the program has shifted from eradication to area-wide control

* *Corresponding author*. Tel.: +1 250 807 8766; fax: +1 250 807 8004.
E-mail address: rebecca.tyson@ubc.ca (R. Tyson).
URL: http://www.people.ok.ubc.ca/rtyson.

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doi:10.1016/j.ecolmodel.2006.12.038

of the population at non-economic levels. By bringing a mathematical modelling approach to the program, we hope to aid the program in its new focus, and shed some light on the reasons for the limited success of this codling moth SIT program.

There is an extensive history of modelling efforts aimed at understanding dispersal of insects and other organisms (Hastings, 1996; Holmes et al., 1994), especially with regard to invasions (Takasu et al., 2000; Shigesada and Kawasaki, 2001; Lewis and Kareiva, 1993; Lewis and van den Driessche, 1993). A great deal of non-spatial modelling work of the SIT, either alone or in combination with other pest control methods (Vreysen et al., 2006; Barclay, 2001 and references therein), provides a detailed picture of the effectiveness of the SIT, when space is not explicitly included in the model. Recent theoretical and experimental work however, has shown that the amount and spatial distribution of suitable habitat is a major driver of population dynamics of species in static (Owen-Smith, 2004; Pe'er et al., 2004; Penteriani et al., 2004; Johnson et al., 2004; Gardner and Gustafson, 2004; Kie et al., 2002) and dynamic (Biedermann, 2004; Lindborg and Eriksson, 2004) landscapes. Some spatial modelling work on the SIT (Plant et al., 1984; Wolf et al., 1971; Lewis and van den Driessche, 1993; Marsula and Wissel, 1994; Barclay, 1992) has confirmed that consideration of spatial effects is important in the development of effective SIT programs. Thus far, spatial modelling work on the SIT has considered only homogeneous landscapes, or landscapes with a periodic pattern of "good" and "bad" patches.

The model in this paper is motivated by extensive field experiments with sterile codling moths (*C. pomonella*) in the Similkameen Valley (Thistlewood and Judd, 2003a,b; Thistlewood et al., 2004). The qualitative results are used here to develop a model describing dispersal of sterile, male codling moths, that will give insight into their movement across orchard boundaries. We use a reaction-diffusion model which describes moth movement in different habitats (pome fruit orchards, fields, non-pome fruit orchards), the effect of wind, and directed moth flight toward individual pome fruit trees or orchards. We consider heterogeneous domains containing a mix of the habitats under consideration, and so the model coefficients and variables are functions of both space and time. Our simulations and analysis indicate that directed moth flight in response to pome fruit trees is probably an important component of moth displacement even when located some distance from host trees (see also Mani et al., 1974). We also find that a non-pome fruit orchard upwind of a pome fruit orchard may serve as a sink for dispersing male moths, suggesting that a buffer strip of non-pome fruit trees may provide another means of control in an integrated pest management program.

In Section 2 we present the experimental results on which our model is based. We develop the model in Section 3, and in Section 4 we perform some analysis. A combination of numerical and analytic techniques are used to investigate solutions to the model equations. We investigate the importance of moth dispersal behaviour at orchard boundaries in Section 6. The paper concludes with a discussion of the model and results in Section 7.

2. Summary of the experiments

2.1. Experimental method

The experiments, from which were obtained the qualitative results motivating the model, are described elsewhere (Thistlewood and Judd, 2003a,b; Thistlewood et al., 2004), and so we present a brief summary here. Over a period of three summers, pheromone traps that are specific for male *C. pomonella* were hung and monitored in a region covering 875 rural hectares. At the moment no effective way of trapping dispersing female moths exists, and so dispersal data was gathered for male moths only. Cherries, peaches, apples and pears are all grown in the experimental region, with apples and pears covering the vast majority (389 and 29 acres, respectively) of orchard acreage. Most of the non-orchard acreage consisted of grassland with isolated trees and a few houses.

During the summer of 2001 and 2002, several mass releases of marked sterile codling moths were carried out in various locations throughout the study area. Both males and females (in a 1:1 ratio) were released, but only male moths were recaptured in traps. The codling moths were released either at a single location (point release) or along a line about 250 m long (line release). Traps hung throughout the 6 km $\times$1.5 km experimental site, at a density of about 1 ha^{-1}, were monitored weekly for recaptured marked moths.

2.2. Experimental results

We review here the general results from the experiments described above, as well as other supporting references. These results must be captured by our model.

2.2.1. Death rate

The sterile males live for a maximum of ca. 4 weeks after release. In the spring, moths only live for a maximum of 2–3 weeks, while in midsummer a few males can live for as long as 5 weeks. Life expectancy estimates are based on mark-release-recapture experiments using sterile male codling moths. It is unclear whether the population numbers decline at a constant rate, or at some rate which varies with time.

2.2.2. Upwind flight

Numerous experimental studies have shown that most male moths fly upwind in response to detecting a conspecific female sex pheromone (Cardé, 1984). In some cases, orientation along these pheromone plumes can occur over many hundreds of metres (Wall and Perry, 1987). Mating occurs when a male successfully follows a female pheromone plume to its source. When searching for a pheromone plume they carry out casting motions which can be described as random motion with upwind drift. When a pheromone plume is encountered, the male moth will fly directly upwind. Higher densities of male moths are found on an orchard's upwind edge, where "upwind" is defined in the sense of the prevailing winds during the codling moth flight period at dusk. Trap catches in these areas, especially those next to open terrain, are generally quite a bit higher than trap catches elsewhere. Orchardists also have observed that damaged fruit tends to be most com-