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Multiannual infestation patterns of grapevine plant inhabiting *Scaphoideus titanus* (Hemiptera: Cicadellidae) leafhoppers

Q1

Ivo E. Rigamonti, Valeria Trivellone, Mauro Jermini, Daniele Fuog, Johann Baumgärtner

Abstract—The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae) was accidentally introduced in Europe, where it became the vector of the 'Candidatus Phytoplasma vitis' phytoplasma causing the 'Flavescence dorée' disease of grapevine plants. A time-varying distributed delay model, simulating the successive occurrences of egg hatching, nymph presence, and adult emergence, is extended here to represent multi-generation infestation patterns of grapevine plants inhabited by eggs, nymphs, and adults. The model extension includes intrinsic mortality, mortality caused by plant dormancy, and low temperatures, development of diapausing and post-diapausing eggs, fecundity rates, and adult longevity. Field observations and published data were used to estimate parameters. The model was validated with five years canopy infestation data from five vineyards not subjected to insecticide treatments and found to have satisfactory explicative and predictive qualities. The model output is most sensitive to a 10% variation in the upper threshold and in the shape parameters of the survivorship function and least sensitive to a 10% variation in the shape parameters of the development function and the survivorship level. Recommendations are made to take into account other factors than temperature and plant phenology and include a wider geographical area in further model development.

Résumé—La cicadelle néarctique *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae) a été introduite accidentellement en Europe dans les années '50, où elle est devenue le vecteur du « Candidatus Phytoplasma vitis » responsable de la maladie de Flavescence dorée de la vigne. Un modèle de délai distribué dans le temps (time-varying distributed delay model), simulant les évènements successifs des éclosions, de la présence des stades juvéniles et de l'émergence des adultes, a été étendu pour représenter les niveaux d'infestation multi-générationnels de la vigne colonisée par des œufs, des nymphes et des adultes. L'extension du modèle inclut la mortalité intrinsèque, la mortalité causée par la dormance de la plante et les basses températures, le développement des œufs diapausants et post-diapausants, les taux de fécondité et la longévité des adultes. Les observations au champ et les données publiées ont servi de base pour l'estimation des paramètres du modèle. Le modèle a été validé avec les données de cinq années d'infestation de la haie foliaire de cinq vignobles sans traitements insecticides et il a montré des qualités explicatives et prédictives satisfaisantes. Le résultat du modèle est plus sensible à une variation de 10% dans le seuil supérieur et dans les paramètres de forme de la fonction de survie et moins sensible à une variation de 10% dans les paramètres de forme de la fonction de développement et du niveau de survie. Des recommandations sont faites pour prendre en compte d'autres facteurs que la température et la phénologie de la plante et inclure un plus large éventail de zones géographiques pour un développement ultérieur du modèle.

I.E. Rigamonti,[1] DeFENS, Università degli Studi di Milano. Via G. Celoria, 2, I-20133 Milan, Italy

V. Trivellone, M. Jermini, Research Station Agroscope Changins – Wädenswil ACW, Centro di Ricerca di Cadenazzo (TI). A Ramél, 18, CH-6593 Cadenazzo, Switzerland

D. Fuog, Syngenta Crop Protection AG. Postfach 4002 Basel, Switzerland

J. Baumgärtner, Center for the Analysis of Sustainable Agricultural Systems (CASAS), Kensington (CA) 94707 United States of America

[1]Corresponding author (e-mail: ivo.rigamonti@unimi.it).

Introduction

The Nearctic leafhopper *Scaphoideus titanus* Ball (Hemiptera: Cicadellidae) was accidentally introduced in Europe in the 1950s (Bonfils and Schvester 1960; Schvester *et al*. 1961). Southwestern and southern European grapevine growing areas were invaded before southeastern European regions that were colonised in the past decade only (Magud and Toševski 2004; Budinščak *et al*. 2005; Zeisner 2005; Der *et al*. 2007; Avremov *et al*. 2011; Chireceanu *et al*. 2011). Currently, *S. titanus* occurs through most of southern Europe, from Portugal to Romania and Bulgaria, but the area of distribution is still expanding.

Scaphoideus titanus is the vector of the 'Candidatus Phytoplasma vitis', a Phytoplasma of the Elm Yellows or 16Sr-V group, an A2 quarantine pest for EPPO causing the Flavescence dorée (FD), an economically very important grapevine plant disease displaying a crisis-recovery-relapse cycle (European and Mediterranean Plant Protection Organization/Commonwealth Agricultural Bureau International 1996). In an area newly invaded by *S. titanus*, FD infestations follow with a time delay of several years if vector control measures are undertaken and less if not (Steffek *et al*. 2007). Once present, the number of FD infected vine plants may increase tenfold every year and reach 80–100% within a few years, if no insect control is undertaken (European and Mediterranean Plant Protection Organization/Commonwealth Agricultural Bureau International 1996).

For these reasons, *S. titanus* control in FD uninfected vineyards and both *S. titanus* and FD control in FD-infected vineyards have become important components of vineyard pest management systems since the 1960s (Carle and Schvester 1964). In FD-infected areas, both the disease and the vector are usually subjected to compulsory control measures, including mandatory insecticide sprayings and mandatory uprooting of symptomatic vines and abandoned vineyards. Despite these measures, the FD is still spreading through southern Europe. In the last 10 years, new FD outbreaks have been reported from Serbia (Duduk *et al*. 2004), Switzerland (Gugerli *et al*. 2006), Slovenia (Seljak and Orešek 2007), Portugal (De Sousa *et al*. 2010), Romania (Irimia *et al*. 2010), Croatia (Šeruga Musić *et al*. 2011), and Austria (Reisenzein and Steffek 2011).

Efficient management strategies and tactics target *S. titanus* densities and disease transmitting capacities by delaying the spread of FD infections, halting an ongoing FD epidemics and retarding an FD relapse. To increase the efficiency of *S. titanus* control, Rigamonti *et al*. (2011) took into account the univoltine development and designed a phenology model simulating the successive occurrences of egg hatching, of nymphal instar presence and adult emergence. From the standpoint of supervised pest control, the model became a useful tool for the adaptive management of populations inhabiting vineyards in southern Switzerland (Jermini *et al*. 2013; Prevostini *et al*. 2013). The focus on the period from egg hatching to adult emergence takes into account an important part of the dynamics of *S. titanus* but has limitations when seeking better insight into within- and between-generation processes to design integrated pest management systems on solid ecological ground. Specifically, the model by Rigamonti *et al*. (2011) excludes diapause development of overwintering eggs as well as adult survival and reproduction.

The scope of this paper is to design, parametrise, and validate an age-structured multigeneration model representing multiannual infestation patterns of *S. titanus* populations. The model is based on theories on poikilothermic development and age-structured population dynamics that determine the explicative properties of the model. Field observations and published data provide the basis for model parameter estimation. Since the purpose of the model is to represent multiannual infestation patterns, model validation procedures test the model's predictive capabilities by comparing simulated patterns with long-term grapevine plant infestation data. In addition, the sensitivity of the final output to model parameter changes is tested for guiding future research work.

Methods

Scaphoideus titanus is a univoltine species whose individuals pass through different life stages according to the insect poikilothermic development mode in temperate countries: the eggs hatch in spring and the egg stage is followed by five nymphal instars that, in summer, develop into adults. Eggs overwinter in diapause, which is a state of low activity associated with reduced morphogenesis,

increased resistance to environmental extremes, and altered or reduced behavioural activity, mediated by hormones (Nechols *et al.* 1999). Diapause is mainly but not exclusively controlled by a combination of temperature and photoperiod (Tauber and Tauber 1976; Tauber *et al.* 1986; Leather *et al.* 1993; Nechols *et al.* 1999). Nevertheless, we focus on temperature as driving variable for diapause development.

In the present model, the development of *S. titanus* has been divided into four morphologically and physiologically different life stages (nymphs, adults, diapausing eggs, post-diapausing eggs). To facilitate model description and provide easy access to the supportive literature, the following methodological sections briefly refer to (1) stochastic cohort development, (2) poikilothermic cohort development with model parameter estimation, (3) simulation model development, (4) validation, and (5) sensitivity probe.

Stochastic cohort development

If the variability in developmental time is high relative the mean developmental time, a stochastic model may be appropriate to model cohort development (Di Cola *et al.* 1999). The time-varying distributed delay of Vansickle (1977) is applied to model the development of *S. titanus* nymphs ($j = 1$), adults ($j = 2$), diapausing eggs ($j = 3$), and post-diapausing eggs ($j = 4$). Manetsch (1976), Plant and Wilson (1986), Di Cola *et al.* (1999), and Severini (2009) contributed to the development of the distributed delay theory in an ecological context. In Manetsch's (1976) and Vansickle's (1977) notation, the model applied to the *j*-th life stage is represented by:

$$\frac{dr_{ji}(t)}{dt} = \frac{k_j}{DEL_j(t)} \left[r_{ji-1}(t) - r_{ji}(t) \left(1 + AR_j(t) \frac{DEL_j(t)}{k_j} + \frac{d\,DEL_j(t)}{k_j dt} \right) \right]$$

(1)

$$j = 1, 2, 3, 4$$

$$i = 1, 2, \ldots, k_j$$

where t is time (days), $r_{ji}(t)$ is the transition rate of the *i*-th substage in the *j*-th life stage, k_j is the number of delay substages in the *j*-th life stage, $DEL_j(t)$ is the time dependent developmental time (days) in absence of losses in the *j*-th life stage, and

$AR_j(t)$ is the time dependent proportional changes or attrition in the *j*-th life stage. In the case under study, the entry rate $r_{11}(t)$ into the nymphal stage is represented by an initialisation function in the first year and by the exit rate of the post-diapausing eggs in the succeeding years. The exit rate of the nymphal stage becomes the entry rate $r_{21}(t)$ into the adult stage; the oviposition is the entry rate $r_{31}(t)$ into the diapausing eggs stage, whose exit rate is the entry rate $r_{41}(t)$ into post-diapausing egg development.

According to Manetsch (1976) and Vansickle (1977), the occurrence $Q_j(t)$ of each life stage can be obtained from

$$Q_j(t) = \sum_{i=1}^{k_j} \frac{DEL_j(t)}{k_j} r_{ji}(t)$$

(2)

For constant conditions, Vansickle (1977) defines the relationships between k_j, DEL_j and AR_j as follows:

$$k_j = \frac{\mu_j^2}{s_j^2}$$

(3a)

$$DEL_j = \mu_j \, \varepsilon_j^{\left(-\frac{1}{k_j} \right)}$$

(3b)

$$AR_j = k_j \left[\frac{1}{\mu_j} - \frac{1}{DEL_j} \right]$$

(3c)

where μ_j is the observed developmental time, s_j^2 is the variance, and ε_j is the stage-specific survival.

Poikilothermic cohort development

Developmental rates and variance. Between the stage-specific lower ^jT_l and the upper ^jT_u thresholds, the developmental rate $z_j(T)$ of nymphs and diapausing eggs, and the senescence rate of adults is represented by the curvilinear model of Brière *et al.* (1999). However, a linear model is used to describe the developmental rate of post-diapausing eggs above the lower and below the upper thresholds; if $^4T_l > T > {}^4T_u$, the rate $z_4(T)$ is equal to 0.001:

$$0.01 \leq z_j(T) = \alpha_j \, T \, (T - {}^jT_l) \left({}^jT_u - T \right)^{\beta_j}$$
$$\text{for } j = 1, 2, 3 \quad (4a)$$

$$0.001 \leq z_j(T) = \alpha_j (T - {}^jT_l) \quad \text{for } j = 4 \quad (4b)$$

where α_j and β_j are parameters. For nymphs and post-diapausing eggs, the estimation procedures and the values for α_j, β_1, ^jT_l, ^jT_u are given in

Rigamonti *et al.* (2011). For adults, Bressan *et al.* (2005) provide data on the senescence rate and associated variance at 26 °C; at temperatures different from 26 °C, the senescence rate is assumed to be proportional to the developmental rate of nymphs (Table 1). Post-diapause development time of eggs was estimated to be 196.6-day degrees above the lower and below the upper thresholds (Rigamonti *et al.* 2011). The inverse of 196.6 is equal to α_4 reported in Table 1. For diapausing eggs, the development rate parameters α_3, β_3 ^3T_l, and ^3T_u were calculated as follows.

To initialise the model, a cumulative Weibull frequency distribution was fitted to the normalised egg hatching data observed in cages set up in 2008 in a vineyard located at Contone, southern Switzerland (Rigamonti *et al.* 2011). The post-diapause development time of 196.6 day-degrees and the Weibull frequency distribution given in Rigamonti *et al.* (2011) allow the calculation of the calendar days on which 0.1%, 25%, 50%, 75%, and 99.9% of egg groups terminated diapause in 2008. The below described simulation model was used to calculate the cumulative oviposition patterns and obtain the calendar days on which 0.1%, 25%, 50%, 75%, and 99.9% of egg groups entered diapause in the preceding year (2007). For each of the five groups, the duration (days) from diapause entry to diapause termination can be computed. Importantly, for each group the respective rate sum detailed by Curry and Feldman (1987) can be calculated. Accordingly, the fraction d_t of the mean development that has occurred after D days is:

$$d_t = \frac{1}{n} \sum_{s=1}^{nD} z(T_s) \tag{5}$$

where $n = 24$ time increments per day, T_s is the discrete environmental temperature measurements for the s-th time increment obtained at the nearby Magadino weather station, nD is the number of increments in D days. Once d_t is equal to 1 the development of a life stage is completed. Using initially α_1 for α_3, different combinations of β_3, ^3T_l and ^3T_u produced different group means and variances. The smallest coefficient of variability among the group means yielded the estimates for β_3, ^3T_l and ^3T_u, while α_3 was finally obtained by equating the sum of equation [4a] equal to 1. The parameter values for the stage-specific developmental rates for all life stages are

Table 1. Parameter estimates for the time varying distributed delay-based model simulating the pluriannual infestation patterns of *Scaphoideus titanus* on grapevine plants, with reference to the relevant equations detailed in the text

Parameter Life stage	Substages equation [3a] k	Development and senescence rate equation [4] α	β	T_l	T_u	Stage-specific survivorship equation [6] λ	ξ	ζ	Relative reproductive potential equation [7] φ	ϕ	τ	Fecundity at 26 °C
1. Nymphs	13[a]	1.91E-05[a]	0.5[a]	8.7[a]	40[a]	1.996E-04[c]	1.5[c]	1.5[c]				
2. Adults (females)	8[d]	1.09E-05[a]	0.5[a]	8.7[a]	40[a]	1.996E-04[c]	1.5[c]	1.5[c]	2.611E-04[c]	1.5[c]	1.5[c]	14.58[d]
3. Diapausing eggs	25[c]	6.86E-08[b]	1.25[b]	0[b]	28[b]	na	na	na				
4. Post-diapausing eggs	25[c]	5.09E-03[b]	na	8.7[a]	40[a]	1.996E-04[c]	1.5[c]	1.5[c]				

[a] Obtained from Rigamonti *et al.* (2011).
[b] Obtained in this paper from field experiments.
[c] Obtained from expert opinions.
[d] Obtained from Bressan *et al.* (2005).
na = not applicable.

Fig. 1. Illustration of temperature-dependent developmental rates for diapausing eggs, post-diapausing eggs, nymphs, and senescence rates of adults of the grape leafhopper *Scaphoideus titanus*. In the temperature range delimited by the lower and upper thresholds a linear model was applied to post-diapausing eggs, while the curvilinear model of Brière *et al.* (1999) was used for all other life stages (the parameter estimates are given in Table 1, the developmental rates below and above the thresholds are given in the text).
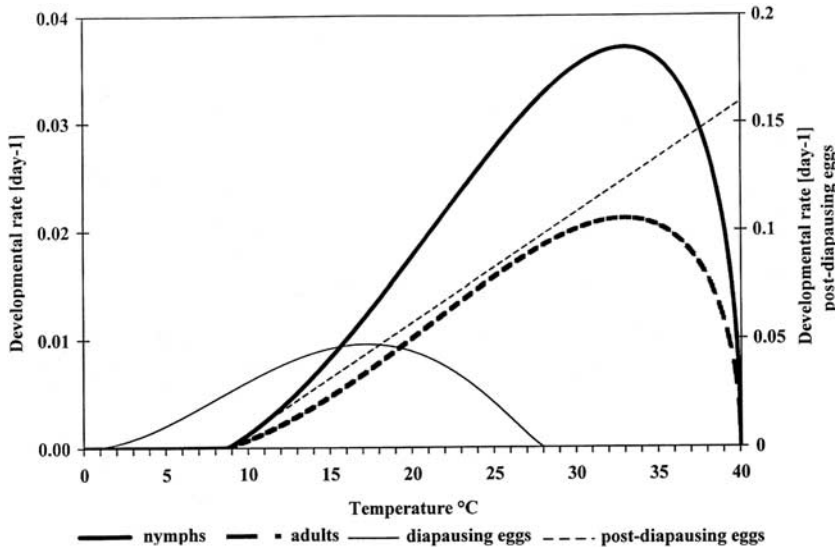
given in Table 1, while the response to temperature is depicted in Figure 1.

The estimates for k_j haven been obtained from the literature or expert opinions. Specifically, the experiments of Rigamonti *et al.* (2011) and the data reported by Bressan *et al.* (2005) provide a series of means and variances in development times for nymphs as well as senescence of adult females, respectively. The mean ratio of the squared means to the variance given in equation [3a] is used to estimate for k_j. For diapausing and post-diapausing eggs, however, expert opinion was considered for setting the values to 25 (Table 1).

Survivorship. All life stages except diapausing eggs are affected by intrinsic mortality and low temperatures. Nymphs and adults survival is also affected by a lack of food during grapevine plant dormancy. The stage specific intrinsic survival ε_j in equation [3b] is tentatively set to 1 for diapausing eggs and represented by a Beta distribution for the other life stages:

$$0.001 \le \varepsilon_j(T) = \lambda_j \left(T - {}^jT_l\right)^{\xi_j} \left({}^jT_u - T\right)^{\varsigma_j}$$
$$\text{for } j = 1, 2, 4 \qquad (6a)$$

$$\varepsilon_j(T) = 1.0 \quad \text{for } j = 3 \qquad (6b)$$

where λ_j, ξ_j and ζ_j are parameters that were estimated on the basis of expert opinions regarding the shape and the level of survivorship between the lower and upper thresholds, assumed to correspond to the respective development thresholds (Table 1).

For the cultivar Pinot noir, Wermelinger *et al.* (1992) reported bud break once 35.8 day-degrees have been accumulated after 1 January above the 10 °C threshold for plant development. In southern Switzerland, the beginning of leaf discolouration is generally observed around Julian day 290. Between this day and bud break in the succeeding year, the plant is assumed to be dormant causing a proportional daily loss rate of $\mu_p = 0.5$ among nymphs and adults.

Temperatures below the lower developmental threshold ${}^jT_l$ are responsible for a proportional loss rate of $0.75 < \mu_T = 0.75 \, (1.0 - 0.1149T)$ for all life stages except diapausing eggs. Expert opinion was considered in the estimation of μ_p and μ_T. The loss rates μ_p and μ_T are added to the attrition term $AR_j(t)$ of equation [1].

Oviposition. According to Curry and Feldman (1987), the reproduction rate for the *i*-th instar is the product of the reproductive profile f_i, *i.e.* the

relative age-specific fecundity rate in the i-th substage, and the temperature-dependent reproductive potential $F(T)$, $i.e.$ the total number of eggs laid by a female conditioned on her living throughout the oviposition period. To represent f_i, we make use of the information provided by Schvester et $al.$ (1962), Vidano (1964), and Bressan et $al.$ (2005) indicating that females pass through a 10 days pre-reproductive period (corresponding to $i = 1, 2$), a 10 days reproductive period (corresponding to $i = 3, 4$), to that we tentatively add a 60 days post-reproductive phase (corresponding to $4 < i \leq 8$). For each substage in the reproductive period ($i = 3, 4$), the relative age-specific fecundity rate per day is 0.5 and 0 otherwise. To obtain $F(T)$ we first calculate the relative reproductive potential $m(T)$ as:

$$m(T) = \phi \left(T - {}^2T_l\right)^{\varphi} \left({}^2T_u - T\right)^{\tau}$$
$$\text{for } {}^2T_l < T < {}^2T_u, \qquad (7)$$

with $m(T) = 0$ for $T \leq {}^2T_l$ or $T \geq {}^2T_u$. The estimates for the parameters ϕ, φ and τ are based on expert opinion on temperature effects on fecundity. To obtain $F(T)$, $m(T)$ is multiplied by the total number of 14.58 eggs per female laid at 26 °C (Bressan et $al.$ 2005). Subsequently, the sum of the products $f_i F(T)$ over the 3rd and 4th substage is related to the daily aging process and multiplied by the occurrence of females, that is $Q_2(t)$ of equation [2] times the sex ratio of 0.5 (Curry and Feldman, 1987). The estimates for the parameters of equation [7] are given in Table 1.

Simulation model development

Manetsch (1976) and Abkin and Wolf (1976) describe the methodology for discretising equation [1] to simulate a delay process where losses, accretions, and delay length varies over time. To assure stability and nonnegative flow rate, a time increment Δt of 1 hour was adequate. In each time increment, the mean temperature is calculated by forcing a cosine function through daily temperature minima and maxima measured at locations and during years of interest (Bianchi et $al.$ 1990). Curry and Feldman (1987) explain in detail how to incorporate discrete environmental temperature measurements T_i into survival and development functions. The model is initialised with a cumulative input equal to 100 obtained from

the Weibull function. For each time increment, instantaneous values for μ_j, ε_j and DEL_j of equation 3a, 3b, 3c are calculated. Likewise, instantaneous mortality and oviposition rates are computed. The model written in the Pascal programming language calculates the daily occurrences of diapausing eggs, post-diapausing eggs, nymphs, and adults that appear as outputs in Figures 2 and 3.

To illustrate the application of time distributed delay simulation models in ecology, the reader is referred to Welch et $al.$ (1978); Fouque and Baumgärtner (1996), Gutierrez (1996), Di Cola et $al.$ (1999), Wearing et $al.$ (2004), Samietz et $al.$ (2007), Arthur et $al.$ (2011), and Gutierrez et $al.$ (2012), for example.

Model validation

In agreement with the purpose of the model (Rykiel 1996), predicted infestation patterns were visually compared with long-term data on infestation patterns in several vineyards. The model produces, distributed over the simulation time period, infestation relative to the initial input. The dynamics of these infestations represent here the calculated infestation patterns.

Over a period of five years, from 2006 to 2010, nymph and adult occurrences were occasionally monitored in five vineyards located in western Switzerland (Yvorne, Lutry) and southern Switzerland (Contone, Biasca, Sessa). The vineyards are located in FD-free zones. Data on nymphs were obtained through the beating tray method, while yellow sticky traps yielded information on adult presence. The details on the sampling technique have been reported in a previous paper (Rigamonti et $al.$ 2011). These counts taken through time represent here the observed infestation pattern.

The daily maximum and minimum temperatures for the vineyards during the period under study were approximated by using the recordings of the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss) made at the Aigle, Pully, Magadino, Comprovasco, and Lugano stations, respectively.

Sensitivity probe

The variation in the output of the model, restricted to the occurrence of diapausing eggs on the last day of the five years simulation period,

Fig. 2. The simulated (lines) and observed (bars) occurrences of *Scaphoideus titanus* life stages on grapevine plants in vineyards located in southern and western Switzerland (A: Contone vineyard, B: Biasca vineyard, C: Sessa vineyard, D: Lutry vineyard, E: Yvorne vineyard). Occasional data were obtained in a monitoring program carried out in FD free zones. The nymphs were obtained through the beating tray method, while yellow sticky traps yielded information on adult presence. The simulated egg occurrences correspond to literature information mentioned in the text. Note that in Figure 2B the observed nymph occurrences are multiplied by ten. Note also that in the Sessa vineyard in 2008 and 2009 adult monitoring was discontinued in the early summer.
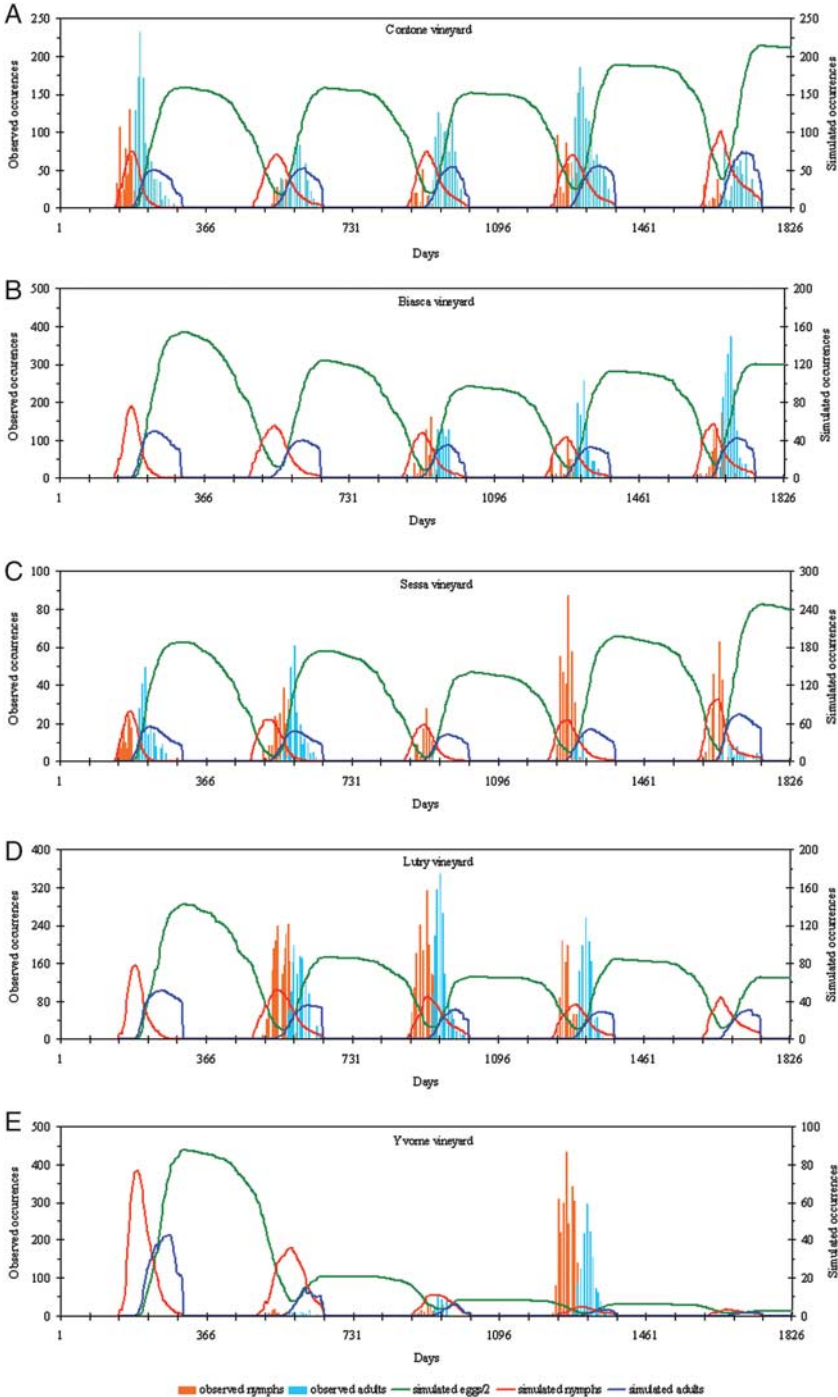
Fig. 3. The simulated occurrences of *Scaphoideus titanus* diapausing (thin line) and post-diapausing (thick line) eggs on grapevine plants in the Contone vineyard (southern Switzerland).
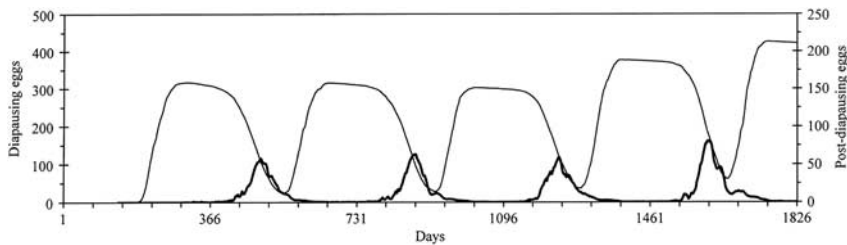
is apportioned to a 10% change in the estimates of the parameters listed in Table 1, with the exception of the fecundity that is tested through the parameter ϕ. Since the development of all non-diapausing life stages is constraint by the same upper and lower thresholds, the 10% change is simultaneously applied to post-diapausing eggs, nymphs, and adults. The test consists in changing one-factor-at-a-time. The results are expressed as relative occurrences (RO), *i.e.* as occurrences relative to the occurrences obtained in the standard model with the parameter estimates given in Table 1.

Results and discussion

The temperature dependencies of stage-specific developmental and senescence rates between the lower and upper thresholds are illustrated in Figure 1. For nondiapausing life stages, the lower threshold of 8.7 °C reported in Table 1 is slightly lower than the threshold of 10 °C for plant development (Wermelinger *et al*. 1991, 1992). Remarkably, the developmental rates of diapausing eggs are lower, and the curve is shifted to a lower temperature range than observed for post-diapausing eggs, nymphs, and adults (Table 1). The shifting of the developmental and the concomitant reduction of the lower and upper temperature thresholds have been hypothesised for and observed in many diapausing insects, including the corn earworm *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) (Logan *et al*. 1979) and the European grape moth *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) (Baumgärtner *et al*. 2012). Note-worthy, the developmental rate of diapausing eggs at 20 °C is much higher than at 5 °C, as reported by Chuche and Thiery (2012).

The model is built on the basis of poiki-lothermic cohort development, with temperature-dependent developmental rate, survival, and fecundity functions, treated by Curry and Feldman (1987); the diapause theory conceptualised by Nechols *et al*. (1999); and stochastic development of age-structured populations according to Plant and Wilson (1986), Gutierrez (1996), and Di Cola *et al*. (1999). A model built on these basic elements has, in our view, satisfactory explicative qualities.

According to Rykiel (1996) the purpose of the model is decisive for validation procedure selection. A monitoring program for supervised management of *S. titanus* made available occasional data from several vineyards. In this program, the monitoring of nymphs was discontinued once adults appeared in sticky traps. No attempt was made to record egg hatching in winter and no data were collected in the presence of diapausing eggs. Moreover, sticky trap catches of adults are affected by weather conditions. These limitations affect the model predictions and field observation comparisons. However, for the purpose of the work, which is the representation of multiannual infestation patterns, the available monitoring information appears to be sufficient for model validation (see subsequent section). A model designed for representing population densities, however, would require more reliable data for validation, changes in model input and a possible revision of mortality functions. Moreover, such a model should include dispersal including the passage of young nymphs through the vineyard floor vegetation (Trivellone *et al*. 2011).

According to Figures 2A–2E, the model generally represents the observed five years infestation pattern at the five locations in a

Table 2. Results of the sensitivity probe, which yields the RO of diapausing eggs on the last day of the five years simulation period in response to 10% changes in model parameters (RO refers to the occurrence of diapausing eggs in relation to the standard model with parameter estimates given in Table 1; since the same upper (^jT_u) and lower (^jT_l) developmental thresholds have been used for all non-diapausing life stages, the respective sensitivity test is carried out simultaneously for eggs, nymphs, and adults)

Parameter Life stage		k	α	β	T_l	T_u	λ	ξ	ζ	φ	φ	τ
1. Nymphs	+10%	1.02	0.61	0.49	6.38	<0.01	>0.99	0.02	0.01			
	−10%	0.98	1.27	1.33	0.11	145.61	<1.01	28.93	43.76			
2. Adults (females)	+10%	0.73	1.15	0.67	6.38	<0.01	>0.99	0.02	0.01	0.59	0.14	0.12
	−10%	1.25	0.85	1.20	0.11	145.61	<1.01	28.93	43.76	1.61	7.11	8.25
3. Diapausing eggs	+10%	0.91	1.02	0.25	0.59	0.07						
	−10%	1.13	0.55	0.01	1.10	0.03						
4. Post-diapausing eggs	+10%	<1.01	0.96		6.38	<0.01	>0.99	0.02	0.01			
	−10%	>0.99	1.02		0.11	145.61	<1.01	28.93	43.76			

RO, relative occurrence.

satisfactory manner. Specifically, the correspondence between field observations and the predicted occurrences of nymphs, the presence of adults, and the appearance of the combined diapausing and post-diapausing eggs is adequate. The simulated egg deposition period coincides with the occurrence of gravid females observed by Cravedi *et al.* (1993) in northern Italian vineyards. The duration of adult presence is also satisfactorily represented by the model, while the predicted nymph occurrence lasts for a longer time period then observed in the field.

The model predicts the beginning of diapause termination as early as in October and the continuing termination of diapause for a small number of eggs throughout the winter. However, the survival of post-diapausing eggs is negatively affected by low winter temperatures. Nymphs not only suffer from the effect of low temperatures but also from a lack of food prior to bud break. In mild winters and at locations with frequent temperatures between 5 °C and 10 °C the plant dormancy effect is particularly high. Under these conditions, the disruption of the phenological synchrony between *S. titanus* and the plant could have a significant effect on infestation patterns. Importantly, the model predicts an overlapping in the occurrence of newly laid eggs and diapausing eggs from the previous year. As a result, diapausing eggs are always present in the vineyards (Fig. 3).

Since here the developed model adequately represents the data in FD uninfested vineyards, it is qualified with satisfactory predictive qualities and assumed to hold the promise for further improve adaptive management of *S. titanus* populations (Jermini *et al.* 2013; Prevostini *et al.* 2013).

Table 2 shows the RO of diapausing eggs on the last day of the five years simulation period in response to a 10% changes in parameter values. Accordingly, the model output is most sensitive to changes in the upper threshold (^JT_u) and in the shape parameters ($ξ_J$ and $ζ_J$) of the beta distribution for the temperature-dependent survivorship. On the other hand, the model is least sensitive to the 10% variation in the shape parameter of the development function (k_J) and the level of survivorship $λ_J$. The small variation of RO in response to the shape parameter (k_J) of the development function and the level of survival ($λ_j$) was not expected, considering the importance given to those parameters in traditional life table studies. Apparently, the model is sensitive to 10% changes in parameters whose estimates are based on expert opinions rather than experimentation (Table 1). Sensitivity analysis is the study of how the uncertainty in the output of a mathematical model or system can be apportioned to different sources of uncertainty in its inputs (Saltelli *et al.* 2008). Since in our case experts did not provide any information on uncertainties, the sensitivity study deals with parameter estimates with both known and unknown reliability. Therefore, we refrained from conducting a comprehensive sensitivity analysis, including the changing of more than

one-factor-at-a-time, and limit the work to a sensitivity probe providing guidance for future research to increase the robustness of the model. For example, experimental work on high temperature effects on development and survival may yield parameters estimates with uncertainties.

The model estimates and the field observations indicate similar infestation patterns at all locations (Figs. 2A–2D) with the exception of Yvorne (Fig. 2E). The predicted decreasing infestation levels in the Yvorne vineyard (Fig. 2E) is in contrast to the respective field observations. Presumably, the discrepancy between predictions and observations is due to the use of unrepresentative weather data from the distant and topographically differently positioned Aigle station. From the response of the predicted infestation patterns to relatively cooler climates, as apparently in the case of the Aigle data, we conjecture that *S. titanus* is approaching the northern limit for distributions (Rigamonti *et al.* 2013). Since the species extends through the United States of America into Canada (Commonwealth Agricultural Bureau International 1992), a critical evaluation of this result is a prerequisite for sketching out the possible area of distribution in Europe. Such a project may benefit from the weather data bank of Yang *et al.* (2010) and the methodology used by Gutierrez *et al.* (2012) to assess the invasive potential of *L. botrana* in North America.

The Weibull input function as well as the developmental rate function of diapausing eggs have been parametrised, and the model has been validated in a narrow range of ecological conditions relative to the inhabited zones in North America and Europe (Commonwealth Agricultural Bureau International 1992). To extend the applicability of the model, it may be necessary to account for other environmental factors than temperature such as humidity and photoperiod. In particular, the diapause theory predicts that diapause is mainly but not exclusively controlled by a combination of temperature and photoperiod (Tauber and Tauber 1976; Tauber *et al.* 1986; Leather *et al.* 1993; Nechols *et al.* 1999).

Acknowledgements

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