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-Soutani 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. Diapauasing 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 diapauasing 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...
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 *DDb* and *DDe*, respectively (i.e. cohorts 1 and 2). As poikilothersms, they develop at temperature-dependent rates. In late summer and fall, both cohorts become overwintering diapause pupae on day *DTb* and *DT*, with diapause terminated on days *DPb* and *DP*, respectively. After passing through the post-diapause phase, the two cohorts emerge as adults on days *DFb* and *DF*, respectively. Also of interest is the size of the cohorts entering the pre-diapause phase during the period *DDb*-*DD*, as these produce the flight patterns of adults during the *DFb*-*DF* 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:

\[
DLc = 10.242 + 0.1226 \times L
\]

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 (DLb = 14.15 h, and DLc = 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 (*DLb*, *DLc*) is:

\[
DLb = A_b + B_b \times L
\]

\[
DLc = A_e + B_e \times L
\]

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

\[
DLb = 9.83 + 0.1226 \times L
\]

\[
DLc = 7.66 + 0.1226 \times L
\]

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

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

$$r_s j = \sum_{i=1}^{D_j} r_j$$  \hspace{1cm} (4)

and state that the stage $j$ is completed once the sum reaches unity ($r_s j (D_j) = 1$). For poikilotherms, the developmental rates depend on daily temperatures where $r_j(D) = r_j(T_D)$ 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 ($T_n D$) rather than daily temperatures are calculated. For $n=24$, the rate sum for the pre-diapause ($j=1$) and post-diapause ($j=3$) phase becomes:

$$r_s j(nD) = \frac{1}{24} \sum_{i=1}^{nD} r_j(T_{nD}) \hspace{1cm} (j=2)$$

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:

$$r_s j(nD, P_0, P_D) = a P_0 + \sum_{i=1}^{nD} r_j(T_{nD}) \hspace{1cm} (j=2)$$

where $P_0$ = photoperiod at the time of entry into diapause ($D_{b}$, $D_{e}$), $P_D$ = 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. $D_{b}$ and $D_{e}$ are the calculated beginnings and endings of the entry into the pre-diapause phase; $D_{f}$ and $D_{F}$, 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 | $D_{b}$, $D_{e}$ | Flight data | Source                                      |
|-----------------|------------------------|------------------|-------------|---------------------------------------------|
| Sachsen (D)     | Dresden-Radebeul/Coswig 51°00'40" 2007-2009 Dresden-Pillnitz 51°06'40" 18.04-22.05 | 203, 237 | 02.05-18.06 | Mrs. E. Harbrecht                             |
|                 | 2 Dresden-Pillnitz 51°00'31" 2003-2005 Dresden-Pillnitz 51°06'40" 12.05-22.06 | 203, 237 | 02.05-18.06 | Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie |
|                 | Rheinland-Pfalz (D) 50°27'53" 2001-2003 Ahr 50°27'53" 09.05-11.06 Meidig* | 202, 237 | 09.05-11.06 | Mr. Fr.-J. Treis                              |
|                 | 4 Bernkastel 49°54'40" 2001-2003 Bernkastel 49°54'40" 10.05-22.06 Hahn* | 202, 238 | 10.05-22.06 | Dienstleistungszentrum Ländlicher Raum, Bernkastel-Kues |
|                 | 5 Piesport 49°52'44" 2004-2006 Piesport 49°52'44" 28.04-01.06 Hahn* | 202, 238 | 28.04-01.06 | D - 0136 Dresden-Pillnitz                     |
|                 | Franken (D) 49°56'10" 2003-2005 Altmannsdorf (Sonneneinzel) 49°56'10" 29.04-10.05 Giebelstadt* | 202, 238 | 29.04-10.05 | http://www.lwg.bayern.de/weinbau/    |
|                 | 7 Castell (Kirchberg) 49°44'34" 2002-2004 Castell (Kirchberg) 49°44'34" 24.04-27.05 Illesheim* | 202, 238 | 24.04-27.05 | rebschutz_liebensraum_weinberg/34270/       |
|                 | Bratislava (SK) 48°20'34" 1978-1980 Modra-Horné 48°20'34" 15.04-24.06 Bratislava* | 200, 239 | 15.04-24.06 | Gabel and Mocko (1984)                        |
|                 | North-and Southeaster Switzerland (CH) 47°13'36" 2000-2002 Wädenswil 47°13'36" 21.04-18.06 | 199, 241 | 21.04-18.06 | Dr. H. Hoehn, AGROSCOPE, CH - 8820 Wädenswil |
|                 | 10 Maifenfeld (Malans) 47°01'28" 2001-2003 Maifenfeld (Malans) 47°01'28" 24.04-27.05 | 199, 241 | 24.04-27.05 | Chur                                        |
|                 | Southern Switzerland (CH) 46°12'15" 2007-2009 Carasso 46°12'15" 04.04-07.05 Magadino | 198, 242 | 04.04-07.05 | Dr. M. Jermini, AGROSCOPE, Centro di Ricerca |
|                 | 12 Mezzana 45°31'11" 2007-2009 Mezzana 45°31'11" 23.04-19.05 Lugano | 198, 242 | 23.04-19.05 | di Cadenazzo,CH - 6594 Contone Mr. L. Colombi, Servizio fitosanitario cantonale CH - 6508 Bellinzona |

*Temperatures corrected for altitude; °if not available, data from Zurich.
the developmental rates of eggs and larval development, and of non-diapausing pupae. The same model is applied here for simulating the three overwintering phases:

\[ r_j(T_{ad}) = \xi_j \left( \frac{\alpha_j(T_{ad} - T_L)}{1 + \beta_j(T_{ad} - T_U)} \right) \quad [j = 1, 2, 3] \]  

(7)

\( T_{ad} \) indicates the ambient hourly temperature, and \( T_L \) and \( T_U \) are the phase-specific lower and upper temperature thresholds, respectively, \( \alpha_j \) and \( \beta_j \) are phase-specific constants, and \( \xi_j \) is a factor changing the developmental rate of the combined egg and larval development (Gutiérrez et al., 2012) into the pre-diapause phase. The factor \( \xi_j \) is applied to phase \( j=1 \) and set to 1 for \( j\neq1 \).

### 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 intrapolation

| Region | Location with latitude | \( DD_b, DD_e \) years, station | Flight data (\( DF_b - DD_b \)) | Source |
|--------|------------------------|-------------------------------|--------------------------------|--------|
| Emilia-Romagna (I) | | | | |
| 13 Carpi 44°46'59" | 197, 244 2007-2009 Parma* | 06.04-23.05 08-16.05 | Dr. Alda Butturini, Dr. T. Rocco, Servizio fitosanitario regionale, 1 - 40127 Bologna |
| 14 San Lodovico di Rio Saliceto 44°47'59" | 197, 244 2007-2009 Parma* | 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. 06.04-28.05 | Delbac (2010) |
| Puglia (I) | | | | |
| 16 Ruvo 41°07′06″ | 197, 250 1976-1978 Bari* | 09.04-23.05 |
| Ribatejo (P) | | | | |
| 17 Lezirão 39°14′10″ | 198, 255 1995-2000 Lisboa | 20.05-24.05 |
| Extremadura (E) | | | | |
| 18 San Serván 38°48′06″ | 198, 256 2006, 2007 Badajoz* | 28.03-28.05 28.03-30.05 | Martin-Vertedor et al. (2010) |
| Attiki (GR) | | | | |
| 19 Spata 37°37′44″ | 199, 258 1996-1998 Lamia* | 05.04-06.04 28.03-28.05 | Moschos et al. (2004) |
| Western and Central Sicily (I) | | | | |
| 20 Marsala 37°47′57″ | 199, 258 2008-2010 Trapani | 02.05-21.05 11.04-07.05 | Prof. Gaetano Siscaro, University of Catania I - 95123 Catania Dr. Luigi Neri, Assessoreto Regionale delle Risorse Agricole e Alimentari I - 93013 Mazzarino |
| 21 Mazzarino 37°18′20″ | 199, 260 2008-2010 Enna* | 05.05-29.05 18.04-20.05 25.04-19.05 |
| Southeastern Sicily (I) | | | | |
| 22 Ispica 36°47′08″ | 200, 261 2008-2010 Gela* | 23.04-26.04 11.05-28.05 |
| 23 Licata 37°06′08″ | 199, 263 2008-2010 Gela | 26.04-21.05 18.04-20.05 |
| Andalucia (E) | | | | |
| 24 Jerez 36°41′12″ | 200, 261 1996-1992 Jerez* | 12.03-01.04 27.05-01.05 07.03-28.04 | Del Tio et al. (2001) |
| Limassol (CY) | | | | |
| 25 Pissouri 34°40′00″ | 203, 268 2008-2006 Larnaca* | 14.03-9.05 22.03-3.05 | Vassilis (2009) |

*Temperatures corrected for altitude; °if not available, data from Bologna; #temperature 1989. Available from: http://www.tutiempo.net/en/Climat/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 ($DD, DD_e$) (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 $DFe$, 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 $\beta$, are given by Gutierrez et al. (2012), while the

| Parameter | Pre-diapause (mature larvae)* ($j=1$) | Overwintering phases diapause (pupae) ($j=2$) | Post-diapause (pupae)* ($j=3$) |
|-----------|-----------------------------------|-----------------------------------------------|-------------------------------|
| $\alpha_j$ | 0.00225 | 3.0257E-04 | 0.00785 |
| $\beta_j$ | 5 | 1.5 | 4.5 |
| $T_l$ | 8.9 | 7.1 | 11.5 |
| $T_u$ | 33.0 | 28.5 | 33.0 |
| $\xi_j$ | 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); $\alpha$, $\beta$ and $\xi$ are constants of the basic rate sum function; $T_l$, $T_u$ 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 | $DD_b$, $DD_e$ year, station | Flight data ($DF_b$, $DD_e$) | Source |
|--------|----------|-----------------------------|-----------------------------|--------|
| Franken (D) | Hammelburg 50°06’55" | 2002, 238 | 9.05-30.05 | http://www.lwg.bayern.de/weinbau/ rebschutz_lebensraum_weinberg/4270/ |
| Rheingau (D) | Eltville 50°01’30’ | 2002, 238 | 17.04° | Reineke (2008) |
| Burgenland (A) | Rast 47°48’09" | 2002, 238 | 28.04-15.05 | Polesny et al. (2000) |
| Moldava (R) | Iași 47°09’25” | 199, 241 | 13.05-08.06 | Cazacu et al. (2009) |
| Western Switzerland (CH) | Begins 46°26’31” | 198, 242 | 9.04-20.06 | Charmillot et al. (1998) |
| | Venthône* 46°18’23” | 198, 242 | 2.04-15.06 | |
| Valtellina (I) | Albosaggia 46°08’35” | 198, 242 | 19.04-22.05 | Pavese (1996) |
| Piemonte (I) | Ghemme 45°36’03” | 198, 242 | 8.05-29.05 | |
| Veneto (I) | Colli goriziano 45°57’04” | 198, 242 | 9.05-2.06 | Zangheri et al. (1987) |

*Temperatures corrected for altitudes; °only beginning of the first flight.
parameters $\alpha_j$, $\beta_j$, $T_{jTl}$, $T_{jTu}$, $a$, and $b$ 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 $\alpha_j$, $\beta_j$, $T_{jTl}$, $T_{jTu}$, $a$, 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.

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 ($DF_b$ – $DF_e$) | Source                        |
|------------------|------------------------|------------------------------|-------------------------------|-------------------------------|
| Aquitaine (F)    | Dordogne 45°08'49"     | 198, 243 2009 Bergerac     | 8.04-1.06                     | Maille (2010)                |
| Aquitaine (F)    | Pessac 44°48'14"       | 196, 243 2005 Bordeaux      | 28.04-9.06                    | Fargeas (2005)               |
| Aquitaine (F)    | Pont de la Maye 44°46'51" | 197, 244 1974 Bordeaux   | 18.04-6.06                    | Roehrich et al. (1976)       |
| Lazio (I)        | Cerveteri 41°59'38"    | 197, 249 1981 Roma*         | 7.05-2.06                     | Cafarelli and Di Cicco (1983) |
| Northwestern     | Arcos de Valdevez 41°50'30" | 197, 249 1999 Pedras rubras* | 20.03-8.05                    | Agular et al. (2008)         |
| Portugal (P)     | Kavala 40°56'12"       | 197, 251 1985 Bitola* (MK)  | 20.04-0.06                    | Stavraki et al. (1987)       |
| California (USA) | Napa 38°18'17"         | 198, 257 2009 Napa          | 19.02-30.05                   | Gutierrez et al. (2012)      |
| Sicily (I)       | Camporeale 37°53'67"   | 199, 258 2010 Palermo*      | 30.04-26.05                   | Prof. Gaetano Siscaro        |
|                  | Noto 36°53'30"         | 200, 261 2010 Gela*         | 26.04-21.05                   | University of Catania 1 - 95123 Catania |

*Temperatures corrected for altitudes.

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 ($DD_b=237$). The latest entries occur in a longer period extending from the northernmost locations ($DD_b=237$) to the southernmost location ($DD_b=268$). Table 3 lists the parameters for the overwintering model.
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 parameterization 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 photoperiod and disregards possible interactions.

The northernmost and southernmost locations considered for model parameterization and validation are Dresden-Radebeul/Coswig at 51°06’40” and Pissouri at 34°40’00” (Tables 1 and 2). The former 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 Palaearctic area providing information for model parameterization 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 tends 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 β2 is smaller than the thresholds β1 and β3, 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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