

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

Received 27 May 2005; received in revised form 8 February 2006; accepted 3 March 2006

Available online 18 April 2006

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.

© 2006 Elsevier B.V. All rights reserved.

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).

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 trees) 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 ($1.987 \text{ cal K}^{-1} \text{ mol}^{-1}$), 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

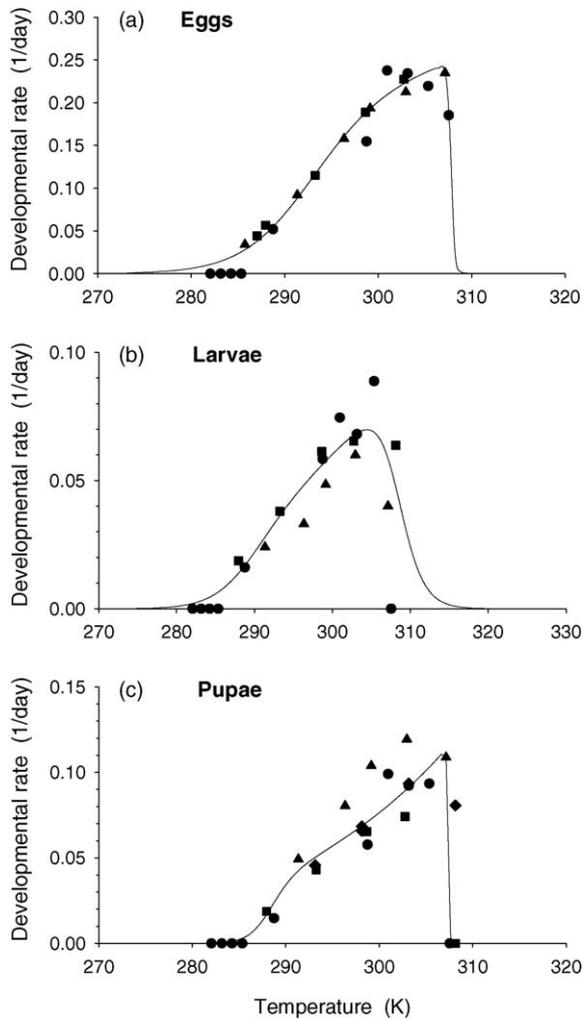


Fig. 1. Developmental rates for different stages of the codling moth from literature data (● – Pitcairn et al., 1991; ▲ – Butturini et al., 1992; ■ – Howell and Neven, 2000; ◆ – Williams and McDonald, 1982) and the fitted non-linear function (line) used for modelling codling moth development (for equation see Section 2).

simulations. The body temperatures of eggs, larvae and pupae was approximated by the temperature of air within the canopy, of apples and of bark of tree trunks, respectively. All habitat temperatures used for the simulations were collected in a field study over one season (2002) in apple orchards in northern Switzerland (cf. Kührt et al., 2006b). The habitat temperatures were measured in an apple orchard with covered and uncovered dwarf trees (height: 3.0 m, canopy diameter: 0.8 m, age 7 years), and in an orchard with standard apple trees (height: 4.5–6.0 m, canopy diameter: 3–4 m, age about 30 years). The standard hailnets on the covered orchard were made of black three-thread nylon (3.8 mm × 10 mm, Frustar, Weiz, Austria). Air temperature within the canopy was measured at noon on selected sunny and overcast days as well as continuously throughout the season. Apple and bark temperatures were taken as surface temperatures from the north- and south-facing side of fruits and tree trunks at noon on selected sunny and overcast days.

Table 1

Parameter values for the non-linear function used for calculation of developmental rates fitted to data of development time at different constant temperatures for codling moth eggs, larvae, and pupae; data obtained from the literature

Stage	Parameter	Value	Literature source
Eggs	ρ_{25}	0.2295 (d ⁻¹)	Pitcairn et al. (1991)
	ΔH_A	1300 (cal mol ⁻¹)	Butturini et al. (1993)
	ΔH_L	-43360 (cal mol ⁻¹)	Howell and Neven (2000)
	ΔH_H	955100 (cal mol ⁻¹)	
	$T_{1/2L}$	292.7 (K)	
	$T_{1/2H}$	307.8 (K)	
Larvae	ρ_{25}	0.05762 (d ⁻¹)	Pitcairn et al. (1991)
	ΔH_A	7094 (cal mol ⁻¹)	Butturini et al. (1993)
	ΔH_L	-55630 (cal mol ⁻¹)	Howell and Neven (2000)
	ΔH_H	125400 (cal mol ⁻¹)	
	$T_{1/2L}$	289.4 (K)	
	$T_{1/2H}$	308.4 (K)	
Pupae	ρ_{25}	0.06879 (d ⁻¹)	Pitcairn et al. (1991)
	ΔH_A	9568 (cal mol ⁻¹)	Butturini et al. (1993)
	ΔH_L	-131500 (cal mol ⁻¹)	Howell and Neven (2000)
	ΔH_H	3961000 (cal mol ⁻¹)	Williams and McDonald (1982)
	$T_{1/2L}$	288.2 (K)	
	$T_{1/2H}$	307.3 (K)	

Standard air temperature, measured 2 m above ground with an agro-meteorological station at the dwarf tree orchard, was subtracted from the respective habitat temperatures. These temperature differences, ΔT_{hab} , could now be added to standard air temperatures provided by any given weather stations to approximate the temperatures experienced by the various codling moth stages through the season.

ΔT_{hab} was estimated for different periods of the season, and separately for clear and cloudy days. Each developmental stage of the codling moth was assigned a series of hourly ΔT_{hab} over the course of the season, separately for either weather condition. Data of solar radiation measured by the agro-meteorological station were used to classify each day of the year to be either “clear” or “cloudy”. Days were considered “clear” when the average radiation between 11.00 and 14.00 h was higher than 500 W m⁻² for April–September, and higher than 300 W m⁻² for the rest of the year. All days with lower radiation means were considered “cloudy”.

Body temperatures of the particular developmental stage were calculated by adding the according hourly ΔT_{hab} to the standard air temperature (T_s). Standard air temperatures used for the simulations were recorded with the meteorological

station Wädenswil (Switzerland) from 1991 to 2004. Egg temperature was calculated by adding ΔT_{hab} of air within the canopy to T_s . For clear days an additional temperature increment was added to $T_s + \Delta T_{\text{hab}}$ due to absorption of radiation (see below). Body temperatures of larvae and pupae were computed by increasing T_s by ΔT_{hab} of apples and tree trunks, respectively. Larval and pupal body temperatures were calculated individually for the north- and the south-facing side of their respective habitats. In addition, for the non-regulating larvae and pupae, the mean temperatures between T_b at the north- and south-facing habitat side were calculated.

All body temperatures were calculated separately for clear and cloudy days. During the daytime (9:00–17:00 CET), ΔT_{hab} measured at noon was added to T_s . For cloudy days, the unmodified ΔT_{hab} was added for every hour. For clear days, ΔT_{hab} was modified by an index to approximate a diurnal course of habitat temperatures. This index was determined by measurements of habitat temperatures in apple orchards on selected sunny days from March to September 2003. Measurements were taken with hand-held type T thermocouple probes (Physitemp Instruments, Clifton, New Jersey, USA) once a month (i.e. 24 March, 24 April, 4 June, 5 August, 18 September) from sunrise until sunset. Air temperature within the canopy and surface temperatures (north and south) on the bark were recorded every 3 h in June and August, and every 2 h on all other sampling dates. Surface temperatures (north and south) of apples were recorded every 3 h in June and August. The index was calculated by dividing the ΔT_{hab} measured at a certain full hour of the day by ΔT_{hab} measured at noon (12:00 h for air and bark temperature, 13:00 h for apple temperature). To calculate the body temperatures during the daytime on sunny days, ΔT_{hab} measured at noon was multiplied by this index, and this product was added to T_s .

For late afternoon and through the night, when radiation was low or absent (17:00–5:00 h CET), habitat temperatures, and thus body temperatures, were assumed to equal air temperatures within the canopy. ΔT_{hab} of the air within the canopy was added to T_s , separately for clear and cloudy days. To consider diurnal changes in radiation on habitat temperatures, the diurnal cycle was further divided into periods: dawn (5:00–9:00 h CET), night (21:00–5:00 h CET), and dusk (17:00–21:00 h CET). Mean values of ΔT_{hab} of air within the canopy for these diurnal periods were added hourly to T_s , according to the time of the season.

The additional increase in temperature experienced by eggs exposed to the sun was calculated with a biophysical model used by Samietz et al. (2005). To approximate the “passive” body temperature or operative environmental temperature (T_e), the following simplified equation (2) of heat balance was used (after Baumgärtner and Severini, 1987):

$$T_e = T_a + a \Phi_R \frac{bA}{kS} \quad (2)$$

where T_a is the ambient temperature, Φ_R the radiation flux density (W m^{-2}), a the absorption coefficient, A the body cross-sectional area towards the radiation source, S the external body-surface area, b the body diameter, and k is the thermal conductivity of the air ($=0.026 \text{ W m}^{-1} \text{ K}^{-1}$).

The size of an egg was approximated by a rotational ellipsoid with half the egg length as the semi-major axis p and half the maximum egg diameter (mean between thorax height and width) as semi-minor axis q . The cross-sectional areas of the eggs towards the radiation source are calculated as a function of the orientation angle α and the projection of the semi-major axis (Samietz et al., 2005). Passive heat gain under a specified condition of radiation assumes a randomly chosen α between 0° and 90° . The operative environmental temperature for eggs at sunny sites in their habitat was calculated by solving the integral given by Samietz et al. (2005) with the dimensions of the eggs.

To estimate the necessary parameters for this biophysical model, absorption coefficient and dimensions of eggs were measured using eggs deposited by females from a laboratory colony. This laboratory strain originated from diapausing larvae collected in cardboard strips on apple trees in north-eastern Switzerland and had been maintained in the laboratory for about 60 generations. All stages were held in a climate chamber at $24 \pm 1^\circ \text{C}$, 60% RH, and LD 16:8 h.

The absorption coefficient for codling moth eggs was measured using a SD 2000 fiber optic spectrometer photo spectrometer (Ocean Optics Inc., Dunedin, FL, USA). One to 2 days after eggs were deposited on cover slips, 25 measurements were taken. The mean absorption coefficient (\pm S.D.) was 0.70 ± 0.00 for the eggs. The mean length of the major axis was $1.3 \pm 0.1 \text{ mm}$, and the mean length of the minor axis was $1.1 \pm 0.1 \text{ mm}$ ($N = 50$).

The radiation flux density (Φ_R) for the estimation of the operative environmental temperature (T_e) was obtained from the meteorological station in Wädenswil, Switzerland, measuring the global radiation during 1991–2004.

2.3. Model validation

To test the phenology model, simulations were run (1) with the approximated body temperatures of the codling moth, and (2) with the standard air temperatures (T_s) obtained over 13 years (1992–2004) from the meteorological station at Wädenswil (Switzerland). The body temperatures of the codling moth were approximated by adding temperature differences between the habitats and a weather shelter, ΔT_{hab} , to T_s . The predicted appearance dates from the simulations were compared to phenology data obtained from male catches in pheromone traps placed in dwarf tree orchards all over Switzerland over the same period (1992–2004). All orchards used for the validation shared similar climatic conditions which were adequately represented by data collected at the weather station in Wädenswil (Heinrich Höhn, unpublished data). Comparisons between the simulated model output and phenological

Table 2
Model validation

Year	N	Deviation of simulated from observed appearance dates of adults (weeks)			
		T_b = habitat temperature		T_b = standard air temperature	
		Regional orchards	Local orchard	Regional orchards	Local orchard
Average		0.1	-0.1	2.9	2.5
2004	14	1	1	4	3
2003	12	-1	0	2	3
2002	6	0	1	4	5
2001	8	0	-1	2	1
2000	7	0	-1	2	1
1999	19	1	1	2	2
1998	12	-1	-2	2	1
1997	15	1	0	4	3
1996	13	1	1	3	3
1995	19	0	0	5	4
1994	8	1	1	4	4
1993	22	-1	-1	2	2
1992	34	-1	-1	2	1

Deviation (in weeks) of simulated vs. observed appearance dates of adult codling moths of the overwintered generation (positive values indicate later, negative values indicate earlier than observed appearance). Observed appearance refers to male catches in pheromone traps in selected orchards in the region with similar climatic conditions (N – number of orchards), and in one local orchard adjacent to the meteorological station Wädenswil (Switzerland). Simulations for model validation were run approximating the insect's body temperatures, T_b , by (1) habitat temperatures, and (2) standard air temperatures from the agro-meteorological station.

observations (pheromone trap catches) were made for all orchards in the region as well as for an orchard adjacent to the weather station in Wädenswil. To avoid any bias due to low moth counts, only orchards with cumulative captures in excess of 50 males over the entire monitoring period (18 weeks) were included in the validations (Table 2). The differences between modelled and observed appearance dates of codling moth adults of the overwintered generation were used as a measure for the validity of the model. Differences between observed and predicted appearance dates were tested for significance by one-sample t -tests. Differences were significant if they deviated from zero.

2.4. Sensitivity analysis

The global site factor (GSF) and all habitat temperatures, i.e. air temperature within the canopy, bark and apple temperatures, were considered most important for codling moth development and were included in the sensitivity analysis of the model. The body temperature of the codling moth was calculated for each time step (1 h) after changing each parameter separately by increasing or decreasing its standard value by 1 S.D. For GSF, the standard deviation from the mean values measured in the field was used (Kührt et al., 2006b). For the different habitat temperatures measured in the field, the standard deviation of the difference to the standard air temperature (T_s) was added or subtracted from the mean values (Kührt et al., 2006b).

For the analysis, the differences between the appearance dates of the codling moth stages for the standard and changed run values were calculated for 5 years separately.

These differences were tested for significance (deviations from zero) using one-sample t -test. Furthermore, the changes in the differences between the appearance dates in dwarf and standard trees and between dwarf trees with and without hail nets were analysed with one-sample t -tests.

3. Results

3.1. Model validation

Using habitat temperatures to approximate insect body temperatures in the simulations, the model agreed well with the data obtained from pheromone trap catches of adult codling moth males. There was no difference between the simulated and observed appearance dates of the first codling moth adults in spring ($t = -0.267$, d.f. = 12, $P = 0.79$ for the local orchard; $t = 0.322$, d.f. = 12, $P = 0.75$ for all other orchards in the region; Table 2).

Using standard air temperatures measured by the meteorological station as the driving variable for simulations resulted in a major delay of adult emergence compared with the observed events in the field ($t = 6.88$, d.f. = 12, $P < 0.001$ for the local orchard; $t = 9.45$, d.f. = 12, $P < 0.001$ for all other orchards in the region; Table 2).

3.2. Phenology model

Plant architecture significantly influenced appearance dates both in temperature-regulating and in non-regulating populations. Simulations with 100% temperature-regulating individuals in the respective stages revealed accelerated

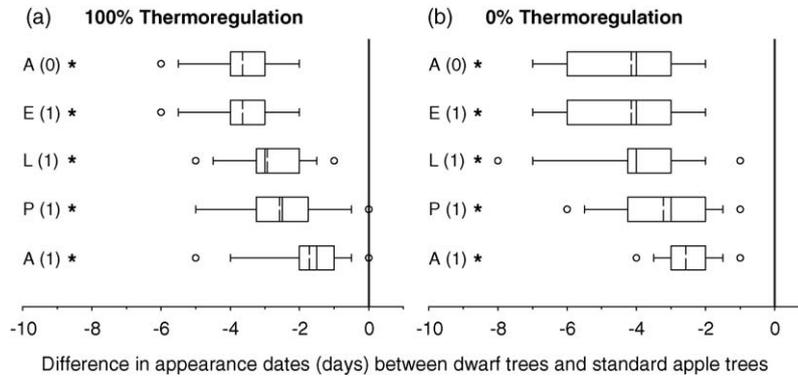


Fig. 2. Comparison of simulated appearance dates of codling moth stages with thermoregulation (a) included and (b) excluded. Shown are differences in appearance dates between individuals in dwarf trees and standard apple trees. Negative values indicate earlier appearance in dwarf trees. A (0) – adults of the overwintered generation, E (1) – eggs, L (1) – larvae, P (1) – pupae, A (1) – adults of the first generation. Boxes show 25–75th percentile with median (solid line) and mean (dashed line); error bars show 10th and 90th percentile; all outliers are plotted as open circles. (*) significant differences according to *t*-test ($P < 0.05$).

development of the codling moth in dwarf trees by on average 2–4 days compared to standard trees (Fig. 2a). On average, adults of the overwintered generation and eggs appeared 4 days earlier, larvae and pupae 3 days earlier, and adults of the first generation 2 days earlier than those developing in standard trees. The total generation time, i.e. from the first adults of the overwintered generation to the first adults of the first generation, was 2 days longer in dwarf trees than in standard trees ($t = 7.87$, d.f. = 13, $P < 0.001$). Excluding thermoregulation behaviour, all codling moth stages appeared on average 3 days (adults of the overwintered generation, eggs, and larvae) to 4 days (pupae and adults of the first generation) earlier in dwarf trees than in standard trees (Fig. 2b). The total generation time was 2 days longer in dwarf trees than in standard trees ($t = 3.46$, d.f. = 13, $P = 0.004$).

Hail nets significantly delayed the appearance dates of the codling moth stages in dwarf trees (Fig. 3). Simulations including thermoregulation showed differences in appearance dates of the various codling moth stages of 4 days except for the adults of the first generation (3 days). The total

generation time was 1 day shorter in trees with hail nets ($t = -2.20$, d.f. = 13, $P = 0.047$). In simulations without thermoregulation, hail nets significantly retarded the development of larvae and pupae of the overwintered generation delaying the appearance of all subsequent stages by 4 days. There was no significant difference in the total generation time between dwarf trees with and without hail nets ($t = -1.05$, d.f. = 13, $P = 0.314$).

Thermoregulation behaviour significantly advanced the appearance of larvae, pupae and adults of the first generation irrespective of orchard type. In both dwarf trees with and without hail nets, larvae of the first generation appeared 2 days earlier when thermoregulation was included. Subsequent stages appeared 1 day earlier (Fig. 4a and b). In standard trees, larvae of the first generation appeared 3 days earlier, while pupae and adults of the first generation appeared 2 days earlier when thermoregulation was included (Fig. 4c). The timing of adult emergence and egg laying were not affected. Thermoregulation behaviour decreased the total generation time by 1 day ($t = -2.51$, d.f. = 13, $P = 0.026$ for dwarf trees without hail nets; $t = -4.19$,

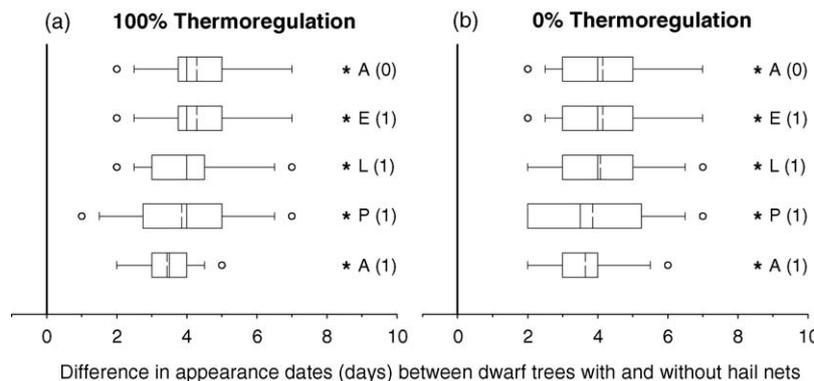


Fig. 3. Comparison of simulated appearance dates of codling moth stages with thermoregulation (a) included and (b) excluded. Shown are differences in appearance dates between individuals in dwarf trees with hail nets and trees without hail nets. Positive values indicate earlier appearance in trees without hail nets. A (0) – adults of the overwintered generation, E (1) – eggs, L (1) – larvae, P (1) – pupae, A (1) – adults of the first generation. Boxes show 25–75th percentile with median (solid line) and mean (dashed line); error bars show 10th and 90th percentile; all outliers are plotted as open circles. (*) significant differences according to *t*-test ($P < 0.05$).

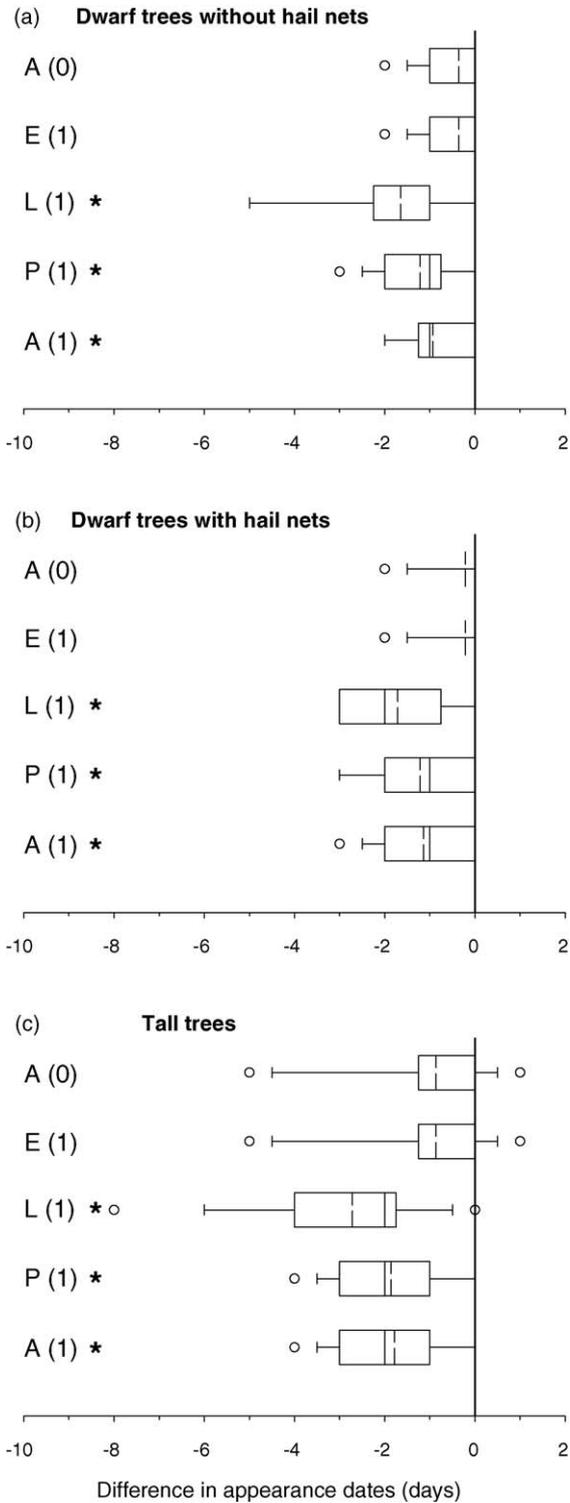


Fig. 4. Comparison of simulated appearance dates of codling moth stages in (a) dwarf trees without hail nets, (b) dwarf trees with hail nets, and (c) standard apple trees. Shown are differences in appearance dates between a temperature-regulating and a non-regulating population. Negative values indicate earlier appearance in the temperature-regulating population. A (0) – adults of the overwintered generation, E (1) – eggs, L (1) – larvae, P (1) – pupae, A (1) – adults of the first generation. Boxes show 25–75th percentile with median (solid line) and mean (dashed line); error bars show 10th and 90th percentile; all outliers are plotted as open circles. (*) significant differences according to *t*-test ($P < 0.05$).

d.f. = 13, $P = 0.001$ for dwarf trees with hail nets; $t = -2.51$, d.f. = 13, $P = 0.026$ for standard trees).

3.3. Sensitivity analysis

Changes in the global site factor (GSF) had no significant effect on the outcome of the simulations. Neither the appearance dates of particular stages nor the differences in the appearance dates between the orchard types were altered by subtracting or adding 1 S.D. to the mean GSF values (Table 3).

Lowering the air temperature within the canopy by 1 S.D. delayed the appearance of all codling moth stages in all orchard types compared with the original air temperatures (Table 3). Due to a noticeable compounding effect, the delay in appearance of various stages increased over the season. Differences in the appearance dates between dwarf and standard trees were only significant for the larvae of the first generation, which appeared 2 days earlier in the dwarf trees (Table 3). Larvae appeared 2 days later in dwarf trees with hail nets when compared to dwarf trees without hail nets.

Increasing the air temperature within the canopy by 1 S.D. did not significantly influence the appearance dates of the codling moth stages in the model, irrespective of the orchard type (Table 3). The only exception were the first generation larvae whose appearance in the standard trees was delayed by 2 days compared with the dwarf trees.

Lowering the bark temperatures by 1 S.D. significantly delayed the appearance of all codling moth stages in all orchard types compared to simulations with the mean temperatures (Table 3). The bark temperatures retarded the development of the pupae of the overwintered and first generation leading to a delayed appearance of adults and eggs. This initial delay was lessened during larval development. The lower bark temperatures increased the delay in the appearance of adults of the overwintered generation, eggs and larvae developing in standard trees by 3 days compared to dwarf trees. The appearance in all other stages was not affected. There was no significant effect on the differences in the appearance dates between dwarf trees with and without hail nets due to lowering the bark temperatures.

Increasing the bark temperatures by 1 S.D. caused all stages to appear earlier compared to simulations with the mean bark temperatures (Table 3). Adults and eggs appeared earlier due to accelerated development of the pupae of the overwintered generation. Increasing the bark temperatures decreased the delay in the appearance of adults of the overwintered generation, eggs and larvae developing in standard trees by 1 day compared to dwarf trees. Differences in the appearance dates between dwarf trees with and without hail nets due to the increase in bark temperatures were only significant for the larvae, which appeared 2 days later in the covered trees.

Lowering the apple temperatures by 1 S.D. had a significant effect on the appearance dates of pupae and adults of the first generation in dwarf trees with and without

Table 3

Sensitivity of the model output to changes in model parameters (GSF – global site factor, T_{air} – air temperature within the canopy, T_{bark} – bark temperature, T_{apple} – apple temperature)

Orchard type	Stage	Difference in appearance dates (d)							
		GSF		T_{air}		T_{bark}		T_{apple}	
		–S.D.	+S.D.	–S.D.	+S.D.	–S.D.	+S.D.	–S.D.	+S.D.
Dwarf trees without hail nets	Adults (0)	0	0	2*	1	4*	–3*	0	0
	Eggs (1)	0	0	2*	1	4*	–3*	0	0
	Larvae (1)	0	0	4*	2	4*	–4*	0	0
	Pupae (1)	0	0	6*	3	2*	–2*	1*	–1*
	Adults (1)	0	0	8*	6	3*	–2*	2*	–1*
Dwarf trees with hail nets	Adults (0)	0	0	4*	2	5*	–3*	0	0
	Eggs (1)	0	0	4*	2	5*	–3*	0	0
	Larvae (1)	0	0	6*	4	5*	–2*	1	0
	Pupae (1)	0	0	7*	4	2*	–2*	2*	–1*
	Adults (1)	0	0	9*	6	2*	–2*	2*	–1
Standard trees	Adults (0)	0	0	4*	1	7*	–4*	0	0
	Eggs (1)	0	0	4*	1	7*	–4*	0	0
	Larvae (1)	0	0	6*	4	7*	–5*	0	0
	Pupae (1)	0	0	6*	4	3*	–3*	1	–1*
	Adults (1)	0	0	8*	5	4*	–3*	1*	–1*
Difference: dwarf – standard	Adults (0)	0	0	–2	–1	–3*	1*	0	0
	Eggs (1)	0	0	–2	–1	–3*	1*	0	0
	Larvae (1)	0	0	–2*	–2*	–3*	1	0	0
	Pupae (1)	0	0	0	–1	–1	2	1	0
	Adults (1)	0	0	0	0	–1	1	0	0
Difference: with hail nets – without hail nets	Adults (0)	0	0	2	1	1	0	0	0
	Eggs (1)	0	0	2	1	1	0	0	0
	Larvae (1)	0	0	2*	2	1	2*	0	0
	Pupae (1)	0	0	1	1	–1	0	1	0
	Adults (1)	0	0	2	1	0	0	1	0

Model parameters were changed by subtracting or adding one standard deviation (S.D.) from/to the original means. Results are shown as mean differences in appearance dates of the codling moth (in days) between model output with changed parameters and those with original parameters for each developmental stage of the codling moth (0 = overwintered generation, 1 = first generation), i.e. values indicate earlier, values indicate later appearance.

* Significant differences according to *t*-test ($P < 0.05$).

hail nets (Table 3). These stages appeared 1 and 2 days later than in simulations with the mean temperatures due to slower larval development in the fruit. In standard trees, lowering the apple temperatures led to a delay in the emergence of the adults of the first generation. The differences in the appearance dates between dwarf and standard trees, and between dwarf trees with and without hail nets, did not change significantly for the different stages when apple temperatures were lowered.

Increasing the apple temperatures by 1 S.D. led to an earlier appearance of pupae and adults of the first generation by 1 day in all orchard types due to accelerated larval development (Table 3). The differences in the appearance dates between dwarf and standard trees, as well as between dwarf trees with and without hail nets, were not significantly changed by increasing the apple temperatures.

4. Discussion

Model validation showed that the explorative model produced plausible results regarding the appearance dates

of adult codling moths. Predicted appearance dates of adults of the overwintered generation agreed well with observed catches of male moths in pheromone traps over 13 years. The weekly interval of pheromone trap counts presented a limitation in the analysis of model accuracy on an even smaller time scale. Estimating body temperature of codling moth by habitat temperature rather than standard air temperature measurements appeared to be more accurate. Using standard air temperature as the estimated body temperature of the codling moth caused large discrepancies of up to several weeks between predicted and observed appearance dates. Thus, model predictions were more precise when habitat temperatures were used as the driving variables instead of standard air temperatures provided by weather stations. Forecasting the emergence of codling moths in spring can be improved when bark temperatures are used, since air temperature insufficiently describes the thermal conditions at the tree trunk. Trunk temperatures at the north- and south-facing sides are highly variable and deviate considerably from air temperature, especially in spring (Graf et al., 2001; Kührt et al., 2006b).

The sensitivity analysis showed that the model was sensitive to changes in habitat temperatures, while changes in the global site factor did not affect simulation results. Lowering the air temperatures within the canopy delayed the appearance of all stages over the season compared to the simulations with mean temperatures. Increasing the air temperatures within the canopy, on the other hand, did not significantly influence appearance dates. These results suggest that when air temperature within the canopy is close to standard air temperature appearance dates are delayed, while a high difference between these two temperatures leads to stable simulation results.

The model was sensitive to changes in bark temperature. The appearance of all stages was affected by changes in bark temperatures, irrespective of orchard type. Particularly the development of overwintered larvae and pupae was retarded when lowering the bark temperatures, and accelerated when increasing them. Changes in bark temperatures had a larger effect in standard trees due to higher temperature variations compared to dwarf trees (Kührt et al., 2006b). Changes in apple temperatures significantly affected the appearance dates of the codling moth. These effects, however, were smaller than effects of the other habitat temperatures.

The simulation results clearly demonstrated influences of habitat parameters on the phenology of the codling moth. Plant architecture and the use of hail nets affect the development and, thus, the appearance dates of the different codling moth stages. Simulations showed that the codling moth appeared several days earlier in dwarf trees than in standard trees. The faster development of the codling moth in dwarf trees is due to higher temperatures in the respective habitats during the day (Kührt et al., 2006b). This accelerating effect on development in dwarf trees during daytime was partly counterbalanced by higher air temperatures within the canopy of standard trees at night. Thus, the difference in appearance dates between dwarf and standard trees was smaller than expected when considering measured differences in habitat temperatures. However, the total generation time of codling moth developing on dwarf trees was 2 days longer than of those developing on standard trees. The differences in appearance dates between dwarf and standard trees were higher in the early season than towards the end of the season. Overwintered larvae and pupae developed faster in dwarf trees than in standard trees due to higher habitat temperatures in spring. Later in the season, differences in habitat temperatures between dwarf and standard trees decreased, and air temperatures within the canopies of standard trees fluctuated less than in dwarf trees (Kührt et al., 2006b). This may have led to slightly faster development of codling moth in standard trees later in the season as indicated by the simulation results.

Hail nets retarded codling moth development by several days. This negative effect on development was due to lower habitat temperatures in dwarf trees with nets (Kührt et al., 2006b; Widmer, 1997). This developmental delay was apparent for the larvae and pupae of the overwintered

generation – during the time of the season when hail nets were kept open. The bundled hail nets and poles itself seemed to alter microclimate (Kührt et al., 2006b), and thus developmental rates of the codling moth. Without thermoregulation, hail nets had no effect on the total generation time, and only a small effect when thermoregulation was included.

Thermoregulation behaviour in codling moth had a less pronounced effect on developmental rates than habitat parameters. Simulations revealed accelerated development for eggs when thermoregulation was included. Thermoregulation behaviour in larvae, however, did not seem to accelerate their development. Possibly, the actual temperatures and temperature gradients in fruit were underestimated by the mean values used for calculations of temperatures experienced by the larvae. Therefore, differences in body temperature between temperature-regulating larvae and non-regulating larvae used in our model were probably too small to cause measurable differences in developmental rates. Nevertheless, thermoregulation behaviour had a small, but significant effect on the duration of one generation, decreasing the total generation time by 1 day. Interestingly, the effect of thermoregulation behaviour on development appeared to be greater in standard trees than in dwarf trees possibly due to higher temperature variations within that habitat, e.g. between the north- and south-facing sides of the tree (Kührt et al., 2006b). The larger temperature gradients in standard trees offer the temperature-regulating individuals a wider temperature range to choose from.

The deviations in phenology modelling between habitat and standard air temperatures as well as due to the habitat influences shown here can have a considerable effect on the efficacy and success of codling moth control. Considering aspects of habitat and behaviour will help to improve current phenology models for this and other pest insects.

Acknowledgements

We thank Oliver Mitesser for his help with model development. We are grateful to Silke Hein, Kathrin Tschudi-Rein, the communicating editor and two anonymous referees for valuable comments on previous versions of the paper. This study was supported by a TH research grant (ETH Zurich) to Jörg Samietz and Silvia Dorn.

References

- Baker, C.R.B., 1980. Some problems in using meteorological data to forecast the timing of insect life cycle. *Bull. OEPP/EPPO Bull.* 10, 83–91.
- Baumgärtner, J., Severini, M., 1987. Microclimate and arthropod phenologies: the leaf miner *Phyllonorycter blancardella* F (Lep.) as an example. In: Prodi, F., Rossi, F., Cristofori, G. (Eds.), *Agrometeorology*, vol. 498. Fondazione Cesena Agric. Publ, pp. 225–243.
- Blago, N., Dickler, E., 1990. Effectiveness of the Californian prognosis model “BUGOFF 2” for *Cydia pomonella* L. (Lepidoptera, Tortricidae) under Central European conditions. *Acta Hort.* 276, 53–62.

- Butturini, A., Tiso, R., Berardinis, E.D., 1993. Influence of temperature on the development of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). Boll. Ist. Entomol. "Guido Grandi" Stud. Bologna 47, 123–134.
- Dorn, S., Schumacher, P., Abivardi, C., Meyhöfer, R., 1999. Global and regional pest insects and their antagonists in orchards: spatial dynamics. Agric. Ecosyst. Environ. 73, 111–118.
- Graf, B., Höpli, H., Höhn, H., 2001. Improving the prediction of adult codling moth (*Cydia pomonella* L.) emergence in a natural environment. IOBC/WPRS Bull. 24, 127–132.
- Howell, J.F., Neven, L.G., 2000. Physiological development time and zero development temperature of the codling moth (Lepidoptera: Tortricidae). Environ. Entomol. 29, 766–772.
- Howell, J.F., Schmidt, R.S., 2002. Codling moth (Lepidoptera: Tortricidae): Development at constant and at orchard temperatures. J. Agric. Urban Entomol. 19, 15–23.
- Kührt, U., Samietz, J., Dorn, S., 2005. Thermoregulation behaviour in codling moth larvae. Physiol. Entomol. 30, 54–61.
- Kührt, U., Samietz, J., Dorn, S., 2006a. Thermal response in adult codling moth. Physiol. Entomol. 31, 80–88.
- Kührt, U., Samietz, J., Dorn, S., 2006b. Effect of plant architecture and hail nets on temperature of codling moth habitats in apple orchards. Entomol. Exp. Appl. 118, 245–259.
- Landsberg, J.J., Powell, D.B.B., Butler, D.R., 1973. Microclimate in an apple orchard. J. Appl. Ecol. 10, 881–896.
- Lischke, H., 1992. A model to simulate the population dynamics of the codling moth (*Cydia pomonella*): parameter estimation, validation and sensitivity analysis. Acta Hort. 313, 331–338.
- Lischke, H., Blago, N., 1990. A model to simulate the population dynamics of the codling moth (*Cydia pomonella* L. (Lepidoptera, Tortricidae)): development and male moth flight. Acta Hort. 276, 43–52.
- Pitcairn, M.J., Pickel, C., Falcon, L.A., Zalom, F.G., 1991. Development and survivorship of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) at ten constant temperatures. Pan-Pac. Entomol. 67, 189–194.
- Pitcairn, M.J., Zalom, F.G., Rice, R.E., 1992. Degree-day forecasting of generation time of *Cydia pomonella* (Lepidoptera: Tortricidae) populations in California. Environ. Entomol. 21, 441–446.
- Rock, G.C., Shaffer, P.L., 1983. Development rates of codling moth (Lepidoptera: Olethreutidae) reared on apple at four constant temperatures. Environ. Entomol. 12, 831–834.
- Samietz, J., Salsler, M.A., Dingle, H., 2005. Altitudinal variation in behavioural thermoregulation: local adaptation vs. plasticity in California grasshoppers. J. Evol. Biol. 18, 1087–1096.
- Schoolfield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. J. Theor. Biol. 88, 719–731.
- Schroeder, C.A., 1965. Temperature relationships in fruit tissues under extreme conditions. P. Am. Soc. Hort. Sci. 87, 199–203.
- Thorpe, M.R., 1974. Radiant heating of apples. J. Appl. Ecol. 11, 755–760.
- Widmer, A., 1997. Lichtverhältnisse, Assimilation und Fruchtqualität unter Hagelnetzen. Schweiz. Z. Obst-Weinbau 8, 197–199.
- Williams, D.G., McDonald, G., 1982. The duration and number of immature stages of codling moth *Cydia pomonella* (L.) (Tortricidae: Lepidoptera). J. Aust. Entomol. Soc. 21, 1–4.