Research Article

Towards an improved understanding of the dynamics of vineyard-infesting *Scaphoideus titanus* leafhopper populations for better timing of management activities

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Abstract

BACKGROUND: This paper deals with supervised management of *Scaphoideus titanus* (Homoptera Cicadellidae) and describes a phenology model designed for improving the understanding of the within-vineyard dynamics and the timing of insect growth regulator (IGR) applications.

RESULTS: The model consists of five components dealing with (a) the beginning of the post-dormancy development of overwintering eggs, (b) the egg hatching patterns, (c) the duration of first-instar nymphs, (d) the development and survival of subsequent instars and (e) the stochastic development of cohorts and their passage into the adult stage. Laboratory data permitted the parameterisation of temperature-dependent development and survival functions. Field data consisting mainly of beating tray catches allowed model parameterisation and validation. The model satisfactorily predicts the dynamics of age structures, the beginning as well as the pattern of egg hatching, the occurrence of the third instar and the emergence of adults.

CONCLUSION: The phenology model is useful for timing IGR applications and for setting up monitoring activities in supervised *S. titanus* control. The model is an entry point into an adaptive management system, in that real-time weather and monitoring data are continuously integrated into the model for improving its explanatory and predictive capabilities.
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Keywords: *Scaphoideus titanus*; egg hatching; nymphal development; adult emergence; phenology model; time-varying delay; insect growth regulator application; sampling

1 INTRODUCTION

The leafhopper *Scaphoideus titanus* Ball is of North American origin and has accidentally been introduced into France, from where it has invaded south-western Europe.[1–3] Currently, it is further expanding its area of distribution, as documented by reports from different European countries.[4–11] A study on the population dynamics reports that *S. titanus* is univoltine and passes the winter in the dormant egg stage.[11] The eggs hatch in late spring, and the nymphs pass through five instars before emerging as adults after the beginning of July.[2,12,13]

The economic importance of *S. titanus* stems from the transmission of the *Candidatus* Phytoplasma vitis, a phytoplasma of the elm yellows or 16Sr-V group, causing flavescence dorée (FD) disease.[14] Both the disease, which is a quarantine organism, and the vector are generally subjected to mandatory control. In Switzerland, for example, the control of *S. titanus* relies on two insect growth regulator (IGR) (Buprofezin®) applications. The date of the first application is crucial because, to be effective, the treatment should target the third instar. The treatment is repeated 2 weeks later.[15]

The studies undertaken so far focus on the disease, on disease transmission and on disease control aspects.[16–20] The information available on the vector primarily refers to life cycles, behavioural aspects, spatiotemporal distributions and sampling for supervised control.[21–27] However, no attempt has been made to analyse the population dynamics through the development and use of models considered as important tools for the dual purpose of improving the understanding of spatiotemporal processes and rationalising decision support in population management.[28,29] Specifically, Peterson *et al.*[30] consider models as useful if they are used within an adaptive management framework that focuses on using a modelling process, rather than a specific model, to learn how a system works.

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Adaptive management (AM) is a systematic, cyclical process for continually improving management policies, strategies and tactics based on lessons learned from operational activities.[31] From a theoretical standpoint, AM is a deliberate plan for learning about the managed system, so that management can be improved in the face of uncertainty.[32] From a practical standpoint, AM establishes a close linkage between monitoring, management and analysis of systems.[33] Within the AM framework, existing knowledge can initially be synthesised in a model that may undergo changes leading to improved predictive and explicative capabilities as soon as more information becomes available.[34]

This work initiates a modelling process in an adaptive management framework and deals with the development of a temperature-driven phenological model simulating the temporal occurrences of *S. titanus* eggs and nymphs in vineyards. The important criteria for the design of the model and the components were parsimony, intelligibility and satisfactory predictive capabilities. The purpose of the model is to improve the insight into the dynamics of *S. titanus* infestations and to seek a better timing of management activities focusing on monitoring operations and IGR applications. For parameter estimation and validation purposes, the work makes use of data collected in western and southern Switzerland, but the model is designed for possible use in much wider areas.

2 MATERIALS AND METHODS

2.1 Model description
The phenology model exclusively deals with the post-dormancy development of eggs and the development of nymphs. An adequate knowledge of these processes should allow a satisfactory prediction of the beginning of egg hatching and the emergence of third-instar nymphs as well as adults. These phenological events are important because they are used to initiate sampling, to time IGR-based chemical control operations and to change the sampling technique from beating trays to sticky traps.[21]

The model consists of five components representing five temperature-dependent processes: the first model component refers to the beginning of the post-dormancy period of overwintering eggs (a), the second component deals with egg hatching patterns and produces cohorts of first-instar nymphs entering the developmental process of nymphs (b), the third component represents the duration of first-instar nymphs on the basis of field observations (c), the fourth component makes use of laboratory data to represent the development of the subsequent instars (d) and the fifth component serves for simulating the development of cohorts and their passage into the adult stage (e). A separate study on the duration of the first-instar nymphs (c) is necessary because of the difficulties in finding eggs in sufficient numbers for studying post-dormancy development. In the final model, however, the duration and survival of first-instar nymphs is combined with the respective development characteristics of the subsequent instars. The components are detailed in the following paragraph.

The duration of egg hatching over a period of about 2 months and the univoltinism lead to the adoption of a single-generation multicohort model for nymph development. The respective model should be able to represent the variability of individual development. In fact, the high ratio of the variance to the mean in development times of individuals, described below, suggests the use of stochastic models.[35] In Vansickle's time-varying distributed delay model, cohorts pass through a series of cascaded delay substages whose number controls the degree

of stochasticity in the developmental process.[36,37] During the past three decades, time-distributed delay models have found a wide application in pest forecasting systems and in demographic ecosystem studies.[38–40] The subsequent section deals with the basic elements only, and the reader is referred to the recent work of Gutierrez,[40] Holst and Ruggle,[41] Alilla *et al.*,[42] Gutierrez and Baumgärtner,[43] Severini[44] and Gama *et al.*[45] for additional explanations and applications.

In model component (e) the model refers to chronological time in units of days, while all other processes are formulated on the basis of physiological time in units of degree-days.[40,46] Physiological time is obtained by summing up $(T_i - T_0)/n$, over time increments with $T_i > T_0$, during the duration of the process under consideration ($i = 1, 2, \ldots, n$ is the time increment per day, $n = 10$ is the number of time increments per day, T_i is the mean temperature during the ith time increment, T_0 is the lower temperature threshold).[47] The value of T_i is obtained from a cosine function forced through the daily maximum and minimum temperatures of the nearest weather station operated by the Swiss Meteorological Service (MeteoSwiss), if available. As detailed in the next section, the SPSS PASW® Statistics 18 software was used to estimate the parameters of the component models and to carry out the simulations on the basis of component (e).

2.2 Model components and parameter estimation
2.2.1 Post-dormancy egg development
The weekly application of the beating tray method in Camorino (2008, 2009), Contone (2006, 2008, 2009), Porza (2008) and Biasca (2009) vineyards provided the dates for the beginning of the first-instar occurrence. Linder and Jermini.[48] provide the details on the sampling technique.

To approximate the day of dormancy termination, the physiological time above $T_0 = 8.7\,^{\circ}\text{C}$ (see Section 4) between the possible days of dormancy termination and the dates with the beginning of egg hatching was calculated. Every day between 1 January and egg hatching was considered, but the one producing the smallest sum of squared differences across years and locations was tentatively identified as the day of dormancy termination.

2.2.2 Patterns of egg hatching
In 2008, egg hatching was observed in a Contone vineyard. Briefly, egg hatching was recorded weekly on 20 caged plants. The cumulative proportion Y of the total number is represented by the cumulative density Weibull function

$$Y(\tau) = 1 - e^{-(\tau/\lambda)^\kappa} \tag{1}$$

with the parameters λ and κ, the values of which were obtained by fitting, via least-squares regression techniques, equation (1) to the experimental data. The physiological time τ above the threshold $T_0 = 8.7\,^{\circ}\text{C}$ is calculated for the time between the fifth interval of the first day of egg hatching and the fifth interval of the day marking the end of the observed egg hatching period. The estimates for the parameters of equation (1) are given in Table 1.

2.2.3 Temperature-dependent development of the first instar
Here, the duration of the first instar (N1) from field observations is calculated on the basis of Manly's model.[49] The density of the N1 and the following instars (N2, N3, N4 and N5) was recorded weekly by applying the beating tray method in a Contone vineyard in 2006. In 2007, additional samples were taken in Lutry, Villeneuve,

Table 1. Parameter estimates for the components of the model representing the phenology of *Scaphoideus titanus*

Developmental rate model parameters				Egg hatching model parameters		Delay model parameters	
Equation (3)			Correction	Equation (1)		Equation (4)	Equation (5)
ξ	T_{min} (°C)	T_{max} (°C)	β	κ	λ	k	ε
1.908×10^{-5}	8.7	40	1.094	1.749	255.831	13	0.01

La Tour de Peilz and Contone vineyards. In 2008, the dataset was completed with samples from Yvorne, Contone and Camorino vineyards. The sampling programme was initiated prior to egg hatching and terminated once there were no more nymphs in the sample. Linder and Jermini[48] provide the details on the sampling technique.

The physiological time, above a 10.4 °C threshold, between the first interval of the day with the beginning and the last interval of the day marking the end of the sampling period was calculated. This threshold was obtained by a preliminary analysis of the dataset described in Section 2.2.4. To obtain data equally spaced in time that allow the application of Manly's model, the field data were interpolated.[49] The basic equation for n samples with entries and q instars is

$$F_{ij} = E_1 B_{1j} + E_2 B_{2j} + \ldots + E_n B_{nj} + \phi_j f_{(i-1)j} + \ldots + \phi_q f_{(i-1)q} \quad (2)$$

where F_{ij} is the number of individuals in instar j and higher instars in the ith sample, E_i is the entry numbers in the ith sample, B_{ij} is the number of individuals in instar j or higher instars at time $i + 1$ that entered instar j after time i, $f_{(i-1)j}$ is the number in instar j in the $(i-1)$th sample, $f_{(i-1)q}$ is the number in instar q in the $(i-1)$th sample and ϕ_j and ϕ_q are the specific survival rates between two sample times for individuals in instars $j = 1, 2, \ldots, q$ at the first of these times. Of interest here are the first $(j = 1)$ and the combined subsequent instars $(q = 2)$. For each vineyard with a specific number n of entries, the parameters $E_1, E_2, \ldots, E_n$ and ϕ_1 and ϕ_2 were estimated via multiple regression techniques. Manly shows how to derive the mean duration of the first instar from basic equation (2). For details, the reader is referred to his publication.[49]

The obtained duration of N1 and the duration of 526.3 degree-days of subsequent instars (N2, N3, N4 and N5) allow the calculation of the proportion of time spent in N1 in relation to the combined duration of all instars and the factor β used below to correct the development time of the subsequent instars whose duration was obtained in the preliminary analysis of the data reported in Section 2.2.4.

2.2.4 Temperature-dependent development of late-instar nymphs
Field-collected N1 were put on leaf discs which were inserted into petri dishes according to the modified leaf–island method of Şengonça and Gerlach.[50] To keep the leaf disc fresh, a blotting paper disc imbibed with Hoagland nutrient solution was put into the dish prior to leaf insertion. Under long-day conditions (14/10 h) and 70 ± 5% RH, groups of about 20 individuals were exposed to constant temperatures of 15, 21, 24, 25, 28 and 32 °C. If possible, dead individuals were replaced with nymphs collected in the field. The key of Della Giustina et al.[51] was used to assign the individuals to the different instars (N1, N2, N3, N4 and N5). Occasionally, daily observations were not possible, and the distribution of individuals in different instars was obtained by interpolating the data prior to and after the period without observations.

At the extreme temperatures of 15 and 32 °C, the experiment yielded data on N3 and N4 only. To obtain an estimate of the development time of the combined late-instar nymphs (N2, N3, N4 and N5) at these temperatures, firstly the ratios of the durations of the combined development of N3 and N4 to the combined development of N2, N3, N4 and N5 at 21, 24, 25 and 28 °C were calculated. The average ratio allowed approximation of the duration of the combined N2, N3, N4 and N5 instars at the 15 and 32 °C temperature extremes.

The non-linear model of Brière et al.[52] was applied to represent the observed developmental rates in the entire range permitting nymphal development, i.e. in the range between the lower (T_{min}) and upper (T_{max}) thresholds:

$$z(T) = \xi T(T - T_{min}) \sqrt{T_{max} - T} \quad (3)$$

where the value for T_{max} was estimated on the basis of opinions expressed by experts, while the values of the parameters T_{min} and ξ were estimated by least-squares regression techniques. Note that the inverse of equation (3) corresponds to the observed development time referred to in the next section. The values for the parameters of equation (3) are given in Table 1.

2.2.5 Time-distributed development
Cohort development for the combined instars is modelled according to Vansickle's time-varying distributed delay

$$\frac{dr_i(t)}{dt} = \frac{k}{DEL(t)} \left[r_{i-1}(t) - r_i(t) \left(1 + AR(t) \frac{DEL(t)}{k} + \frac{dDEL(t)}{dt} \right) \right],$$
$$i = 1, 2, \ldots, k \quad (4)$$

with the transition rates $r_i(t)$, the number of delay substages k, the attrition $AR(t)$ and the time-varying development time $DEL(t)$. For each cohort, system (4) produces a distributed output $r_k(t)$ of emerging adults from the input $r_0(t)$ of hatching eggs. In the phenology model developed here, the cumulative input (hatching eggs) into the delay process is set to 1 so that the model produces occurrences rather than population densities. The number k of substages was calculated as the mean ratio of the squared observed development times to the variance of development times of N3 at 24 °C.

To obtain the observed development time μ of all instars combined, the observed development time for N2, N3, N4 and N5 was corrected by β to obtain the duration of the combined instars.

The instantaneous $DEL(t)$ at time t with temperature T is calculated by

$$DEL(T) = \mu(T)\varepsilon^{-1/k} \quad (5)$$

where ε is the survival, i.e. the ratio of emerging adults to hatching eggs. Here, ε takes into account the high intrinsic mortality observed in the laboratory and an unknown extrinsic mortality under field conditions.

The instantaneous attrition *AR(t)* is obtained from observations on the durations at constant temperatures *T*:

$$AR(T) = k \left[\frac{1}{\mu(T)} - \frac{1}{DEL(T)} \right] \quad (6)$$

The parameter estimates are given in Table 1. Equation system (4) has been discretised by Vansickle and is implemented here for a time increment of 0.1 days on EXCEL spreadsheet software.[36]

2.3 Model validation

The validation method depends on the intended use of the model, which is a satisfactory representation of the phenology, beginning with dormancy termination and ending with adult emergence on the basis of an age-structured model.[53] Here, validation relies on a visual comparison of model predictions with field observations. From a pest management standpoint, the model should provide satisfactory predictions of the beginning of egg hatching, the occurrence of N3 and the emergence of adults.

The field data consist of catches obtained by applying the beating tray technique.[48] In apple orchards, this technique produces estimates with high systematic and random errors.[54] In vineyards, the technique appears to be inefficient for estimating the density of early instars, which preferentially infest the shoots growing from the trunk, and of the highly mobile adults. However, the technique appears to yield acceptable information on N3 occurrences. The validation procedure consists of two steps.

1. The capacity of the model to predict the dynamics of age structures is evaluated with samples taken in Lutry (2007), Riex (2007), Giubiasco (2010) and Sessa (2010) vineyards. The respective temperatures were measured at the Pully, Dezaley, Locarno Magadino and Lugano meteorological stations. In all cases, except Dezaley, the nearest weather station operated by the Swiss Meteorological Service (MeteoSwiss) provided the daily maximum and minimum temperatures. The corresponding data for Dezaley were kindly made available by Dr P Linder (Agroscope, Switzerland). With the exception of Lutry, the sampling data from these vineyards have not been used for parameter estimation. For comparison purposes, the proportions of N3 catches per vineyard and year relative to the highest number of N3 caught in the respective samples are calculated. Moreover, the simulated N3 occurrence and adult emergence are plotted as a proportion of the simulated maximum N3 and adult occurrences.
2. The capacity of the model to predict the dates for the beginnings of egg hatching, N3 occurrences and adult emergences is plotted against the corresponding dates observed in nine vineyards that have occasionally been monitored between 2006 and 2010. Only some of these data have been used for parameter estimation. The simulated beginning of egg hatching, N3 occurrences and adult emergence occurs on the date at which 1% of the population has reached the respective life stage.

3 RESULTS

3.1 Model components and parameter estimation

The sum of squared differences in the durations between the calculated dates of dormancy termination and the beginning of egg hatching decreased rapidly until 15 April and increased slowly
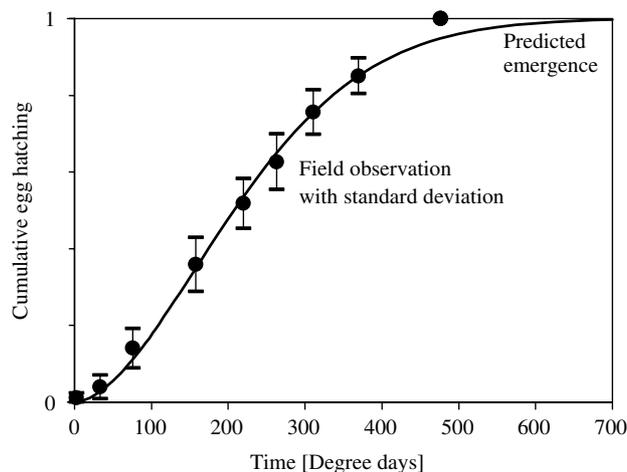

Figure 1. Observed (dots) and predicted (line) cumulative hatching of *Scaphoideus titanus* eggs in caged vine plants.
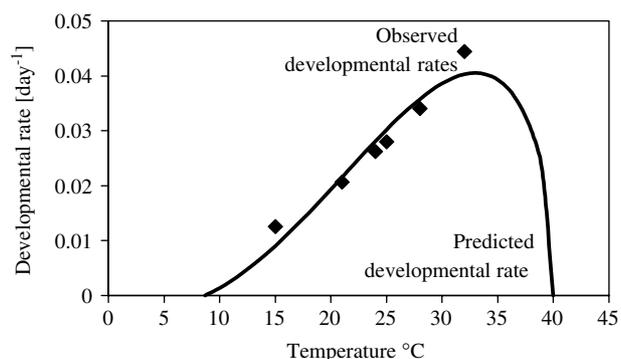

Figure 2. Observed (diamonds) and predicted (line) developmental rates of all instars following the first instar of *Scaphoideus titanus*.

thereafter. The physiological time elapsing between this date and the beginning of egg hatching was 196.6 degree-days, with little variability between the seven cases under study. In fact, the low coefficient of variation (CV = 0.04) encouraged the tentative use of the empirically established date for modelling post-dormancy development of eggs.

The observed and the predicted cumulative emergence of N1 in the field cage plant experiment in relation to the physiological time that elapsed between the beginning and the end of egg hatching are depicted in Fig. 1. Accordingly, equation (1) satisfactorily represents egg hatching over a period of about 50 days and provides the information required to calculate the input into the time-distributed delay process. The extended duration of the egg hatching period is consistent with the results reported in the literature.[2,13]

Manly's method allowed the calculation of the mean duration of N1 for each of the nine vineyards.[49] The mean duration was 49.3 degree-days, with a standard error of 3.88. The coefficient of variation of 0.079 indicates a reliable estimate of the mean duration. Based on the estimate of the duration of N1 and the duration of subsequent instars, the development of the combined instars was calculated as being $\beta = 1.094$ longer than the duration of the N2 to N5 instars (Table 1, parameter β).

Figure 2 shows that the model of Brière *et al.*[52] satisfactorily represents the developmental rate in the entire range of
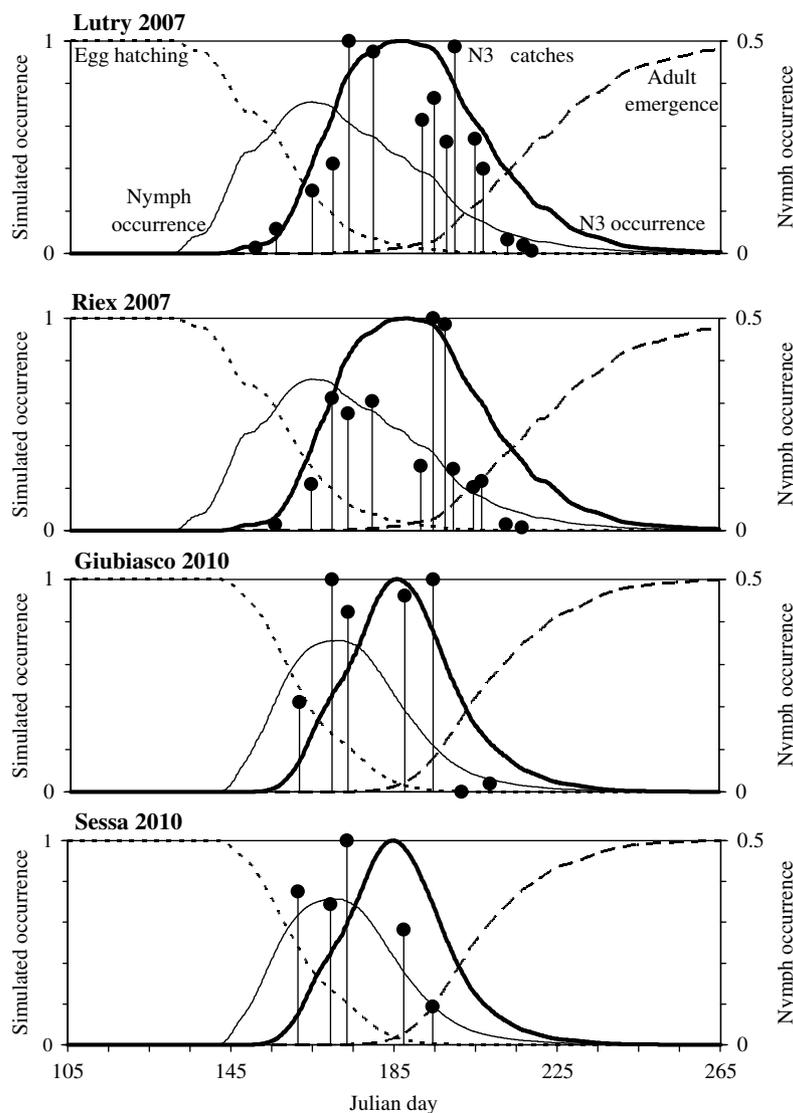
Figure 3. Validation of the phenology model for *Scaphoideus titanus*: the dynamics of the predicted age structure in different vineyards and the observed catches of third-instar nymphs relative to the respective maximum number. The simulated occurrences of third-instar nymphs and adults are related to the respective maximum occurrence. (All the variables, with the exception of nymph occurrence, are represented on the axis labelled 'simulated occurrence').

temperatures, i.e. between $T_{min} = 8.7\,°C$ and $T_{max} = 40\,°C$, that permit nymphal development. The preparation of the data produced mean values at which the model was fitted. Table 1 reports the estimated values for ξ and T_{min} for which standard errors of 2.97×10^{-6} and 2.61 have been obtained.

The number of substages is low ($k = 13$) in relation to the much higher number that is obtained when using the empirical relationship between variance and development time established by Shaffer.[55] This indicates a high variability in development times between individuals. According to equation (5), the low survival ($\varepsilon = 0.01$) and the low number of substages ($k = 13$) result in a considerable difference between observed $\mu(T)$ and calculated $DEL(T)$ development times.

3.2 Model validation

The changing age structure predicted by the model for four vineyards located in southern and western Switzerland is illustrated in Fig. 3. The hatching eggs enter the nymphal stage,

which is represented by simulated N3 occurrences relative to the maximum occurrences in the N3. The adults emerging from the fifth instars are accumulated in the adult stage, which, for illustrative purposes, reaches 1 in Fig. 3. In fact, the dotted line representing the occurrences of the combined instars shows that, after a relatively fast increase, there is an exponential decrease to very low adult occurrences. This decrease is due to the high intrinsic and extrinsic mortality.

The pattern of N3 occurrences is compared with the numbers of N3, relative to the maximum, of the monitoring data. In general, the model satisfactorily predicts the beginning of N3 occurrences but delays the ending of this instar. Possibly, the difference is due to mortality factors not considered in the model. The delay may be responsible for the late adult emergence that begins at the end of June and continues until September. Interestingly, the beginning of adult emergence partially coincides with the period of egg hatching. The long period of adult emergence is due to the long egg hatching period and to the high variability in
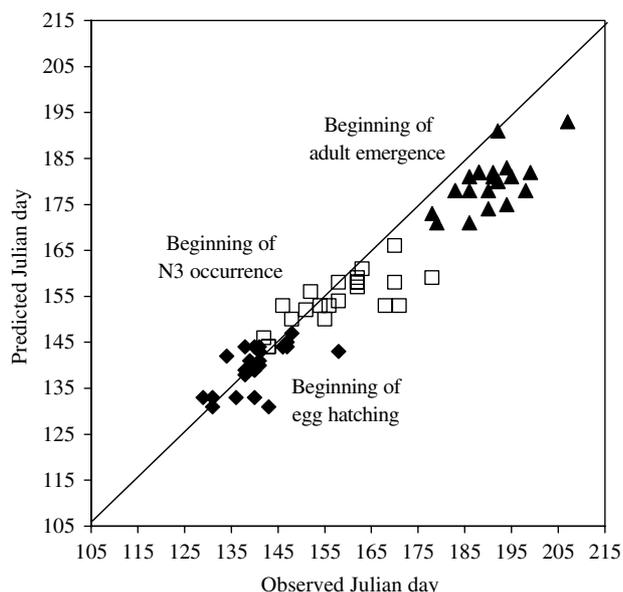
Figure 4. Validation of the phenology model for *Scaphoideus titanus*: the correspondence between the simulated and observed dates relevant for control operations.

development times of nymphs, which are both caused by intrinsic and environmental factors.

The relationships between the observed and the predicted beginnings of egg hatching, N3 occurrences and adult emergence are depicted in Fig. 4. The calendar days have been chosen because they easily allow predicted and observed data to be compared. According to Fig. 4, the dates for the beginning of egg hatching are close to the line of correspondence indicating a satisfactory prediction. Likewise, the occurrences of N3 are predicted with a satisfactory degree of reliability. However, the prediction of adult emergence is less reliable, presumably owing to the accumulation of errors in the predictions of preceding events and in using inappropriate sampling methods. In fact, the model predicts a faster development of nymphs than observed under field conditions.

4 DISCUSSION

The simple model components dealing with dormancy termination and egg hatching produce a satisfactory prediction of events that initiate and control the monitoring programme. The work of Chuche and Thiéry, however, showed how egg hatching is influenced by environmental conditions, including temperature, affecting the dormancy of overwintering eggs.[11] The results of their study should be taken into account if more realistic representations of egg hatching are necessary. It is anticipated that this will become particularly important if the model is applied for regions other than the one considered in this study. Specifically, warm winters may require changes in the method used to represent egg hatching.[11]

Manly's model proved to be very useful for calculating the development times of N1 on the basis of field data.[49] Moreover, this model component also provides a methodology for estimating the mortality under field conditions, which becomes important when extending the current phenology model to a population model representing the densities rather than the occurrences of

S. titanus. The structural elements such as population density, spatial distributions, sex ratio and net migrations may become particularly important once the model is further extended to disease transmission.

The beginning of adult emergence has been recorded by the beating tray technique. This technique is unreliable for recording the presence of adults, and the use of sticky traps is recommended instead.[21] Hence, the planned extension of the phenology model to the adult stage would require changes not only in the model but also in the monitoring technique. As sticky traps provide unreliable estimates for adult densities, the further development of the phenology model into a population model may require a thorough revision of the sampling technique.

Vansickle's time-varying distributed delay was useful for dealing with variability in temperature-dependent development times and associated variability, as well as with changes in the population structure.[36,39,56] If future studies or the result of adaptive management require corrections, the model could easily be changed.

In general, the validation procedure shows a close correspondence between the predicted and the observed beginning of N3 occurrences. The less satisfactory correspondence for Sessa (Fig. 3) may be due to the use of unsuitable temperatures recorded at the relatively distant weather station located near a lake in the centre of Lugano. This indicates that insight into the dynamics of the population system has been improved and has contributed to better prediction of the occurrence of important events. A satisfactory prediction of N3 appearance is very important for the timing of IGR applications. The use of other insecticides may be based on different criteria. The capability of the model to represent the dynamics of age structures may satisfy the needs of users targeting nymphal instars other than the N3 considered in this work. Importantly, the work deals with model development, parameter estimations and validations on the basis of historical data. The analysis of existing information is an important step in an adaptive management process.[34]

The possibilities of further improving explicative and predictive capabilities are limited if the model is not developed for easy integration of new information including real-time weather and monitoring data. As previously stated, Peterson *et al.*[30] consider models to be useful if they are used within an adaptive management framework that focuses on using a modelling process, rather than a specific model, to learn how a system works. The discussion section provides suggestions on how to update the model in the next step of the modelling process. Currently, attempts are being made to update the model continuously with monitoring information, to replace historical temperatures with real-time recordings from an intelligent sensor network and to provide, via a web-based system, the phytosanitary service and pilot farms with increasingly reliable predictions of the occurrence of pest-management-relevant phenological events (Prevostini M, unpublished).

5 CONCLUSIONS

The application of insect growth regulators for *S. titanus* control requires the correct timing of N3 appearance. This can be achieved by the development and implementation of a phenological model. Formulated on a mechanistic basis, it serves as a building block for more comprehensive models dealing with the dynamics of vineyard-infesting pest population systems across wide geographical areas.

Standard experiments under laboratory and field conditions as well as historical information obtained in routine monitoring programmes can efficiently be used to parameterise and validate an initial phenology model for *S. titanus*. This model can be integrated into an adaptive management process where real-time weather and monitoring data are used continuously to improve the predictive and explanatory capabilities of the model.

ACKNOWLEDGEMENTS

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