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Autor: Johnsen, S. / Gutierrez, A.P. / Freuler, J.

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The within season population dynamics of the cabbage root fly (*Delia radicum* [L]). A simulation model

S. JOHNSEN^{1,4}, A. P. GUTIERREZ² & J. FREULER³

¹ Division of Biological Control, University of California Berkeley. Present address: Dep. of Ecology and Molecular Biology, Royal Vet. & Agric. University, Bülowsvej 13, DK-1870 Frederiksberg C, Denmark

² Division of Biological Control, University of California, Berkeley, Albany, CA 94706, USA

³ Station fédérale de recherches agronomiques de Changins, CH-1260 Nyon, Switzerland

Based mainly on published data a simulation model for the within season phenology of *Delia radicum* is developed. It is based on the concept of physiological time and simulates the stochastic variation in developmental times. It incorporates features of the flies biology such as diapause and “aestivation”. It further demonstrates the importance for the egg dynamics of carabid predation and the influence of hot weather on oviposition. Areas where further biological information is needed are pointed out. These are: the response of overwintering pupae to temperature during diapause, the biological details of why oviposition declines during hot weather and the functional and numerical response of the carabids to *D. radicum* egg densities. The model successfully simulates previously collected data on field egg dynamics with respects to timing and where carabid density/activity is known also egg density patterns.

INTRODUCTION

General life cycle

Depending on temperatures, the cabbage root fly – cabbage maggot in North America – (*Delia radicum* [L.]) may have 1–3 generations during the season. Adult females must feed on nectar and pollen to mature eggs (MILES, 1953), and generally begin oviposition after 50 D° (above 6 °C). They continue to oviposit for the duration of the adult life but the oviposition rate is age specific (HARRIS & SVEC, 1966; ZOHREN, 1968) and depends on the availability of adult food (FINCH, 1971). The eggs hatch into larvae, and their feeding on roots of cruciferous crops may be economically important.

Several investigations have attempted to predict the emergence of adults from overwintering pupae and the time of oviposition using physiological time (COAKER & WRIGHT, 1963; ECKENRODE & CHAPMAN, 1971; WYMAN *et al.*, 1977; COLLIER & FINCH, 1985). In Great Britain, a phenological model was developed for predicting these events, and is used by some farm advisors and growers to forecast the time of cabbage root fly attack, and for timing pesticide applications to control these insects (FINCH, 1989). The specifics of this model are not published.

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Diapause

In north temperate regions, the cabbage root fly overwinters as a diapausing pupa (COLLIER & FINCH, 1983a). TAUBER *et al.* (1986) refer to this type of overwintering as a diapause mediated winter-dormancy. Diapause in cabbage root fly and the terminology used is discussed by JOHNSEN *et al.* (1990). In spring, pupae begin post diapause development when temperatures exceed the threshold for morphological development, and compared to the variation in time of pupation during fall, spring emergence of the flies is highly synchronized (COLLIER & FINCH, 1983a). In temperate areas where winter conditions are not harsh (e.g., along the coast of Northern California or the north coast of Spain), part of the population does not go into diapause during winter, and hence synchronization of the population does not occur (C. PICKEL, A. P. GUTIERREZ, pers. comm.). In these regions development may occur year round.

The terminology concerning the phases of diapause is confusing (TAUBER *et al.*, 1986), and the physiology is only partially understood. Cabbage root fly development in response to temperature in the phases preceding post diapause is only partially known (COAKER & WRIGHT, 1963; COLLIER & FINCH, 1983a, b), but the time of transition of some field populations from diapause to post diapause stage has been defined empirically (COLLIER & FINCH, 1983a, b). Several reports indicate that some post diapause populations consist of subpopulations that have average developmental times of 150–170 D°, but others that require longer diapause periods before postdiapause development is initiated (COLLIER *et al.*, 1989b). The subpopulations are termed “normal” and “late emerging” types respectively (COLLIER & FINCH, 1983b; COLLIER *et al.*, 1989a, b). Here the terms “Type I” and “Type II” will be used. In addition, there may be considerable local variation in the proportion of Type II individuals in the population (FINCH *et al.*, 1988).

In this paper a simulation model for the within season dynamics of cabbage root fly is developed and used to simulate the dynamics of a field egg population. It is compared to field data reported by FREULER (1975a, b).

DEVELOPMENT OF THE CABBAGE ROOT FLY MODEL

The dynamics model

The population model for the cabbage root fly is a bookkeeping device for tracking births and deaths, diapause development, ageing and other relevant biological factors. Ageing in the model may be viewed as a series of boxes (an array in a computer model), with individuals flowing from one box to the next at rates that are determined by physiological time. The concept of physiological time and age is well known and is reviewed by CURRY & FELDMAN (1987). Individuals may be recruited or die at age specific and time varying rates. In the model, we are able to keep track of cabbage root fly numbers and their masses (see GUTIERREZ *et al.*, 1988).

The distributed delay dynamics model of MANETSCH (1976) with attrition added (VANSICKLE, 1977) was used to model egg, pupal and adult dynamics. The application of this model to plant and insect demography is described by GUTIERREZ & BAUMGÄRTNER (1984). A simpler model is used for the larval dynamics (see below). The distributed delay model simulates the observed dispersion in the ageing process of a cohort of individuals born at the same time. It requires that

the mean developmental time (DEL) and number of age classes (k) be specified. These parameters were estimated from the literature and from experiments conducted on a California population of the cabbage root fly (Tab. 1).

Tab. 1. The age specific developmental statistics for cabbage root fly.

STAGE	DEL (D°)	k	DEVELOPMENTAL THRESHOLD (°C)
Post- diapausing pupae	150 ^{a)}	25 ^{a)}	4.3 ^{b)}
Eggs	50 ^{a,b)}	25 ^{a)}	6.0 ^{b)}
Larvae	225 ^{b)}	75 ^{a)}	6.0 ^{b)}
Pupae	200 ^{b)}	13 ^{a)}	6.0 ^{b)}
Adults	350 ^{c)}	7 ^{a)}	6.0 ^{d)}

a) Based on our data.

b) Collier & Finch, 1985.

c) Computed from, Zohren, 1968.

d) Computed from Riedel, 1967.

In this section it is necessary to discuss the components of the model before reporting and discussing the simulation results. The parameter k is the parameter of the Erlang distribution, and defines the number of age classes in the model. It is computed as the ratio of $DEL^2/\text{variance}$ (VANSICKLE, 1976). k for the larval stage was large (Tab. 1.) due to a very small variance of developmental times; therefore using the distributed delay model for this life stage makes little sense. To make computations more efficient, a deterministic ageing-process was used for larvae (GILBERT *et al.*, 1976; CUFF & HARDMAN, 1980) using the physiological time at calendar time t as the time step. In this model, all individuals in a cohort age at the same rate, much as predicted by a LESLIE (1945) matrix model.

In contrast, k values for the other stages were small making the distributed delay model an appropriate form. The pattern of adult longevities (i.e., survivorship) predicted by the model is similar to that reported by ZOHREN (1968). However, a small k causes a loss of accuracy when computing age specific oviposition rates. Hence, as a compromise, a k of 20 was arbitrarily chosen for the adult stage. This k, in combination with an age specific mortality rate, reproduced the longevity data quite well. The mortality rate (μ_a) per D° was computed as:

$$0 \leq \mu_a = 0.079/|300-a| \leq 0.0086, \quad [1]$$

where a is physiological age of an individual, $|300-a|$ is the absolute value of $(300-a)$ and 0.0086 is the maximum mortality rate per D°.

Biological data and components of the model

The field oviposition data for 1971 and 1972, and predator dynamics data for 1971 used here were previously reported by FREULER (1975a, b). These data were used to test the model and to estimate some parameters of the model. The simulations were started with the initial value of 40 post diapause pupae on 1 January for 1971 and 80 for 1972, and daily maximum and minimum temperatures at 2 m above ground and 5 cm below ground were used to drive the model. Ageing

of eggs, larvae and pupae was simulated using physiological time computed from soil temperature data. For adults, air temperatures were used.

In the field and in the model the season begins in the spring with the emergence of adults from post diapause pupae, followed by oviposition, development of eggs, larvae, pupae and adults over 1 or more generations until diapause is induced in an increasing fraction of the pupae in the fall. The principal factors inducing diapause are photoperiod and temperature (SONI, 1976). This seasonal sequence is followed in the development of the model.

Post diapause development

Field emergence of type I post diapause pupae occur over a period of $120-220 D^{\circ} > 4.3^{\circ}C$ (COLLIER & FINCH, 1983b; Johnsen, unpubl.). The females complete most oviposition within $330 D^{\circ}$ after emergence. The generation time

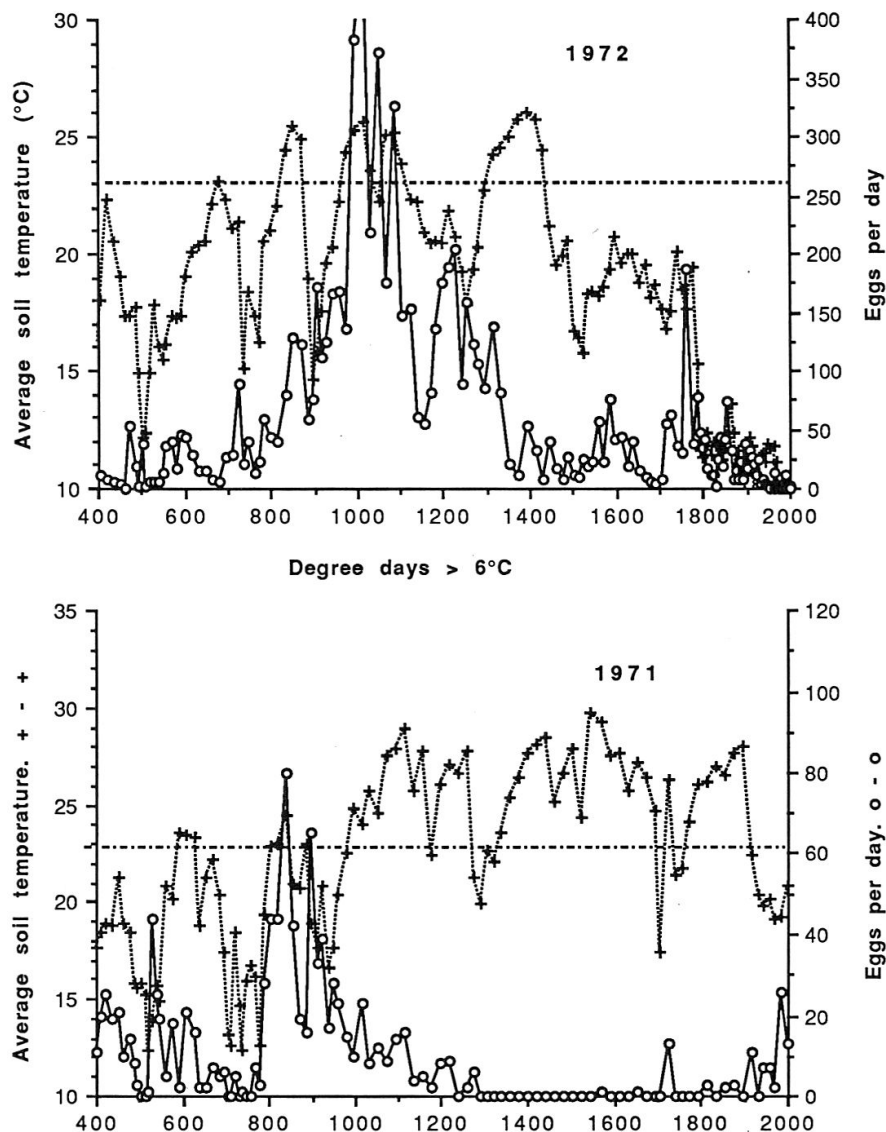


Fig. 1. Average soil temperatures (..+..) measured during FREULER's experiments in 1971 (top) and 1972 (bottom) and observed daily egg catches (o) on physiological time ($D^{\circ} > 6^{\circ}C$). The horizontal dashed line indicates $23^{\circ}C$.

(egg to adult) for non diapausing cabbage root fly is about 600 D° (Tab. 1.). However, FINCH *et al.* (1988) reported that two Swiss cabbage root fly populations from Lausanne and Wädenswil also contained “late emerging” (here “Type II”) individuals. FREULER’s data on egg phenology from Changins, Switzerland (Fig. 1) also suggests that Type II, “late emerging” post diapause individuals occur there, as the peak in oviposition around 500 D° – for the above reasons – can have no other explanation. In the model, 40% post diapause individuals were assumed to be type II, requiring an additional 400 D° mean developmental time but the same variance of developmental times as normal post diapause pupae. This accounted for the second peak observed in FREULER’s data. The adult oviposition rates are computed next.

Oviposition

Per capita age specific oviposition rates ($R[a,t]$)(eggs D°⁻¹) at time t were incorporated in the simulations using the function

$$R(a,t) = \frac{C_1 a}{C_2^a}, \quad [2]$$

The constants of the function were fitted to laboratory data reported by HARRIS & SVEC (1966) and ZOHREN (1968). These data were collected under laboratory conditions. Data reported by HARRIS & SVEC are much higher than the field fecundity estimates reported by FINCH (1971). Presumably the lower fecundity in the field is due to a shortage of adult food. In the simulation, the parameter values chosen ($C_1 = 0.125$, $C_2 = 1.013$) estimate the average cumulative oviposition per female of 75 eggs reported by FINCH (1971).

Effects of weather on oviposition rates

MILES (1953, 1954) and HUGHES & MITCHELL (1960) reported that oviposition rates per day increased with temperature until high temperatures limited oviposition. MILES (1953, 1954) suggested that the lower threshold for female activity was 15.5 °C and that oviposition was reduced at temperatures above 21 °C (see also READ, 1965). The field oviposition data considered here confirms these general relationships, but suggest that the lower threshold is near the developmental threshold for adults of 6 °C. This latter threshold and increasing daily oviposition rates with temperature follow in the model in a straightforward way from calculating oviposition rates per degree day.

MILES (1954) also found that “oviposition declined during long periods of hot weather”. In Changins, the summer of 1971 was much hotter than in 1972. Such temperatures are also known to slow pupal development (see below). Apparent differences are seen between the two years with regards to patterns of temperatures and oviposition (Fig. 1). In 1972, the peak egg density occurred around 850–1300 D° and declined thereafter. In 1971, a decline in egg density began around 900 D° concurrent with a steep increase in soil temperatures, and little oviposition occurred thereafter. A very similar pattern was observed by MILES (1953) in her field study.

In the model, if maximum soil temperatures (T_{sm}) are above 23 °C, the scalar $\tau \geq 1$, expressing the effects of high temperatures on daily oviposition is computed as:

$$1 \leq \tau(t) = \begin{cases} \tau(t-1) + 0.1 (T_{sm} - 23.0)^{1.15}, & \text{if } T_{sm} > 23.0^\circ\text{C} \\ \tau(t-1) \cdot 0.8, & \text{if } T_{sm} \leq 23.0^\circ\text{C} \end{cases} \quad [3]$$

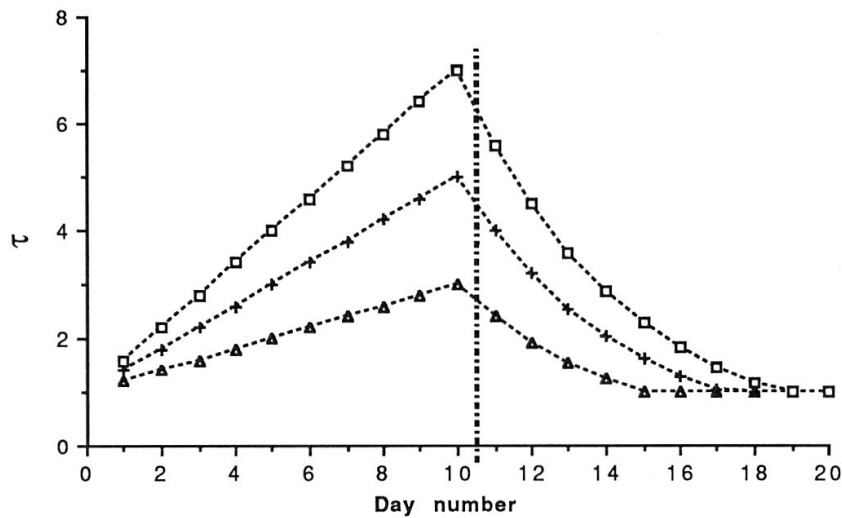


Fig. 2. The scalar τ expressing the influence of hot weather on daily oviposition rates of *D. radicum*, as it would develop over successive days at constant temperatures. The curves represent the temperatures 25° (Δ), 27° (+) and 29°C (\square). At the vertical dashed line, a drop in temperatures to below 23°C is assumed.

This equation (Fig. 2) was one of several alternatives tried and gave the best simulation of the field data. The daily oviposition rate (R^*) corrected by t is computed as follows:

$$R^* = R(a,t)/\tau(t) \quad [4]$$

Other factors affecting oviposition

Humidity in the top soil layers may also be important for oviposition and egg survival (NAIR & MCEWEN, 1975). Cabbage root fly eggs are known to have poor survival at RH below 90% (SWAILES, 1963; MAACK, 1977). Of course, RH at the soil surface depends on rainfall patterns, soil moisture and water potential as well as temperature. The interactions are not known, and are in part in equation [5]. In hot weather the females utilize a larger proportion of their food and reserves to meet respiration demands. This too is likely to reduce oviposition. Furthermore, MILES (1953) suggests that hot weather may be associated with reduced occurrence of the flowering plants, from which the females feed, and this in turn may affect oviposition negatively. All of these factors are not known in detail and are incorporated in an *ad hoc* way in [3].

Egg mortality due to temperature

High and low temperatures are lethal to eggs (RIEDEL, 1967), hence soil temperatures where the eggs are placed by the female should be considered in the model. Unfortunately, data to formulate this mortality function were not available and the effect is ignored.

Carabid predation of cabbage root fly eggs

FREULER (1975b) also studied the dynamics of carabid and staphylinid populations (as systematic groups) using pit fall traps during 1971. Carabids are known to be important predators of *Delia radicum* eggs and were the most numerous of the two predators. Unfortunately information in the literature is insufficient to formulate a functional response for the predators, but FREULER (1975b) found that there was an average 56% mortality rate of eggs per day due to predation across the whole experiment. Given daily counts of carabids, the function used to estimate the number of eggs in age class a killed by carabids ($N_{c,a}$) was formulated as:

$$N_{c,a} = (0.1 \cdot d_{e,a})^{0.85} \cdot c^{0.65} \quad [5]$$

with $d_{e,a}$ being the density of eggs in the a^{th} age class, c the number of carabids caught that day. Function [5] behaves like the Nicholson-Bailey functional response with respects to predator density, and as a type II model with respects to egg densities. This three dimensional concave surface predicts the number of eggs killed. The coefficients in [5] were fit to data presented by ANDERSEN *et al.* (1983), who found that individual carabids of the common species *Bembidion lampros* consumes an average of 1.4 egg per predator and day when offered 15 eggs per day of the cabbage root fly's close relative *Delia floralis*.

The model does not include larval or pupal mortality except pupal mortality at high temperatures, but does include high temperature effects on developmental delays (see below).

Pupal development at high temperatures

Developmental rates of young pupae are slowed at high temperatures, and in the literature they have been assumed to enter "aestivation" (FINCH & COLLIER, 1985). As we shall see, this phenomenon is merely a developmental delay due to high temperatures. This effect was quite evident in FREULER's data (Fig. 1). This response was simulated using equation [6] (FINCH & COLLIER, 1985), which predicts the fraction of pupae (f_{ae}) of age 0–75 D° induced into "aestivation" when maximum soil temperatures (T_{sm}) are above 21.0 °C:

$$0 \leq f_{ae} = (T_{sm} - 21) \cdot 0.13 \leq 1. \quad [6]$$

If temperatures are above 21 °C on consecutive days, the fraction of non "aestivating" pupa induced into "aestivation" was computed using [6], with the highest previous temperature experienced replacing 21 °C. When soil temperatures drop below 21 °C, all "aestivating" pupae resume normal development.

The data of FINCH & COLLIER (1985) show that the time required for "aestivating" pupae to complete development when favorable conditions return is shorter than expected if a total arrest of development in "aestivation" is assumed. This suggests that some development occurs during "aestivation". FINCH & COLLIER (1985) also showed that some flies will eventually emerge if the pupae are kept long enough at high temperatures, but many will die. The rate of development curve of post diapause pupae in response to temperature [7] described in JOHNSON *et al.* (1990) was used to model the developmental rates of "aestivating" pupae.

$$\Delta a = (\Delta t \cdot e^{(-0.1\phi)}, \text{ where } \phi = \begin{cases} 0, & \text{if } T_{sm} \leq T_u \\ T_{sm} - T_u, & \text{if } T_{sm} > T_u \end{cases} \quad [7]$$

and $T_u = 21.5^\circ\text{C}$ is an upper threshold for linear development in response to increasing temperature.

The data suggests that the so-called aestivation is simply a slowing of developmental rates due to high temperatures generally observed in poikilotherms (see CURRY & FELDMAN, 1987). Applying function [7] in the model predicts accurately the emergence times of flies reported by FINCH & COLLIER (1985) for cohorts of individuals held at constant temperatures. (JOHNSEN *et al.*, 1990)

Pupal mortality due to high temperatures

FINCH & COLLIER observed an increased pupal mortality at “aestivating” temperatures. Higher temperatures yielded higher mortality. But they did not quantify this close enough to allow a function to be derived. In the model, the daily mortality rate (μ_{ae}), was estimated as a function of maximum soil temperature (T_{sm}). The following equation was chosen as the best of several alternatives tried in the simulations:

$$0 \leq \mu_{ae} = 0.03 \cdot (T_{sm} - 21.5)^{1.2} \leq 1. \quad [8]$$

Diapause induction during fall

Induction of diapause occurs in the larval stage in response primarily to photoperiod, but there may be an interaction with temperature (SONI, 1976). A more comprehensive discussion of winter diapause in this species is given in JOHNSEN *et al.* (1990). Different populations of cabbage root fly respond differently to these factors. For example, populations from higher latitudes are induced into diapause at longer daylengths than more southerly populations (COLLIER *et al.*, 1988). The proportion (f_d) induction of pupal diapause during fall was simulated using an empirical fit to data from COLLIER *et al.* (1988), [9]

$$0 \leq f_d = 3.5 \sqrt{(L - 20)} - 4.3 \leq 1 \quad [9]$$

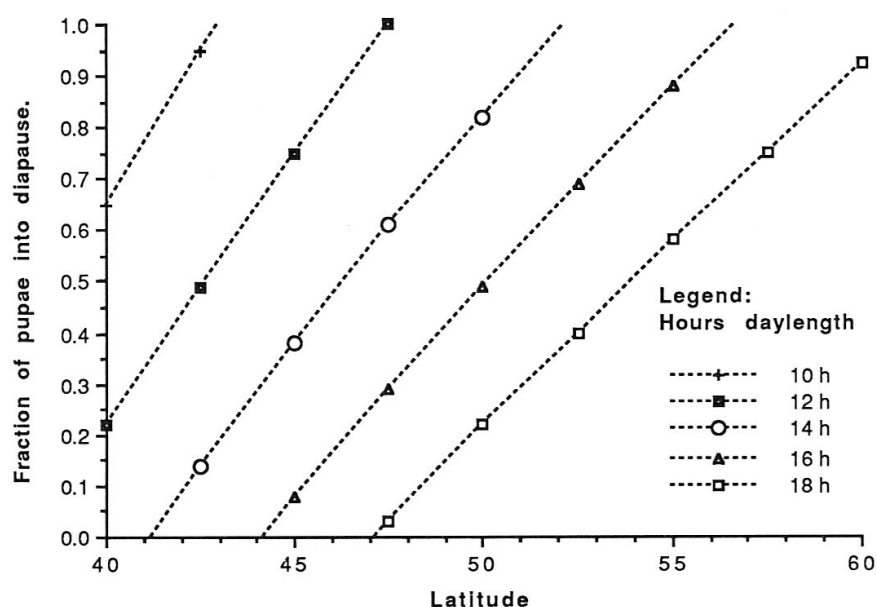


Fig. 3. A: graph of the function for predicting diapause in newly formed pupae at different latitudes. Numbers in the legend refers to daylength (hours).

where L is latitude and D is the daylength (Fig. 3). In the model, diapause is distinguished during the transition from the larval to the pupal stage. It is not known exactly when in their development larvae are receptive to the inducing stimuli (SONI, 1976), hence using the time of pupation is convenient and it introduces no biological problems to the model.

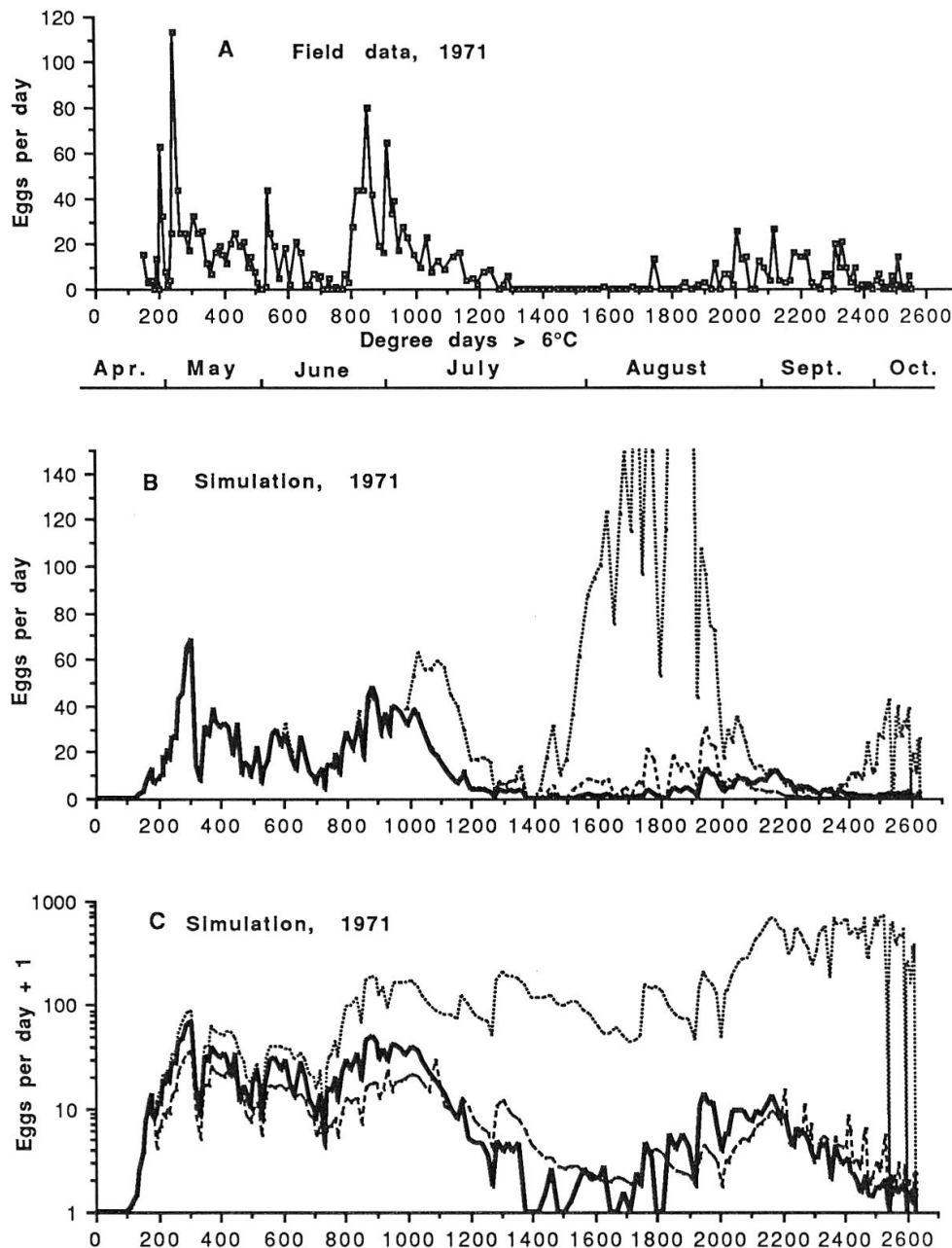


Fig. 4. A: Field data, 1971. B: Simulation data. (—) is the simulation with all weather effects on oviposition and carabid predation included; (---) “aestivation” is excluded; (...) “aestivation” and effects of high soil temperatures on oviposition are excluded. C: Predation effects on a logarithmic scale: (—) is the simulation with all the described environmental effects on a logarithmic scale: (---) is the simulation with all the described environmental effects on oviposition and predation included; (---) is with carabid predation replaced by a constant mortality of 60%; (...) is carabid predation excluded all together.

SIMULATION RESULTS

The field data and simulated data computed incorporation the various effects of weather and carabid predation on cabbage root fly eggs are shown for 1971 (Fig. 4) and 1972 (Fig. 5).

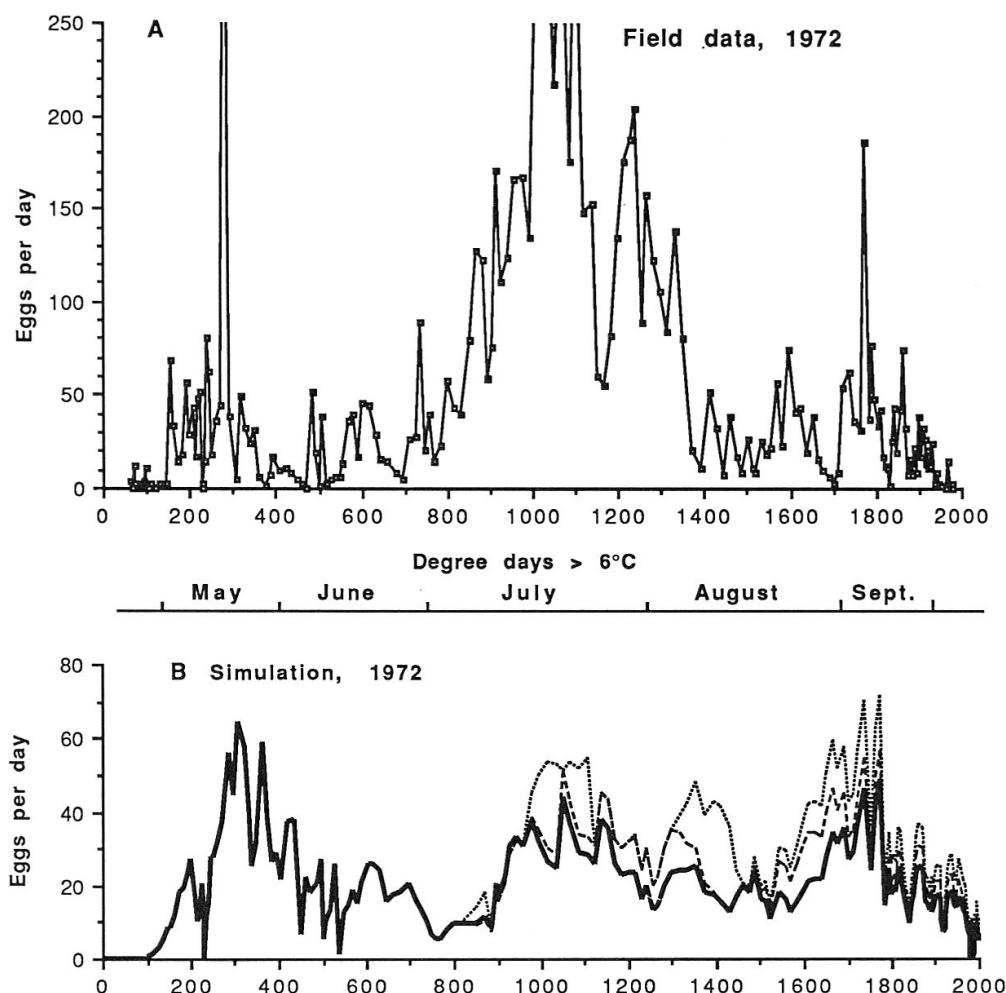


Fig. 5. The 1972 cabbage maggot egg dynamics data from (A) 10 cauliflower plants (o) and (B) The simulated egg dynamics. (—) is the simulation with all weather effects on oviposition included, (--) "aestivation" is excluded, (...) "aestivation" and the effects of high temperatures on oviposition are excluded.

The 1971 season: For 1971, Fig. 4.A presents the field data, and Fig. 4.B examines in a stepwise fashion weather effects given predation: the simulation results with all factors included, without pupal "aestivation", and with the effects of high temperatures on fecundity removed. Fig. 4. C examines the effects on egg dynamics of carabid predation given weather effects. This figure shows the effects of observed carabid numbers, a constant 60% egg mortality, and the effects of carabid predation removed. Note that the solid lines in Fig. 4 B and 4. C are the same simulated data plotted on a different scale.

The observed and simulated data, when all factors are present (Fig. 4 A and B), are very similar with respects to magnitude and phenology. The effects of high

temperatures on oviposition appear more important to cabbage root fly dynamics in the 1971 data than are the effects of "aestivation". Fig. 4. C shows that the dynamics with predation are similar to the observed patterns (4.A), but with predation removed cabbage egg populations continue to increase throughout the season. The results using the constant 60% mortality rate per day are dissimilar to the observed values only during time 1400 to 1900 D°.

The 1972 season was relatively cool and hence high temperature effects on oviposition were not very important. Estimates of carabid densities were not available, and a 60% per day egg mortality rate was used in the simulation. The observed data are given in Fig. 5.A and the simulation results with all factors included and minus high temperature effects are given in Fig. 5.B. The model underestimated egg numbers during midsummer (800–1300 D°), but the pattern is correct. Lowering the constant mortality rate merely increased the magnitude of the egg population, especially in the third peak. This suggests that either the midsummer egg mortalities were lower than 60% or the oviposition rate was higher than simulated. It is not possible to separate these effects. The biggest gap in the model is our ignorance of the numerical response of carabid predators to increasing egg densities. The functional response model would also be improved by further work.

DISCUSSION

The simulation model captures much of the 1971 oviposition dynamics of *D. radicum*, and illustrates the importance of weather in determining the egg dynamics in the field. The model confirms that carabid predation may be an important factor affecting egg numbers and subsequent cabbage root fly population dynamics. The model could provide a valuable tool for monitoring the pest and for evaluating biological (and possibly chemical) control measures against it, given a background of weather.

The model reproduced the number of eggs observed in 1971 much better than the numbers in 1972. This in part is due to the fact that 1972 predator activity was not known, and the constant mortality applied overpredicted the effect during midsummer. This of course needs further study to get a more precise description of the numerical and functional responses of carabids to cabbage root fly egg densities. However, the model provides a good framework for incorporating these effects as they are discovered.

Other factors may also account for the discrepancies between observed and simulated egg numbers, and these may adversely affect simulations of predator activity and the influence of high temperatures on oviposition. Neither of these aspects were modelled based on experimental data. Among the factors that might be important are the availability of adult food which varies over the season and influences fecundity directly (FINCH, 1971), larval mortality due to shortage of food, diseases of the adults (FINCH, 1989), female size preference of plants selected for oviposition (MAACK, 1977) and other factors. These factors, as discovered could be incorporated in the model.

The model does not include development during winter diapause because the temperature response of the pupae during most of this period is not known. For regions with cold winters as occur in much of the distribution area of *D. radicum*, this poses little problem as diapause ends during winter before weather warms and temperatures reach the lower threshold for post diapause develop-

ment. For warmer areas, the temperature response during diapause has to be known in greater detail before simulations of this development can be successful. For populations with type II individuals, the model would have to be able to predict what proportion occurs in the population.

ZUSAMMENFASSUNG

Im wesentlichen anhand publizierter Daten wird ein Simulationsmodell für die Phänologie der kleinen Kohlflye *Delia radicum* [L.] entwickelt. Es ist auf dem Konzept der physiologischen Zeit aufgebaut und simuliert die stochastische Variation der Entwicklungszeiten. Eigenheiten der Biologie der kleinen Kohlflye wie Diapause und «Aestivation» sind eingebaut. Das Modell zeigt, dass die Carabiden in ihrer Aktivität als Eiräuber und das heisse Wetter wichtige Faktoren sind, welche den Eiablageverlauf beeinflussen. Weitere biologische Daten werden benötigt bezüglich der Reaktion überwinternder Diapausepuppen auf die Temperatur, der negativen Wirkung des heissen Wetters auf die Eiablage und der funktionellen und numerischen Reaktion der Carabiden auf die Dichte der Kohlflyeneier. Das Modell simuliert erfolgreich den Zeitpunkt der Eiablage und, sofern Carabidendichte und -aktivität bekannt sind, auch ihre Verteilung.

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