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Life table statistics and cohort parameters for potato tuber moth *Phthorimaea operculella* (Zeller)

Abstract - A study has been undertaken to create a solid ground for the integrated control of the potato tuber moth *Phthorimaea operculella* Zeller in Tunisia. This paper presents the life table statistics, i.e. the generation time, the net reproductive rate, the intrinsic rate of increase and the finite rate of increase, at optimal conditions for development. Assuming that the population would increase exponentially with a stable age distribution the population would grow 0.169 fold per day per individual. The comparison of the life table statistics obtained for the Tunisian strain of the potato tuber moth with the same statistics of other strains showed that the Tunisian strain is not different from other strains. As a consequence, the wide range of data reported in the literature was used to calculate the stage-specific cohort parameters, i.e. developmental time and variability, stage-specific survival and age-specific fecundity. The stage-specific cohort parameters are calculated and expressed as functions of temperature.

Riassunto - *La statistica delle tavole di sopravvivenza e i parametri delle coorti per la tignola della patata* Phthorimaea opercullela *(Zeller).*

È stato effettuato uno studio per creare una base solida all'elaborazione di programmi di lotta integrata contro la tignola della patata *Phthorimaea operculella* Zeller in Tunisia. In questo lavoro si espongono le tavole di sopravvivenza, cioè la durata di generazione, il tasso netto di riproduzione, il tasso intrinseco di accrescimento e il tasso di accrescimento per unità di tempo della popolazione. Le statistiche sono state calcolate per condizioni permettenti uno sviluppo ottimale delle popolazioni. Ammettendo un accrescimento esponenziale di una popolazione avente una struttura d'età stabile, la popolazione aumenterebbe 0.169 volte per giorno e per individuo. Il confronto delle statistiche delle tavole di sopravvivenza ottenute per una linea tunisina con quelle di altre linee dimostra che la linea tunisina non è diversa dalle altre. Di conseguenza i numerosi dati della letteratura sono stati usati per il calcolo dei parametri di coorte, specifici per gli stadi, cioè per la durata di sviluppo e la sua variabilità, per la sopravvivenza e per la fecondità dipendente dall'età. Questi parametri, sono stati calcolati ed espressi come funzioni della temperatura.

Résumé - *Les statistiques des tables de survie et les paramètres des cohortes de la teigne de la pomme de terre* Phthorimaea operculella *(Zeller).*

Une étude a été entreprise pour créer une base solide à l'élaboration de programmes de lutte intégrée contre la teigne de la pomme de terre *Phthorimaea operculella* Zeller en Tunisie. Ce travail présente les statistiques des tables de survie, à savoir la durée d'une génération, le taux net de reproduction, le taux intrinsèque accroissement naturelle et le taux d'accroissement par unité de temps. Ces statistiques sont calculées pour des conditions optimales de développement des populations. En supposant que la population augmente de manière exponentielle avec une distribution stable des âges, la population augmenterait de 0.169 par jour et par individus. La comparaison entre les statistiques des tables de survie pour la lignée tunisienne avec les mêmes statistiques calculées pour des lignées observées ailleurs dans le monde montre que la population tunisienne de la teigne de la pomme de terre n'est pas différente des autres populations. En conséquence, les nombreuses données rapportées dans la littérature ont été utilisées pour calculer les paramètres des cohortes spécifiquement aux stades, à savoir le temps de développement et sa variabilité, la survie et la fécondité spécifiques à l'âge. Les paramètres des cohortes sont étudiés et exprimés en tant que fonctions de la température.

Key words: *Phthorimaea operculella,* Gelechiidae, life table statistics, temperature-dependent cohort parameters, potato.

INTRODUCTION

The potato tuber moth *Phthorimaea operculella* Zeller is the only economically significant insect pest of potatoes in Tunisia and throughout North Africa (von Arx et al., 1988). Studies on *P. operculella* conducted in Tunisia generally focused on the observation of damage symptoms in rustic stores, i.e. holes in the potato tubers (von Arx et al., 1987; von Arx et al., 1988; Essamet et al., 1988). These studies were useful for assessing the economic losses and for developing simple control techniques, but proved to be a poor basis for studying the mechanisms underlying population dynamics which is considered as a prerequisite for the design of integrated pest management systems.

The best way for understanding the dynamics of a populations is the construction and analysis of life tables (Dempster, 1975). In applied entomology age-specific or cohort life tables are most commonly used, and cohort development is often observed under different constant temperature regimes to account for the poikilothermisms; a cohort is defined as a group of individuals born at the same time. The so obtained life tables are used to calculate the *life table statistics,* i.e. the net reproductive rate R_0, the generation time G, and, as a summary statistics, the intrinsic rate of increase r_m (Birch, 1948; Krebs, 1985). Under constant and unlimiting environmental conditions these parameters reflect the performance of a population with a stable age-structure (Birch, 1948; Krebs, 1985). Because of these restrictions, the statistics have limited applicability in applied demographic analyses. For the purpose of this study, however, they are useful since they permit the comparison of the performance of a Tunisian strain of the potato tuber moth populations with the performances of other strains. In case of agreement the vast literature on *P. operculella* can be consulted and used to explain, by means of population models, the dynamics of Tunisian potato tuber moth populations.

A more general method for modeling the population dynamics can be derived from a mechanistic representation of the flow of cohort members through the different life stages (Severini et al, 1990; Baumgärtner & Gutierrez, 1989; Baumgärtner et al., 1990). Based on the observed flow rates a simulation model can be constructed which accounts for variabilities in individual developmental times and considers time-dependent entries into the developmental process as given by the age-specific fecundity (see for example, Bianchi et al., 1990; Cerutti et al., 1991). In this paper the relevant temperature-dependent functions for cohort development, survival and fecundity, i.e. the *cohort parameters*, are presented while the simulation model for the population dynamics under time-varying environmental conditions will be presented elsewhere.

MATERIAL AND METHODS

Life table statistics (reference cohort)

Life table data. This experiment was conducted at the "Institut National de Recherche Agronomique de Tunisie" (INRAT), 2094 Ariana, Tunis. The experimental method used for the elaboration of the potato tuber moth life table is similar to the one found in Chi (1988). Fifty tubers of variety Spunta were placed each in a plastic container of 500 ml. A layer of 1 cm of sterile sand was provided for pupation. Each tuber was then inoculated with one potato tuber moth egg taken from a permanent stock culture held at INRAT. The eggs were all of the same age, i.e. laid during the 12 h preceding the experiment. The containers were then closed with fine mesh organdy and placed in an open room at ambient conditions. Checks were made every day for egg hatching, presence of symptoms on the tubers and pupation occurrence. Five days after egg hatching, tubers that did not show symptoms of attack were dissected to assess larval mortality. As soon as pupation occurred, pupae were sexed.

Couples were each placed in a smaller plastic container covered with a piece of organdy adequate for egg-laying. On top of it, we placed a piece of black oviposition paper which was wetted daily. In order to keep a close contact between the paper and the organdy and to stimulate oviposition, a slice of fresh potato was put on the paper. The adults were fed every day with a 5 to 10% sugar solution. The daily survival and fecundity of each individual was recorded.

Temperature and humidity were recorded. Oscillations ranged from 18°C to 34°C and from 30% to 90%. In two cases, two larvae per tuber were observed. These two cases are disregarded in the analysis so that the life table cohort is build up on a basis of 48 eggs.

Life table analysis. Data obtained as described above were then compiled in a standard cohort life table following the usual method found in literature (Birch, 1948; Southwood, 1978; Krebs, 1985). The following two population statistics were first calculated:

mx : number of female offspring per female of age *x*
lx : proportion of organisms surviving to start of age interval *x*

A sex ratio of 1:1 is used for obtaining m_x. This sex ratio has been reported by several authors to be stable under different conditions (Graf, 1917; Attia & Mattar, 1939; Al-Ali et al., 1975; Foot, 1979; Briese, 1980; Salas & Quiroga, 1985). The life table statistics are computed with an algorithm kindly provided by Dr. Fred L Hulting, Florida (Hulting, 1990). Accordingly, the net reproductive rate (R_0), the intrinsic (or instantaneous) rate of increase (r_m), the mean generation time (G), and the finite rate of increase (λ) are calculated as follows,

$$R_0 = \sum m_x\, l_x \qquad [1]$$

$$1 =^{r_m x} l_x\, m_x \longrightarrow r_m \qquad [2]$$

$$G = \frac{\ln R_0}{r_m} \qquad [3]$$

$$\lambda = e^{r_m} \qquad [4]$$

In order to associate variation to the intrinsic rate of increase, the standard error and confidence interval are computed using the Jacknife method as demonstrated, for example, by Meyer et al. (1986) and Wermelinger et al. (1991). This iterative procedure calculates pseudo-values r_j of r_m by successively dropping one individual j of the original data set of size n

$$r_j = n r_m - (n-1) r_{mj} \qquad [5]$$

where r_{mj} is the solution of equation [2] obtained by omitting observation j. The pseudo-values r_j, which are assumed to be normally distributed (Hogg & Chen, 1988), are then averaged for calculating the "Jacknife Estimate of r_m". The standard error and the confidence interval of the mean are calculated.

Cohort parameters

The cohort has been identified as the basic unit in population models which are based on flow rates of individuals with varying developmental times (Severini et al.,1990) and should thus be considered in parameter estimation procedures for population models.

The individuals of a group entering a life stage at the same time do not emerge simultaneously but appear distributed in time; consequently, the mean developmental time DEL, according to Manetsch's (1976) and Vansickle's (1977) notation, and its frequency distribution, proven to be an Erlang Density Function (Severini et al. 1990) with shape and scale parameters k and c, are studied for each life stage, i.e. for eggs, larvae, pupae and adults. During development and at the end of the life span the cohort suffers from mortality, expressed here as stage-specific survival ϵ.

Since the input into the egg stage originates from mature females, the age-specific fecundity will be studied; thereby, the age of the female is expressed by a senescence rate function.

The developmental time, the stage-specific survival and the fecundity are controlled by temperature and therefore, each of these cohort parameters is expressed in relation to temperature. There is some experimental evidence that the variation coefficient of developmental time is constant and exclusively varies at temperature extremes. Since the data available do not permit an adequate study of developmental time variability under such conditions, we refrain from expressing this statistics as a function of temperature.

Developmental times. We will consider the inverse values of developmental time DEL(T), i.e. the developmental rates $r(T)$, as a function of the constant temperatures T and defined as

$$r(T) = \frac{1}{\mathrm{DEL}(T)} \qquad [6]$$

Accordingly, $r(T)$ is the proportion of development completed in one day at constant temperature T. To describe the function $r(T)$, the model of Sharpe & DeMichele (1977) is chosen because of its explanatory capabilities. This model postulates that the development of a poikilotherm organism is driven by a rate-determining enzyme or enzyme complex which has three basic reversible energy states: inactive by cold temperature, active and inactive by hot temperature. Sharpe & DeMichele (1977) based their model on the fact that the mean transition rate between energy states is determined by the Eyring equation and that the probability of transition times is exponentially distributed:

$$r(T) = \frac{T \exp\left[\left(\Phi - \frac{\Delta H_A^{\neq}}{T}\right)/R\right]}{1 + \exp\left[\left(\Delta S_L - \frac{\Delta H_L}{T}\right)/R\right] + \exp\left[\left(\Delta S_H - \frac{\Delta H_H}{T}\right)/R\right]} \qquad [7]$$

where T is the absolute temperature [°K], Φ is a conversion factor [°K^{-1} mol^{-1}], R is the universal gas constant (1.987 [cal °KE-1 mol^{-1}], $\Delta H_A^{\neq}$ is the enthalpy of activation of the reaction that is catalyzed by the enzymes [cal mol^{-1}], $\Delta S_{L,H}$ is the change in entropy associated with low (L) respectively hot (H) temperature [cal °K^{-1} mol^{-1}] and D$H_{L,H}$ is the change in enthalpy associated with low (L) respectively hot (H) temperatures [cal mol^{-1}].

Very high correlations between the estimated parameters render parameter estimation procedures for equation [7] difficult. Schoolfield et al. (1981) have overcome this problem in rewriting [7] as

$$r(T) = \frac{\rho \frac{T}{298.16} \exp\left[\frac{\Delta H_A^{\neq}}{R}\left(\frac{1}{298.16} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_{1/2\,L}} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_{1/2\,L}} - \frac{1}{T}\right)\right]} \qquad [8]$$

where ρ is the developmental rate at T = 298,16 °K = 25 °C, $T_{1/2,H}$ is the temperature [°K] at which the enzyme is 1/2 active at low (L) respectively hot (H) temperatures, $\Delta H_{L,H}$ and $\Delta H_A^{\neq}$ have already been defined above.

The values of the six unknown parameters in equation [8] are estimated via least square techniques using developmental rates measured at several constant temperatures. The data used to establish these relations originate from Koizumi (1955), Broodryk (1971), Salama et al. (1972), Gergis (1987) and, only for the eggs, Hovey (1943). Only observations made under constant temperatures are used. Since variations between the data from different sources are small, developmental times were averaged for each observed temperature.

Variability in developmental times. As stated above the probability density function for the developmental times is adequately represented by an Erlang distribution with scale c and shape k (Severini et al., 1990). The reference cohort study is used to obtain the stage specific developmental time DEL(T), as well as its variance of VAR(T). T is the mean temperature recorded during the experiment. An estimate of k for each stage is then obtained from the following equation (Manetsch, 1976):

$$k = \frac{(\mathrm{DEL}(T))^2}{\mathrm{VAR}(T)} \qquad [9]$$

For visual examination purposes the Erlang density function with scale $c = \mathrm{DEL}/\mathrm{k}$, where DEL is the mean developmental time, and shape k is plotted with the observed data.

Survival. As pointed out by Feldman & Curry (1984), survival of organisms can be viewed as three competing processes: 1) development completion (for adults), 2) innate mortality, and 3) external mortality. All three categories are dependent on environmental factors such as temperature. In this work the innate mortality (or survival) of immature life stages, as affected by constant temperature, is investigated. Since a satisfactory mechanistic model for the temperature response does not exist, we join Cerutti et al. (1991) and follow Curry & Feldman (1987), who used equation [8] to describe the response of survival to temperature. Accordingly, equation [8] may be rewritten as

$$\epsilon(T) = \frac{p1 \dfrac{T}{298.16} \exp\left[\dfrac{p2}{R}\left(\dfrac{1}{298.16} - \dfrac{1}{T}\right)\right]}{1 + \exp\left[\dfrac{p3}{R}\left(\dfrac{1}{p4} - \dfrac{1}{T}\right)\right] + \exp\left[\dfrac{p5}{R}\left(\dfrac{1}{p6} - \dfrac{1}{T}\right)\right]} \qquad [10]$$

where *p1* ... *p6* are the parameters to be estimated. Data were found in various literature sources. As above, only observations made under constant temperatures are used.

Fecundity. The age-specific fecundity rate $f(a)$ is examined on the basis of the data collected for the standard reference cohort in the above life table analysis. The function of Bieri et al. (1983), as modified by Bianchi et al. (1990), is used to describe $f(a)$

$$f(\mathrm{a}) = \frac{e_1(\mathrm{a} - e_2)}{e_3{}^{(\mathrm{a}-e_2)}} \qquad [11]$$

where a is the age of the female expressed in days and $e_1 \dots e_3$ are parameters which are estimated via least square procedures. Like the immature development, the aging of the adults depends on temperature. The senescence rate of the females is calculated as follows. In a temperature range in which the effect of temperature on the innate survival of aging females is presumably small, the life span is calculated. The inverse of the life span is plotted against the temperature for deriving an adequate estimation of the adult senescence rate.

To describe the response $g(T)$ of the fecundity to constant temperatures T, several data sets found in the literature and the fecundity of the standard reference cohort, used for life table analyses, are plotted in fig. 7. According to visual inspection, data sets which best reflect the observations on the reference cohort are selected, and a polynomial regression model of second order with coefficients a, b and c is used to represent $g(T)$

$$g(T) = a + bT + cT^2 \qquad [12]$$

RESULTS AND DISCUSSION

Life table statistics

Fig. 1 displays the number of female offspring per female (m_x) and the survival rate of the adult (l_x) with respect to age class $x = 1$ day. For the calculation of the l_x, the emergence time of the adult females and the preimaginal mortality are taken into account. As a result of this, l_x linearly increases during the period of emergence to a maximum of 0.69, which is the observed preimaginal mortality. The m_x increases rapidly, reaches its maximum at the time the last adult has emerged and decreases thereafter. This pattern of the l_x and m_x curves has been reported by Briese (1980) to be characteristic of *P. operculella.*

The life table statistics calculated from the reference cohort studied in Tunisia are displayed on table 1 together with findings from other sources. For similar experimental temperatures, the statistics of the reference cohort compare favorably to other studies. For example, the observations of Gergis (1987) made at several constant temperatures in Egypt are practically the same as the ones found in

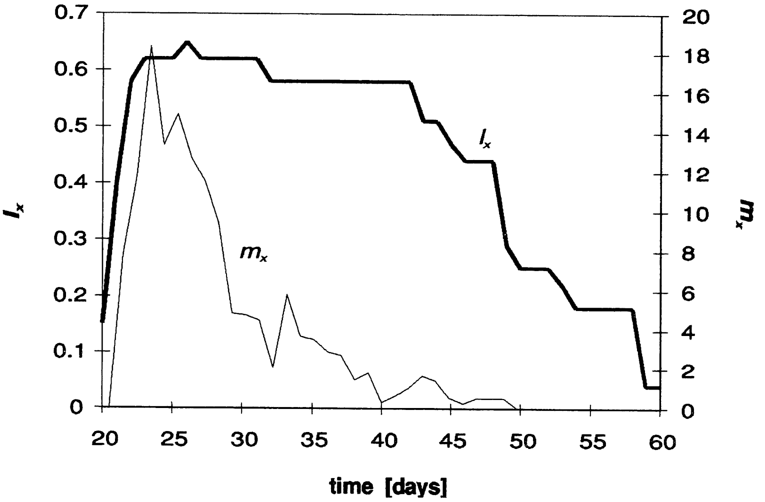

Fig. 1 - Number of female offspring per female (m_x) and survival rate of the adults (l_x) with respect to age x.

Tunisia. It is more difficult to make comparisons with the statistics reported by von Arx & Gebhardt (1990), because they used a day-degree scale (cumulated temperature above the 13 °C threshold) to express l_x and m_x. Nevertheless, an approximation of the intrinsic rate of increase can be found by multiplying r_m by 13, yielding an r_m of 0.136. This is low compared to the other results in table 1 and may be due to the different experimental design they used.

Assuming that the population would increase exponentially with a stable age distribution the population will grow 0.169 fold per day per individual. One generation will elapse in about 26 days, and its size will be 86 times larger than the previous one. However, it must be stressed that these statistics have a limited practical value. Nevertheless, they are useful for comparing the performance of

Table 1 - Population statistics based on a reference cohort and comparison with the literature. T: temperature, r_m: intrinsic rate of increase, R_0: net reproductive rate, G: mean generation time, and λ: the finite rate of increase. Jacknife: *estimation of r_m using the Jacknife procedure;* S.E. *and* C.I.: *standard error and confidence interval of the estimate. [1]) Temperature not constant. [2]) Calculated from data expressed in day-degrees with a lower threshold of 13°C.*

Source	*T*	r_m	R_0	*G*	*λ*
[1]) Reference cohort	25.0	0.169	86.18	26.3	1.18
Jacknife		0.170			
S.E.		0.007	12.17		
C.I.	0.156–0.183				
Chi (1988)	24.0	0.136	69.70	31.2	1.15
Cardona & Oatman (1975)	23.9	0.121	63.51	34.3	1.13
	26.7	0.176	73.08	24.4	1.19
	29.4	0.196	56.15	20.5	1.22
	32.2	0.207	46.13	18.5	1.23
	35.0	negative	–	–	–
Gergis (1987)	15.0	0.039	37.60	93.00	1.04
	20.0	0.101	94.16	45.0	01.11
	25.0	0.170	70.10	25.00	1.18
	30.0	0.212	69.41	20.00	1.24
	35.0	negative	–	–	–
[1,2]) von Arx & Gebhardt (1990)	26.1	0.0105	30.1	326.9	

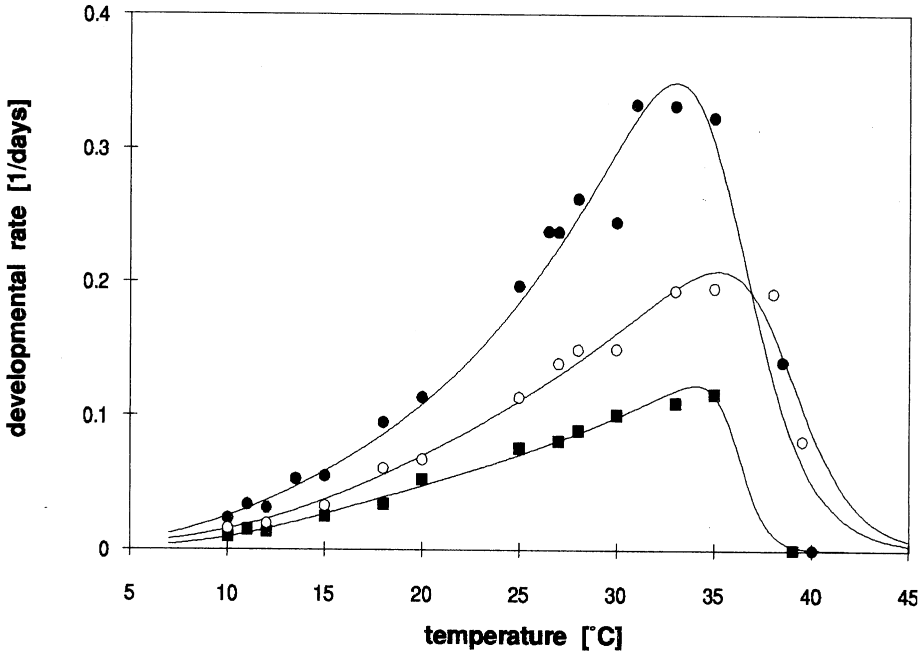

Fig. 2 - Temperature-dependent developmental rates of *Phthorimaea operculella* immature life stages represented by the kinetic model of Sharpe & DeMichele (1977) (see equation [8], ● = eggs; ○ = pupae; ■ = larvae).

populations under specific conditions. For instance, table 1 shows that the Tunisian potato tuber moth exhibits similar population performances when compared to strains from other parts of the world. Data reported in the literature can therefore be used whenever necessary.

Cohort parameters

Developmental time and variability. The response of the developmental rate to constant temperatures, ranging from 10°C to 40°C, is depicted in fig. 2. In the temperature range between 20°C and 32°C the developmental rate increases almost linearly and consequently, a linear model would have been satisfactory to fit the data. However, temperatures below 20°C and above 32°C are frequently encountered in Tunisia, and it is therefore necessary to represent $r(T)$ over a wider temperature range. The kinetic model [8] is particularly adequate for this purpose. The parameters of this model are presented in table 2.

According to the ρ values given in table 2 the developmental times at 25°C (DEL*(25°*C)) of the eggs, larvae and pupae are about 6, 14 and 8 days (DEL*(25°*C)

$= 1/\rho$). In addition, the development completion from eggs to adults requires about 28 days. This result is in accordance with G values of table 1.

The $T_{1/2\,L,H}$ values (table 2), i.e. the temperatures at which half of the enzymes are deactivated by low (L) or hot (H) temperatures, denote an important aspect of the developmental pattern of *P. operculella*, which is the fact that *P. operculella* can develop in a wide temperature range. The developmental rate of the pupae, for example, is still the half of its maximum value at 38.5°C (311.681°K), whereas $T_{1/2\,L}$ for the eggs lies as low as 7.8°C (280.897°K). This feature confirms the ability of *P. operculella* to inhabit a large range of ecological zones (Broodryk, 1971; Hains, 1977; Whiteside, 1985; Briese, 1986). However, at high and low temperature, mortality can be quite high and hence must be accounted for.

Other factors that could influence the developmental time are humidity and food. Humidity has been reported to have no significant influence on the potato tuber moth population statistics (Hovey, 1943; Broodryk, 1971; Haines, 1977), whereas the food effect was studied by Traynier (1983) and Tamò (1986). In Tunisia, the variety Spunta is cultivated in more than 95% of the potato crop area (von Arx et al., 1990) and available in large quantities in the stores (Roux et al., 1992). Hence, food can be considered as unlimited and homogenous.

Variability in the stage developmental times is displayed in fig. 3. The estimated mean developmental time DEL(T), variability VAR(T) and k values are respectively 3.16, 0.15 and 71 for the eggs, 11.5, 0.42 and 314 for the larvae and 6.6, 1.18 and 37 for the pupae. Note the high value of k for the larval stage which is the result of the small observed variance of developmental times when compared to the mean duration of the larval stage. The fit of the Erlang Density Function on the actual data is presented in fig. 3. By visual examination, the fit appears to be satisfactory.

Table 2 - Parameter values of the kinetic model (Sharpe & DeMichele, 1977) describing the stage specific developmental rate $r(T)$ response to temperature. Note that the temperature is given in Kelvin degrees (273.16°K = 0°C) (see equation [8]).

	ρ	$\Delta H_A^{\neq}$	ΔH_L	$T_{1/2\,L}$	ΔH_H	$T_{1/2\,H}$	R^2
	[rate]	[cal mol^{-1}]	[cal mol^{-1}]	[^{0}K]	[cal mol^{-1}]	[^{0}K]	
Eggs	0.168	17250	-48000	280.987	121830	308.913	0.989
Larvae	0.072	11000	-50000	285.008	275000	309.361	0.997
Pupae	0.119	11500	-35000	285.533	125000	311.681	0.990

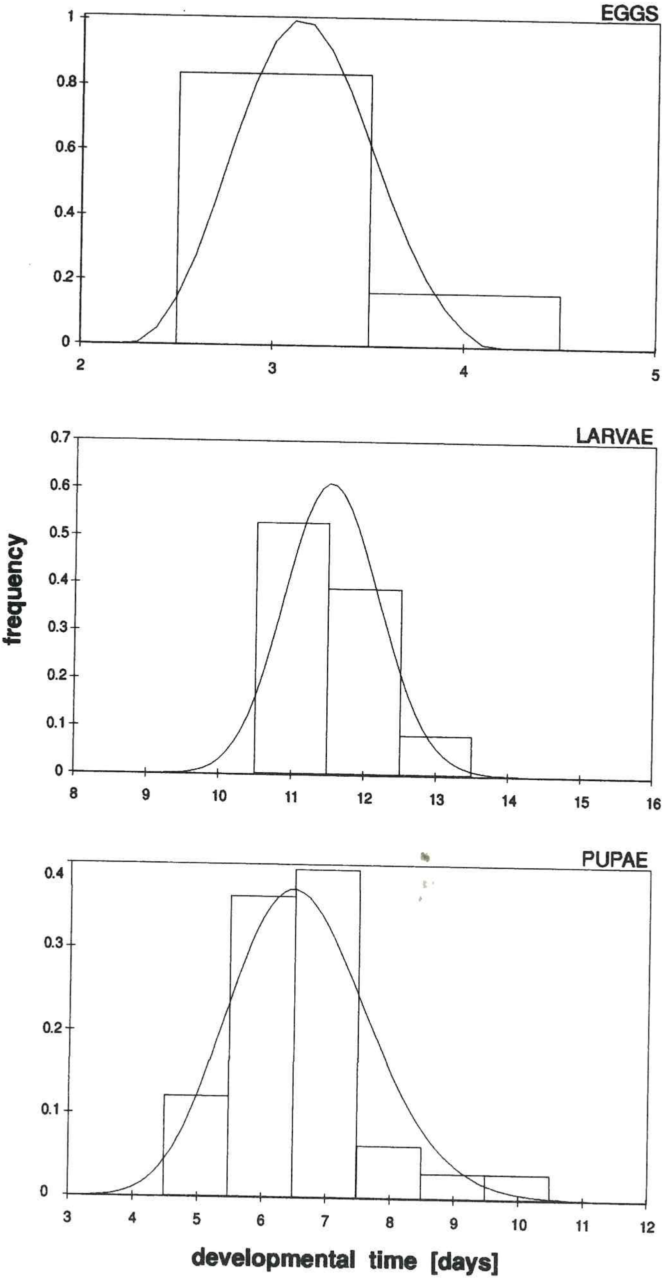

Fig. 3 - Developmental times distribution of *Phthorimaea operculella* immature life stages. The Erlang Density Function is plotted with the observed data. Parameters are estimated as described in the text.

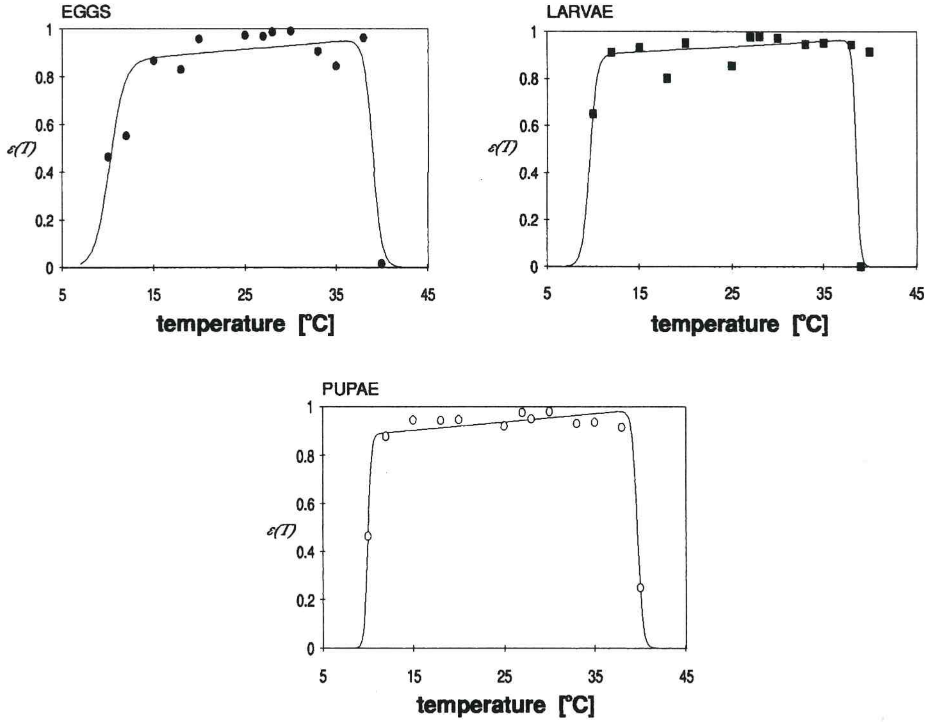

Fig. 4 - Temperature-dependent survival rates $\epsilon(Tc)$ of *Phthorimaea operculella* immature life stages as represented by the kinetic model of Sharpe & DeMichele (1977). Equation [10] is fitted to the observations drawn from Koizumi (1955) and Broodryk (1971).

Survival. The effect of temperature on the survival rates $\epsilon(T)$ of immature life stages is displayed in fig. 4, and the parameter values for equation [10] are presented in table 3. All the observed data originate from Koizumi (1955) except the point $\epsilon(39) = 0$ for the larvae which was found in Broodryk (1971).

A visual examination of fig. 4 and the R^2 values in Table 3 indicate that the selected model represents the stage-specific survival rate response to temperature in a satisfactory way. In the temperature range between 13°C and 37°C, the survivorship of the immature stages remains between 90% and 100%. At lower and higher temperatures, all stages suffer from drastic mortalities. Such extreme situations normally do not occur in the stores. Under field conditions, however, cold and hot temperatures can frequently be encountered in winter and mid-summer. In the summer larvae can probably avoid these adverse conditions by dispersing to cooler places at the ground level where they can feed and find protection inside the tubers during summer. In the winter they may develop in protected places like stores.

Table 3 - Stage specific parameters for the influence of temperature upon survivorship of Phthorimaea operculella *immature stages (see equation [10]).*

	P1	P2	P3	P4	P5	P6	R^2
Eggs	0.914	50	–200000	283.347	400000	312.187	0.987
Larvae	0.937	–150	–400000	282.782	900000	311.650	0.919
Pupae	0.937	50	–800000	283.140	700000	312.858	0.999

Fecundity. The number of eggs laid per female, may be considered as the most variable cohort statistics. The reason might be that besides temperature, other factors such as food, presence of host plant (odor) or even the photoperiod appear to influence the egg production (Labeyrie, 1957; Briese, 1981; Traynier,1983) more than they influence, in general, immature development and survival.

The age specific fecundity observed in the reference cohort study is displayed in fig. 5. The estimation of equation [11] via least square procedures yields the following age specific parameters: $e_1 = 40.276, e_2 = 0.717, e_3 = 1.518$. Recall that the mean temperature recorded during the observations (from 1st egg laid to the last female alive) was 24.1°C, which corresponds approximately to the optimal temperature discussed below. It is therefore possible to calculate the daily fecundity at any temperature T by multiplying the daily fecundity for $T_{24.1}$ (equation [11]) by a correction factor $f(T_{opt})/f(T)$, where the function $f(T)$ is as defined in equation [13]. The age of the female is given by the temperature-dependent se-

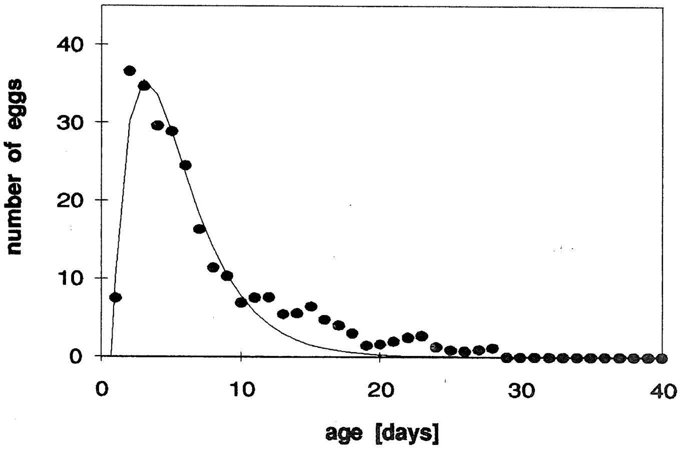

Fig. 5 - Age-specific fecundity for *Phthorimaea operculella* at a mean temperature of 24.1 °C. Equation [11] is fitted to the reference cohort data.

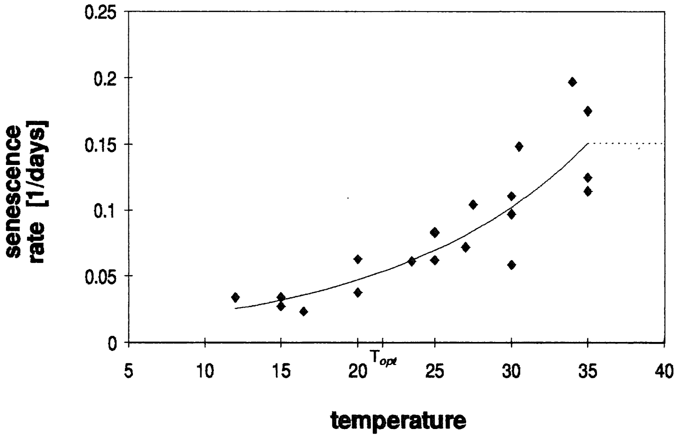

Fig. 6 - Temperature-dependent senescence rate for adult females of *Phthorimaea operculella*. Data sources: Koizumi, 1955; Salama et al., 1972; Briese, 1980; Gergis, 1987. T_{opt} is the optimal temperature for oviposition. Equation [13] is fitted to the reference cohort data.

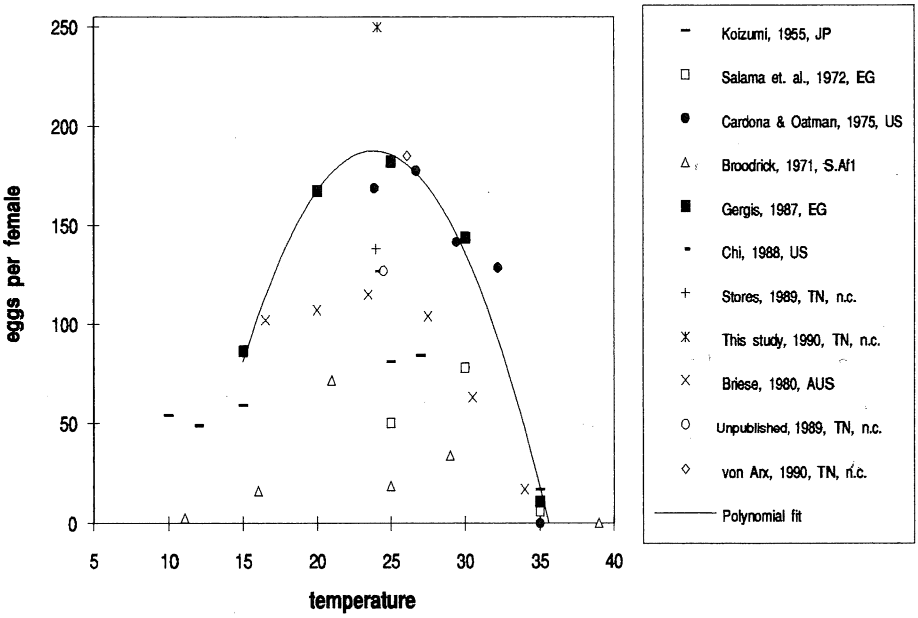

Fig. 7 - Fecundity response to temperature of *Phthorimaea operculella*. Equation [12] is fitted to the data of Gergis's (1987) and Cardona & Oatman's (1975) observations.

nescence rate depicted in fig. 6. A non-linear regression was used to fit the data for the temperatures ranging from 12°C to 35°C. The senescence rate $r(T)$ is assumed to be maximal, i.e. equal to the rate at 35°C at higher temperatures, and to be zero for temperatures lower than 12°C. As a result, the aging of the female can be described by

$$r(T) = \begin{cases} 0 & \text{for} {<} 12 \\ \exp(-4.0604 + 0.77T_c & \text{for } {\leq} T {\leq} 35 \\ r(35) & \text{for} {>} 35 \end{cases} \qquad [13]$$

The effect of temperature upon fecundity is presented in Fig. 7. Data originate from several sources. For the Tunisian potato tuber moth, only a few values obtained at variable temperature regimes are available: one value has been obtained from the standard reference cohort study, a second from a follow-up of a cohort in a store, a third from a study conducted at INRAT, Tunis (unpublished data), and a fourth from von Arx & Gebhardt (1990). The mean fecundity observed in the reference cohort is 250 eggs per female at a mean temperature of 24.1°C. Such high fecundity was also obtained by Traynier (1983) who recorded 244 eggs per female when potato leaves were placed in oviposition cages, by Labeyrie (1957) who showed that feeding the adults with a honey solution can result in a fecundity of up to 236 eggs per female, and by Trehan & Bagal (1944) who report that substituting a sugar solution for water (or nothing) increased the number of eggs laid from 110 to 213 and extended the adult life span.

A visual comparison of the Tunisian observations with data reported from other parts of the world suggests that the data sets of Gergis (1987) and Cardona & Oatman (1975) are the most appropriate to describe the Tunisian potato tuber moth fecundity response to temperature (fig. 7). Hence, equation [12] is applied to these data values yielding $g(T) = -585.672 + 64.858T - 1.36(T)^2$. The lower temperature for egg laying is then T_{min} =12.1°C, which corresponds to the beginning of flight activity (Goldson & Emberson, 1977), while the maximal temperature lies at T_{max} =35.6°C. Note that temperatures higher than 35°C are known to induce male sterility (Koizumi, 1955; Cardona & Oatman, 1975). The optimal temperature Topt is 23.8°C, which is in the range of temperature encountered both in the rustic stores and during the first nocturnal hours in the last weeks of the main growing season.

CONCLUSION

From a demographic standpoint the performance of the Tunisian strain of the potato tuber moth is similar to the performances of other strains studied elsewhere. Therefore, the vast literature on *P. operculella* can be consulted and used to relate the cohort parameters to temperature. Once field-specific information is used to complete the temperature-dependent cohort parameters a simulation model representing the flow rates of individuals can be constructed.

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