

A model for the overwintering process of European grapevine moth *Lobesia botrana* (Denis & Schiffermüller) (Lepidoptera, Tortricidae) populations

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Abstract

The paper deals with the development, parametrization and validation of a phenology model of the overwintering process of European grapevine moth *Lobesia botrana* (Denis & Schiffermüller) populations in northern latitudes. The model is built on diapause and poikilothermic population development theories and represents the phenological events of entries into and emergence from pre-diapause, diapause and post-diapause phases. The rate sum models for pre-diapause and post-diapause development are based on published non-linear temperature dependent rate functions. The rate sum model for diapause, however, is negatively affected by the photoperiod during diapause and positively influenced by the photoperiod at the time of diapause entry. The diapause model is parametrized with 3-year data from 25 locations in Europe and Cyprus, and validated with 1-3 year observations from 18 locations in Europe and California. Despite restrictive assumptions and limitations imposed by weather data recorded at variable distances from the observation sites, and the variable qualities of observation data, the model's predictive and

explanatory capabilities are useful for adaptive pest management and assessments of the invasive potential. The need for controlled experiments is recognized and suggestions are made for improving the model.

Introduction

The polyphagous European grapevine moth [*Lobesia botrana* (Denis & Schiffermüller): Tortricidae] is found in Southern Russia, Japan, the Middle East, the near East, and Northern and Western Africa, and the Mediterranean Basin where it is considered the most important pest of grapes (Savopoulou-Soultani *et al.*, 1990; Venette *et al.*, 2003; Frolov and Saulich, 2005; Thiéry and Moreau, 2005; De Yong, 2010). In 2009, *L. botrana* was discovered in Napa County, California (Varela *et al.*, 2010), and in their prospective analysis of the invasive potential in California, Gutierrez *et al.* (2012) use the extensive European experimental and modeling literature. However, most of these studies focused on population development during the grape growing season and only a few dealt with aspects of diapause during overwintering (Kharazinov *et al.*, 1980; Tzanakakis *et al.*, 1988; Roditakis and Karandinos, 2001; Andreadis *et al.*, 2005).

Annual cycles in resources and unfavorable conditions characterize virtually all biological environments, and according to Nechols *et al.* (1999), insects have developed a set of adaptations that leads to appropriate timing of recurring events in their life cycles. Among them is diapause which is a hormonally mediated state of low metabolic activity associated with reduced morphogenesis, increased resistance to environmental extremes, and altered or reduced behavioral activity. Diapausing stimuli are perceived only during species-specific, genetically determined life stages in response to token environmental cues that precede unfavorable conditions. The life stages with diapause in the life cycle may be different from those responding to diapausing stimuli. Photoperiod and temperature are the most important stimuli.

Diapause development is mainly, but not exclusively, controlled by a combination of temperature and photoperiod (Tauber and Tauber, 1976; Tauber *et al.* 1986; Nechols *et al.*, 1999). According to Leather *et al.* (1993), one of the major functions of temperature is to maintain the condition by acting as a regulatory factor on the rate of diapause development. In many species, the temperature range over which diapause development occurs is different from that for non-diapause development; in such insects, the low optimum temperatures for diapause development ensure that warm autumn conditions do not result in the resumption of development. According to Leather *et al.* (1993), the length of day at the time of induction has no effect on the maintenance or termination of diapause in many insects, while in others the

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conditions prevailing at this point have been shown to affect the duration of the diapause period. Many insects appear to have evolved to take advantage of the seasonal progression of photoperiods during winter, and diapause development often involves responses to a series of photoperiods that exert their influence as diapause proceeds rather than to a single critical photoperiod (Tauber *et al.*, 1986; Leather *et al.*, 1993).

The study is a phenology model for overwintering of *L. botrana* populations across a wide geographical range where the pest may occur. Phenology deals with the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species (Lieth, 1976). The model should have satisfactory predictive and explanatory capabilities and be useful for further developing the population model (*e.g.* Gutierrez *et al.* 2012) by explicitly dealing with overwintering in a wide range of latitudes. Model development, parametrization and validation rely on the efficient use of available information within the conceptual framework provided by the theory of diapause (Leather *et al.*, 1993; Nechols *et al.*, 1999) and the rate sum approach to poikilothermic development formalized by Stinner *et al.* (1974) and Curry and Feldman (1987).

Materials and methods

Model description and initialization

Overwintering process

The *L. botrana* overwintering model starts with diapause induction and represents the development through pre-diapause ($j=1$), diapause ($j=2$) and post-diapause ($j=3$) phases that eventually lead to the emergence and the flight of the adults (Figure 1). With a decrease in the length of day during late summer and fall, eggs and larvae respond increasingly to photoperiod and enter the pre-diapause phase. Newly formed pupae pass first through diapause followed by a post-diapause phase (Gutierrez *et al.*, 2012). Of particular interest in this paper are the first individuals (labeled with subscript b) and the last individuals (labeled with subscript e) stimulated to enter the winter diapause on days D_b and D_e , respectively (*i.e.* cohorts 1 and 2). As poikilotherms, they develop at temperature-dependent rates. In late summer and fall, both cohorts become overwintering diapause pupae

on day DT_b and DT_e with diapause terminated on days DP_b and DP_e , respectively. After passing through the post-diapause phase, the two cohorts emerge as adults on days DF_b and DF_e , respectively. Also of interest is the size of the cohorts entering the pre-diapause phase during the period DD_b - DD_e as these produce the flight patterns of adults during the DF_b - DF_e period.

Diapause induction

Riedl (1983) published data on life cycle of *Cydiapomonella* that showed a linear dependence of the critical length of day (DLc) of diapause initiation on latitude L measured in decimal degrees in California. Specifically, DLc for 50% of the larvae entering diapause is:

$$DL_c = 10.242 + 0.1226 L \quad (1)$$

Roditakis and Karandinos (2001) working at Heraklion with a local *L. botrana* population showed that the diapause depends on length of day (DL). Gutierrez *et al.* (2012) obtained DL values for the beginning and the ending of the diapause induction ($DL_b = 14.15$ h, and $DL_e = 11.98$ h). Assuming that Riedl's (1983) equation can also be applied to *L. botrana* overwintering at different latitudes (L), the length of day for the beginning and the ending of diapause entry (DL_b , DL_e) is:

$$\begin{aligned} DL_b &= A_b + B_b \cdot L \\ DL_e &= A_e + B_e \cdot L \end{aligned} \quad (2)$$

To apply (2) to the Roditakis and Karandinos (2001) data, we have a system of two equations with four unknowns (A_b , B_b , A_e , B_e). In order to solve the system, we assume from Riedl (1983) that $B_b = B_e = 0.1226$. Now, we are able to calculate the numerical values $A_b = 9.83$ and $A_e = 7.66$ and obtain two equations for determining the lengths of day (DL_b , DL_e) at the beginning and the ending of diapause induction:

$$\begin{aligned} DL_b &= 9.83 + 0.1226 \cdot L \\ DL_e &= 7.66 + 0.1226 \cdot L \end{aligned} \quad (3)$$

Once these latitude-dependent day lengths are known, the method of Glarner (2010) can be used to calculate the dates DD_b and DD_e , *i.e.* the latitude-specific Julian days on that cohort 1 (DD_b) and cohort 2 (DD_e) enter pre-diapause development.

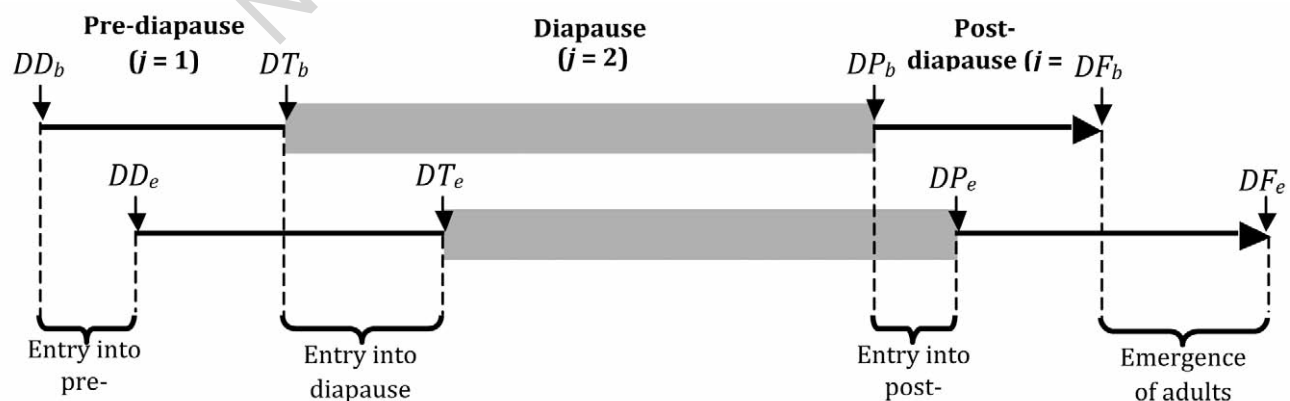


Figure 1. The overwintering phases of *L. botrana* (pre-diapause, diapause, and post-diapause) for cohorts 1 and 2 responding to length of day on days DD_b and DD_e , entering diapause on days DT_b and DT_e , terminating diapause on days DP_b and DP_e , and emerging as adults on days DF_b and DF_e .

Overwintering model

Stinner *et al.* (1974) and Curry and Feldman (1987) represent the duration D_j of a life stage j by the sum rs_j of daily rates $r_j(D)$:

$$rs_j(D) = \sum_{n=1}^{D_j} r_j(D) \quad (4)$$

and state that the stage j is completed once the sum reaches unity ($rs_j(D_j)=1$). For poikilotherms, the developmental rates depend on daily temperatures where $r_j(D)=r_j(T_D)$ where $r_j(T_D)$ is called *rate function* of the j -th stage. Knowledge of the beginning of phase j , the temperature profile during phase j , and the rate function $r_j(T_D)$ allows the emergence on day D_j to be predicted.

Here, this model is applied to the three overwintering phases of *L. botrana* (Figure 1) and different rate functions are used as if these phases were life-stages. In addition, hourly (T_{nd}) rather than daily temperatures are calculated. For $n=24$, the rate sum for the pre-dia-

pause ($j=1$) and post-diapause ($j=3$) phase becomes:

$$rs_j(nD) = \frac{1}{24} \cdot \sum_{b=1}^{D_j} \sum_{n=1}^{24} r_j(T_{nb}) \quad [j \neq 2] \quad (5)$$

For diapausing pupae, however, the development rate, summed up over 24 time increments per day, is modified by photoperiodic effects and the rate sum for the diapause phase ($j=2$) becomes:

$$rs_j(nD, P_0, P_D) = a P_0 + \sum_{b=1}^{D_j} \left[b P_D + \frac{1}{24} \sum_{n=1}^{24} r_j(T_{nb}) \right] \quad [j = 2] \quad (6)$$

where P_0 = photoperiod at the time of entry into diapause (DT_b, DT_e), P_D = photoperiod on the D -th day, a and b = constants. As to the analytical form of $r_j(T_{nd})$ in eqs. 2 and 3, Gutierrez *et al.* (2012) used a modified form of the Brière and Pracros (1998) model to represent

Table 1. Overwintering model for *L. botrana*: data set used for parameter estimation. DD_b and DD_e are the calculated beginnings and endings of the entry into the pre-diapause phase; DF_b and DF_e are the observed beginnings and endings of the first flight; the temperatures for the different weather stations are from Yang *et al.* (2010).

Region		Location with latitude	DD_b, DD_e year, station	Flight data ($DF_b - DD_e$)	Source	
Sachsen (D)	1	Dresden-Radebeul/Coswig 51°06'40"	203, 237	18.04-22.05	Mrs. E. Harbrecht Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie D - 01326 Dresden-Pillnitz	
			2007-2009	07.05-18.06		
	2	Dresden-Pillnitz 51°00'31"	203, 237	16.05-23.06		
			2003-2005	28.04-16.06		
Rheinland-Pfalz (D)	3	Ahr 50°27'53"	202, 237	09.05-11.06	Mr. Fr.-J. Treis Dienstleistungszentrum Ländlicher Raum, D - 54470 Bernkastel-Kues	
			2001-2003	26.04-03.06		
			Mendig*	17.04-08.05		
	4	Bernkastel 49°54'40"	202, 238	10.05-22.06		
			2001-2003	24.04-03.06		
	5	Piesport 49°52'44"	Hahn*	17.04-26.05		
			202, 238	28.04-01.06		
			2004-2006	01.05-02.06		
	Franken (D)	6	Altmansdorf (Sonnenwinkel) 49°56'10"	202, 238	29.04-10.05	http://www.lwg.bayern.de/weinbau/ rebschutz_lebensraum_weinberg/34270/
				2003-2005	03.05-30.05	
Giebelstadt*				04.05-29.05		
7		Castell (Kirchberg) 49°44'34"	200, 238	24.04-27.05		
			2002-2004	23.04-30.05		
			Illesheim*	03.05-31.05		
Bratislava (SK)	8	Modra-Horné 48°20'34"	200, 239	15.04-24.06	Gabel and Mocko (1984)	
			1978-1980	29.04-24.06		
			Bratislava*	23.04-25.06		
North- and Southeastern Switzerland (CH)	9	Wädenswil 47°13'36"	199, 241	21.04-18.06	Dr. H. Hoehn, AGROSCOPE, CH - 8820 Wädenswil	
			2000-2002	30.04-08.06		
	10	Maienfeld (Malans) 47°01'28"	Wädenswil°	10.04-10.06		
			199, 241	30.04-07.06		
Southern Switzerland (CH)	11	Carasso 46°12'15"	2001-2003	24.04-01.06	Dr. M. Jermini, AGROSCOPE, Centro di Ricerca di Cadenazzo, CH - 6594 Contone Mr. L. Colombi, Servizio fitosanitario cantonale CH - 6500 Bellinzona	
			2007-2009	28.04-01.06		
			Chur	28.04-01.06		
	12	Magadino Mezzana 45°51'11"	198, 242	04.04-07.05		
			2007-2009	23.04-16.05		
		Lugano	13.04-22.05			
			12.04-09.05			
			23.04-19.05			
			17.04-07.05			

*Temperatures corrected for altitude; °if not available, data from Zurich.

the developmental rates of eggs and larvae combined, and of non-diapausing pupae. The same model is applied here for simulating the three overwintering phases:

$$r_j(T_{nD}) = \xi_j \frac{\alpha_j (T_{nD} - {}^jT_l)}{1 + \beta_j (T_{nD} - {}^jT_u)} \quad [j = 1, 2, 3] \quad (7)$$

T_{nD} indicates the ambient hourly temperature, and jT_l and jT_u are the phase-specific lower and upper temperature thresholds, respectively, α_j and β_j are phase-specific constants, and ξ_j is a factor changing the developmental rate of the combined egg and larval development (Gutierrez *et al.*, 2012) into the pre-diapause phase. The factor ξ_j is applied to phase $j=1$ and set to 1 for $j \neq 1$.

Model parametrization

Information available

The beginning (DF_b) and the end (DF_e) of the first flight at 25 different locations in Europe and Cyprus were provided by extension services personnel, retrieved from the internet or obtained from the scientific literature (Tables 1 and 2). The information consisted of verbal and written communications, published tables or graphics. All the latitudes were obtained from www.google.com using information provided by the data sources. When available, observations over three consecutive years were used (Tables 1 and 2).

For the overwintering periods of the two cohorts (*i.e.* DD_b , DD_e), daily maximum and minimum temperature from nearby weather stations were retrieved from Yang *et al.* (2010). The cosine intrapopulation

Table 2. Overwintering model for *L. botrana*: data set used for parameter estimation. DD_b and DD_e are the calculated beginnings and endings of the entry into the pre-diapause phase; DF_b and DF_e are observed dates of the beginning and endings of the first flight; the temperatures for the different weather stations are from Yang *et al.* (2010).

Region		Location with latitude	DD_b , DD_e years, station	Flight data ($DF_b - DD_e$)	Source
Emilia-Romagna (I)	13	Carpi 44°46'59"	197, 244 2007-2009 Parma°	06.04-06.05 12.04-14.05 08.04-16.05	Dr. Alda Butturini, Dr. T. Rocco, Servizio fitosanitario regionale, I - 40127 Bologna
	14	San Lodovico di Rio Saliceto 44°47'59"	197, 244 2007-2009 Parma°	08.04-16.05 06.04-28.05 09.04-19.05	
Aquitaine (F)	15	Villeneuve d'Ornon 44°46'20"	197, 244 2007-2009 Agen	03.04-n.a. 09.04-n.a. 06.04-n.a.	Delbac (2010)
Puglia (I)	16	Ruvo 41°07'06"	197, 250	09.04-23.05	Moleas (1979)
			1976-1978 Bari*	05.04-18.04 09.04-23.05	
Ribatejo (P)	17	Lezirão 39°14'10"	198, 255 1985-1987 Lisboa	28.03-26.04 20.03-24.05 27.03-20.05	Gonçalves (1989)
Extremadura (E)	18	San Serván 38°48'06"	198, 256 2006, 2007 Badajoz*	28.03-28.05 28.03-30.05	Martín-Vertedor <i>et al.</i> (2010)
Attiki (GR)	19	Spata 37°57'44"	199, 258 1996-1998 Lamia*	29.03-n.a. 05.04-n.a. 28.03-n.a.	Moschos <i>et al.</i> (2004)
Western and Central Sicily (I)	20	Marsala 37°47'57"	199, 258 2008-2010 Trapani	02.05-21.05 11.04-07.05 n.a.-03.06	Prof. Gaetano Siscaro, University of Catania I - 95123 Catania Dr. Luigi Neri, Assessorato Regionale delle Risorse Agricole e Alimentari I - 93013 Mazzarino
	21	Mazzarino 37°18'20"	199, 260 2008-2010 Enna*	05.05-29.05 18.04-29.05 25.04-19.05	
Southeastern Sicily (I)	22	Ispica 36°47'08"	200, 261	23.04-26.04	
			2008-2010 Gela*	29.04-22.05 26.04-21.05	
	23	Licata 37°06'08"	199, 263	16.05-30.06	
			2008-2010 Gela	21.04-18.05 11.05-28.05	
Andalucia (E)	24	Jerez 36°41'12"	200, 261	12.03-01.04	Del Tio <i>et al.</i> (2001)
			1990-1992 Jerez#	27.03-01.05 07.03-28.04	
Limassol (CY)	25	Pissouri 34°40'00"	203, 268	14.03-9.05	Vassilis (2009)
			2005-2006 Larnaca*	22.03-3.05	

*Temperatures corrected for altitude; °if not available, data from Bologna; #temperature 1989. Available from: http://www.tutiempo.net/en/Climate/Jerez_de_la_Frontera_aeropuerto/84510.htm

method of Bianchi *et al.* (1990) was used to compute hourly temperatures. At some locations (Tables 1 and 2), temperature differences between phenological observation sites and corresponding weather stations were corrected for altitude using an environmental lapse rate of 0.7°C per 100 m, as used by the International Civil Aviation Organization (Aguado and Burt, 2007).

Development of larvae stimulated to become diapause pupae

Based on twice weekly data, Gutierrez *et al.* (2012) estimated that cohorts (e.g. DD_b) completed 5/6 of the combined egg and larval development at the time of entry into diapause (DT_b), and are presumed to

emerge as the first adults on day DF_b (Figure 1). The same pattern is assumed for other cohorts during the period (DD_bDD_e) (Figure 1). This assumption is made because during fall, eggs and young larvae are unlikely to survive pre-diapause development. Estimates of DF_b and DF_e , and on the duration of post-diapause development allows the calculation of DT_b and DT_e . Values for the parameters for the rate sum functions of pre-diapause and post-diapause phase obtained from Gutierrez *et al.* (2012) are listed in Table 3.

Diapause development

The values for β_j are given by Gutierrez *et al.* (2012), while the

Table 3. Developmental rate parameter estimates for the model on overwintering *L. botrana*.

Parameter	Overwintering phases		
	Pre-diapause (mature larvae)* ($j=1$)	diapause (pupae) ($j=2$)	Post-diapause (pupae)* ($j=3$)
α_j	0.00225	3.02579E-04	0.00785
β_j	5	1.5	4.5
iT_l	8.9	7.1	11.5
iT_u	33.0	28.5	33.0
ξ_j	6.0	1.0	1.0
a	n.a.	-3.0258E-06	n.a.
b	n.a.	2.42064E-04	n.a.

*Parameters provided by Gutierrez *et al.* (2012); α , β and ξ are constants of the basic rate sum function; iT_l , iT_u are lower and upper temperature thresholds; a and b are constants for the linear latitude correction; n.a., not applicable.

Table 4. Overwintering model for *L. botrana*: data set used for validation purposes. Predictions of the beginning and the ending of the first flight. DD_b and DD_e are the calculated beginnings and endings of the entry into pre-diapause; DF_b and DF_e are the observed beginnings and endings of the first flight; the temperatures for the different weather stations were obtained from Yang *et al.* (2010).

Region	Location with latitude	DD_b, DD_e year, station	Flight data ($DF_b - DD_e$)	Source
Franken (D)	26 Hammelburg 50°06'55"	202, 238 2005 Giebelstadt*	9.05-30.05	http://www.lwg.bayern.de/weinbau/rebschutz_lebensraum_weinberg/34270/
Rheingau (D)	27 Eltville 50°01'30"	202, 238 2008 Zweibrücken	17.04°	Reineke (2008)
Burgenland (A)	28 Rust 47°48'09"	200, 240 1998 Eisenstadt	28.04-15.05	Polesny <i>et al.</i> (2000)
Moldava (R)	29 Iași 47°09'25"	199, 241 2007 Iași	13.05-08.06	Czacu <i>et al.</i> (2009)
Western Switzerland (CH)	30 Begnins 46°26'31"	198, 242 1997 Genève*	9.04-20.06	Charmillot <i>et al.</i> (1998)
	31 Venthône* 46°18'23"	198, 242 1997 Sion*	2.04-15.06	
Valtellina (I)	32 Albosaggia 46°08'55"	198, 242 1995 Sondrio*	19.04-22.05	Pavese (1996)
Piemonte (I)	33 Ghemme 45°36'03"	198, 243 1995 Novara*	8.05-29.05	
Veneto (I)	34 Colli goriziano 45°57'04"	198, 242 1980 Ronchi dei Legionari*	9.05-2.06	Zangheri <i>et al.</i> (1987)

*Temperatures corrected for altitudes; °only beginning of the first flight.

parameters $\alpha_j, jT_i, jT_u, a, b$ were estimated by simulating the overwintering process for the two cohorts at all the locations and years given in Tables 1 and 2. The values for the parameters $\alpha_j, \beta_j, jT_i, jT_u, a$ and b are obtained as follows. For varying parameter values, the diapause model, applied to the calculated diapause duration at the different locations (Tables 1 and 2) for the two cohorts, yielded different mean rate sums with associated variances. The parameter values producing the smallest coefficient of variation were accepted as model parameter estimates.

Model validation

The intended use of the model has improved understanding of the overwintering process for use in pest emergence forecasting (Rykiel, 1996). Implicitly, the models representing pre-diapause and post-diapause development have been examined by Gutierrez *et al.* (2012), allowing us to focus here on the diapause process. For model validation, we make use of information on DF_b and DF_e at 17 different locations in Europe and one location in California (Tables 4 and 5) and calculate the observed date of diapause termination by means of the post-diapause function described by Gutierrez *et al.* (2012). As in the aforementioned case of model parametrization, the information was provided by extension services personnel, retrieved from the Internet or obtained from the scientific literature. Likewise, an altitude-dependent correction of some data was carried out.

Results

The location-specific days for the beginning (DD_b) and the end (DD_e) of diapause induction are reported in Tables 1, 2, 4 and 5. Across the latitudes, the earliest entries occur during a small time period delimited by the central location 40 ($DD_b=196$) and both the northernmost and southernmost locations ($DD_b=203$). The latest entries occur in a longer period extending from the northernmost locations ($DD_e=237$) to the southernmost location ($DD_e=268$). Table 3 lists the parameters for the overwintering model.

The model for pre-diapause development ($j=1$) predicts the entry into diapause after about 1-3 weeks after DD_b and DD_e at all 18 locations, depending on temperature (eq. 3). According to Figure 2, diapause is terminated in cohort 1 on December 21 at location 42 in Sicily and on February 23 at location 27 in Germany's Rheingau. Cohort 2 terminates diapause between March 19 at location 39 in Portugal and on May 27 at location 29 in Romania. Hence, for cohort 1, the earliest and latest dates of diapause termination are in the southernmost and northernmost regions under study. However, the corresponding extreme dates for diapause termination in cohort 2 are in the westernmost and easternmost European regions under study.

Figure 2 shows the predicted and observed dates for diapause termination at the 18 locations listed in Tables 4 and 5. The average difference between the predicted and the observed diapause duration is

Table 5. Overwintering model for *L. botrana*: data set used for validation purposes. Predictions of the beginning and the ending of the first flight. DD_b and DD_e are the calculated beginnings and endings of the entry into pre-diapause; DF_b and DF_e are the observed beginnings and endings of the first flight; the temperatures for the different weather stations were obtained from Yang *et al.* (2010).

Region	Location with latitude	DD_b, DD_e year, station	Flight data ($DF_b - DD_e$)	Source
Aquitaine (F)	35 Dordogne 45°08'49"	198, 243 2009 Bergerac	8.04-1.06	Maille (2010)
Acquitaine (F)	36 Pessac 44°48'14"	196, 243 2005 Bordeaux	28.04-9.06	Fargeas (2005)
Aquitaine (F)	37 Pont de la Maye 44°46'51"	197, 244 1974 Bordeaux	18.04-6.06	Roehrich <i>et al.</i> (1976)
Lazio (I)	38 Cerveteri 41°59'38"	197, 249 1981 Roma*	7.05-2.06	Cafarelli and Di Cicco (1983)
Northwestern Portugal (P)	39 Arcos de Valdevez 41°50'50"	197, 249 1999 Pedras rubras*	20.03-8.05	Agular <i>et al.</i> (2008)
Macedonia (GR)	40 Kavala 40°56'12"	197, 251 1985 Bitola* (MK)	20.04-01.06	Stavraki <i>et al.</i> (1987)
California (USA)	41 Napa 38°18'17"	198, 257 2009 Napa	19.02.-30.05	Gutierrez <i>et al.</i> (2012)
Sicily (I)	42 Camporeale 37°53'67"	199, 258 2010 Palermo*	30.04-26.05	Prof. Gaetano Siscaro University of Catania I - 95123 Catania Dr. Luigi Neri Assessorato Regionale delle Risorse Agricole e Alimentari I - 93013 Mazarino
	43 Noto 36°53'30"	200, 261 2010 Gela*	26.04-21.05	

*Temperatures corrected for altitudes.

8.3 days for cohort 1 and 21.4 days for cohort 2, respectively. If the observation on day 45 is disregarded, the average difference among the data for cohort 1 is only 6.8 days. Accordingly, eq. 3 is better able to predict diapause development in cohort 1 than in cohort 2. In general, the predicted number of days for cohort 1 are slightly higher than the observed number of days, while the corresponding numbers of days for cohort 2 are scattered around the line of correspondence (Figure 2).

Discussion

The model is based on the diapause theory which states that development is mainly but not exclusively controlled by a combination of temperature and photoperiod (Tauber and Tauber, 1976; Tauber *et al.* 1986; Nechols *et al.*, 1999). Driven by photoperiod and temperature, the model satisfactorily predicts the overwintering of *L. botrana* under the conditions considered in this study. Since satisfactory forecasting on solid theoretical grounds is possible, the model exhibits adequate predictive and explanatory capacities.

The favorable qualification of the model is possible in spite of shortcomings in the data used for model parametrization and validation. First, model development relied primarily on information on the beginnings and the endings of the first flight recorded by pheromone traps. The quality of this information, however, is limited, since pheromone trap catches are negatively affected by adverse weather conditions. Pheromone trap catches represent activities of males and may, therefore, provide more reliable information on flight beginnings than endings. To some extent, this may explain the difference between the quality of the predictions for cohort 1 and cohort 2 (Figure 2). Moreover, the pheromone traps were deployed for supervised pest management rather than research purposes and hence, the observations focused on specific periods rather than on the entire flight period. In many cases, the time resolution of the observations was imprecise making it difficult to estimate the beginning and the end of flights. Since vineyards are generally set up in environments favorable for grape production, we assume that the temperature experienced by *L. botrana* is higher than those recorded even after the altitude correction. The quality of the temperature data is further limited by the variable distances between the weather stations and vineyards being monitored. The correction of temperatures is particularly important since it may influence the temperature range for diapause development discussed below. Biased temperature data may also explain the deviation of location 42 from the line of corresponding observations and predictions in Figure 2. Furthermore, the effects of adverse weather on flight activities, the quality of observations and the difference between vineyard and weather station temperatures may have varied through time. This would also help explain the difference in the quality of the predictions for the flights of the two cohorts (Figure 2).

The model has been developed on the basis of restrictive, albeit plausible assumptions. First, we assumed that the response seen in *C. pomonella* to latitude (Riedl, 1983) can be used as a model for *L. botrana*. Next, we assumed that both cohorts consist exclusively of mature larvae that do not suffer from overwintering mortality and successfully pass the pre-diapause, diapause and post-diapause phases. To be able to use the information available for modeling the population phenology, we had to assume that male trap catches were related to population densities. Finally, the model for diapause development assumes only additive effects of temperature and photoperiods and disregards possible interactions.

The northernmost and southernmost locations considered for model parametrization and validation are Dresden-Radebeul/Coswig at 51°06'40" and Pissouri at 34°40'00" (Tables 1 and 2). The former

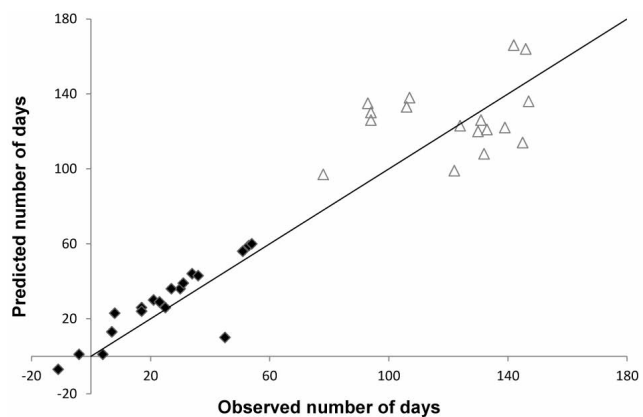


Figure 2. Validation of the diapause model for *L. botrana*: observed and predicted days for diapause termination for the first (filled diamonds) and the last (empty triangles) cohort of pupae entering diapause at different geographical locations (the reference day is 1 January, the 45 degree line represents correspondence between observed and predicted values, observed days' refer to the dates obtained by subtracting post-diapause development from observations on the beginning and the end of the first flight).

location may be at the limit of the distribution in the north (Frolov and Saulich, 2005; De Yong, 2010). Portuguese locations in the West and Cypriot locations in the East further delimitate the palaeartic area providing information for model parametrization and validation. The literature suggests, however, that the explicit consideration of other environmental factors may be needed when dealing with locations outside this area. For example, the distribution in the Palaearctic extends further to the south and towards desert environments than taken into account in this paper (Al-Zyoud and Elmosa, 2001; El-Wakeil *et al.*, 2009). For these areas, it may be necessary to build the effect of relative humidity explicitly into the overwintering model. In Israel, Rakefet *et al.* (2009) reported a significant effect of cultivars on the numbers of trapped males and a cultivar effect on female host choice. In this case, the explicit consideration of host plant effects may be necessary for obtaining satisfactory forecasts. Sciarretta *et al.* (2008) studied the spatial distribution of pheromone trap catches in Mediterranean landscape. Since a time-varying part of the population inhabits areas outside vineyards, an explicit consideration of a wide range of plant species and movements between vineyards and their surroundings may improve predictive and explanatory model capabilities.

The explanatory capabilities of the model allow us to tentatively assign *L. botrana* to an insect diapause type characterized by temperature and photoperiod influence on diapause development (Leather *et al.*, 1993). In comparison to pre- and post-diapausing individuals (Table 3), the pattern of the diapause development rates occurs in a slightly lower temperature range (the lower threshold β_2 is smaller than the thresholds β_1 and β_3 , Table 3) and the temperature allowing fastest development is shifted towards lower temperatures. A shift of the temperature range for diapause development has been recorded for other insects and may prevent individuals from resuming development under warm autumn conditions (Nechols *et al.*, 1999). The sensitivity to the photoperiod at the time of entry into diapause is known for other insects (Leather *et al.* 1993). To verify these assumptions, to study alternative models for representing photoperiodic and temperature influences, and to explicitly include other environmental factors and ascertain the shift in the temperature response curve, observations from other sites may be useful. To overcome the limitations of observation and temperature data, specific measurements should be to provide more reliable data for model development.

More promising for model improvements, however, are experiments under controlled conditions, possibly complemented with gas exchange measurements (Kharizanov *et al.*, 1980).

In conclusion, the conceptual framework provided by diapause theory (Leather *et al.*, 1993; Tauber and Tauber, 1976; Tauber *et al.*, 1986; Nechols *et al.*, 1999) and the rate sum approach to poikilothermic development formalized by Stinner *et al.* (1974) and Curry and Feldman (1987) allowed efficient use of existing data and yielded a model with satisfactory explanatory and predictive capacities. The predictive capabilities are considered sufficient to allow the model to be used as part of an adaptive vineyard pest management system (Rigamonti *et al.*, 2011), while predictive and explicative capabilities are satisfactory for considering the model as a component in the ongoing prospective analysis of the invasive potential of this pest (Gutierrez *et al.*, 2012).

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