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Article

Temperature-Dependent Population Model of Apple Leafminer, *Phyllonorycter ringoniella* (Lepidoptera: Gracillariidae)

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Simple Summary: The Asiatic apple leafminer *Phyllonorycter ringoniella* is a significant pest of apple crops in Korea, Japan and China. We are presenting a comprehensive population model of its development. The model comprises three primary sub-models: the spring emergence model, the immature stage transition model, and the adult oviposition model. Tested under six different scenarios, the simulations revealed that the Asiatic apple leafminer has five per year. The model accurately predicted the peak times of each generation, with a discrepancy of only seven days compared to actual field data. Sensitivity analyses demonstrated that population size was primarily influenced by total fecundity and the larval stages, although the timing of peak occurrences remained the same despite variations in these parameters. Increased temperatures caused earlier adult peaks, particularly for the summer generations. To manage this pest effectively, our population model can be a valuable tool for estimating population dynamics, understanding abundance fluctuations and determining optimal periods for pesticide application in apple orchards.

Abstract: The Asiatic apple leafminer, *Phyllonorycter ringoniella* (Matsumura), is a significant secondary pest of apple trees in Northeast Asia. To better understand its population dynamics, a population model based on temperature-developmental relationships was constructed. This model includes three sub-models: spring emergence, immature stage transition, and adult oviposition. Field data were collected from sex-pheromone baited traps in apple orchards in Andong, Korea, during 2015 and 2016 to validate the model. Simulations under six pesticide-natural enemy scenarios showed that the population size of each generation was best simulated when weighted mortality factors for pesticides and natural enemies were applied. Using daily temperature inputs, the model demonstrated that *P. ringoniella* typically undergoes five generations per year, with peak times predicted within a seven-day margin of field data. Sensitivity analyses revealed that population size was influenced by total fecundity and the larval stage model, but peak times remained consistent despite parameter changes. Higher temperatures led to earlier adult peak dates, especially in summer generations. This model serves as a fundamental tool for estimating population dynamics and abundance changes of *P. ringoniella* and can guide the timings of pesticide application. Further validation is necessary to test the model's efficacy in controlling pests in apple orchards.

Keywords: apple leafminer; temperature; development; oviposition; emergence model

1. Introduction

The Asiatic apple leafminer, *Phyllonorycter ringoniella* (Matsumura), is a significant insect pest of apple trees in Korea, Japan, and China [1–4]. This pest can produce four to six generations per year, which with their leaf mines affect photosynthesis, hasten defoliation, inhibit new bud growth, and ultimately cause premature ripening and premature fruit drop [2,4,5].

Temperature is a crucial abiotic factor affecting various biological processes of insects, including development, survival, longevity, fecundity, and demographic parameters [6–12]. Understanding the relationship between temperature and these biological processes is essential for comprehending population growth and dynamics, predicting seasonal occurrences and outbreaks [13–18], and developing effective pest management strategies [19–22].

Mathematical models are critical tools for describing insect responses to variable environmental conditions and predicting population dynamics across different geographic zones and climates [23,24]. Various studies have introduced mathematical functions to depict these relationships based on an insect's thermal characteristics at different temperatures. A population model can enhance our understanding of insect pest dynamics under a variety of environmental factors and aid in developing integrated pest management tactics through simulations [7,24].

In temperate regions, a population model for arthropod species typically requires three basic components: a spring emergence model, a temperature-dependent development model for immature stages, and an oviposition model [6,7,25–27]. These models have been mathematically described and applied to various temperature-dependent and stage-structured models of insects and mites. They can also be used to calculate developmental thresholds, optimal temperatures, thermal constants, survival rates, longevity, and fecundity, aiding in predicting geographic distribution, phenology, and providing precise forecasting systems [9,11].

Understanding the population dynamics of *P. ringoniella* in apple orchards is vital for developing effective management strategies. The objective of this study is to develop and validate a population model for *P. ringoniella* using field data. This information will help us comprehend the population dynamics of this pest and formulate effective management strategies for apple orchards.

2. Materials and Methods

2.1. Model Construction

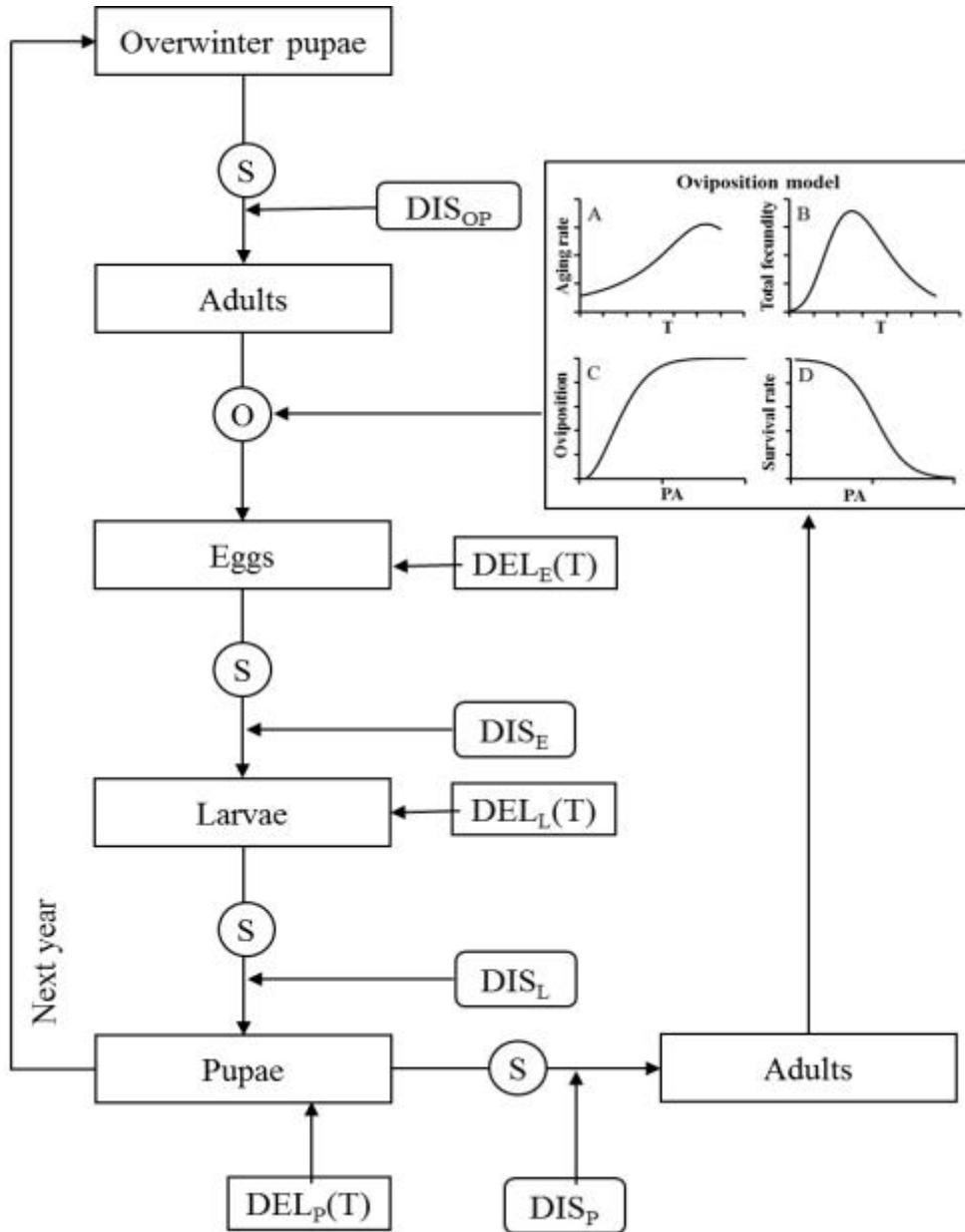
The *P. ringoniella* population model was constructed to include five developmental stages: overwinter pupa, egg, larva, pupa, and adult (Figure 1). Each stage was divided into separate cohorts of individuals, which entered the stage on a given day and were treated as different age groups within the stage [24,28]. However, the overwintering pupae with which the model started, consisted of a single cohort, with the assumption that individuals of this cohort were physiologically identical [25].

The population model was consisted of three component models (Figure 1): the spring emergence model [29], the oviposition model [30], and the stage transition model [31]. The spring emergence model predicted adult emergence from overwintering pupae using the two-parameter Weibull function based on accumulated degree days. The adult oviposition model consisted of four temperature-dependent components: the developmental (aging) rate model, total fecundity model, age-specific oviposition rate model, and age-specific survival rate model. The stage transition model for each immature stage included the temperature-dependent developmental rate model and the developmental distribution model.

At any given time, each cohort was defined by two variables [23]: $aij(t)$, the physiological age of cohort j within stage i at time t ; and $Nij(t, a)$, the number of individuals in cohort j of physiological age a at time t . The output of the model is $Ni(t)$, the total number in stage i at time t , calculated by summing over the cohorts.

Temperature was the only meteorological factor included in the model; other variables, such as relative humidity, were not considered. The model starts with the overwintering pupal stage with an arbitrarily defined number of individuals. Model computations used a daily time-step, assuming all mortality occurred at the transition to the next stage. It was also assumed that there was no

emigration or immigration of *P. ringoniella* adults. The population model was simulated using PopModel 1.5 [32].



DIS: distribution model for each stage (Eq. 1), DEL: developmental model (Eq. 2, Eq. 3), S: survival rate (Eq. 5), O: Oviposition model, T: temperature, and PA: physiological age. OP, E, L, and P indicate overwinter pupae, eggs, larvae, and pupae, respectively.

Figure 1. Schematic diagram of the population model for *Phyllonorycter ringoniella*.

2.2. Sub-Models and Their Process Functions

The process functions and their parameters (Table 1, Table 2) were obtained from previous studies, the spring emergence model from Geng and Jung (2018) [29], the adult oviposition model from Geng and Jung (2017) [30], and the stage transition model from Geng and Jung (2018) [31].

Spring Emergence Model: daily spring adult emergence was estimated using Weibull distribution model (Eq. 1). This model uses cumulative degree-days with a base temperature of 7.06 °C from January 1 as an independent variable [29].

Adult Oviposition Model: this model included four component functions, the adult aging rate function (Eq. 4), temperature-dependent total fecundity function (Eq. 5), age-specific oviposition rate function (Eq. 6), and age-specific survival rate function (Eq. 7). Since total egg production by female adults could be influenced by temperatures experienced by them earlier, the average temperature during the 5 days prior to oviposition was taken as input variable in the total fecundity model. Daily egg production was estimated by the PopModel 1.5 [32] according to the computational process of Kim and Lee (2003) [26]. The sex ratio (female proportion) was assumed to be 0.5 [33].

Stage Transition models: These models simulate the proportion of individuals transitioning from one stage to the next, comprising a temperature-dependent development rate function and a cumulative distribution function.

Immature Survival Model: the survival rates of eggs, larvae, and pupae at different constant temperatures (13.3-32.2°C) were examined in the laboratory. The survival rates were simulated using an extreme value equation (Eq. 5), with parameter values presented in Table 2.

External Mortality Model: Parasitism is a major biological external mortality factor for the apple leafminer [5], while insecticides are the major non-biological external mortality factor [34]. Given the mining behavior of the larvae, an insecticide-driven mortality averaging 86.1%, was considered only for the egg stage, which is directly exposed to the pesticide spray [34]. The insecticide was assumed to be effective against eggs oviposited five days before and five days after the spraying date [24,34]. Parasitism rates of larvae and pupae were assumed to be 29.5% in a conventional orchard [5] and 54.9% in a pesticide-free orchard (unpublished data).

Table 1. Equations used in the population model of *Phyllonorycter ringoniella*.

No.	Model	Equation
1	Two-parameter Weibull function	$y = 1 - \exp\left[-\left(\frac{x}{a}\right)^b\right]$
2	Lactin-1	$r(T) = e^{\rho T} - e^{\left(\rho T_{max} - \left(\frac{T_{max}-T}{\Delta T}\right)\right)}$
3	Briere-1	$r(T) = aT(T - T_{min})\sqrt{(T_{max} - T)}$
4	Inverse second-order polynomial	$r(T) = \frac{a}{1 + b \cdot T + cT^2}$
5	Extreme value function	$f(T) = \omega \cdot \exp[1 + (\varepsilon - T)/\delta - \exp((\varepsilon - T)/\delta)]$
6	Three-parameter Weibull function	$p(P_x) = 1 - \exp\left[-\left(\frac{P_x - \alpha}{\beta}\right)^r\right]$
7	Sigmoid function	$s(P_x) = \frac{1}{1 + \exp[(\eta - P_x)/\theta]}$

The same parameter symbols used in different equations may assume different meanings.

Table 2. Parameter values of each equation used in the population model of *Phyllonorycter ringoniella*.

Models	Eqs.	Parameters (\pm SEM)	r^2
Spring emergence model	1	a	b

		353.349 ± 3.1223	4.104 ± 0.1909		0.83
Development model		ρ	T_{max}	ΔT	
Eggs	2	0.1575 ± 0.00489	34.3922	\pm	6.3332 ± 0.19438 0.99
			0.18388		
		a	T_{min}	T_{max}	
Larvae	3	0.00004 ± 0.000005	4.8463	\pm	33.5695 ± 0.32969 0.97
			2.02694		
Pupae	3	0.00011 ± 0.000009	7.5904	\pm	35.5845 ± 0.44517 0.99
			0.89274		
Distribution of development time		a	b		
Eggs	1	0.9786 ± 0.00707	$7.2970 \pm$ 0.54226		0.96
Larvae	1	1.0343 ± 0.00660	$5.5455 \pm$ 0.27600		0.92
Pupae	1	0.9866 ± 0.00401	$14.8415 \pm$ 1.03858		0.98
Survival rate model		ω	ε	δ	
Eggs	5	0.914 ± 0.0272	$20.340 \pm$ 1.3763	20.457 ± 5.3569	0.57
Larvae	5	0.759 ± 0.0536	$17.988 \pm$ 0.4533	6.947 ± 1.1520	0.87
Pupae	5	0.923 ± 0.0351	$21.845 \pm$ 0.4333	8.353 ± 0.6850	0.94
Oviposition model					
Adult aging rate	4	a	b	c	
		0.0213 ± 0.00323	-0.0542	\pm	0.0009 ± 0.00009 0.98
			0.00342		
Total fecundity	5	ω	ε	δ	
		71.3686 ± 4.90491	17.8132	\pm	6.1431 ± 0.68516 0.95
			0.46966		
Oviposition rate	6	α	β	γ	
		0.0545 ± 0.02963	0.5286	\pm	1.7591 ± 0.13074 0.98
			0.03284		
Survival rate	7	η	θ		
		1.0416 ± 0.00529	-0.1926	\pm	
			0.00472		0.99

The same parameter symbols in different models may indicate different meanings.

2.3. Simulations under Six Scenarios

The population model was simulated under six scenarios:

Scenario A: original run, was without insecticide effects or natural enemies. The population increased naturally.

Scenario B: based on scenario A, with the pesticide effect added to the egg stage. Pesticide was sprayed ten times, starting on Julian date 115, at 15-day intervals.

Scenario C: based on scenario B, with the natural enemy effect added to the larval stage. A parasitoid rate of 29.5% was applied.

Scenario D: based on scenario C, with the natural enemy effect added to the pupal stage. A parasitoid rate of 29.5% was applied.

Scenario E: based on scenario A, with the natural enemy effect added to the larval and pupal stages. A parasitoid rate of 29.5% was applied.

Scenario F: same as scenario E, but with a parasitoid rate 54.9 %.

These scenarios were simulated using PopModel 1.5, with meteorological data from 2015 and 2016 in Andong, South Korea.

2.4. Field Population DATA collection

To validate the model against field data, the flight occurrences of *P. ringoniella* adults were monitored in 28 conventional and one pesticide-free apple orchard in Andong, from April 10 to October 24, 2015, and from March 1 to October 26, 2016. Most apple orchards were cultivated by mix varieties but dominated by 'Fuji' and 'Hongro'. Commercial pheromone traps (GreenAgro Tech, Kyeongsan, Korea) baited with synthetic sex pheromone lures containing a 6:4 ratio of E4,Z10-14:Ac and Z10-14:Ac [35], were used for monitoring. One trap was hung 1.5 meters above ground in each orchard and checked weekly or twice a week. The lures were changed every two months, and the sticky inserts were changed weekly.

2.5. Meteorological Data

The meteorological data of daily average, maximum, and minimum temperatures, were obtained from Andong meteorological station (<http://www.kma.go.kr>). The biofix for degree day accumulation was set to January 1 for simplicity [36].

2.6. Sensitivity Analysis

Temperature data of 2015 were used for all simulations during the sensitivity analyses. Simulations were carried out under Scenario F, starting from the spring emergence model with 100 overwintered pupae as the initial input.

The sensitivity of parameter changes was examined by altering certain parameter values by 10% [23,24]. Several model outputs were evaluated: the total number of eggs, larvae, pupae, and adults, and the peak date (Julian date) of each generation. The parameters of the developmental models were excluded from the sensitivity analyses due to invalid equation solutions with parameter changes. The average effect and non-linearity index were used for sensitivity analysis [23,24]:

$$\text{Average effect} = 0.5[F(1.1p_0) - F(0.9p_0)]$$

$$\text{Non-linearity index} = 0.5[F(1.1p_0) + F(0.9p_0)] - F(p_0)$$

Where $F(p)$ is the output at parameter value p , and p_0 is the parameter value in original run.

The sensitivity of temperature change was conducted by running the model with temperatures in 2015 decreased or increased 1°C.

3. Results

3.1. Simulation and Validation

The seasonal population dynamics of *P. ringoniella* in the conventional and pesticide-free orchards in 2015 and 2016 are shown in Figure 2. *P. ringoniella* exhibited five annual occurrences with

overlapping 4th and 5th generations. The population model successfully simulated the typical pattern of *P. ringoniella*, accurately predicting the number of generations and the peak time of each generation (Figure 3, Figure 4, Table 3). However, the model did not accurately predict the population size for each generation. To test the effects of pesticides and natural enemies on population dynamics, the population model was simulated under six scenarios (Figure 3, Figure 4). The pesticide influenced both population size and peak time (Table 3), whereas natural enemies only decreased the population size without affecting the peak time of each generation.

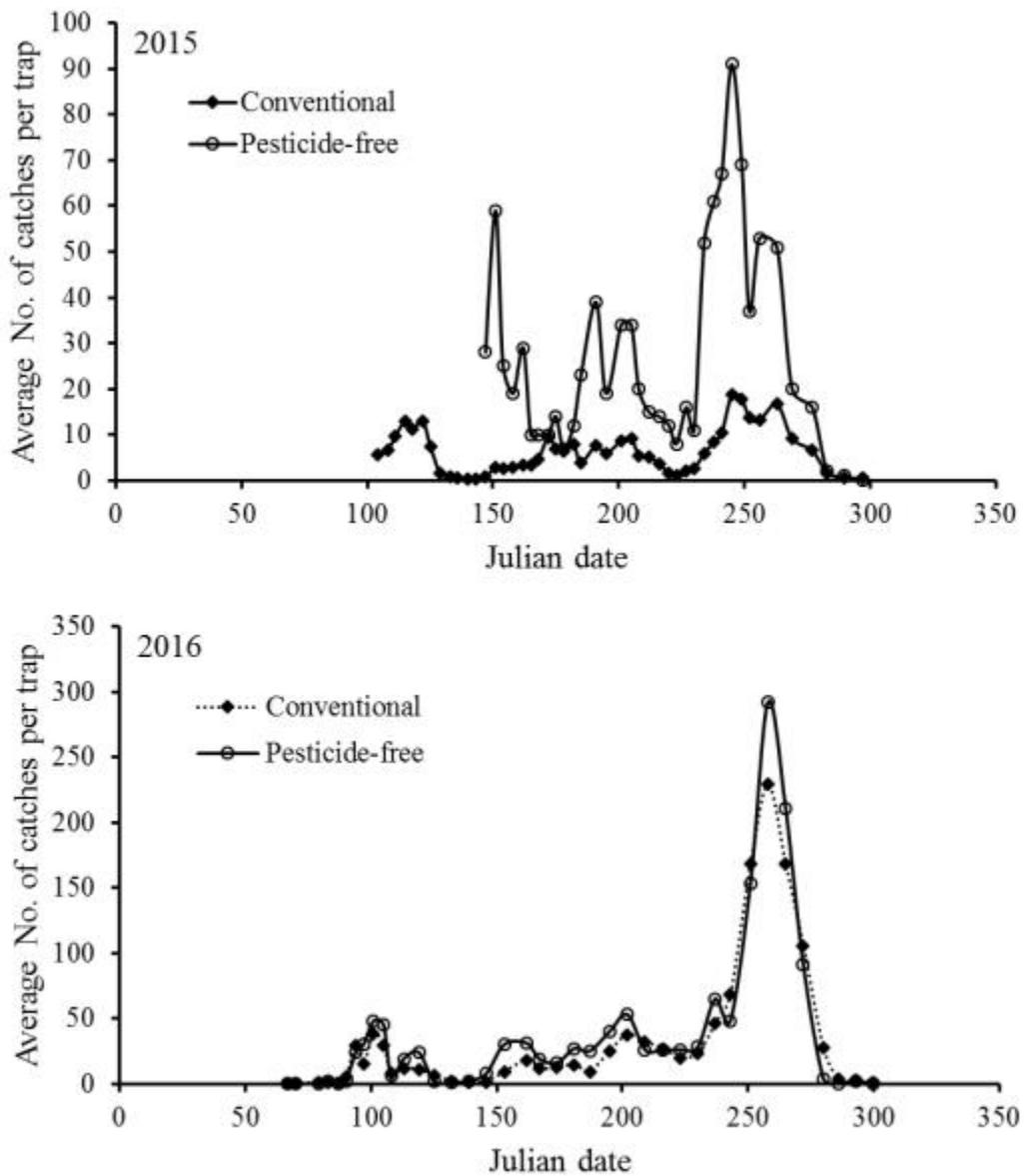


Figure 2. Seasonal occurrence patterns of *Phyllonorycter ringoniella* males caught in pheromone traps in 28 conventional apple orchards and one pesticide-free orchard in Andong in 2015 and 2016.

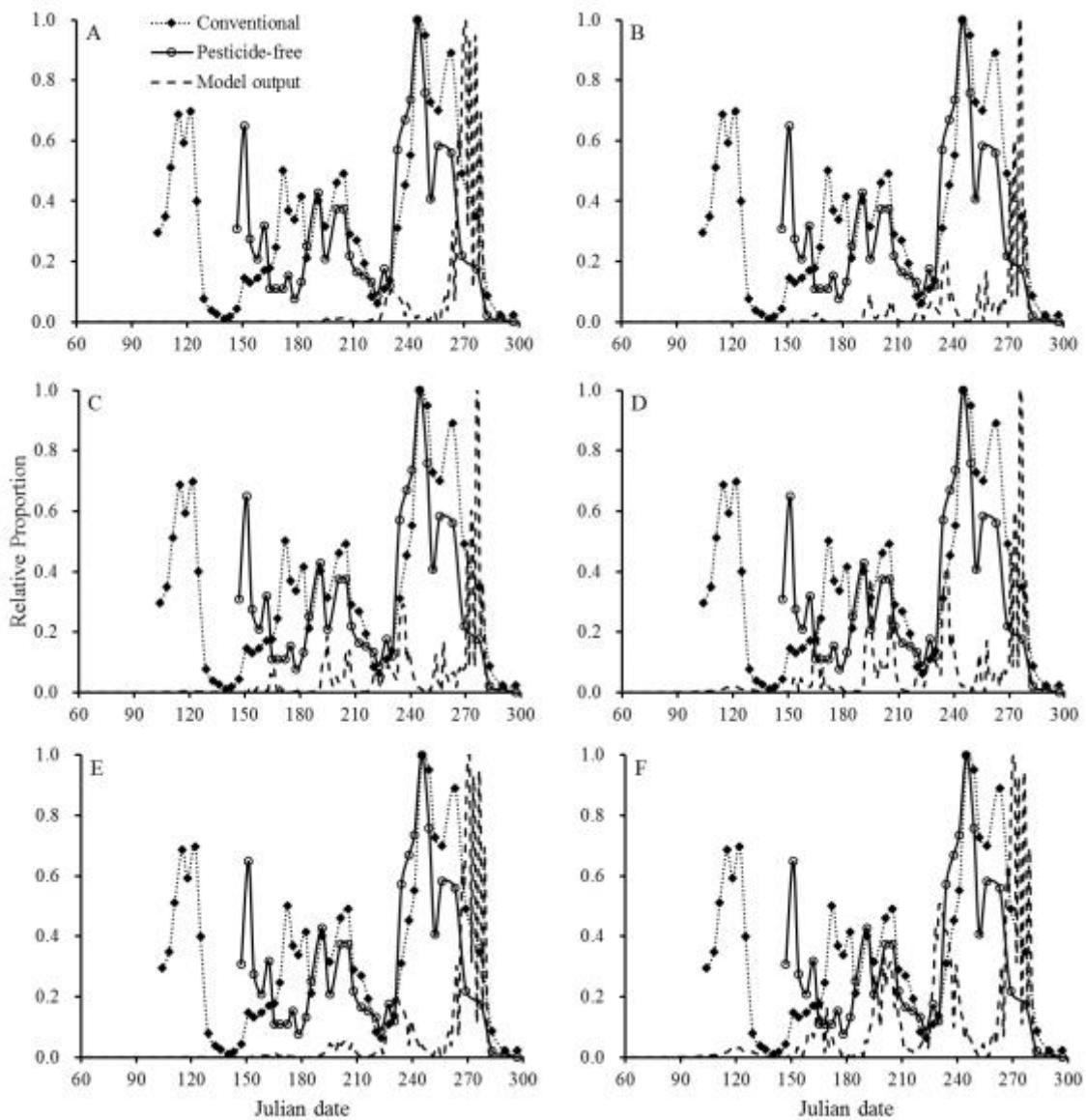


Figure 3. Comparison of model outputs with actual pheromone trap data in 28 conventional apple orchards and one pesticide-free apple orchard in Andong in 2015. The population model was simulated under six scenarios (A-F, detailed information in the methods).

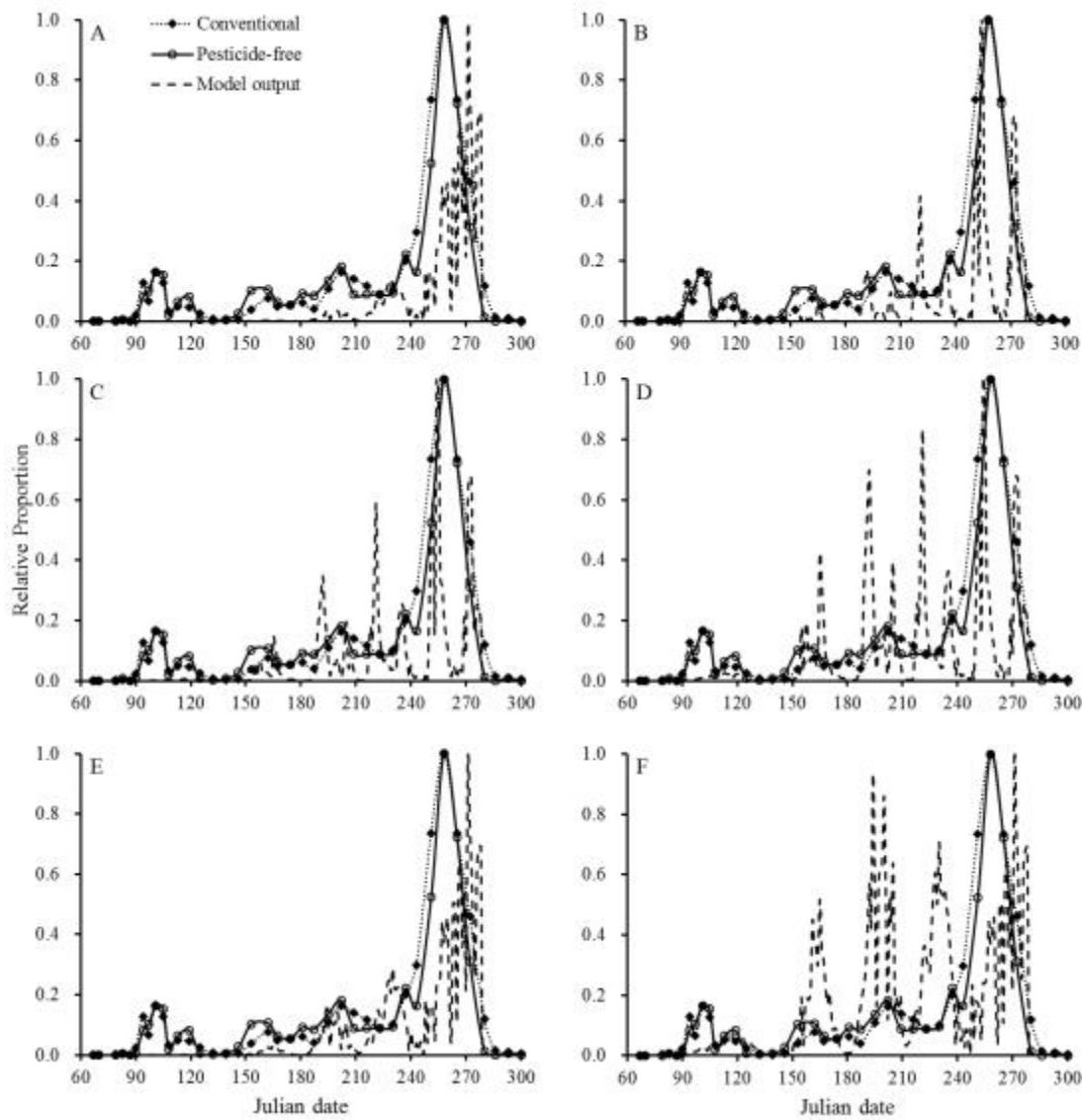


Figure 4. Comparison of model outputs with actual pheromone trap data in 28 conventional apple orchards and one pesticide-free apple orchard in Andong in 2016. The population model was simulated under six scenarios (A-F, detailed information in the methods).

Table 3. The predicted and actual peak time (Julian date) of each generation of *Phyllonorycter ringoniella* in 2015 and 2016.

Year	Generation	Model output under scenarios*						Actual data	
		A	B	C	D	E	F	Conventional	Pesticide-free
2015	1st	122	122	122	122	122	122	122	-
	2nd	164	166	166	166	164	164	172	151
	3rd	204	195	195	195	204	204	205	191
	4th	231	236	236	236	231	231	245	245
	5th	271	276	276	276	271	271	263	256

2016	1st	117	117	117	117	117	101	101
	2nd	165	165	165	165	165	162	162
	3rd	200	192	192	192	200	202	202
	4th	230	235	235	235	230	243	237
	5th	271	253	254	254	271	271	258

*Six scenarios were described in context.

3.2. Sensitivity Analysis

The average effect is proportional to a numerical approximation of the partial first derivative of the output with respect to the parameter, and the non-linearity index is proportional to an approximation of the partial second derivative [23,24]. In most cases, the absolute value of the average effect is larger than the non-linearity index, indicating a stronger linear relationship between model outputs and the parameters (Table 4). Negative average effect values imply that model outputs decrease as parameter values increase. Negative non-linearity values indicate a convex curve relationship between the outputs and parameters. If both values are negative, the model outputs decrease along a convex curve with increasing parameter values [24]. The most influential parameter was found in the total fecundity model. The total number of eggs, larvae, pupae, and adults increased as the parameters ω and/or ε increased. Both average effects and non-linearity were observed in our sensitivity results, suggesting that parameter changes can influence the population model in a complex manner.

Increased temperature led to earlier adult peak dates, especially for the summer generations, while decreased temperature delayed the adult peak time (Figure 5).

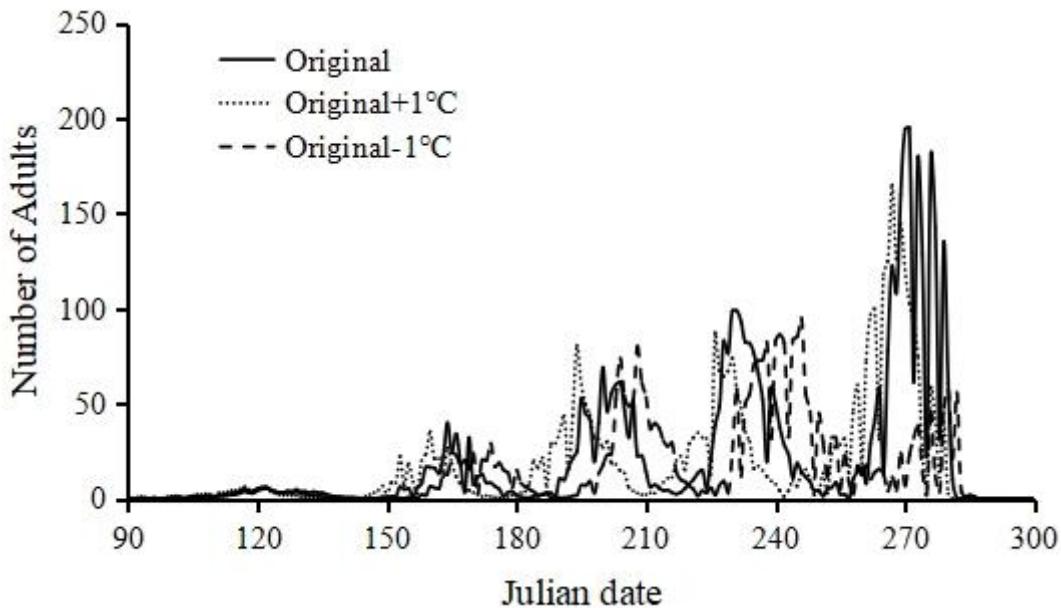


Figure 5. Sensitivity of population model outputs to temperature changes.

4. Discussion

The population model provided a fundamental structure for understanding the population dynamics of *P. ringoniella* in apple orchards. While the model successfully simulated the typical occurrence patterns of *P. ringoniella*, it showed some discrepancies when compared with actual field observations. Specifically, the peak times of each generation, especially the 4th and 5th generations,

differed between the actual data and the simulated results. Additionally, the model tended to overestimate the population sizes of the summer generations, particularly when pesticide and natural enemy effects were not included.

The most influential factors affecting peak times were the parameters of the developmental models. When these models are based on lower and upper threshold temperatures, insect development can be underestimated or overestimated at extreme temperatures [24]. Previous insect population dynamic models have demonstrated that considering micro-environmental weather conditions can significantly improve model accuracy regarding population peak times and sizes [37,38]. Internal temperatures of leaves and fruits can differ from ambient air temperatures by as much as 13-14°C [39,40]. Overestimating these internal leaf temperatures results in a leftward shift in the larval distribution model, leading to earlier peak times for the 3rd generation in this study.

The population occurrence patterns of *P. ringoniella* were estimated under six scenarios. However, the simulated outputs were not sufficient to fully explain actual field observations, because the model incorporated pesticide and natural enemy effects in a simplified manner. To improve the model, factors such as pesticide residue effects, pupae diapause, and adult survival should be included [24].

The present population model demonstrated the typical patterns of *P. ringoniella* population dynamics in apple orchards. Similar temperature-dependent models for other insect species have been reported in previous studies to predict developmental rates [20,21], spring emergences [14,16,17], and population dynamics [15,18]. This model enhances our understanding of the role of a warming climate in the population dynamics and ecology of this insect pest, providing useful guidance for managing this pest species as suggested by Shaffer and Gold (1985) [23].

For a population model to be used as a practical management tool, it must accurately reflect actual observations and predict the timing and number of control procedures [13,23,24]. While the current model can predict adult peak times effectively, further validation is needed to test the model's efficacy in controlling *P. ringoniella* in apple orchards. Consequently, we expect the model to be useful in evaluating new management practices and in estimating population dynamics and abundance changes of *P. ringoniella* in response to climate changes, such as global warming.

Author Contributions: Conceptualization, S.GENG and C.J.; methodology, C.J.; software, L.Q. and S.Guo; validation, Z.Z. and H.T.; formal analysis, S.GENG and L. CHEN; investigation, S.GENG and H.H.; data curation, L.Q.; writing—original draft preparation, S.GENG and H.H.; writing—review and editing, S.GENG and C.J.; visualization, S.Guo; supervision, C.J.; project administration, S.GENG and C.J.; funding acquisition, S.GENG and C.J. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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