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Modelling the phenology of codling moth: Influence of habitat and thermoregulation

Ute Kührt [a], Jörg Samietz [a,*], Heinrich Höhn [b], Silvia Dorn [a]

[a] Institute of Plant Sciences, Applied Entomology, Swiss Federal Institute of Technology (ETH), CH-8092 Zurich, Switzerland
[b] Agroscope Changins-Wädenswil, Swiss Federal Research Station, CH-8820 Wädenswil, Switzerland

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Abstract

This study used an explorative, individual-based model to evaluate the influences of (1) plant architecture, i.e. dwarf versus standard trees, (2) the use of hail nets, and (3) insect behaviour on the phenology of the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), a major pest in apple orchards worldwide. Body temperatures of the different codling moth stages were approximated by microhabitat temperatures, behavioural response to temperature, and biophysically modelled temperature increments due to absorption of solar radiation. Results indicate a significant influence of habitat parameters on the phenology of the codling moth. Under the simulated conditions, adults appeared up to 6 days earlier in dwarf trees than in standard trees, and up to 5 days later in trees covered with hail nets than in trees without them. In contrast, thermoregulation behaviour, which is documented for the larval and adult stages, appeared to be of relatively low influence on the insect's overall phenology. Model validation using reported pheromone trap catches of male moths agreed with the simulated appearance dates of adults of the overwintered generation. Simulated and observed appearance dates did not deviate when habitat temperature was used, but deviated considerably when standard air temperature was used as driving variable. Considering habitat and behaviour will help to improve current phenology models for the codling moth.

Keywords: Insect phenology; Habitat temperature; Developmental rate; Model; Hail net; Plant architecture; Apple; *Cydia pomonella*

1. Introduction

The codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is one of the most devastating pest insects in apple orchards worldwide (Dorn et al., 1999). Understanding the factors governing its development and implementing this knowledge into forecast models enables to time interventions and increases efficacy and success of control measures. Standardised air temperature measurements from agro-meteorological stations and developmental rates from laboratory studies are commonly used as driving variables to forecast codling moth phenology (e.g. Baker, 1980; Blago and Dickler, 1990; Lischke and Blago, 1990; Pitcairn et al., 1992; Rock and Shaffer, 1983).

However, there is evidence that standard air temperatures used to drive models deviate considerably from the microenvironmental temperatures experienced by insects (Graf et al., 2001; Howell and Schmidt, 2002; Landsberg et al., 1973; Schroeder, 1965; Thorpe, 1974). Furthermore, recent studies have shown that microenvironmental temperatures in typical habitats of the different codling moth stages are altered by plant architecture and by the application of hail protection nets (Kührt et al., 2006b).

Additionally, thermoregulation behaviour has been documented for certain codling moth stages. Feeding codling moth larvae within apples perform cryptic basking, i.e. they feed preferably in the warmer side of the fruit thereby increasing their body temperature and possibly

* Corresponding author at: Agroscope Changins-Wädenswil, Swiss Federal Research Station, PO Box 185, CH-8820 Wädenswil, Switzerland. Tel.: +41 44 783 61 93; fax: +41 44 783 64 34.
E-mail address: joerg.samietz@faw.admin.ch (J. Samietz).

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accelerating their development (Kührt et al., 2005). This positive thermal response disappears when mature larvae leave the fruit in search of cocooning sites and overwintering shelters. A similar shift in thermal response is documented for adults. Unmated adults rest preferably in sites with lower temperatures, while mated females prefer to deposit their eggs at sites with temperatures around 30 °C (Kührt et al., 2006a).

Habitat parameters such as plant architecture (traditional standard trees versus commercial dwarf tress) and application of hail nets as well as thermoregulation behaviour likely alter the temperatures experienced by the various codling moth stages. Therefore, the purpose of this study was to examine the influence of these factors on the rate of development of immature stages and study their effects on the seasonal phenology of the codling moth using an exploratory, individual-based model.

2. Materials and methods

2.1. Phenology model

The phenology model simulated the development of individuals within a population. Development was divided into four stages: egg, larva, pupa, adult; diapause was not considered. Each individual had the following characteristics: body temperature (T_b), developmental stage, thermoregulation (included or excluded), mortality (stage-dependent), maximum oviposition rate (eggs per day), fertility (eggs per female). The different codling moth stages were not distinguished by male and female. Body temperatures of the different developmental stages were approximated by the measured temperatures in the respective microhabitats (canopy, bark, and apple; see Section 2.2). Stage-dependent mortality, maximum oviposition rate per day, and life-time fertility were drawn from data available in the literature (Lischke, 1992).

Thermoregulation was included into the model by assigning body temperatures to individuals according to their thermal preference (Kührt et al., 2005, 2006a). Eggs from temperature-regulating females were given a body temperature that is obtained at sun-exposed sites in the canopy. Temperature-regulating larvae were assigned a body temperature that they potentially experience in the south-facing half of an apple. Late fifth-instar larvae do not choose their pupation site by temperature, and, thus, pupae were assigned the mean bark temperatures for T_b. In the simulations without thermoregulation, eggs were randomly assigned a T_b at sunny or shady sites depending on the potential global radiation (GSF) at this site, which was estimated in the apple orchards throughout the season (cf. Kührt et al., 2006b). Non-regulating larvae were assigned the mean apple temperature for T_b.

The hourly temperature-dependent developmental rates were calculated with a non-linear function derived from an equation for enzyme kinetics, modified by Schoolfield et al. (1981):

$$r(T_c) = \frac{\rho_{25}\left(\frac{T_c}{298.16}\right)\exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{298.16}\ \frac{1}{T_c}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2L}}\ \frac{1}{T_c}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2H}}\ \frac{1}{T_c}\right)\right]} \quad (1)$$

where T_c is the temperature (K), ρ_{25} the developmental rate at 25 °C assuming no enzyme inactivation (d^{-1}), R the universal gas constant (1.987 cal K^{-1} mol^{-1}), ΔH_A the enthalpy of enzyme activation (cal mol^{-1}), ΔH_L the change in enthalpy connected with low temperature inactivation of the enzyme (cal mol^{-1}), ΔH_H the change in enthalpy connected with high temperature inactivation of the enzyme (cal mol^{-1}), $T_{1/2L}$ the temperature at which the enzyme is 1/2 active and 1/2 low temperature inactive (K), and $T_{1/2H}$ is the temperature at which the enzyme is 1/2 active and 1/2 high temperature inactive (K).

This function was fitted to data of development time at different constant temperatures for all codling moth stages obtained from the literature (Fig. 1 and Table 1). Hourly developmental rates were accumulated. When the cumulative developmental rate r reached 1, development was completed and the individual transitioned to the next stage. Calculation of the development time started on 1 January with the accumulation of the hourly developmental rates of the pupae. The initial number of pupae was set to 100 individuals.

Simulations were run with habitat temperatures measured in dwarf trees with and without hail nets, and in standard trees (Kührt et al., 2006b). The phenology of the codling moth was compared between uncovered dwarf and standard trees to estimate effects of plant architecture on development time. To evaluate the influence of hail nets on codling moth phenology, development time was compared between dwarf trees with and without hail nets. For all orchard types, the impact of thermoregulation on the phenology of the codling moth was assessed by comparing populations of temperature-regulating and non-regulating individuals. The appearance dates of the first individuals of each stage, and the total generation time (period between the appearance of adults of the overwintered and the first generation) were used for data analysis. The effects of plant architecture, hail nets, and thermoregulation were evaluated by testing for differences in the appearance dates of corresponding codling moth stages using one-sample *t*-tests.

2.2. Determination of body temperature

The body temperatures of the different codling moth stages were approximated by the temperatures in their typical habitats which were then used for the different