

Predicting the phenology of codling moth, *Cydia pomonella*, for sustainable pest management in Swiss apple orchards

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Abstract

The effects of temperature on post-diapause development, female lifespan, and reproduction of *Cydia pomonella* L. (Lepidoptera: Tortricidae) were studied under controlled conditions to determine the respective parameters for a temperature-driven phenology model. Lower thermal thresholds of 10.0 and 9.7 °C and thermal constants of 417.2 and 427.7 degree days were established for post-diapause development of females and males, respectively. Female lifespan was found to be 202.6 degree days on average, with a lower thermal threshold of 11.2 °C. Total fecundity was highest at 27.7 °C with an average of 241.9 eggs per female. Literature data were used to quantify the lower thermal thresholds and the thermal constants for eggs, larvae, and pupae. For validation, the model was run with weather data from 13 consecutive years and the output was compared with pheromone trap catches from 39 to 63 different orchards, depending on the year. The model proved to be a reliable and useful tool to forecast codling moth phenology under Swiss conditions not only for a whole growing season but also during several years with very variable weather conditions. Hence, it can be used to support apple growers in pest management decisions on the one hand and to predict changes in codling moth phenology with respect to climate change on the other.

Introduction

The codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), is a key pest of apple and other pome fruits, causing significant economic damage worldwide (Barnes, 1991). Due to the high potential for yield losses, various control measures have been developed. Currently, in addition to the classical chemical control, alternative methods such as biological control with pathogens (Huber & Dickler, 1977), mating disruption with pheromones (Thomson et al., 2001; Witzgall et al., 2008), or the sterile insect technique (Bloem et al., 2007) are successfully applied. Whatever strategy is chosen, optimal timing of monitoring and control measures is crucial for an efficient and effective control. In recent years, pest forecasting models have been increasingly used to support growers in their management decisions for numerous crops (Chambers et al., 2015; Cormier et al., 2016). In Switzerland, SOPRA (www.sopra.admin.ch), a decision

support system for insect pest management in fruit orchards, was developed in the late 1990s (Graf et al., 2002a) and has constantly been expanded since then to include 10 species to date (Samietz et al., 2008, 2011). The system basically consists of structurally identical phenology models for each species. The models are based on the time-varying distributed delay approach (Manetsch, 1976) and require the thermal thresholds, the thermal constants, and the variability in individual maturation times for each developmental stage, as well as the age-specific reproduction rate of adult females as biological parameters (Severini et al., 2003).

In this study, we established the above-mentioned model parameters for the post-diapause development as well as the adult lifespan and reproduction of the codling moth based on experiments under controlled conditions in climate chambers and in the greenhouse. The parameters for egg, larval, and pupal development were estimated from literature data (Glenn, 1922; Sokolowski et al., 1978; Williams & McDonald, 1982; Rock & Shaffer, 1983). For validation, the parametrized model was subsequently run with weather data from 13 consecutive years, from 2003 to

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2015, and the model predictions on the phenology of moth flight of the overwintering (first) and the summer (second) generations were compared with corresponding pheromone trap catches from 39 to 63 different sites, depending on the year.

Materials and methods

Post-diapause development

The effect of temperature on the post-diapause development of *C. pomonella* was studied on a total of 4 721 individuals in climate chambers at six constant temperatures: 12.7, 15.1, 17.6, 19.9, 22.4, and 25.1 °C. Fifth instars were collected from a natural codling moth population on untreated high-stem apple trees at two sites in the upper Rhine Valley in Switzerland (47°11'N, 9°27'E, 460 m above sea level, and 46°59'N, 9°33'E, 560 m asl). At the end of July, just before the beginning of diapause, corrugated cardboard bands were wrapped tightly around the stems of infested trees to attract larvae in search of hibernation sites. The bands were protected with an additional layer of jute against bird predation. A month later, at the end of August, the bands were removed and opened, and the larvae were put in plastic jars filled with recoiled corrugated cardboard strips as hibernation shelter. They were stored in field conditions in an insectary until the end of January. From the beginning of February to the end of March, they were relocated to a climate chamber at 1 °C in order to maintain the dormancy (Geier, 1963b). Five days before the exposure to the experimental conditions, temperature was increased gradually to 10 °C to allow for gentle adaptation.

At the beginning of April, the 4 721 diapausing larvae were split into six more or less equal groups and exposed to the experimental temperatures in climate chambers: 621 at 12.7 °C, 769 at 15.1 °C, 817 at 17.6 °C, 874 at 19.9 °C, 880 at 22.4 °C, and 760 at 25.1 °C (Table 1). In daily observations, hatching of adult moths and their sex were recorded. To assure undisturbed development,

hibernation cocoons were not opened and, hence, pupation could not be observed.

At each temperature, the mean duration of post-diapause development was established for females and males. For all individuals, the developmental rates were determined as the reciprocal values of the developmental times, and two separate linear regression models were applied to describe the effect of temperature on the post-diapause development of females and males, respectively. Based on these regressions, the thermal constants (i.e., the reciprocal value of the regression slope or the average developmental time in degree days), the lower thermal thresholds (i.e., the x-intercept of the regression), and the corresponding standard errors were computed according to Campbell et al. (1974).

Adult lifespan and reproduction

The effect of temperature on the lifespan and reproduction of *C. pomonella* females was studied in two experiments, one in the greenhouse at temperatures fluctuating between 15 and 29 °C, and one in climate chambers at four constant temperatures: 15.9, 19.1, 24.6, and 27.7 °C. Mean lifespan and reproductive performance were established with 178 and 142 females, respectively (Table 2).

In the greenhouse, 30 females and 30 males originating from the experiment on post-diapause development (17.6, 19.9, and 22.4 °C treatment) were kept in pairs from the first day of the adult stage until the natural death of the female in 30 gauze cages measuring 15 × 15 × 25 cm³. Each pair was offered water and a 10% (wt/vol) sugar solution in soaked cotton wool, and, for oviposition, a daily supply of one new immature 3- to 4-cm-diameter apple and a fresh apple leaf from an untreated orchard. The greenhouse was ventilated, and temperature corresponded approximately to field conditions, fluctuating in a daily rhythm around an overall average of 22 °C, with a minimum of 15 °C and a maximum of 29 °C. The light regime followed natural day length during the experimental period from the end of May to the end of July (minimum

Table 1 Number of observations, sex ratio (females/males), mortality (%), and mean (\pm SD) duration (days) of post-diapause development of *Cydia pomonella* at various constant temperatures

Temperature (°C)	Diapausing larvae	Living adults	Sex ratio (♀:♂)	Mortality (%)	Duration (days)	
					Females	Males
12.7	621	471	1.22	24.2	129.8 \pm 17.4	124.1 \pm 15.5
15.1	769	634	1.22	17.5	80.7 \pm 11.8	79.1 \pm 11.7
17.6	817	669	1.19	18.2	60.9 \pm 12.8	58.1 \pm 9.4
19.9	874	701	1.16	19.8	46.5 \pm 9.8	44.5 \pm 9.7
22.4	880	698	1.18	20.7	37.0 \pm 10.1	37.1 \pm 9.3
25.1	760	652	1.29	14.2	29.1 \pm 8.7	29.0 \pm 8.2

Table 2 Effect of temperature on mean (\pm SD) female lifespan (days) and fecundity (no. eggs per female) of *Cydia pomonella*

Temperature (°C)	Female lifespan		Total fecundity	
	n	No. days	n	No. eggs/female
Constant				
15.9	38	47.1 \pm 11.7	29	200.7 \pm 20.6bc
19.1	36	28.0 \pm 7.8	28	214.3 \pm 30.3b
24.6	35	17.4 \pm 6.6	27	161.8 \pm 24.2d
27.7	40	13.0 \pm 3.0	29	241.9 \pm 37.4a
Fluctuating				
15–29 (mean 22.0)	29	21.9 \pm 5.8	29	186.7 \pm 28.1c

Means followed by different letters differ significantly (Scheffé's test: $P < 0.01$).

L15.3:D8.7, maximum L15.5:D8.5). Relative humidity was maintained constant at 75% with an air humidifier.

In the climate chambers, 120 pairs of simultaneously emerged females and males were confined in groups of three pairs in cages identical to those used in the greenhouse. They were exposed to four constant temperatures in 10 cages (i.e., 30 pairs) at 15.9, 19.1, 24.6, and 27.7 °C, respectively. Photoperiod was L16:D8 and relative humidity was kept constant at 75% at all temperatures. Water and sugar solution were provided, as in the greenhouse, but the three females in each cage received three immature apples and three apple leaves for oviposition per day.

In both the greenhouse and the climate chambers, the apples and leaves were replaced at 24-h intervals and examined for eggs under the binocular microscope. Individual egg-laying performance was observed in the greenhouse, but in the climate chambers, the number of eggs had to be averaged because three females were laying their eggs in the same cage. Dead males were substituted with newly emerged ones so that females had mating partners available for the entire lifespan. The date of death and longevity were recorded for both females and males, but only female data were used for further analysis. In the climate chambers, nine additional couples (15 at 27.7 °C) were kept in separate cages for extra observations of longevity. Though apples and leaves were offered for oviposition, eggs were not counted, in order to limit labor input.

Individual data on female lifespan were subjected to the Grubbs test ($\alpha = 0.05$) to identify and exclude outliers (Grubbs, 1969). The remaining data were then transformed to aging rates by taking the reciprocal values, and a linear regression model was applied to describe the effect of temperature on female aging. The statistical approach suggested by Campbell et al. (1974) was subsequently used to compute the lower thermal threshold, the thermal constant, and the corresponding standard errors for female

aging in the same way as it was done for the post-diapause development (see above).

Total fecundity of females at the various temperatures was compared with Scheffé's multiple contrasts test (Zar, 1974) to reveal a possible effect of temperature on reproductive potential. Non-linear regression statistics were applied to describe age-specific cumulative fecundity. The data from the greenhouse and the climate chambers were pooled after transforming the egg-laying performance from absolute to relative values (% of the maximum value) and applying a physiological time scale, that is, degree days above the thermal threshold established for female aging (see above). A modified Weibull function was fitted to the pooled data using the XLSTAT 2015 software package (v.2015.1.02; Addinsoft, Brooklyn, NY, USA), as follows:

$$F(x) = 100 \cdot \{1 - \exp[-c_1 \cdot (x - 20)^{c_2}]\} \text{ for } x \geq 20, \quad (1)$$

where F is the cumulative relative fecundity rate, x is the age of females in physiological time units (degree days) and c_1 and c_2 are the estimated parameters.

Egg, larval, and pupal development

Literature data were used to establish the model parameters for the preimaginal stages. Glenn (1922) provided a comprehensive dataset on the effect of temperature on the development of eggs, larvae, and pupae, which was suitable for parameter estimation. His data were supplemented with experimental results from Sokolowski et al. (1978) on egg development, and from Williams & McDonald (1982) and Rock & Shaffer (1983) on larval development. Developmental times at different temperatures were transformed to developmental rates (reciprocal values of the developmental times), and three separate linear regressions were applied to describe the effect of temperature on egg, larval, and pupal development, respectively, in the same way as it was done for post-diapause development and female aging (see above). Again, Campbell et al.'s (1974) approach was used to compute the lower thermal threshold, the thermal constant, and the corresponding standard errors.

Modeling phenology

Time-varying distributed delay models (Manetsch, 1976) were applied to simulate the transition of individuals through the consecutive developmental stages. The underlying mathematical principles and the internal structure of this approach and its implementation to describe insect phenologies have been reviewed in detail by Severini et al. (1990) and Gutierrez (1996). It has already been used successfully to forecast the phenology of various fruit pests such as codling moth and Oriental fruit moth, *Grapholita molesta* Busck (Welch et al., 1978; Croft & Knight, 1983),

summer fruit tortrix, *Adoxophyes orana* F. v. R. (Baumgärtner & Charmillot, 1983), rosy apple aphid, *Dysaphis plantaginea* Pass. (Graf et al., 1985, 2006), apple sawfly, *Hoplocampa testudinea* Klug (Graf et al., 1996, 2001a, 2002b), smaller fruit tortrix, *Grapholita lobarzewskii* Nowicki (Graf et al., 1999, 2015, 2016), pear psylla, *Cacopsylla pyri* L. (Schaub et al., 2005), apple blossom weevil, *Anthonomus pomorum* L., and cherry fruit fly, *Rhagoletis cerasi* L. (Samietz et al., 2008).

The driving variables of the model are hourly values of air temperature and solar radiation, where the latter is employed to emulate the temperature in the hibernation habitat (Graf et al., 2001b; Samietz et al., 2011). The temperatures are used to compute the instantaneous developmental and reproduction rates in each stage based on the specific regressions described above. An algorithm originally developed by Abkin & Wolf (1976) was adapted to compute the process of aging within the various developmental stages and to continuously keep track of the age structure of the population. For each hour from January 1 until December 31, the model predicts the relative abundance of the various developmental stages – that is, hibernating larvae/pupae, adults of the overwintering generation, eggs, larvae, pupae, and adults of the first and eventually of the second-generation or diapausing larvae. The code was written in Object Pascal with Delphi 6 (Borland, Cupertino, CA, USA, 2001).

Model validation

For validation, the model was run with weather data from 13 consecutive years (2003–2015) recorded at the meteorological station of MeteoSwiss (Swiss Federal Office of Meteorology and Climatology) in Wädenswil, Switzerland. The resulting model predictions on relative moth abundance were compared with pheromone trap catches in the corresponding years at 39–63 sites with comparable climatic conditions (Schweizerische Meteorologische Anstalt, 2000). The quality of the predictions was assessed by visual comparison of simulated and observed moth abundance on the one hand, and by computing the coefficients of determination (r^2) of the linear regressions between predicted and observed values on the other. Two exceptionally warm, two average, and two cold years were chosen for graphic presentation and for discussion of the effect of climate change on the population dynamics of codling moth.

Results

Post-diapause development

Post-diapause development was monitored with a total of 4 721 individuals at 12.7, 15.1, 17.6, 19.9, 22.4, and

25.1 °C (Table 1). At all temperatures, females outnumbered males, the female-to-male ratio being 1.21 on average. Overall mortality was 19.0%, varying between 14.2% at 25.1 °C and 24.2% at 12.7 °C. Though mortality was highest at the lowest temperature and lowest at the highest temperature, distinct temperature dependence was not observed. However, at all temperatures, mortality decreased with progressing development: 17% of the initial population died in the larval stage, whereas only 1.9 and 0.1% died as pupae or adults, respectively. Temperature had a significant effect on the duration of post-diapause development (Table 1). At 12.7 °C, females needed on average 129.8 days to reach the adult stage, whereas at 25.1 °C the same developmental step took just 29.1 days. Generally, males developed slightly faster than females; however, the difference became obvious only at temperatures below 20 °C (Table 1). Linear regressions appear to adequately describe the effect of temperature on post-diapause developmental rates of both females and males within the temperature range under study, the r^2 -values being 0.68 and 0.69 for females and males, respectively (Figure 1, Table 3). Based on these regressions, lower thermal thresholds of 10.0 and 9.7 °C and thermal constants of 417.2 and 427.7 degree days were computed for the post-diapause development of females and males, respectively.

Adult lifespan and reproduction

Female lifespan and reproduction were studied on 178 and 142 individuals, respectively, at four constant temperatures: 15.9, 19.1, 24.6, and 27.7 °C, and at temperatures

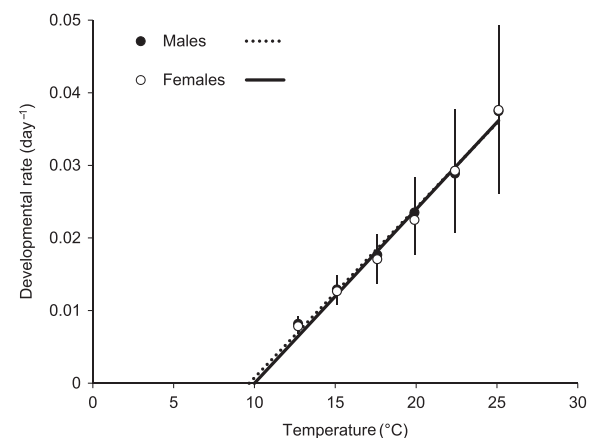


Figure 1 Temperature effects on mean (\pm SD) post-diapause development rates (per day) of *Cydia pomonella* females and males (for parameters, see Table 3).

Table 3 Linear regression statistics for the temperature effects on female and male post-diapause development, female aging, and egg, larval, and pupal development of *Cydia pomonella*: regression coefficients, thermal constant (K, degree days), and lower thermal threshold (THR, °C) with corresponding standard errors (SE_K and SE_{THR})

Stage	Slope	Intercept	r ²	K ± SE _K (degree days)	THR ± SE _{THR} (°C)	Source
Female post-diapause development	0.002397	−0.02397	0.68	417.2 ± 6.3	10.0 ± 0.2	This study
Male post-diapause development	0.002338	−0.02260	0.69	427.7 ± 6.9	9.7 ± 0.2	This study
Female aging	0.004935	−0.05531	0.62	202.6 ± 13.1	11.2 ± 0.7	This study
Egg development	0.012699	−0.13686	0.93	78.7 ± 6.0	10.8 ± 1.2	Glenn 1922, Sokolowski et al. 1978
Larval development	0.002661	−0.02744	0.62	375.8 ± 82.1	10.3 ± 2.7	Glenn 1922, Williams & McDonald 1982, Rock & Shaffer 1983
Pupal development	0.006257	−0.05783	0.99	159.8 ± 5.6	9.2 ± 1.1	Glenn 1922

fluctuating between 15 and 29 °C (mean 22.0 °C) (Figure 2). Average lifespan decreased with increasing temperature, from 47.1 days at 15.9 °C to 13.0 days at 27.7 °C (Table 2). Total fecundity varied between 241.9 eggs per female at 27.7 °C and 161.8 eggs per female at 24.6 °C. Although the reproductive performance differed significantly between temperatures, no consistent trend could be observed with respect to the effect of temperature on total fecundity within the temperature range under study (Table 2). However, the temporal pattern of oviposition appeared to be affected: the higher the temperature, the higher and earlier the peak and the shorter the reproductive period (Figure 2). At 27.7 °C, females laid on average 37.4 eggs per day on day 4 of adult life and the last surviving individuals ceased reproducing after 26 days. At 15.9 °C, the peak of 10 eggs per day was reached only after 16 days, and reproduction of the oldest females lasted 64 days.

A linear regression adequately described the effect of temperature on female aging rates within the temperature range under study ($r^2 = 0.62$; Figure 3, Table 3). Based on this regression, a lower thermal threshold of 11.2 °C and a thermal constant of 202.6 degree days were calculated for the development of adult females.

Age-specific reproduction was generalized for all temperature conditions using relative oviposition rates and a physiological time scale based on the thermal threshold for females. On average, a female laid 50% of the eggs within the first 93 degree days and 95% within 265 degree days of the adult life (Figure 4). The modified Weibull function (equation 1) allowed an accurate mathematical description of the relationship between female age and relative cumulative fecundity ($r^2 = 0.97$; Figure 4).

Egg, larval, and pupal development

Temperature-dependent life table statistics for the immature developmental stages were derived from data published by Glenn (1922), Sokolowski et al. (1978), Williams & McDonald (1982), and Rock & Shaffer (1983). Again, linear regressions described the effect of temperature on egg, larval, and pupal developmental rates in a satisfactory manner, with r^2 -values of 0.93, 0.62, and 0.99, respectively (Table 3). For the egg stage, a thermal threshold of 10.8 °C and a thermal constant of 78.7 degree days were established. The corresponding values for the larval stage were 10.3 °C and 375.8 degree days, and for the pupal stage, 9.2 °C and 159.8 degree days (Table 3).

Model predictions and validation

Driven with weather data from 2003 to 2015, the phenology model predicted the relative abundance of the consecutive developmental stages of the codling moth, beginning with diapausing larvae/pupae and proceeding with adults of the spring generation, eggs, larvae, diapausing larvae or pupae, and adults of the summer generation and their progeny for the corresponding years. For validation, the predicted abundance of spring and summer generation adults were compared with pheromone trap catches from 39 to 63 orchards with comparable climatic conditions. Generally, model predictions fit well with the observations, with r^2 -values usually exceeding 0.50 (Table 4). Onset and end of moth flight of both spring and summer generations were well reproduced (Figure 5). Yet, the predicted peaks seemed to be slightly delayed as compared to the observations. The model also proved to capture the effect of exceptional temperature conditions. Up to now, in most apple-growing regions of Switzerland the codling moth

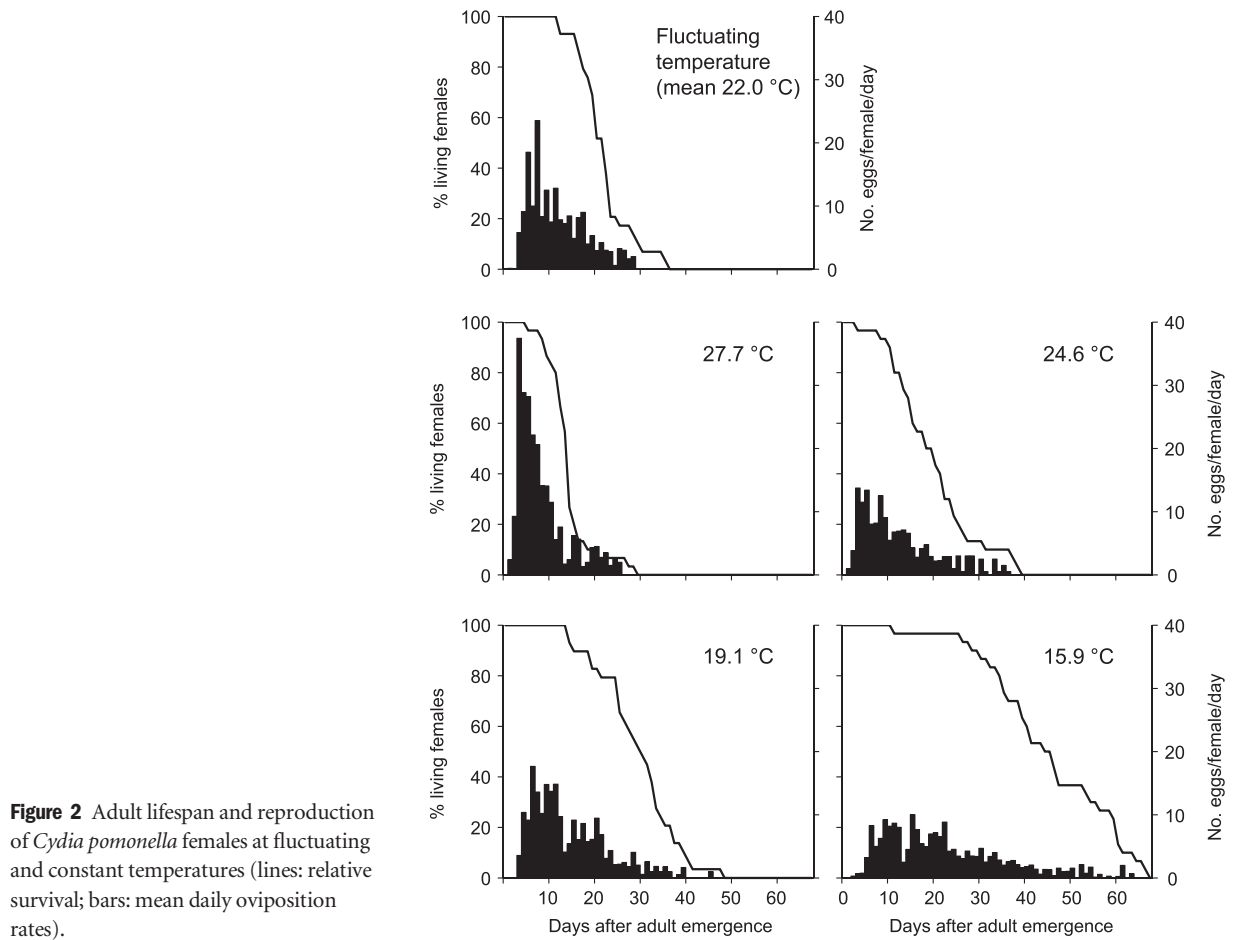


Figure 2 Adult lifespan and reproduction of *Cydia pomonella* females at fluctuating and constant temperatures (lines: relative survival; bars: mean daily oviposition rates).

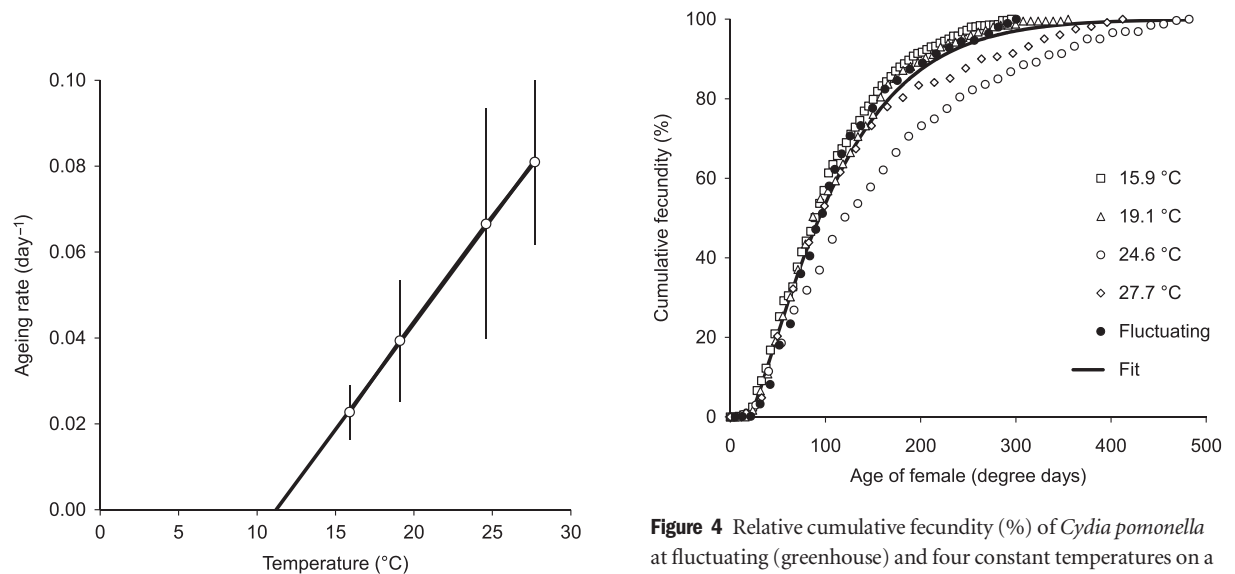


Figure 3 Temperature effects on mean (\pm SD) female aging rates (per day) of *Cydia pomonella* (for parameters, see Table 3).

Figure 4 Relative cumulative fecundity (%) of *Cydia pomonella* at fluctuating (greenhouse) and four constant temperatures on a physiological time scale (degree days above 11.2 °C; see Table 3) and global fit with a modified Weibull model (see equation 1: $c_1 = 0.003786 \pm 0.000537$, $c_2 = 1.2135 \pm 0.03$; $r^2 = 0.97$).

Table 4 Number of observation sites with pheromone traps (n) and coefficients of determination (r^2) for the linear regressions between predicted and observed *Cydia pomonella* populations for the period from 2003 to 2015

Year	n	r^2
2003 ¹	44	0.598
2004 ¹	44	0.489
2005	40	0.580
2006 ¹	50	0.627
2007	50	0.157
2008	50	0.567
2009	50	0.470
2010	63	0.577
2011 ¹	43	0.686
2012 ¹	40	0.677
2013	39	0.500
2014	43	0.625
2015 ¹	40	0.504

¹Years shown in Figure 5.

spring generation has been significantly more important than the summer generation in most years. In 2011 or 2012, 2 years with medium spring temperatures (15.3 °C from April to July), the model predicted a ratio between the spring and summer generation of roughly 4:1. In 2003 and 2015, two extraordinarily warm years (16.5 °C from April to July), the model forecasted similar peaks for both generations, whereas in 2004 and 2006, two rather cold years (14.2 °C from April to July), the summer generation was practically non-existent. These model predictions are confirmed with pheromone trap catches in the corresponding years (Figure 5).

Discussion

Only very few studies have been conducted on the effect of temperature on post-diapause development of codling moth. In a comprehensive study, Shelford (1927) investigated the response of codling moth to weather and climate in Illinois (USA) based on his

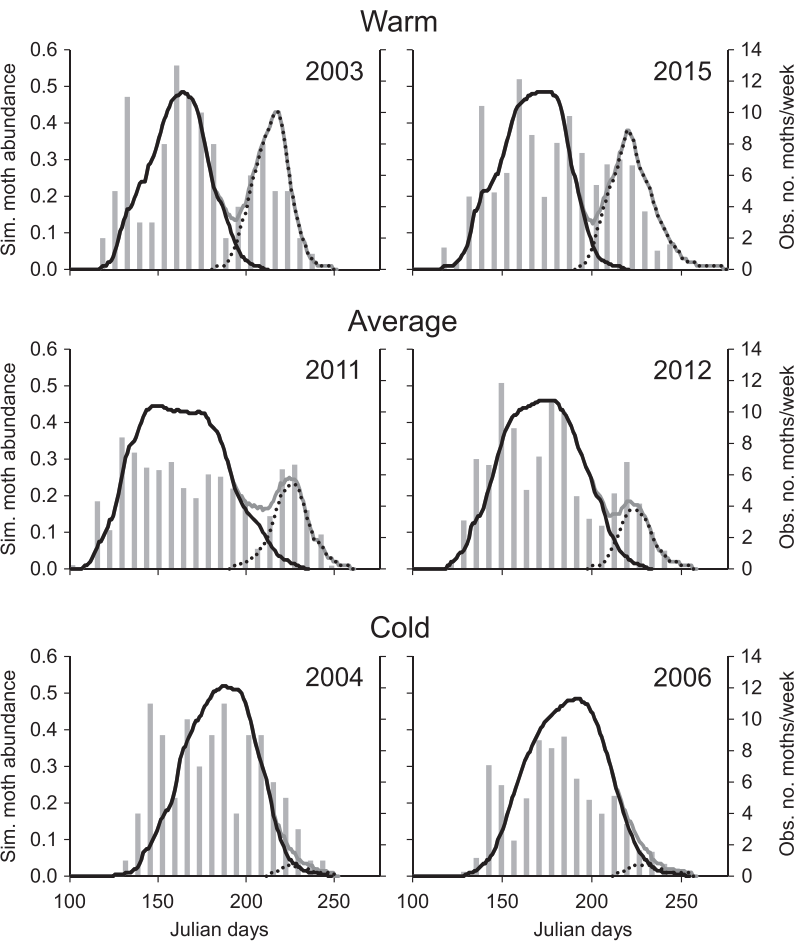


Figure 5 Model predictions (sim.) on relative abundance of first (solid line) and second (dotted line) generation of *Cydia pomonella* compared with pheromone trap catches (obs.; gray bars) in two warm years (2003 and 2015, average temperature April–July: 16.5 °C), two average years (2011 and 2012, April–July: 15.3 °C), and two cold years (2004 and 2006, April–July: 14.2 °C).

own and Glenn's (1922) data. From his findings, a lower thermal threshold of 10.5 °C and a thermal constant of 320 degree days can be derived for post-diapause development. Considering the large geographical distance between the examined populations, these values compare fairly well with the parameters found in the present study (10.0 °C and 420 degree days).

The longevity and fecundity of codling moth females are better investigated. The mean female lifespan of roughly 200 degree days established in this study lies within the range of outcomes reported in the literature (Geier, 1963a; Geier & Briese, 1978; Howell, 1981; Vickers, 1997; Jones & Wiman, 2008; Wenninger & Landolt, 2011). With a total of 160–240 eggs per female, the fecundity we observed is close to the 100–280 reported by Wenninger & Landolt (2011), but roughly twice as high as the values published in other studies (Geier, 1963a; Geier & Briese, 1978; Howell, 1981; Vickers, 1997; Mansour, 2007; Jones & Wiman, 2008; Aghdam et al., 2011). Based on Wiesmann's (1935) observation that newly emerged females usually contain 150–200 discernible oocytes, we assume that the rearing conditions in our experiments were close to optimal and females fully exploited the intrinsic potential.

In this study, we estimated the developmental parameters for eggs, larvae, and pupae based on literature data (Glenn, 1922; Sokolowski et al., 1978; Williams & McDonald, 1982; Rock & Shaffer, 1983). For the embryonic development, we calculated a lower thermal threshold of 10.8 °C and a thermal constant (average developmental time) of 79 degree days. Both values are in close agreement with the more recently published results of Howell & Neven (2000), Aghdam et al. (2009), and Blomefield & Giliomee (2009). For larval development, we found the same thermal threshold as Howell & Neven (2000) – i.e., 10.3 °C – but Aghdam et al. (2009) and Blomefield & Giliomee (2009) estimated lower thresholds of 8.9 and 7.9 °C, respectively. The thermal threshold of 9.2 °C for pupal development is again in the range of 9.2 to 10.7 °C established by these studies. Our estimation of 376 degree days as the thermal constant for larvae is slightly higher than those by Howell & Neven (2000), Aghdam et al. (2009), and Blomefield & Giliomee (2009). On the other hand, our thermal constant of 160 degree days for pupal development is lower than the values in the above-mentioned studies. However, the thermal constant of roughly 600 degree days for the whole immature development (egg, larva, and pupa) is the same in all studies.

The validation showed good agreement of model predictions on the relative abundance of first- and second-

generation moths compared with pheromone trap catches. Aside from one exception (2007), the r^2 -values were generally within the range of 0.5 to 0.7, although relative abundance (model prediction) was compared with flight activity (pheromone trap catches), which can be significantly hampered by short-term weather effects such as low evening temperatures or precipitation. In fact, the poorest fit was achieved in 2007, the year with the most rainfall in the summer months (165% of long-term average).

In the model we chose linear regressions to describe the effect of temperature on developmental rates for all stages. It is known that with most arthropods this relationship is non-linear in the low and in the high temperature range. Therefore, many authors (e.g., Logan et al., 1976; Sharpe & DeMichele, 1977; Régnière & Powell, 2013) suggested more realistic non-linear models. However, for the sake of simplicity and because we got satisfactory phenological predictions we opted for the linear approach.

Conclusion

The temperature-driven phenology model we designed, predicts the relative abundance of all development stages of the spring and summer generations of the codling moth, beginning with hibernating larvae. Integrated in SOPRA, a web-based decision support system, the model can be used by fruit growers and farm advisors for decision support in codling moth control in general and for the timing of monitoring and control measures in particular. The validation over a 13-year period indicated not only the model's usefulness for sustainable codling moth management but also its capacity to predict phenological changes as a consequence of global warming. Currently, the summer generation is of minor importance in Switzerland, but with increasing temperatures it will become more important, and codling moth control strategies will have to be adapted accordingly (Samietz et al., 2015).

To date the model stood the test under Swiss conditions. However, its general structure would allow an application in other apple-growing regions as well. Yet, thorough local verification would be needed to further expand the geographical range of validity.

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