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Insights into *Cydia pomonella* adaptability to different climatic conditions: voltinism characteristics and suitability of phenological models for flight predictions

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Abstract

The codling moth (*C. pomonella*) is a notorious pest of apples, pears and other pome fruits, causing significant economic damage during outbreaks. This study investigated the voltinism of codling moth across various climatic conditions at three distinct Moroccan apple orchards; two in the Atlas Mountains and one in the plain. Our objective was to assess the voltinism of the pest and to analyze its evolution in relation with the temperature factor through different locations. We employed phenological models to predict insect generation patterns and the onset of adult flights, and compared predictions with observed data obtained from trap catches. At all study sites, a single generation required an average accumulation of 549 DD close to some models assumptions. The study also highlighted the significant impact of temperature on the insect's voltinism and indicated that a warmer climate could lead to an additional generation. In the mountainous regions, the pest typically occurs on three generations, with a potential fourth one if the growing season exceeds 2000 DD. In the plain, the moth completes four generations. Furthermore, the advent of flights varied among locations, highlighting the need to account for the synchrony between insect emergence and host tree phenological stages when predicting the onset of moth activity. Finally, the study suggests that different models should be used in Morocco to predict moth flights accurately as observed data were consistently aligning with specific models at each location.

Key Words

Cydia pomonella, degree days, phenological models, temperature, voltinism

Introduction

The codling moth, *C. pomonella* (L.) (Lepidoptera: Tortricidae), is one of the most devastating pests affecting pome tree fruits globally (Barnes 1991). Primarily targeting apples, along with pears and walnuts, this pest induces severe damage with economic losses predominantly attributed to larval feeding on both fruit seeds and flesh (Du et al. 2012). Infestation rates of *C. pomonella* typically exceed 50%, and might reach up to 90% in unprotected apple orchards (Brunner et al. 1982; Shao et al. 2014).

C. pomonella is an ectothermic organism profoundly influenced by temperature fluctuations, with significant implications on its life cycle (Deutsch et al. 2008). As temperatures rise, insect development rates generally increase, potentially leading to shortened life cycles and increased population growth rates. Moreover, temperature changes can disrupt voltinism patterns, which are crucial for understanding the moth's life cycle and implementing effective integrated pest management strategies (Rosenzweig et al. 2001; Trnka et al. 2007; Stoeckli et al. 2012).

The voltinism of *C. pomonella* varies among regions due to differences in temperature, photoperiod, and food availability (Stoeckli et al. 2012; El Iraqui and Hmimina 2016). These factors play a crucial role in regulating developmental rates and diapause induction. Diapause, a fundamental physiological mechanism in the codling moth's life cycle, results from the complex interaction between temperature and photoperiod. Photoperiod acts as a major environmental cue, triggering diapause when day length decreases and thus limiting the number of generations in temperate regions. Laboratory experiments by Setyobudi (1989) demonstrated that diapause induction is higher under fluctuating temperatures than under constant ones. Similarly, El Iraqui and Hmimina (2016) reported that, under Moroccan conditions, the high temperatures prevailing during the period conducive to diapause (July to early August) delay its induction. Consequently, in regions where summer temperatures remain high and photoperiodic variations are less pronounced, temperature becomes the dominant factor influencing voltinism (El Iraqui and Hmimina 2016). For instance, southeastern France typically observes two complete generations and a partial third one, whereas Croatia experiences two generations annually, with the second often being partial due to diapause induction (Boivin et al. 2003). In contrast, Morocco usually witnesses three generations annually, with a potential fourth emerging during periods of high spring temperatures (El Iraqui and Hmimina 2016). Similarly, northeastern China displays a two-generation life cycle of *C. pomonella* and is considered highly invasive in this region (Wan and Yang 2016; Fang et al. 2018). In North American production areas, reports suggest the occurrence of more than two generations per year (Jones et al. 2013). In Central Italy, Piskorski et al. (2010) reported that *C. pomonella* populations can complete two to three generations within the same region, depending on the host plant.

Despite the development and adoption of various sustainable control methods, such as biological control, mating disruption, and the sterile insect technique, pesticide reliance remains prevalent for codling moth management (Damos 2015), and these applications lead to numerous issues such as insecticide resistance along with adverse environmental and health impacts (Damalas and Eleftherohorinos 2011). Effective management of *C. pomonella* is based on appropriate treatment interventions during the optimal stage of pest development (Knight 2000; Knight and Light 2005). However, while using pheromone traps as a monitoring method, their predictive accuracy is hindered by various environmental factors (such as initial pest status, rain and wind), making them less optimal for forecasting species phenology and establishing IPM programs (Knight and Light 2005). Moreover, spatial heterogeneity in pest distribution within and among orchards further complicates management decisions, with studies showing that codling moth populations exhibit clumped distributions influenced by landscape structure, host plant availability, and dispersal patterns (Trematerra and Sciarretta 2017).

Consequently, phenological models driven by degree days accumulation have emerged as valuable tools for pest management and to support the reliability of sexual traps particularly in apple-producing regions (Riedl et al. 1976; Brunner et al. 1982; Knight 2007; Jones et al. 2013). These models have been globally deployed by researchers to forecast critical stages of the pest life cycle, including egg hatch, pupae development, and adult emergence, thereby enabling effective treatment scheduling (Tomkins et al. 1987; Blago 1992; Ahmad et al. 1995; Knight 2007; Samietz et al. 2007; Jones et al. 2008; Barros-Parada et al. 2015). It has been noted that models developed and validated in California, Italy, and Portugal are routinely utilized by regional agricultural extension services for crop protection (Welch et al. 1978; Pitcairn et al. 1992; Bugiani et al. 1996; Rosa 2000). Furthermore, in Michigan, a newly developed model for *C. pomonella* emergence has been successfully applied for field forecasting (Chappell et al. 2014). Degree day models have also been instrumental in predicting the potential impact of global warming on the dynamics and phenology of *C. pomonella* in future scenarios (Schneider et al. 2023; Jha et al. 2024).

To contribute to environmentally friendly management practices for *C. pomonella* in Moroccan orchards, our study aims to comprehensively understand the pest voltinism across three distinct localities. This involved illustrating the current situation and adaptability of the pest in contrasted climatic conditions in Morocco and gaining insight into its evolution over an extended period of 10 years (2009–2018). Furthermore, we sought to elucidate the significant temperature impact on both the number and duration of generations in each region. Furthermore, we assessed the applicability and consistency of four published models in predicting the phenology of *C. pomonella*, particularly targeting the first second and third emergences, as their accurate determination ensures successful control of the pest. By comparing predictions with observed adult flight activity obtained from male captures, we aimed to demonstrate the reliability of these phenological tools in improving pest forecasts which would help enhancing an efficient monitoring and management of the pest in Moroccan orchards.

Materials and methods

Studied sites

Field observations were conducted in three stations representing distinct climatic conditions (Table 1, Fig. 1). The classification of these sites was based on differences in elevation and seasonal temperature patterns, which influence local climate characteristics such as winter severity and summer dryness. Meteorological data were obtained from INRA's FieldClimate database (https://www.fieldclimate.com). Data were collected in Azrou (Station 1) from 2009 to 2018, in Laanoceur (Station 2) during 2021–2022, and in Ain Taoujdate (Station 3) during 2022–2023. All orchards were part of the experimental

Table 1. Climatic characteristics of the studied stations.

Studied Sites	Region	Location	Elevation m asl	Whether characteristics	Max T°C	Min T°C
Station 1	Middle Atlas Mountains	33°43'00"N, 5°22'00"W	1295	cold winters and dry summers	35 °C	-3 °C
Station 2	Middle Atlas Mountains	33°41'03"N, 4°51'11"W	1350	cold winters and dry summers	40 °C	-7 °C
Station 3	Saïss Plain	33°55'59"N, 5°12'60"W	500	dry summers and cool winters	37 °C	2.8 °C

Figure 1. Experimental orchards of the survey locations. https://earth.google.com/web (Accessed on 07 February 2024).

stations of the National Institute of Agricultural Research (INRA) and are located in major apple-producing regions of Morocco, where apple is the dominant crop, ensuring a uniform host-plant environment; surrounding crops do not serve as hosts for *C. pomonella*. Phytosanitary practices were properly managed, and conventional control strategies were applied throughout the study period.

Insect monitoring and generation delimitation

Based on trap catches

In each experimental apple orchard, the monitoring of *C. pomonella* flight was studied using pheromone traps, the most commonly used survey method for *C. pomonella*. Four Delta traps (Univers Horticole) were placed in station 1, from mid-April until mid-September, during the period 2009–2018. In the station 2, during the period 2021–2022, seven traps were installed from April 1st until the harvest and four ones were installed from March 1st until the harvest in station 3. Traps were positioned in each orchard at a minimum distance of 50 m from each other, maintaining a space of about 10 m from the borders. Hung on the trees at human height, the sexual traps were equipped with a sticky plate and a pheromonal capsule (rubber septa loaded with 43.48 g/kg (E,E)-8,10-dodecadien-1-ol, Univers Horticole). According to the manufacturer, the dispensers remain active for 4 to 6 weeks under field conditions and were replaced accordingly. The sticky boards were replaced based on the amount of impurities deposited on them. The survey of the trap catches was conducted twice per week. In the context of this study, treatments were suspended. The delimitation of generations was based on male flight activity recorded by pheromone traps at each station overall the growing seasons. *C. pomonella* adults that emerged from overwintering larvae constituted the first flight. The start of this flight was determined by the first moth catches in early spring. The second flight corresponded to the emergence of adults from the first generation, and the third flight consisted of adults issue from the second generation. The start of these subsequent flights was assumed when moth catches began to rise consistently following a period with few or no catches. Hence, the period between the start of each flight and the start of the subsequent flight was considered as the generation time (Milonas and Savopoulou-Soultani 2006; Damos and Savopoulou-Soultani 2010). Given the phytosanitary management protocol adopted throughout the study period and the predominance of apple as the main host plant, any external captures from surrounding sites are expected to be minimal and therefore do not affect the estimation of flight onset.

Based on degree days (DD) accumulation

Data on temperature were collected from Azrou, Lannoceur, and Ain Taoujdate climatological stations, and degree days were accumulated from January the 1st of each year across the three stations. In this study, we employed the single sine curve method with horizontal cut-off to calculate degree days. This method assumes that temperatures above a defined upper threshold do not contribute to degree days accumulation, and insect development occurs at a constant rate when the daily temperature exceeds the upper threshold and does not increase or stop above this threshold (Beasley and Adams 1996). The horizontal cutoff method has been widely recommended and used for degree days estimation globally (Allen 1976; Pruess 1983; Zalom et al. 1983). Degree days were calculated based on daily records of both minimum and maximum temperatures, using lower and upper temperature thresholds of 10.0 and 31.1 °C, respectively.

Prediction of generations

For each station and across all growing seasons, we explored four published phenological models to predict insect generation patterns, particularly focusing on their duration, and the onset of the first, second and third flights. These forecasts were then compared with observed generations determined from trap catches. We compared the degree days required for the development of a single generation in Moroccan conditions with the values of "556 DD" as suggested by Riedl et al. (1976) [Model 1] and "619 DD" following the model proposed by Pitcairn et al. (1992) [Model 2]. Forecasts for the onset of the first, second and third flights were established using two models: one outlined by Damos et al. (2018) [Model 3], which suggests the occurrence from the 1st January, of the first emergence, the second flight and the third flight at 250–300 DD, 850–900 DD and 1500 DD respectively. In contrast, the model by Juszczak et al. (2013) [Model 4] estimates the first emergence at 110 DD, the second flight at 650 DD, and the third flight at 1190 DD, all starting from January 1st.

Statistical analysis

Data were processed with SPSS software to analyze the effect of temperature on pest number of generations. The correlation between annual accumulated degree days and the number of generations in each year across all stations was determined by the Pearson correlation coefficient.

Results

Flight patterns of *C. pomonella* based on trap captures and comparison of observerd generations with theoretical ones

Across all three stations and over the years, a pattern of three generations was generally observed in the mountain regions (stations 1 and 2), while four generations were assessed in the plain (station 3). On average, the accumulated degree days required for the completion of a single generation were 524 ± 22 DD at station 1, 554 ± 44 DD at station 2, and 570 ± 80 DD at station 3. These values closely align with the 556 DD proposed by Model 1 rather than the 619 DD suggested by Model 2.

Station 1:

Observing the data set presented in Table 2, the life cycle of *C. pomonella* exhibited three major generations during the periods 2009–2012, 2014–2016 and the year 2018. The first generation started in April, the second one occurred around mid-late June, while the third one began between late July and the first week of August. During the same years, both Models (1 and 2) predicted three generations. However, the differences in generation durations were more pronounced with Model 2. In fact Model 2 forecasted longer durations and later termination dates for each generation compared to both Model 1 and the observed data. Notably, Model 1 predicted the first generation to last about 10 days longer than observed generation, but it showed a closer alignment with the actual timing of the second and third generations.

The year 2013 was an exception, and recorded only two generations and a third partial one. The first generation ended around June 30 recording 576 DD and the second one extended until August 13 requiring 665 DD. Both Models (1 and 2) predicted three generations, which does not align with the observed generations. However, concerning the end of the second generation, Model 2 was close to the actual observed data. The year 2017, the

Table 2. Comparison between observed (based on sexual trap catches) and theoretical generations in the three stations across different years and degree days requirement for each generation.

		Based on trap catches		Model 1 556 DD	Model 2 619 DD
Years	Generations	Limits of generations	Generations length (DD °C)	Limits of generations	Limits of Generations
			Station 1		
2009	G1	08/04–14/06	421	08/04–25/06	08/04–01/07
	G2	14/06–01/08	655	25/06–03/08	01/07–12/08
	G3	01/08–02/09	460	03/08–09/09	12/08–08/10
2010	G1	05/04–14/06	418	05/04–30/06	05/04–04/07
	G2	14/06–24/07	516	30/06–03/08	04/07–12/08
	G3	24/07–02/09	547	03/08–15/09	12/08–06/10
2011	G1	07/04–15/06	412	07/04–26/06	07/04–30/06
	G2	15/06–01/08	645	26/06–04/08	30/06–12/08
	G3	01/08–05/09	460	04/08–14/09	12/08–02/10
2012	G1	10/04–17/06	465	10/04–25/06	10/04–28/06
	G2	17/06–05/08	708	25/06–01/08	28/06–09/08
	G3	05/08–07/09	466	01/08–07/09	09/08–23/09
2013	G1	12/04–30/06	576	12/04–30/06	12/04–04/07
	G2	30/06–13/08	655	30/06–04/08	04/07–12/08
	G3P	13/08–29/08	209	04/08–15/09	12/08–06/10
2014	G1	08/04–01/06	390	08/04–18/06	08/04–25/06
	G2	01/06–20/07	535	18/06–01/08	25/06–10/08
	G3	20/07–31/08	590	01/08–09/09	10/08–27/09
2015	G1	06/04–01/06	386	06/04–20/06	06/04–26/06
	G2	01/06–26/07	700	20/06–26/07	26/06–03/08
	G3	26/07–07/09	567	26/07–05/09	03/08–24/09
2016	G1	03/04–16/06	410	03/04–28/06	03/04–03/07
	G2	16/06–25/07	639	28/06–04/08	03/07–12/08
	G3	25/07–04/09	508	04/08–09/09	12/08–29/09
2017	G1	02/04–06/06	464	02/04–13/06	02/04–17/06
	G2	06/06–10/07	458	13/06–20/07	17/06–28/07
	G3	10/07–18/08	645	20/07–22/08	28/07–04/09
	G4P	18/08–04/09	231	22/08–06/10	04/09–15/11
2018	G1	10/04–30/06	444	10/04–08/07	10/04–12/07
	G2	30/06–01/08	471	08/07–12/08	12/07–21/08
	G3	01/08–11/09	585	12/08–23/09	21/08–13/10
			Station 2		
2021	G1	01/04–23/06	499	01/04–29/06	01/04–04/07
	G2	23/06–11/08	612	29/06–10/08	04/07–18/08
	G3	-	-	10/08–27/09	18/08–20/10
2022	G1	11/04–23/06	545	11/04–24/06	11/04–02/07
	G2	23/06–05/08	556	24/06–05/08	02/07–14/08
	G3	05/08–15/09	512	05/08–16/09	14/08–14/10
			Station 3		
2022	G1	01/03–26/05	567	01/03–25/05	01/03–30/05
	G2	26/05–01/07	473	25/05–05/07	30/05–12/07
	G3	01/07–10/08	654	05/07–06/08	12/07–18/08
	G4	10/08–15/09	536	06/08–11/09	18/08–04/10
2023	G1	08/03–18/05	671	08/03–27/05	08/03–01/06
	G2	18/05–30/06	650	27/05–06/07	01/06–14/07
	G3	30/06–02/08	531	06/07–07/08	14/07–20/08
	G4	02/08–05/09	475	07/08–12/09	20/08–07/10

DD: degree days; G: generation; P: partial generation.
Limits of generations: Day/Month.

hottest season with 2085 DD, was distinct by three generations and an additional partial one. The first generation started from early April, the second one began on the first week of June, while the third occurred on early July and ended around August 18 allowing the development of a partial fourth generation stopped by diapause and harvest in September. For this season, predictions of Model 1 attested the possibility of three generations and the high potential of a fourth one which differs from Model 2 assumptions forecasting a weak possibility of a fourth flight.

Station 2:

The table 2 shows that the 2021 season was characterized only by two generations conversely to Model 1 and Model 2 predicting 3 generations. In fact, as attested in the field, the absence of captures in subsequent weeks indicated the manifestation of diapause since august 11. The first generation started in early April and concluded around June 23 requiring 499 DD for its accomplishment. The second one began on June 23 and its development required an average of 612 DD. The season 2022 was distinguished by the succession of three generations of codling moth as predicted by the two models. The first, the second, and the third generations accomplishment required the accumulation of 545, 556, and 512 DD, respectively and their limits corresponded more to the Model 1 rather than Model 2.

Station 3:

The life cycle of *C. pomonella* was characterized by four complete generations during the two seasons of 2022 and 2023 (Table 2). The phenological Model 1 predicted four major generations for both 2022 and 2023 seasons, matching more with the observed generations in terms of their timing compared to Model 2. The discrepancy between the observed data and Model 1 predictions was minimal, typically ranging from one to four days.

Accumulated degree days across years and key periods

Table 3 illustrates the relationship between temperature variations and the voltinism of *C. pomonella* during critical phases of its life cycle. The analysis focuses on January-April, which corresponds to the first emergence period, and May-June, which generally aligns with the first flight and the beginning of the second flight due to overlapping generations. July-August corresponds to the second flight and the start of the third flight, with the possibility of diapause induction in insect populations.

At station 1, the patterns of degree days accumulation throughout the growing seasons (January to mid-September) remained relatively stable with an average of 1816 ± 115 DD. The highest annual degree days accumulation was recorded in 2017 (2085 DD); the year where four generations were recorded for codling moth population. The coldest year 2018 with 1624 DD, has experienced extreme temperatures during July-August as usually observed in summer at station 1. This year has recorded three generations.

At Station 2, located in the Atlas Mountains, the years 2021 and 2022 differed in temperature and the number of generations observed. The year 2021, which was slightly colder than 2022, recorded two generations of codling moth. In contrast, three generations were observed in 2022.

At station 3, both seasons 2022 and 2023 recorded high temperatures exceeding 2000DD, and they experienced the succession of four generations. Statistical analysis showed a significant positive correlation between the annual accumulation of degree days and the number of generations ($P = 0.001$; $r = 0.783$**) and showed also a significant correlation between the number of generations and the temperatures prevailing during July-August, the period conducive to diapause ($P = 0.001$; $r = 0.766$**).

Prediction of *C. pomonella* flights

Based on Damos et al. (2018) and Juszczak et al. (2013) models and exploiting the thermal data from all studied seasons in all stations, the emergence of the overwintering generation and the advent of the second and the third flights were estimated (Table 4).

Based on observed findings throughout all studied seasons at station 1, the first captures occurred from early to April 10, with an average accumulation of 82 DD from January 1. These emergences were 27 DD earlier than the first flight predicted by Model 4 which was expected at 110 DD, and much earlier than Model 3 prediction of 250 DD. The initial moths of the second generation were captured between early June (2014, 2015, 2017), mid-June (2009,

Table 3. Voltinism of *C. pomonella* based on accumulation of degree days across years and key periods (January-April, May-June, July-August).

Year	DD January-April	DD May-June	DD July-August	DD from 1st January-15 September	Number of Generations
			Station 1		
2009	151	543	918	1813	3
2010	226	415	910	1780	3
2011	194	497	865	1764	3
2012	123	598	926	1843	3
2013	176	461	919	1751	2
2014	215	520	861	1828	3
2015	178	570	910	1851	3
2016	167	486	930	1821	3
2017	236	643	975	2085	4
2018	112	367	931	1624	3
			Station 2		
2021	256	470	811	1643	2
2022	205	554	859	1827	3
			Station 3		
2022	506	764	1001	2527	4
2023	746	812	1012	2782	4

Table 4. Comparison between the estimated and effective dates underlining the start of the first, the second and the third flights of *C. pomonella.*

	Model 3			Model 4			Based on trap catches					
	1st Emergence	2nd Flight	3rd Flight	1st Emergence	2nd Flight	3rd Flight	1st Emergence	DD	2nd Flight	DD	3rd Flight	DD
					Station 1							
2009	16/05–20/05	10/07–14/07	21/08	10/04	24/06	01/08	08/04	99	14/06	521	01/08	1195
2010	03/05–18/05	10/07–13/07	25/08	06/04	29/06	02/08	05/04	103	14/06	522	24/07	1057
2011	12/05–18/05	10/07–13/07	24/08	10/04	26/06	03/08	07/04	92	15/06	493	01/08	1156
2012	18/05–25/05	09/07–12/07	20/08	28/04	25/06	01/08	10/04	76	17/06	547	05/08	1273
2013	11/05–25/05	13/07–16/07	24/08	16/04	30/06	04/08	12/04	77	30/06	655	13/08	1343
2014	05/05–10/08	09/07–13/07	23/08	11/04	20/06	01/08	08/04	86	01/06	470	20/07	1023
2015	08/05–12/05	06/07–09/07	16/08	15/04	22/06	27/08	06/04	85	01/06	464	26/07	1182
2016	20/05–25/05	13/07–16/07	23/08	18/04	28/06	03/08	03/04	73	16/06	498	25/07	1044
2017	03/05–09/05	26/06–30/06	070/8	09/04	13/06	19/07	02/04	83	06/06	556	10/07	1032
2018	05/06–13/06	24/07–26/07	03/09	28/04	11/07	14/08	10/04	53	30/06	498	01/08	987
					Station 2							
2021	27/04–09/05	04/07–10/07	24/08	22/03	19/06	02/08	01/04	156	23/06	673	11/08	1326
2022	10/05–15/05	05/07–08/07	20/08	12/03	17/06	29/07	11/04	159	23/06	726	05/08	1337
					Station 3							
2022	08/03–21/03	29/05–02/06	13/07	05/02	14/05	21/06	01/03	224	26/05	816	01/07	1332
2023	15/03–21/03	14/05–18/05	26/06	13/02	21/04	26/06	08/03	209	18/05	903	30/06	1571

DD: degree days from the 1st of January.
Model 3: 1st Emergence (250-300 DD); 2nd Flight (850-900 DD) and 3rd Flight (1500DD).
Model 4: 1st Emergence (110 DD); 2nd Flight (650 DD) and 3rd Flight (1190DD).

2010, 2011, 2012, 2016), and late June (2013, 2018) with an average of 522 DD from January 1. This reflects a relatively low energy accumulation compared to the thresholds suggested by Model 3 at 850–900 DD, and the 650 DD proposed by Model 4. The third flight was observed annually between late July and early August, at an average of 1129 DD from January 1. It occurred quite earlier than the dates and heat units predicted by Model 4 and deviated considerably from the flight timing projected by Model 3.

At Station 2, the first emergence occurred within the first 10 days of April at an average of 157 DD. This was 47 DD later than the predictions by Model 4 and 92 DD earlier than the projections by Model 3 The second flight, on June 23, with an average of 699 DD, closely aligned with the timing predicted by Model 4, but was remarkably different from Model 3. The third flight, beginning at an average of 1331 DD, occurred in the first 10 days of August. This timing was slightly close to the prediction by Model 4, which estimated it for late July/early August, but was considerably earlier than the projections by Model 3.

At the warmest station in 2022 and 2023, the accumulated degree days required for the initiation of the first, second and third flights were noted to align more closely with Model 3, especially for the second and third generation predictions. Conversely, Model 4 anticipated the beginning of all flights, unmatching with the observed data (a difference of 106 DD for the 1st flight, 209 DD for the 2nd Flight and 261 DD for the 3rd one).

Discussion

To investigate the factors affecting the voltinism of *C. pomonella*, we studied its presence in three diverse localities of Morocco: stations 1 and 2 in the Atlas Mountains, relatively cold, and station 3 in the plain. We compared the observed generations of *C. pomonella* at each site with those predicted by models to determine the reliability of using them for codling moth control in Moroccan conditions. The predicted generations were estimated using the models proposed by Riedl et al. (1976) [Model 1] and Pitcairn et al. (1992) [Model 2]. The first emergence of diapausing larvae and the advent of the second and third flights of *C. pomonella* were estimated based on two models outlined by Damos et al. (2018) [Model 3] and Juszczak et al. (2013) [Model 4]. Remarkable insights were unveiled, shedding light on the intricate relationship between temperature effect and the host plant phenology with the dynamics of *C. pomonella*.

At first, the present study highlighted the temperature impact on the voltinism of codling moth supported by the positive correlation between accumulated annual degree days and number of generations. Years recording elevated temperatures, exceeding 2000 DD in a growing season, such as 2017 in station 1 and 2022–2023 in station 3 have experienced the succession of four generations. While the season 2021 in station 2, recording 1643 DD, has recorded two generations. This fact has been reported in many studies. Stoeckli et al. (2012) attested that high temperatures could lead to a pronounced second generation and a substantial risk of an additional third one under future climatic conditions. Similarly, Gheban et al. (2014) investigated the impact of temperature on the voltinism of *C. pomonella* over two consecutive years in Romania. Their findings showed that in 2011, only one generation and an incomplete second one were observed, while in 2012; a warmer year; two complete generations were assessed. These results are consistent with our findings, highlighting the significant role of temperature on *C. pomonella* voltinism. Interestingly, our study was conducted in orchards where apple is the predominant crop, creating a homogeneous host plant environment that allowed us to focus specifically on temperature effects on insect voltinism. Otherwise, within the same region and under similar climatic conditions, Piskorski et al. (2010) demonstrated variability in insect voltinism according to host plant species, finding that *C. pomonella* exhibits trivoltine cycles on apple compared to bivoltine cycles in walnut populations, suggesting that genetic adaptation to specific hosts and host plant phenology may modulate generation number simultaneously with temperature.

At stations 1 and 2, three generations were generally observed, consistent with the study by El Iraqui and Hmimina (2016) led in a mountain region. However, certain years were exceptional such as 2017, 2018 and 2021. 2017 was noticeable by the highest accumulated degree days (2085 DD), which resulted in three major generations and a fourth partial one. In contrast, the seasons 2018 and 2021 were marked by the lowest accumulated degree days, 1624 DD and 1643DD respectively, but have recorded a different number of generations. A detailed comparison of temperatures between the two years showed that 2018 experienced low temperatures during the first two key periods (January-April and May-June), in contrast to July-August recording a high degree days accumulation (931 DD). However, this same period, corresponding to diapause induction, was relatively cooler in the 2021 season, with 811 DD. These conditions could explain the absence of field captures since august 11 and the occurrence of only two generations in 2021. In fact, the high temperatures during the period conducive to diapause (July/August) could reduce induction of diapause as has been previously reported by Gomi et al. (2007) and facilitate the development of a full third generation (case of the 2018 season). The interaction between diapause and temperature is well documented, as lower temperatures require longer daylengths to prevent diapause (Sheldeskova 1967; Riedl and Croft 1978). However, under Moroccan conditions, the exceptionally high summer temperatures may delay diapause induction, thereby extending generation development despite photoperiods that would normally trigger dormancy (El Iraqui and Hmimina 2016). The year 2013 shared similar conditions in terms of accumulated degree days with the other seasons. However, despite a substantial accumulation of degree days in July /August, only two generations and a third partial one have occurred. This underscores that the voltinism of *C. pomonella*, could be influenced by the combination of several factors such as host plant species, food availability, genetic variability, and photoperiod as attested in various studies (Sheldeshova 1967; Brown et al. 1978; Riedl and Croft 1978; Setyobudi 1989; Piskorski et al. 2010).

Station 3 is characterized by a warm climate, and as a consequence of high temperatures, the recording of four generations has been noted. The advent of more generations has been reported in several studies (Stoeckli et al. 2012; El Iraqui and Hmimina 2016). This station might exemplify the broader implications of climate change on insect physiology and population dynamics. In fact, in Morocco, the mean annual temperature has increased by about 0.9 °C since the 1960s. These rising temperatures are likely to impact various aspects of *C. pomonella* life cycle, such as its adaptability and phenology. A study conducted in California predicted an additional generation for *C. pomonella* between 2030 and 2099. It indicates that the biofix date is projected to shift earlier by up to 28 days and the length of generations expected to be shortened by up to 19 days (Jha et al. 2024). This underscores the significant influence of global warming on the insect's phenology.

One of the core interests of our study was to predict theoretical generations using models proposed by Riedl et al. (1976) and Pitcairn et al. (1992) along with forecasting the first emergence, and the start of the second and third flights using models developed by Damos et al. (2018) and Juszczak et al. (2013). The comparison between the predictions and the observed data offers valuable insights into the accuracy of these predictive tools. These models have been applied to forecast the phenology of *C. pomonella* and other species in both present and future climatic scenarios across various regions (Pitcairn et al. 1992; Haavik et al. 2013; Joshi et al. 2017). Across all studied stations, the average accumulation of DD necessary for a single generation was close to 556 DD aligning with Riedl et al. (1976). However, this value should be considered only as an approximation, as each generation has its own specific heat requirements, notably the first one which presented different accumulated degree days in the three stations (439 DD in station 1, 522 DD in station 2 and 619 DD in station 3). These differences can be partly attributed to microclimatic variability within and among orchards, as slight variations in temperature, sun exposure, and canopy position can influence the developmental rates of larvae, leading to differences in emergence timing among individuals, even within the same tree (Greiser et al. 2022).

Forecasting the onset of flights seems reliable with Juszczak et al. (2013) model at stations 1 and 2, and Damos et al. (2018) model at station 3. In particular, at station 3, the advent of the first, second and third flights occurred respectively at 217, 860 and 1452 DD from January 1 aligning perfectly with Damos et al. (2018) predictions. This suggests that this model could be adapted and applied in the context of warm temperatures. In the Atlas Mountains, the flight dates corresponded more to Juszczak et al. (2013) predictions. More precisely, at station 1, the observed dates were marginally earlier than those predicted by Juszczak et al. (2013), while at station 2, the observed dates were slightly later than predicted ones. The observed reliability and alignment of the studied models with observed data, suggest their potential success as tools for forecasting pest phenology under diverse Moroccan climatic conditions. These results are consistent with findings of Joshi et al. (2017) in Pennsylvania, who employed two models based on accumulated degree days to forecast the phenology of *C. pomonella*. The results facilitated the prediction of critical events, including the appearance of the first and second generations. Several studies have also employed phenological models to predict various developmental stages of *C. pomonella* including egg hatch, larvae development and pupae emergence, under different climatic conditions, in Switzerland (Graf et al. 2018), in Chile (Wilson and Barnett 1983), and in Washington (knight 2007). In these studies, the deployed models demonstrated reliability and utility as effective tools for forecasting codling moth phenology, not only for an entire growing season but also over multiple years characterized by varying weather conditions.

The accurate determination of the first flight is essential for an effective pest monitoring, as it indicates the onset of pest activity and guides management strategies to schedule timely interventions. At stations 1 and 2, the first flight occurred at an average of 120 DD, in the first days of April, while at station 3, it was observed at an average of 217 DD, typically in early March. These discrepancies emphasize the importance of understanding the synchronization between pest activity and host plant phenology. In fact, even when the heat requirements for development are fully satisfied, the insect's life cycle may still align with early or late plant development. Changes in plant phenology, particularly shifts in flowering and leaf development, can greatly influence the timing of insect activity, such as the onset of adult flight. Insects like the codling moth are closely synchronized with the development of their host plants. For instance, an earlier bloom can trigger an earlier start to insect activity, as their life cycles are often aligned with the availability of resources such as leaves and fruits for egg-laying and larval development (Menzel and Fabian 1999; Morin Lechowicz et al. 2009; Vitasse et al. 2011).

Conclusion

This study provides a comprehensive assessment of *C. pomonella* voltinism under contrasting Moroccan climatic conditions, highlighting the strong influence of temperature on the pest's developmental dynamics. In cooler areas, the codling moth generally completes three generations, with a possible fourth during warm years, while in warmer regions up to four full generations can occur. These findings confirm the remarkable plasticity of *C. pomonella* and its potential to adapt rapidly to temperature shifts.

Beyond describing voltinism patterns, our results underline the reliability of specific phenological models for predicting moth development in Moroccan conditions. Model 1 (Riedl et al. 1976) proved most accurate for estimating the number of generations, whereas Model 3 (Damos et al. 2018) and Model 4 (Juszczak et al. 2013) performed best under warm and cool climates, respectively. These outcomes suggest that model calibration by climatic zone could substantially improve forecasting accuracy and decision support for Integrated Pest Management (IPM) programs.

Finally, the findings provide valuable insights into how *C. pomonella* populations may respond to ongoing climate warming. The warmer conditions observed in the Saïss plain could serve as a proxy for future thermal scenarios across Morocco, implying a probable increase in voltinism and thus higher management challenges. Future research should focus on integrating temperature-based models with apple tree phenology and other ecological drivers to enhance predictive tools under changing environments. Ultimately, tailoring phenological models to regional climate variability will be crucial for designing sustainable and climate-resilient pest management strategies.

Author contributions

Conceptualization: Salma EL Iraqui El Houssaini; Methodology: Salma EL Iraqui El Houssaini and Dina Akroute; Software: Dina Akroute; Validation: Salma EL Iraqui El Houssaini and Dina Akroute; Formal analysis: Dina Akroute and Rachid Boulamtat; Investigation: Salma EL Iraqui El Houssaini and Dina Akroute; Resources: Rachid Benkirane; Data curation: Dina Akroute and Rachid Boulamtat; Writing-original draft preparation: Salma EL Iraqui El Houssaini, Dina Akroute and Rachid Boulamtat; Writing-review and editing: Salma EL Iraqui El Houssaini; Dina Akroute, Rachid Boulamtat, Khaoula Habbadi, Rachid Lahlali and Rachid Benkirane; Supervision: Salma EL Iraqui El Houssaini; Funding acquisition: Mohamed Sbaghi. All authors have read and agreed to the published version of the manuscript.

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Data availability statement

The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

Conflicts of interest

The authors declare no conflicts of interest.

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