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Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **56 (1983)**

Heft 3-4

PDF erstellt am: **21.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-402095

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MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
56, 389-399, 1983

Developmental Biology of Bemisia tabaci (Genn.) (Sternorrhyncha, Aleyrodidae) on cotton at constant temperatures

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The developmental rate (1/D, D = duration in days) of *Bemisia tabaci* (Genn.) immature life stages (eggs, larvae and nymphs) is studied on cotton in relation to constant temperatures. A nonlinear model based on Longan's function (Logan *et al.*, 1976) is used to describe the developmental rate - temperature relationship. At 27 °C the age specific fecundity and adult survival is invstigated and expressed with models proposed by Bieri *et al.* (1983) and Gompertz (Batschelet, 1980). Reproduction is affected both by adverse temperature and by the age of the leaves of the host plant. Likewise the effect of adverse temperature conditions on egg survival is assessed.

The white fly *Bemisia tabaci* (Genn.) is a widespread pest of many agricultural crops in subtropical and tropical areas (Mound & Halsey, 1978). It affects the quantity and the quality of yield through feeding respectively through excreting honeydew (Fowler, 1956; Gameel, 1970) and is known as a vector of viruses (Mound, 1973; Bird & Maramarosch, 1978). Damage to cotton has been reported from various countries, e. g. Pakistan (Ahmed & Mohsin, 1969), Egypt (Azab *et al.,* 1971), Brazil (Costa *et al.,* 1973), Mexico (De Leon & Sifuentes, 1973), Iran (Habibi, 1975), Turkey (Sengonca, 1975), Israel (Gerling *et al.,* 1980) and USA (Johnson *et al.,* 1982). In the Sudan Gezira the white fly is now considered as the most important cotton pest (Hakim & Nasr El Din, 1978).

For poikilotherm organisms, basic information on development and reproduction characteristics as affected by temperature and host plant are needed for parameter estimates which are used in population models (Gutierrez *et al.,* 1977; Gutierrez & Baumgärtner, in press; Gutierrez & Getz, in press). Previous studies on the life cycle of *B. tabaci* has been made mainly under field conditions (Husain & Trehan, 1933; Avidov, 1956; El Khidir, 1965; Khalifa & El Khidir, 1965; Azab *et al.,* 1971; Abdelrahman & Saleem, 1977, 1978; Gameel, 1978), making it difficult to establish relations between the biological characteristics of the insect and the different environmental factors. Thus development and reproduction were studied under controlled conditions to provide an experimental basis for parameter estimates in population models. A similar study in constant temperature cabinets was recently undertaken by Butler *et al.* (1983).

MATERIAL AND METHODS

Experimental procedures

Cotton leaves infested with *B. tabaci* were collected in the Sudan Gezira in January 1979 and brought to Switzerland (St-Aubin: laboratories of Ciba-Geigy, and Zürich: Institut für Phytomedizin, ETH). The insects were used to build up a stock culture and to undertake investigations on cotton (cv. Deltapine) conducted in temperature cabinets with controlled environments as described in tab. 1. The light intensity varied between 20 and 200 W/m^2. For all experiments the relative humidity (r. h.) was kept within the range of 60–70%. The plants were grown at long day (16/8) conditions in 1 liter pots either on fertilized soil (14% N, 7% K, 14% P; 3 g per pot; St-Aubin) or on a similar soil irrigated with nutrient solution (1.7% N, 1.7% P, 3.0% K, Zürich). As a rule the first fully grown leaves were used for rearing the insects.

In a first experiment, the development of the white fly at different constant temperatures was studied. To obtain oviposition the white fly adults were kept in clip-on cages of 3.5 cm diameter during 24 h at 27 °C. After removal of the cages, the oviposition area was encircled with a mixture of equal parts of canada balsam and castor oil (Azab *et al.*, 1971) to avoid the escape of the crawlers (first stage larvae). The cotton plants were then placed at different temperatures (t) to investigate the rate ($R = 1/D$, D = duration in days) of egg and of total immature stage development (tab. 1, fig. 1 and 2). As it was difficult to watch individual crawlers, larval and nymphal development was calculated as the difference between total immature stage development and egg development. The influence of temperature on egg survival (SE) was recorded.

Tab. 1: Environmental conditions for biological studies of *Bemisia tabaci.*

Experiment	Temp. (°C)	Radiation (W/m2)	Plant-age (DDP)	Leaf-age (DDP)	Replicates
Stock culture	27	20 - 200	450	-	-
Developmental rates (R) vs. temperature (t)	15	20	450	150	165, 0 1)
	21	20	450	150	- , 91
	24	200	450	150	227, 137
	27	200	450	150	458, 195
	30	20	450	150	476, 367
	35	20	450	150	296, 5
Fecundity (FR) and adult survival (SA) vs. age (z)	27	200	450	150	50 2)
	27	200	450	150	40 3)
	27	200	450	150	40 4)
Oviposition rate (ROT) vs. temperature (t)	15	20	450	150	29
	21	20	450	150	26
	27	200	450	150	30
	33	20	450	150	29
	38	20	450	150	16
Oviposition rate (ROL) vs. plant- and leaf age (la)	27	200	450	150	52
	27	200	750	150	25
	27	200	750	400	32
	27	200	1365	150	31
	27	200	1365	400	29

(r. h. = 60–70%; long day (16/8) conditions; DDP = day-degrees above the 12 °C developmental threshold for cotton)

1) Replicates for egg and total immature development, respectively
2) Replicates for females manipulated daily (treatment A)
3) Replicates for females manipulated every 10 days (treatment B)
4) Replicates for males

In a second experiment, the age specific fecundity rate (FR) and the adult survival rate (SA) were studied at 27 °C. At this temperature the development of immature stages appeared to be fastest. FR and SA were expressed as a function of age (z) measured in days. To calculate FR, females were kept individually in small clip-on cages of 1 cm diameter with at least one male. The cages were moved to a new leaf every day (treatment A, tab. 1). The manipulation of the adults occurred at 4 °C to prevent their escape. Exposure time at such a low temperature was about 2 min including 1 min to immobilize the adults. They were transferred by means of a small hair brush. The effect of this procedure on survival and fecundity was studied by comparing the manipulated insects with a group of caged females moved to a new leaf at 4 °C at an interval of 10 days (treatment B, tab. 1). The survival of males was studied separately in the same way.

In a third and fourth experiment the effects of temperature, plant age, and leaf age (la) on reproduction was investigated with a group of insects selected at random from the stock culture (tab. 1). They were exposed during one day either to various temperature conditions or reared at 27 °C on main stem leaves and plants of different age (tab. 1). The age was expressed in day-degrees (DDP) above the 12 °C plant developmental threshold (Gutierrez *et al.,* 1975). Thereby the age of the leaves was approximated by counting the nodes (50 DDP per node; Gutierrez *et al.,* 1977). For each temperature, each leaf age, and plant age the number of eggs (NE) laid per day was calculated. The oviposition rate was related either to temperature or to leaf age. The oviposition rate related to temperature (ROT) was defined as the ratio of NE to the value found at the reference temperature of 27 °C. The oviposition rate related to leaf age (ROL) was expressed as the ratio of NE on 400 DDP old leaves to the value found on the 150 DDP old reference leaves (tab. 2).

Tab. 2: Models and corresponding parameters to describe the *Bemisia tabaci* developmental biology.

Relationship	Model used	Life Stages	Parameter estimates a	b	c	d	DF
Developmental rate (R) vs. temperature (x)[1]	$R = \begin{cases} 0. & 0 \geq x \geq d \\ a(\exp(b*x)-\exp(b*d-(d-x)/c)) & 0<x<d \end{cases}$	Eggs	0.0267	0.1056	1.3923	25.2	1619
		Immatures	0.0641	0.2135	4.5929	22.2	788
		Nymphs	0.3044	0.2278	4.3657	21.2	3
Fecundity rate (FR) vs. age (z)	$0 \leq FR = a(z-c)/b^{(z-c)}$	Females 1	8.9413	1.2264	0.4344	-	16
Adult survival (SA) vs. age (z)	$1 \geq SA = a*\exp(-b*\exp(c*z))$	Males	1.3081	0.2104	0.1678	-	15
		Females 1	1.1370	0.0758	0.2401	-	22
		Females 2	1.4344	0.2561	0.1185	-	22
Oviposition rate (ROT) vs. temperature (t)	$0 \leq ROT = a - b*t + c*t^2 - d*t^3$	Females	4.8916	0.7778	0.0384	0.0006	126
Oviposition rate (ROL) vs. leaf age (la)	$0 \leq ROL = a - b*la$	Females	1.1989	0.0013	-	-	185

DF = degrees of freedom
Females 1 = manipulated daily (treatment A)
Females 2 = manipulated every 10 days (treatment B)

[1] x = t-THR, d = TM-THR, while: t = temperature in °C, THR = developmental threshold, TM = lethal, maximum temperature.

Statistical analysis

The different relationships were described by linear or nonlinear regression models as summarized in tab. 2. The parameters were estimated via least square methods using SPSS (Nie *et al.,* 1975) or BMDP (Jennrich, 1979) statistical software. In general the fit of the data to these models (tab. 2) was evaluated visually. For a range of temperature data (15–30 °C), however, a test was made to check the adequacy of a linear model (Sachs, 1978; Baumgärtner *et al.,* 1981) in describing the developmental rate-temperature relationship for eggs. Because the variance in developmental rates differed with temperatures (fig. 1), a weighted procedure was used in the BMDP program to compute the regression statistics (Baumgärtner & Charmillot, 1983). The weight assigned to each case is here proportional to the inverse of the variance (Dixon, 1981). Data from 15 and 35 °C were excluded from the calculation on total development of immature stages because of extremely small survival, 0 and 1.7% respectively. Differences in fecundity (tab. 3) between treatments A and B were tested with the SPSS one-way analysis of variance programs (Kim & Kohout, 1975), while changes in egg survival (equation 1) at different temperatures were tested after Newman-Keuls multiple range test (Zar, 1974).

Tab. 3: Fecundity of *Bemisia tabaci* as affected by short manipulations at intervals of one and ten days at 4 °C (treatment A and B, respectively, see tab. 1).

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MEANS AND S.DEV.


Manipulated          Mean   S.Dev.   N    95% Conf. Int.
daily                116.3   70.8    50     96.2 - 136.4
every 10 days        127.5   82.5    40    101.1 - 153.9



ONE-WAY ANALYSIS OF VARIANCE


Source of    Sume of          Mean             Significance
Variation    Squares    DF    Square     F         of F

Treatment     2800.0     1    2800.0   .482       0.489
Residual    511050.5    88    5807.4
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RESULTS AND DISCUSSION

Developmental rates

Assuming that egg development is a linear function of the temperature for the range of 15–30 °C, a threshold (THR) of 10,8 °C was calculated. However, if the linear model is submitted to an F-test (Nie *et al.,* 1975), it appears that at a high significance level ($P \ll 0.001$) the model is not adequate to express the relationship for the temperature range mentioned above. In experiments carried out at 35 °C, much lower developmental rates than calculated by the linear model were observed (fig. 1 and 2). Because under Sudanese conditions the daily mean temperature exceeds 30 °C in September and October, the nonlinear function based on Logan's model (Logan *et al.,* 1976) was used to describe developmental rates (tab. 2). The base temperature considered in this equation is the developmental threshold (THR) as calculated above (Baumgärtner *et al.*, 1981). Up to 28 °C the developmental rate of eggs is consistent with the results obtained by El Helaly *et al.* (1971), Gameel (1978), and Butler *et al.* (1983). Above this temperature the rate differs considerably from the values found by El Helaly *et al.* (1971, 1977) and Gameel (1978).

The same base temperature (THR) was used to calculate the rate - temperature relationship for the total development of immature stages (fig. 2, tab. 2). This was fastest below 30 °C while for egg development it was fastest around 33 °C (fig. 1). The calculated lethal, maximum temperature (TM) with 100% mortality was 4 °C lower for the larval and nymphal than for the egg development. The shortest life cycle of about 17 days is observed if eggs are exposed to 33 °C and nymphs to 27 °C (fig. 1 and 2). This corresponds to the duration of immature stage development observed by Razoux Schultz & Ahmed (1962) or Abdelrahman & Saleem (1977, 1978) in October or at the beginning of November on Sudanese cotton. Shorter developmental times have been reported, for example, by Husain & Trehan (1933) on cotton in India, and by El Khidir (1965) and Khalifa & El

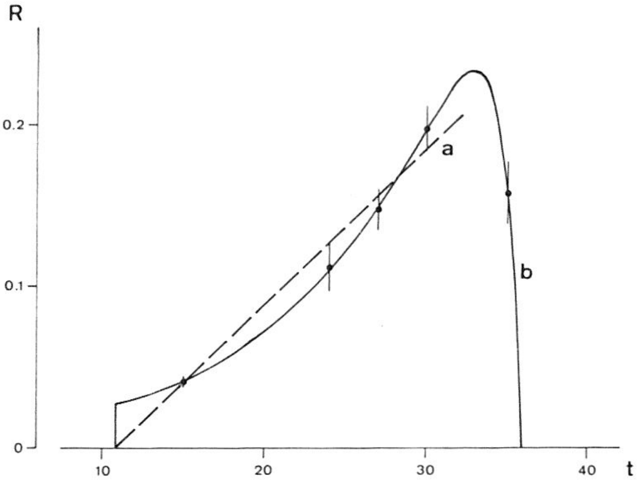


Fig. 1: Rate (R) of egg development as a function of temperature (t) in °C (R = 1/D, D = Developmental time in days; a = linear regression for the temperature range of 15-30 °C; b = nonlinear model after Logan *et al.*, 1976; means of the observed values are given with standard deviations; parameter estimates are given in tab. 2).

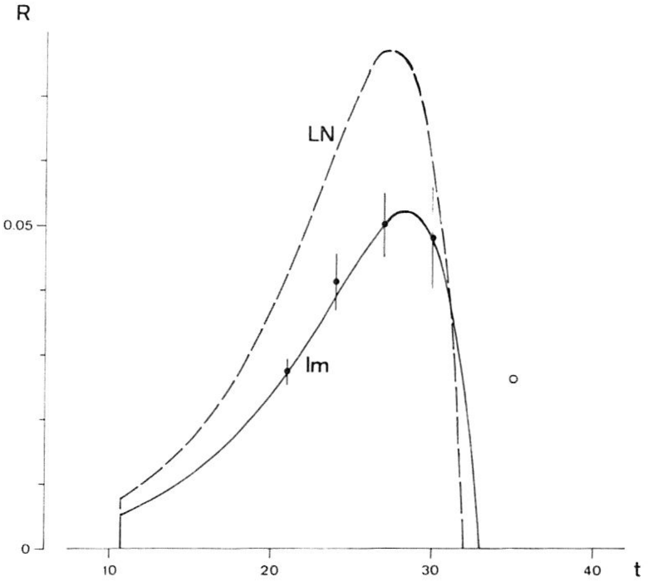


Fig. 2: Rate (R) of total immature stage (Im) and larval and nymphal (LN) development as a function of temperature (t) in °C (The non-linear model is based on Logan *et al.*, 1976; means of the observed values are given with standard deviations. ○ = value excluded from regression calculations, because of only 5 replicates; parameter estimates are given in tab. 2).

Khidir (1965) on lubia *(Dolichos lablab)* in the Sudan. The duration of the development of the immature stages studied by Azab *et al.* (1971) on sweet potatos *(Ipomoea batatas)* in Egypt and most recently by Butler *et al.* (1983) on cotton seedlings in Arizona is comparable to that observed for Sudanese material on cotton for the temperature range of 20 to 27 °C. At lower and higher temperatures the developmental rates observed by these workers, however, were faster. In Sudanese cotton fields Gameel (1978) observed longer developmental periods. The discrepancies may be due either to variations in the host plant quality, which is known to have a profound influence on white fly biology (Joyce, 1958, 1959; Razoux Schultz & Ahmed, 1962; Van de Merendonk & Van Lenteren, 1978), or to variable temperatures, which have been shown to promote faster development than comparable constant temperatures (Messenger, 1959).

Fecundity and adult survival

The fit of Bieri's *et al.* (1983) model to the age specific fecundity (FR) data was satisfying when a preoviposition period (c, tab. 2) was included (fig. 3). The daily manipulation at 4 °C (treatment A) didn't appear to reduce the fecundity significantly (P = 0.48, tab. 3). The average number of 128 eggs per female in treatment B is less than that reported by Azab *et al.* (1971) and by Gameel (1978) (161 and 160, respectively) and higher than the number observed by El Khidir (1965) or by Butler *et al.* (1983) (108 and 81, respectively) at 26.7 °C. Hassan (1982) used white flies which were retrieved from our stock culture for investigations on fertility. He found an average of more than 309 eggs per female when

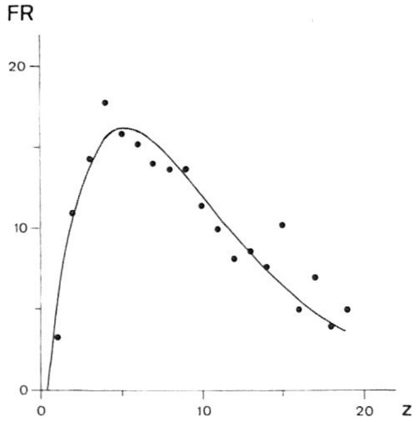


Fig. 3: Age specific fecundity (FR) as a function of female age (z) in days at 27 °C (Model after Bieri *et al.*, 1983; parameter estimates are given in tab. 2).

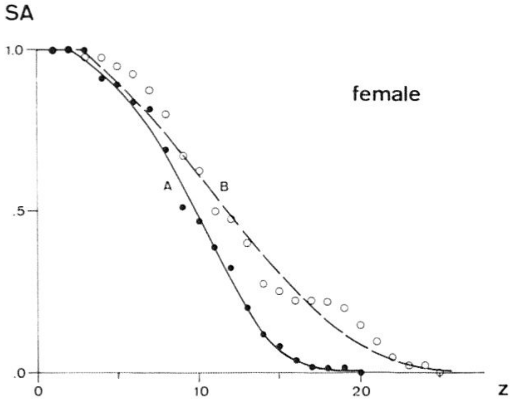
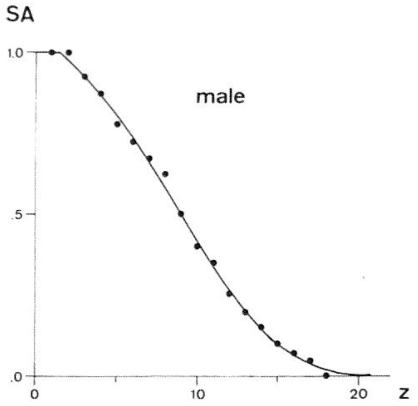


Fig. 4: Survival (SA) of females as a function of age (z) in days at 27 °C (A = females manipulated daily at 4 °C, treatment A; B = females manipulated every ten days at 4 °C, treatment B; model after the Gompertz function; parameter estimates are given in tab. 2).

Fig. 5: Survival (SA) of males as a function of age (z) in days at 27 °C (Model after the Gompertz function; parameter estimates are given in tab. 2).



kept on leaf-discs at 25-26 °C constant temperature. The age specific survival (SA) described by the Gompertz function (Strehler, 1977; Batschelet, 1980; tab. 2) differred between sexes and between females in the two treatments (fig. 4 and 5). The average longevity of females from treatment B was 12.9 days at 27 °C and considerably shorter than that observed by El Khidir (1965), Gameel (1978) and Hassan (1982), i. e. 18.5, 61.5 and more than 29.4 days, respectively, but longer than reported by Butler *et al.* (1983), i. e. 8.0 days at 26.7 °C. However, there is an agreement in the longevity of males being shorter than the longevity of females. Male longevity was 6.0, 7.6, 13.2 and 9.7 days, after El Khidir (1965), Butler *et al.* (1983), Gameel (1978) and the experiment reported in this paper (fig. 5), respectively. Gameel's (1978) and El Khidir's (1965) observations were made under field conditions so that a direct comparison with experiments in controlled environments is almost impossible. The discrepancies between the results of Hassan (1982), Butler *et al.* (1983) and those reported here are more difficult to explain. Different food quality and relative humidity may be responsible factors for them.

Effects of temperature and nutrition on reproduction

The relative oviposition rate per day as affected by temperature (ROT) is highest around 31 °C (fig. 6, tab. 2), i. e. about the same temperature found most favorable for the egg development. The relative oviposition rate as affected by the host plant (ROL) decreases with increasing leaf age (la; fig. 7, tab. 2). ROL appears to be less influenced by the age of the host plant. Temperature and the nutritional value of the host plant are known to change the fecundity of the greenhouse white fly *(Trialeurodes vaporariorum* Westwood) significantly (Weber, 1931; Hussey & Gurney, 1959; Van Boxtel *et al.,* 1978; Van Sas *et al.,* 1978). Before being exposed for one day to different temperatures or leaf qualities, the females were reared under favorable conditions. Any changes in the relative oviposition rates (ROT, ROL) are the result of an immediate response to the experimental conditions and may be different if females are adapted to them. Furthermore, due to the experimental facilities available, the host plants were presumably suffering from a light stress (20 W/m^2; tab. 1). Because the relative oviposition rate responds clearly to temperature (ROT) and host plant conditions (ROL) both relationships are likely to have a profound influence on the population dynamics of *B. tabaci* (Von Arx *et al.,* in press) and deserve further studies at full length.

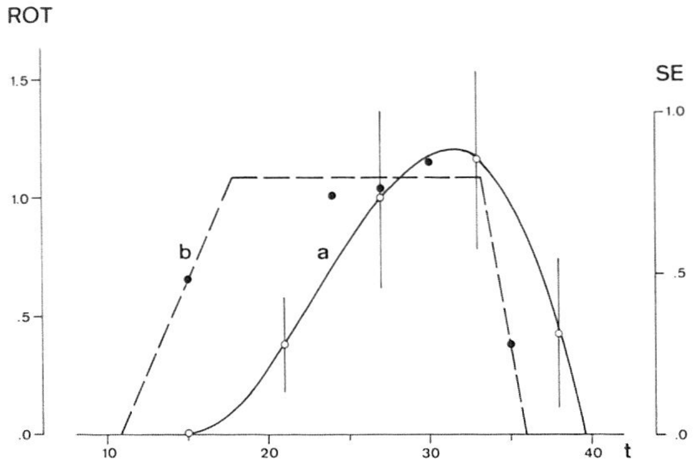


Fig. 6: Relative oviposition rate (ROT, a) per day and egg survival (SE, b) as a function of temperature (t) in °C (o = means and standard deviations of the observed values for ROT; ● = observed SE; parameter estimates for ROT are given in tab. 2; the relationship for SE is described in the text, equation 1).

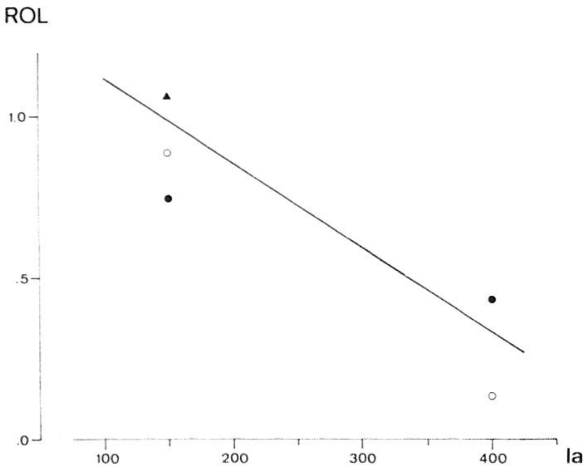


Fig. 7: Relative oviposition rate (ROL) per day as a function of leaf age (la) in day-degrees (DDP) (DDP = °C ≧ 12.0; ▲ = plant age 450 DDP, o = plant age 750 DDP, ● = plant age 1360 DDP; parameter estimates are given in tab. 2).

Survival of immature stages

Egg survival (SE) was significantly ($P \leqq 0.001$) affected by the experimental temperatures (fig. 6, equation 1) and appeared to be lower than reported by GAMEEL (1978). After the Newman-Keuls multiple range test (ZAR, 1974; KIM & KOHOUT, 1975) survival at 35 °C was significantly ($P \leqq 0.05$) reduced as compared to the values between 24 and 30 °C. Survival at 15 °C, however, was not significantly ($P \geqq 0.05$) different from other values.

$$SE = \begin{cases} 0. & 10.8 \geqq t \geqq 36.0 \\ 0.1145 \bullet (t\text{-}THR) & 10.8 < t < 17.7 \\ -\,0.2879 \bullet (t\text{-}TM) & 33.3 < t < 36.0 \\ 0.7903 & 17.7 \leqq t \leqq 33.3 \end{cases} \qquad (1)$$

where: SE = egg survival
t = temperature
THR = lower developmental threshold for eggs
TM = upper lethal temperature for eggs

Besides temperature, host plant quality seems to be a limiting factor for the survival of larvae and nymphs. Since plant quality was not assessed in detail and was probably reduced by the light stress mentioned above, it was impossible to separate the two effects.

ACKNOWLEDGEMENTS

The research work was financed by Ciba-Geigy AG, from which most of the equipment and facilities were available. The authors are particularly indebted to Mr. A. MEIER, Dr. B. SECHSER, Dr. V. DITTRICH and Mr. A. VONLANTHEN for their assistance during the study. Thanks are due to Prof. Dr. O. I. GAMEEL for his advice, on whose work on *B. tabaci* these investigations are mainly based. Dr. H. R. ROTH and Dr. W. BERCHTOLD, Institut für Tierproduktion der ETH, Zürich, advised us in planning the statistical analyses, and Mrs. E. FREI and Mr. S. MANCUSO, Institut für Phytomedizin der ETH, Zürich, carried out a part of the experiments. We thank Mrs. B. HERREN and Prof. Dr. A. P. GUTIERREZ, University of California, Berkeley, for the review of the manuscript.

RESUMÉ

Le taux de développement (1/D, D = durée en jours) des stades préimaginaux de *Bemisia tabaci* (GENN.) a été étudié sur coton à des températures constantes. La relation température - taux de développement a été décrite en utilisant le modèle non-linéaire basé sur la fonction de LOGAN *et al.* (1976). La fécondité et la survie des adultes ont été étudiées à 27 °C en fonction de l'âge des adultes et décrites en utilisant les modèles proposés par BIERI *et al.* (1983) et GOMPERTZ (BATSCHELET, 1980). La fécondité journalière moyenne est influencée non seulement par les températures défavorables, mais aussi par l'âge physiologique des feuilles de la plante hôte. La survie des œufs à des températures défavorables à leur développement a été également quantifiée.

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(received June 8, 1983)