Environmental factors affecting the life tables of *Tetranychus urticae* KOCH (Acarina). I. Temperature

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The literature of the past 20 years concerning temperature effects on spider mite development is briefly reviewed. In an experiment with apple trees the effect of temperature as a key element of the life system of *Tetranychus urticae* Koch was quantified. Life tables were constructed at five different constant temperatures between 15 °C and 35 °C, from the preadult developmental time, mortality, adult oviposition pattern, longevity and sex ratio of the twospotted spider mite. Ratios of the duration of the quiescent and active stages were calculated as well as life table statistics such as net reproductive rate, R_0, intrinsic rate of natural increase, r_m, generation time, G, and doubling time of the populations. Developmental rates were linearly related to temperature and the proportion of the quiescent stages declined with higher temperatures. With rising temperatures adult life span became shorter and the ovipositional rate increased as well as r_m which was linearly related to temperature in the range under study. Generation time and doubling time accordingly decreased.

INTRODUCTION

In the life system of the twospotted spider mite *Tetranychus urticae* KOCH, temperature is considered one of the most important component affecting the development and reproduction of this poikilothermic organism. Therefore, temperature was the first element to be analyzed in a series of investigations on environmental influences. The analysis relies on life tables constructed at different temperatures on detached apple leaves.

LITERATURE REVIEW

The response of demographic parameters of spider mites to temperature is well documented for a wide range of tetranychids feeding on various host plants, which is the reason for some of the variation of the results. In this short review, the literature of the past 20 years on spider mites in general and on *T. urticae* in particular is summarized (for earlier literature the reader is referred to VAN DE VRIE *et al.*, 1972).

Preadult development

Rising temperatures between 10 °C and 30 °C linearly increase in most cases the developmental rates of eggs and juvenile stages of tetranychid species (KEETCH, 1971; GUPTA *et al.*, 1972; HAZAN *et al.*, 1973; TANIGOSHI *et al.*, 1975; RABBINGE, 1976; HERBERT, 1981a; CAREY & BRADLEY, 1982; LANDWEHR & ALLEN, 1982; YASUDA, 1982; BOYNE & HAIN, 1983; CONGDON & LOGAN, 1983;

DELRIO & MONAGHEDDU, 1986; DE MORAES & McMURTRY, 1987; YANINEK *et al.*, 1989). After a steady increase the developmental rates reach a peak and decline thereafter (PERRING *et al.*, 1984b; DELRIO & MONAGHEDDU, 1986). The maximum rates and the slopes are species-specific. A linear increase of the developmental rates (1/DT) is equivalent to a curvilinear decrease of the developmental time (DT) with increasing temperature (cf. Fig. 1).

For *T. urticae* the developmental rates were found to be linear between 15 °C and 29 °C (HERBERT, 1981b; CAREY & BRADLEY, 1982).

Reproduction

The fecundity of various tetranychids often reaches a maximum level at a range of approx. 20−30 °C (KEETCH, 1971; GUPTA *et al.*, 1972; RABBINGE, 1976; YASUDA, 1982; DELRIO & MONAGHEDDU, 1986; DE MORAES & McMURTRY, 1987), and is reduced at lower (HERBERT, 1981a) as well as at higher (HAZAN *et al.*, 1973) temperatures. Other sources report increasing (TANIGOSHI *et al.*, 1975; CONGDON & LOGAN, 1983) or decreasing (BOYNE & HAIN, 1983; PERRING *et al.*, 1984a) fecundity with rising temperatures. However, the ovipositional rate per day typically increases (TANIGOSHI *et al.*, 1975; RABBINGE, 1976; LANDWEHR & ALLEN, 1982; BOYNE & HAIN, 1983; CONGDON & LOGAN, 1983; DE MORAES & McMURTRY, 1987) approaching a maximum rate and collapsing thereafter (DELRIO & MONAGHEDDU, 1986; HOLTZER *et al.*, 1988). This is connected to a reduced oviposition period at higher temperatures.

Between 15 °C and 21 °C egg production of females of the twospotted spider mite is enhanced by a factor of three (HERBERT, 1981b), CAREY & BRADLEY (1982) reported less progeny at 29 °C than at 24 °C.

Mortality

A wide number of studies has described a fairly distinct reduction of the adult life span at increasing temperatures (KEETCH, 1971; GUPTA *et al.*, 1972; HAZAN *et al.*, 1973; TANIGOSHI *et al.*, 1975; RABBINGE, 1976; CAREY & BRADLEY, 1982; BOYNE & HAIN, 1983; CONGDON & LOGAN, 1983; PERRING *et al.*, 1984a; DELRIO & MONAGHEDDU, 1986; DE MORAES & McMURTRY, 1987; YANINEK *et al.*, 1989). Juvenile survival was found to be impaired both at high and low temperatures (HERBERT, 1981a; LANDWEHR & ALLEN, 1982; DELRIO & MONAGHEDDU, 1986).

A rearing temperature of 15 °C invoked a shorter oviposition period in *T. urticae* than higher temperatures (HERBERT, 1981b), but longevity was reduced at 29 °C by 5 days compared with 24 °C (CAREY & BRADLEY, 1982).

Sex-ratio

The sex-ratio, i.e., the proportion of females in the progeny did not reveal a consistent reaction of *T. urticae* to temperature (HERBERT, 1981b; CAREY & BRADLEY, 1982). DE MORAES & McMURTRY (1987) found a higher proportion of *T. evansi* females at both ends of the temperature range of 15° to 35 °C.

MATERIAL AND METHODS

Young apple trees of the variety "Golden Delicious" on M9 rootstocks were used to supply the leaf material for the experiments. They were potted in 8 liter

containers and cultivated at 21 °C. The spider mites originated from an apple orchard near Sion, Canton Valais, in Southwestern Switzerland and were reared in the laboratory on the apple trees at 20 °C.

In the experiments, young larvae of *T. urticae* that had hatched on the apple trees were transferred to detached leaves or leaf disks lying upside down on moist tissue in plastic trays. The lids obtained gauze-covered holes to prevent dew formation. The juvenile stages developed on leaf disks of 19 mm diameter which were renewed every two or three days. The adulds were kept on leaves being replaced every four or five days. The trays were exposed to constant temperatures of 15, 21, 25, 30, or 35 ± 0.5 °C and a photoperiod of 16:8 h under controlled conditions. The temperatures inside the trays went up to 0.5 °C above the ambient temperatures and the relative humidity was 90−95%. Development of the preadult stages (eggs + juveniles), oviposition and longevity were recorded daily. For the embryonic developmental time females were allowed to oviposit for two days on detached leaves and these leaves were subjected to the same temperatures as mentioned above. The number of replications per treatment in all experiments varied in a range from 19 to 210 observations, the respective numbers are listed in the tables. The variability between individuals was disregarded. The recorded data were compiled in age-specific life tables.

On these life tables some analyses were carried out. The ratio of quiescent to active stages in the juvenile development for different temperatures were calculated. For the developmental rates a linear model $DR = f(T)$ proved appropriate. In the life table statistics, only females suffering a natural death were considered, i.e., individuals leaving the leaf disks were excluded from the calculations. Net reproductive rate (R_0), intrinsic rate of natural increase (r_m), and mean generation time (G) were calculated according to SOUTHWOOD (1978). First, an approximate value for r_m was calculated ($\ln R_0/ G$) and from this initial value the accurate r_m was computed by the means of an iterative computer program (based on an algorithm made available by Prof. A.P. GUTIERREZ, UC Berkeley). Since only developmental times and oviposition were measured in these experiments, the missing parameters were extracted from the literature: the sex ratio was set to 0.75 (CAREY & BRADLEY, 1982; WERMELINGER & DELUCCHI, 1990), and the mean preadult survival to 0.8, although it may vary with temperature (HERBERT, 1981b).

RESULTS

In general, the developmental times and longevity decreased with increasing temperatures (Tab. 1). The developmental rates, i.e. the fraction of development accomplished each day, were positively and linearly related to temperature (Fig. 1), or vice versa, the developmental time showed a curvilinear decline with rising temperature. Calculating the intersection of the developmental rate regression line with the temperature axis, the overall threshold for total preadult development was found to be 9.7 for *T. urticae*.

Younger stages were much more susceptible to temperature than older ones: embryonic development differed by a factor of more than 5 in the temperature range under study, whereas the longevity of the adults varied only threefold. An atypical increase of the longevity occurred at 35 °C. These data can be further analyzed beyond the needs of life table statistics by splitting the juvenile development into active and quiescent phases for each of the two sexes (Tab. 2). Gener-

Tab. 1: Duration of the life stages, egg production, and average oviposition rate (OR) of *Tetranychus urticae* at different temperatures (n = total replications)

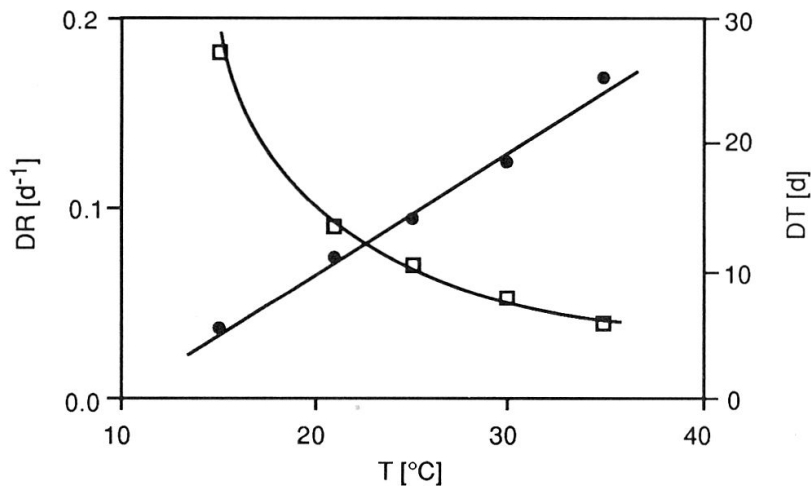| | Temperature | | | | | |
	15°C	21°C	25°C	30°C	35°C	n
Egg [d]	10.8	4.9	3.9	2.6	1.9	710
Juvenile [d]	16.6	8.6	6.6	5.4	4.0	206
Adult [d]	16.6	14.7	8.9	5.3	8.5	74
fecundity [eggs]	21.5	40.0	27.7	20.0	39.9	74
OR [eggs/fem./d]	1.2	2.7	3.0	3.7	4.7	74

Fig. 1: Relationship between temperature (T) and developmental rate (DR,●) and developmental time (DT,□) of *Tetranychus urticae* DR = $-0.063 + 0.0065 \cdot T$, $R^2 = 0.991$)

Tab. 2. Duration [d] of active (A = larva, protonymph, deutonymph) and quiescent stages (Q = proto-, deuto-, teleiochrysalis) during the preimaginal development of *Tetranychus urticae* (Q/A = ratio of quiescent to active stages of both sexes, n = replications per treatment)

	females			males			Q / A	n
	A	Q	A + Q	A	Q	A + Q		
15°C	9.4	7.5	16.9	8.5	7.6	16.1	0.83	43
21°C	4.4	4.4	8.8	4.2	3.7	7.9	0.96	37
25°C	3.7	3.0	6.7	3.9	2.5	6.4	0.76	45
30°C	3.9	1.6	5.5	4.0	1.0	5.0	0.39	43
35°C	3.1	0.9	4.8	3.1	0.7	3.8	0.27	38

ally, females tened to have a longer developmental time. At 35 °C the ratio of quiescence to mobile stages declined to less than a third of the ratio at the two lowest temperatures. At increasing ambient temperatures quiescence length was reduced more markedly than the active phases and may be completed at high temperatures within hours.

Tab. 3. Life table parameters of *T. urticae* at various rearing temperatures under long-day conditions

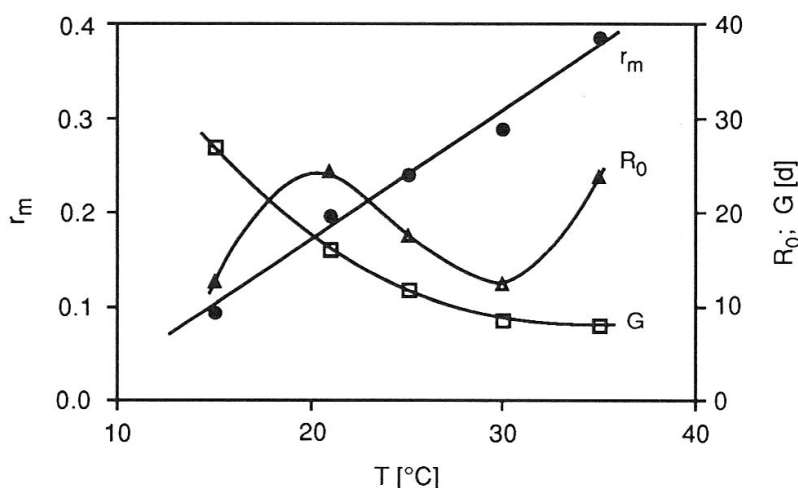|	Temperature				
	15°C	21°C	25°C	30°C	35°C
Net reproductive rate (R_0)	12.7	24.3	17.6	12.4	23.9
Intrinsic rate of increase (r_m)	0.094	0.197	0.242	0.288	0.386
Generation time (G)	27.1	16.2	11.9	8.7	8.2
Doubling time [d]	7.4	3.5	2.9	2.4	1.8

Fig. 2: Relationship between temperature (T) and intrinsic rate of natural increase (r_m), net reproductive rate (R_0) and generation time (G) of *Tetranychus urticae* ($r_m = -0.107 + 0.014 \cdot T$, $R^2 = 0.985$)

The dependence of the total egg production on temperature was less clear-cut (Tab. 1). The daily ovipositional rate steadily increased with higher temperatures. However, total fecundity shows two peaks at 21 °C and 35 °C. The latter peak was caused by the prolonged oviposition period at 35 °C relative to the one at 30 °C (cf. Tab. 1).

The population life table parameters are listed in Tab. 3. The intrinsic rate of natural increase r_m, i.e. the growth capacity of a population at given conditions, demonstrated a clear dependence on temperature (Fig. 2). Within the range of 15 °C to 35 °C the rate r_m could be described by a linear regression model while the generation time G gradually decreased. The net reproductive rate R_0 peaked at the temperatures 21 °C an 35 °C corresponding to the fecundity pattern (Tab. 1) (G and R_0 curves fitted by eye). According to the low R_0 at 30 °C, r_m was reduced too. As an expressive value of the speed of multiplication the doubling time of a stable-age population can be computed as $\ln 2/r_m$ (cf. eqn. 1) which decreased markedly with rising temperatures.

DISCUSSION

Typical of poikilothermic animals, the duration of the life stages clearly varied with temperature. The speed of immature development showed a linear re-

lationship to temperature and coincided with results of HERBERT (1981b) with the same mite and host plant species. The proportion of quiescent stages decreased with increasing temperature. This agrees with findings on other tetranychids by RABBINGE (1976) and PERRING et al. (1984b). However, other authors report temperature-insensitive ratios of quiescent to active stages (HERBERT, 1981a; CAREY & BRADLEY, 1982; LANDWEHR & ALLEN, 1982; DE MORAES & McMURTRY, 1987) for various tetranychids as well as for T. urticae (HERBERT, 1981b; CAREY & BRADLEY, 1982). The metabolic processes during quiescence are, presumably, mainly dependent on temperature, while a shortening of the active stages may be limited by nutrition (quality, food acquisition). Among the life stages, it was the embryonic development which depended most on temperature. Temperature is the prevailing factor affecting the egg stage as this is least susceptible to other environmental factors like wind, rainfall, plant nutrition etc. In all temperature regimes, the developmental time of males was shorter than that of females. This may be associated with the mating behavior of males. The previously emerged males guard the female teleiochrysales before their emergence. They even assist the females in casting off the exuvia, mating immediately with the females as soon as their opisthosoma is accessible (LAING, 1969; own observations). In a young mite cohort on a newly settled plant, the shorter developmental time would allow the lower number of males to find emerging females and to inseminate them at the earliest possible time, before the females disperse.

Total fecundity varied only by a factor of two despite a more sensitive ovipositional rate. The reason for this is that total production at high temperatures was restricted by a shorter oviposition period. This mechanism also explains the two fecundity peaks at 21 °C and 35 °C: at 35 °C the increased ovipositional rate dominated over the short longevity, at 21 °C the longer longevity outstripped the low ovipositional rate, and at the intermediate temperature 25 °C the two opposite effects added up to lower egg production.

In general, there exist three main phenomena at increasing temperatures: decreasing longevity, increasing development speed, and increasing ovipositional rate per day. The interplay of these partly opposite processes determines the growth of a population, which can be expressed as an overall performance index r_m. This rate of population increase is the exponent in the exponential growth equation

$$N_t = N_0 \cdot e^{r_m t} \qquad [1]$$

where N_t means the size of the population (number of individuals) at time t, and N_0 is the initial population size. r_m was linearly related to temperature (cf. HERBERT, 1981a,b), but was overestimated at both very low and very high temperatures, since survival is reported to be adversely affected by these temperatures (SHIH et al., 1976; HERBERT, 1981a; LANDWEHR & ALLEN, 1982). The intrinsic rates of natural increase r_m compare well to the rates for T. urticae reported by WATSON (1964), LAING (1969), and CAREY & BRADLEY (1982), but are much lower than those found by SHIH et al. (1976) and HERBERT (1981b). All of these studies were made with host plants other than apple except for the one of HERBERT (1981b). It is evident that plant species, experimental conditions, mite strain, but also the physiological condition of the host plant (WERMELINGER et al., 1985) affect the population development of spider mites.

Since eqn. 1 is limited to stable-age populations at unlimited conditions, comprehensive simulation models are required for the study of field populations

with time-varying age structure. The results of these experiments formed a part of the data basis used for the parameterization of an explanatory computer simulation model on the interactions between spider mites and predatory mites (ZAHNER & BAUMGÄRTNER, 1988).

ZUSAMMENFASSUNG

Eine kurze Zusammenfassung der Literatur der letzten 20 Jahre vermittelt eine Übersicht über die Temperatureffekte auf die Spinnmilbenentwicklung. In einem Versuch auf Apfelbäumen wurde die Wirkung der Temperatur als einer der wichtigsten Komponenten des Lebenssystems der Gemeinen Spinnmilbe *Tetranychus urticae* KOCH quantifiziert. Bei fünf verschiedenen konstanten Temperaturen zwischen 15 °C und 35 °C wurden Lebenstafeln aus Entwicklungsdauer, Mortalität, Eiablagedynamik, Lebensdauer und Geschlechtsverhältnis erstellt. Aus diesen Lebenstafeln konnten die Anteile der Ruhestadiendauer an der Gesamtentwicklung sowie die Lebenstafel-Statistik berechnet werden: Nettoreproduktionsrate R_0, spezifische natürliche Wachstumsrate r_m, Generationszeit G sowie die Populations-Verdoppelungszeit. Im untersuchten Temperaturbereich erhöhten sich die Entwicklungsraten linear mit zunehmender Temperatur, und das Verhältnis Ruhestadien/aktive Stadien nahm stetig ab. Ebenso nahmen die Eiablagerate und r_m zu, wobei r_m im ganzen untersuchten Bereich Linearität aufwies. Generationszeit und Verdoppelungszeit nahmen mit höheren Temperaturen ab.

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