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Accumulation of Photoperiodic Information During Diapause Development in the Spider Mite *Tetranychus urticae*

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Photoperiodic control of diapause development was studied in three strains of the spider mite, *Tetranychus urticae*, originating from different latitudes in Europe. Diapause was almost fully maintained by a long-night regime during the first month of diapause, but was terminated rapidly and synchronously by a short-night regime. Diapause termination in continuous light was almost as rapid as in short nights; in continuous darkness diapause termination proceeded much slower, probably revealing the “spontaneous” rate of diapause development of these mites. The effect on diapause termination of successive short-night cycles appeared to be accumulated in a way comparable to cycle summation during diapause induction. The threshold for diapause termination by short nights, expressed as the number of cycles required for 50% diapause termination, was found to be lower the more southern the origin of the strain of mites. However, considerable differences in the number of cycles required for diapause termination were also present within strains: some mites needed only 3–4 short nights to terminate diapause, whereas others needed more than 10. In contrast with short-night cycles the effect of long-night cycles was not accumulative. Intensification of diapause under the influence of long-night cycles during its early stages appeared not to take place. Long nights were capable of maintaining the state of diapause if experienced before short-night cycles, but not afterwards. Short and long nights seem to act independently from each other, the former accelerating diapause development (“activation”), the latter slowing down diapause development (“diapause maintenance”). No antagonistic effect of long and short nights was found on the photoperiodic maintenance of diapause, in the sense that the effect of short nights might be diminished or even reversed by long nights, and *vice versa*, as found in photoperiodic induction of diapause in *T. urticae*. Therefore diapause maintenance does not seem to involve a photoperiodic counter mechanism comparable with the counter involved in the photoperiodic induction of diapause in these mites.

Photoperiodism Diapause Spider mites Acarina *Tetranychus urticae*

INTRODUCTION

Females of the spider mite *Tetranychus urticae* display two different photoperiodic reactions, *viz* the induction of a reproductive diapause by daylengths shorter than the so-called critical daylength, and the maintenance of the state of diapause, also by short daylengths. Stages sensitive for the induction of diapause are from the late embryo to the teneral female (Veerman, 1977a, 1985); the sensitive stage for the photoperiodic maintenance of diapause is the diapausing female herself (Veerman,

1977b). During the state of diapause unknown physiological changes occur (named “diapause development” by Andrewartha, 1952), which prepare the mites for the termination of diapause. According to Tauber *et al.* (1986), diapause development ends when photoperiodic control of diapause maintenance is lost. From that moment on further development in the spider mite is controlled only by prevailing temperature; if temperatures are too low the mites remain in a state of rest that has been called post-diapause quiescence by Tauber *et al.* (1986) (*cf* Koveos *et al.*, 1993a).

Diapause development must be viewed as a dynamic process which proceeds in these mites, as in many insects (*cf* Hodek, 1983), at a certain rate even at low temperature in constant darkness, and eventually may end “spontaneously” (Veerman, 1977b; Koveos *et al.*, 1993b). The rate at which diapause development progresses depends on photoperiod and temperature

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(Veerman, 1977b), as well as on the geographic origin of the population of spider mites under examination (Koveos *et al.*, 1993a,b). Diapause intensity, studied in several strains from different localities in Europe, and expressed as the length of the period of diapause development, was found to be lower the more southern the origin of the strains.

The physiological mechanism of photoperiodic induction of diapause in the spider mite is known to comprise both a photoperiodic clock, measuring nightlength, and a so-called photoperiodic counter, which accumulates, integrates and stores the photoperiodic information contained in the long- and short-night cycles perceived by the animal during its sensitive stages (Vaz Nunes and Veerman, 1982; Veerman and Vaz Nunes, 1984, 1987). Recently it was found that the photoperiodic clock controlling diapause maintenance in these mites is most likely the same as the one controlling the induction of diapause (Koveos *et al.*, 1993b). Therefore the next question that arose was whether the parallel between both photoperiodic mechanisms might go even further, i.e. whether or not some kind of photoperiod counter is also involved in the photoperiodic maintenance of diapause in the spider mite. Evidence that a photoperiodic counter may not only be involved in the induction of diapause but also in its termination has been presented by Numata (1992) for adult diapause in the bean bug, *Riptortus clavatus*. In this paper evidence is presented for the accumulation of short-night cycles, but not long-night cycles, during diapause development in the spider mite. The number of cycles required for 50% diapause termination is shown to depend on the geographic origin of the mites.

MATERIALS AND METHODS

Three strains of *T. urticae* were used in this study, *viz* the strain Leningrad, originating from 60°N in Russia, the strain Voorne, from 52°N in the Netherlands; and the strain Thessaloniki-II, from 40.5°N in Greece. A detailed description of the origin of these strains may be found elsewhere (Koveos *et al.*, 1993a). The mites were reared in the laboratory on detached-leaf cultures of bean (*Phaseolus vulgaris*) under a short-night photoperiod (LD 17:7) at 22.5°C. The terms short-night cycle and long-night cycle for photoperiodic regimes with nights shorter or longer than the "critical nightlength" (the nightlength at which 50% of the population enters or terminates diapause) are preferred above the terms long-day and short-day, as the scotophase was found to be more important than the photophase for both induction and termination of diapause in these mites (Veerman and Vaz Nunes, 1987; Koveos *et al.*, 1993b).

For the experiments, mite cultures were started on freshly excised bean leaves, each leaf kept separately on a pad of moist cotton wool. Female mites (25–30 per leaf) were allowed to lay eggs for 24 h at LD 17:7 and 25.5°C; leaves with eggs (differing no more than 24 h in age) were incubated for another 3 days under the same

regime, whereupon the eggs were ready to hatch. Subsequently the cultures were transferred to a diapause inducing regime (LD 10:14 and 19°C), at which the mites completed their entire post-embryonic development. Under these conditions all females entered diapause, except for the Greek strain in which diapause incidence was about 80%. Next, diapausing females were stored in a cold room at 4°C for variable periods of time, depending on the experiment, as explained in the Results section. For the experiments mites were transferred onto fresh bean leaves and exposed to various photoperiodic regimes at 19°C in light-proof wooden cabinets placed in a climatic room. Air of constant temperature and humidity was forced through the cabinets. Each cabinet was equipped with two daylight fluorescent tubes of 8 W, separated from the working space of the cabinet by a plexiglass screen and controlled by electronic timers. Light intensity at the level of the mites was approx. 1000 lx. In some of the experiments, as indicated in the Results section, mite cultures were kept for a number of days in temperature-controlled incubators with either constant light (LL) or constant dark (DD). Criteria for the termination of diapause were the change in colour of the females, from the orange winter coloration to the greenish summer colour, and the start of oviposition (*cf* Veerman, 1985). Between 100 and 200 females were used in each experimental treatment.

In both field and laboratory studies it has been established that the functional significance of the photoperiodic response displayed by diapausing females of *T. urticae* lies in the maintenance of diapause during autumn and early winter (Veerman, 1977b; Gotoh, 1986; Veerman and Koveos, 1989). The effect that has actually been measured in the present experiments on diapause maintenance and diapause development is whether or not diapausing females terminate diapause and resume activity; in these experiments the possible presence of a short period of post-diapause development (*sensu* Tauber *et al.*, 1986) has been neglected. Therefore, with regard to the experiments performed, the term diapause termination is preferred above the term diapause maintenance; responses observed will be expressed as percentage diapause termination.

RESULTS

Figure 1 shows the effect of photoperiod on diapausing females of the Voorne strain of *T. urticae*, which had spent the first 3 weeks of diapause at 4°C before being transferred to the different photoperiodic regimes at 19°C. As found before (Veerman, 1977b), diapause is almost fully maintained by the long-night regime during the 31 days of the experiment, but is terminated rapidly in the short-night regime. The effect of the aperiodic regimes continuous light and continuous darkness was unexpected, in view of their weak effects on diapause induction (*cf* Veerman and Vaz Nunes, 1987): after a short delay diapause termination in continuous light appears to be as rapid and synchronous as in short

FIGURE 1. Time course of diapause termination in the Vooorne strain of *Tetranychus urticae* under 4 different regimes at 19°C, after a cold rest of 3 weeks at 4°C. Closed circles: short-night regime (LD 17:7); open circles: long-night regime (LD 10:14); closed triangles: continuous darkness (DD); open triangles: continuous light (LL).

nights; continuous darkness, on the other hand, first seems to maintain diapause as strongly as long nights do, but after about 2 weeks control is lost and the percentage diapause termination starts to increase rather steeply.

The next experiment, the results of which are shown in Fig. 2, was devised to examine whether the diapause-terminating effect of short-night cycles is accumulated by the mites. After a cold rest at 4°C for 2 weeks samples of diapausing females were exposed to 1–12 cycles of LD 17:7 at 19°C, after which they were transferred to continuous darkness (DD), also at 19°C. Diapause termination was determined on the 12th day after transfer from the cold room. DD was thought to be the best choice for a “neutral” regime in view of its effects shown in Fig. 1, considering the short duration of the experiment. The experiment was performed with three strains: Leningrad, Vooorne, and Thessaloniki-II. In all three strains the percentage diapause termination increased in proportion to the number of short-night cycles experi-

FIGURE 2. Number of short-night (LD 17:7) cycles required for diapause termination at 19°C in three strains of *Tetranychus urticae* after a cold rest of 2 weeks at 4°C. After experiencing the indicated number of short-night cycles the mites were transferred to continuous darkness at 19°C. Percentages diapause termination were determined 12 days after removal from cold storage. Closed circles: Leningrad; open squares: Vooorne; open circles: Thessaloniki-II.

enced by the mites. The number of cycles required for 50% diapause termination appeared to be higher the more northern the origin of the strains: it increased from 2–3 cycles in Thessaloniki-II to 5–6 in Vooorne and 6–7 in Leningrad. However, the number of cycles required for diapause termination differs not only between strains, but appears to vary rather widely also within strains. In the Vooorne strain, for instance, some mites require only 3 short nights to terminate diapause, whereas others need more than 10 short-night cycles (Fig. 2). A comparable variation in individual diapause thresholds has been found before for the induction of diapause in this strain of mite (Veerman, 1977a; Veerman and Vaz Nunes, 1987). The conclusion from this experiment is that some kind of cycle summation takes place in the photoperiodic termination of diapause by short-night cycles which is comparable in its kinetics with the reverse effect, the summation of long-night cycles in the induction of diapause (*cf* Veerman, 1977a; Veerman and Vaz Nunes, 1987).

Next we investigated the effect of the duration of the initial cold treatment on the number of short-night cycles required to terminate diapause. The results for the strains Thessaloniki-II and Leningrad, after periods of cold of respectively 2, 3 and 5 weeks, are shown in Fig. 3. The experimental setup is the same as in Fig. 2. The experiments show that the number of short-night cycles required for diapause termination decreases in both strains with the duration of the cold treatment the mites had experienced before; for instance, the number of short-night cycles required to terminate diapause in 50% of the mites in the Leningrad strain decreased from 6–7 cycles after 2 weeks of cold to 5–6 cycles after 3 weeks cold and 2–3 cycles after a cold rest of 5 weeks (Fig. 3). The experiments again demonstrate that diapause development in these mites proceeds at a certain rate even at 4°C; the number of short-night cycles required for diapause termination becomes less the further the process of diapause development has proceeded. This is completely in agreement with the graphical model for “horotelic” and “tachytelic” completion of diapause proposed by Hodek (1983), in which horotelic stands for the standard rate of diapause development (e.g. under a long-night regime) and tachytelic for “activation” (e.g. by a short-night regime).

In an analysis of the operation of the photoperiodic counter in diapause induction in the spider mite it was found that long- and short-night cycles have opposite effects; short-night cycles may diminish or even cancel the diapause inductive effect of long-night cycles, irrespective of the sequence in which the long- and short-night cycles are experienced by the mites (Veerman and Vaz Nunes, 1987). To see whether long- and short-night cycles might act in a comparable way in the photoperiodic termination of diapause we investigated in the next experiment the effect of an increasing number of short-night cycles preceded and/or followed by long-night cycles, DD or LL (Table 1). The series B–E, F–I, K–N and O–R all show that the percentage diapause termin-

FIGURE 3. Number of short-night (LD 17:7) cycles required for diapause termination at 19°C in the strains Thessaloniki-II (a) and Leningrad (b) of *Tetranychus urticae* after a cold rest at 4°C of 2 weeks (closed circles), 3 weeks (open squares) or 5 weeks (open circles). Further treatment the same as in Fig. 2.

ation increases with the number of short-night cycles given to the mites, as seen in Fig. 2. From the experiments B–I it appears that long-night cycles are not capable of stopping, let alone reversing, the diapause terminating effect of the short-night cycles. The lower percentage diapause termination in F–I compared with B–E might indicate that long nights may maintain diapause to a certain extent if experienced before the short-night cycles, but not after diapause development has undergone an acceleration by preceding short-night cycles. The diapause terminating processes which started under the influence of the short nights probably continue at a certain rate under the subsequent long-night regime; this may explain the fact that the percentage diapause termination is lower in the series F–I, with a smaller number of long-night cycles following the short nights, than in the series B–E. This is also evident if we compare the series B–E with K–N: the effect of long-night cycles is the same as that of DD, which shows that the long-night cycles are not capable any more of actively maintaining the state of diapause. Comparing F–I with O–R shows, however, that the long-night cycles do

actively maintain diapause, compared with DD, if they are experienced before the short-night cycles, which corroborates the conclusion drawn from the comparison between B–E and F–I. With LL instead of DD, percentage diapause termination is very high in all experiments T–ZA; this is not amazing, however, in view of the fact that Fig. 1 showed the diapause terminating effect of LL to be almost as strong as that of short nights.

The effect of alternating short-night cycles with either long-night cycles, DD, or LL, is shown in experiments ZB–ZD in Table 1. Alternating short nights with long nights (ZB) yields a percentage diapause termination comparable with H and I, but not with D and E, which indicates that in ZB the long nights are still capable of maintaining the state of diapause to a certain extent, possibly because the long-night cycles are preceding as well as following the short-night cycles. The very low percentage diapause termination in ZC, when short nights are alternated with DD, is at first sight surprising, but may be explained by the fact that the regime the mites experienced in fact consisted of 7 cycles of LD

TABLE 1. Diapause termination at $19 \pm 1.0^\circ\text{C}$ in the Voorne strain of *Tetranychus urticae*, after a cold rest of 3 weeks at 4°C.

Experiment	Photoperiodic regime	% Diapause termination
A	*14 LN	2
B	2 SN + 12 LN	14
C	4 SN + 10 LN	44
D	6 SN + 8 LN	90
E	8 SN + 6 LN	97
F	6 LN + 2 SN + 6 LN	13
G	6 LN + 4 SN + 4 LN	28
H	6 LN + 6 SN + 2 LN	45
I	6 LN + 8 SN	53
J	14 DD	8
K	2 SN + 12 DD	15
L	4 SN + 10 DD	40
M	6 SN + 8 DD	86
N	8 SN + 6 DD	94
O	6 DD + 2 SN + 6 DD	13
P	6 DD + 4 SN + 4 DD	43
Q	6 DD + 6 SN + 2 DD	74
R	6 DD + 8 SN	82
S	14 LL	79
T	2 SN + 12 LL	89
U	4 SN + 10 LL	96
V	6 SN + 8 LL	96
W	8 SN + 6 LL	95
X	6 LL + 2 SN + 6 LL	97
Y	6 LL + 4 SN + 4 LL	98
Z	6 LL + 6 SN + 2 LL	98
ZA	6 LL + 8 SN	98
ZB	1 SN + 1 LN + 1 SN ... (14 cycles)	46
ZC	1 SN + 1 DD + 1 SN ... (14 cycles)	14
ZD	1 SN + 1 LL + 1 SN ... (14 cycles)	88

The regimes consisted of increasing numbers of short-night cycles (SN: LD 17:7), preceded and/or followed by long-night cycles (LN: LD 10:14), continuous darkness (DD), or continuous light (LL).

*Numbers before the symbols denote the number of 24-h periods employed.

TABLE 2. Diapause termination at $19 \pm 1.0^\circ\text{C}$ in the Voorne strain of *Tetranychus urticae*, after a cold rest of 3 weeks at 4°C .

Experiment	Photoperiodic regime	% Diapause termination
A	*3 LN + 7 SN	45
B	6 LN + 7 SN	43
C	9 LN + 7 SN	49
D	12 LN + 7 SN	44
E	15 LN + 7 SN	41
F	18 LN + 7 SN	47
G	21 LN + 7 SN	43
H	24 LN + 7 SN	46
I	3 LN + 7 SN + 21 LN	100
J	6 LN + 7 SN + 18 LN	100
K	9 LN + 7 SN + 15 LN	89
L	12 LN + 7 SN + 12 LN	81
M	15 LN + 7 SN + 9 LN	87
N	18 LN + 7 SN + 6 LN	81
O	21 LN + 7 SN + 3 LN	70
P	24 LN + 7 SN	46
Q	31 LN	12

The regimes consisted of 7 short-night cycles (SN: LD 17:7) given at consecutively later times during the first month of diapause, either preceded by an increasing number of long-night cycles (LN: LD 10:14) (experiments A–H), or applied against a “background” of long-night cycles (experiments I–P). Diapause termination was determined immediately after the treatments shown.

*Numbers before the symbols denote the number of 24-h periods employed.

17:31; this is apparently interpreted as a long-night regime which strongly maintains diapause. Similarly, the regime applied in experiment ZD may be interpreted as 7 short-night cycles of LD 41:7, which may explain the high percentage of diapause termination found. An effect of the very long light phase (comparable with the effect of LL shown before) may also be present. However, on the basis of the present data it is not possible to decide to what extent the outcome of experiment ZD is attributable to either one of the above effects (SN or LL), or both.

The last experiment was designed to investigate whether the effect of long-night cycles is accumulated independently of the effect of short-night cycles. At the same time the experiment shows whether any changes in sensitivity occur with respect to the diapause terminating effect of short-night cycles during the early phase of diapause (Table 2). After a cold treatment of 3 weeks samples of diapausing females of the Voorne strain were exposed, at 19°C , to 7 short-night cycles given at consecutively later times during the first month after transfer from the cold room. In the first series (A–H) the 7 short-night cycles were preceded by an increasing number of long nights; diapause termination was determined immediately after application of the 7 short-night cycles. For all regimes the percentage diapause termination was between 40 and 50%, which shows that the effect of long nights is not cumulative: although the long nights may maintain the state of diapause for a certain period of time at a more or less constant “depth”, the “tachytelic” processes leading to an accelerated termination of dia-

pause start as soon as the mites experience the short nights and proceed with the same “strength”, irrespective of the preceding number of long nights. Sensitivity to the 7 short-night cycles appears not to change over the test period of 1 month; this shows that no intensification of diapause by long nights takes place during the early stages of diapause. The same conclusion has been drawn before based on other experiments with the same strain of spider mites (Koveos *et al.*, 1993a).

After the percentage diapause termination had been determined in the experiments A–H the mite cultures were transferred back to the long-night regime; diapause termination was determined again in all cultures on the 31st day after transfer from the cold room. In the series I–P, therefore, all mites had lived for an equal number of days since the start of the experiment. As Table 2 shows, the percentage diapause termination is higher as the mites experienced the 7 diapause terminating short-night cycles earlier during the period of 31 days. This illustrates again the above conclusion that long nights are capable of maintaining the state of diapause if experienced before the short nights, but not after. Comparison of the series A–H with the series I–P shows that the process leading to diapause termination, initiated by the short-night cycles, apparently even continues (albeit probably with a lower speed) during the long-night cycles applied after the short nights, resulting in a higher percentage diapause termination the longer the period after experience of the short nights. The effect of long-night cycles is therefore not antagonistic with respect to the effect of short-night cycles, in the sense that the effect of short-night cycles might be reversed by long-night cycles.

DISCUSSION

The analysis of the accumulation of photoperiodic “information” during diapause development may well be more difficult than of that occurring during diapause induction because of the complex dynamics and “spontaneous” changes which occur during diapause development (*cf* Hodek, 1983; Tauber *et al.*, 1986). In experiments on the photoperiodic induction of diapause in the spider mite it has been found that the photoperiodic counter accumulates both long- and short-night cycles; the long and short nights have about equal strength, but opposite effects. Accumulation takes place irrespective of the sequence (short–long or long–short) in which the mites experience the photoperiodic cycles (Vaz Nunes and Veerman, 1982; Veerman and Vaz Nunes, 1987). Short nights given after a number of long nights were found to be capable of reversing the inductive effect of the long nights; if the mites received a number of short-night cycles before being transferred to a long-night regime, more long-night cycles were required for diapause induction to take place than when the mites had experienced a “neutral” regime (LL or DD) before the transfer to long nights. In diapause induction therefore a clear antagonistic effect is present between long-

and short-night regimes (Veerman and Vaz Nunes, 1987). If we now look at the present results on diapause termination it is evident from Fig. 2 that short-night cycles are accumulated in a way comparable to that described above for diapause induction. Figure 1 shows us that long-night cycles actively maintain diapause, at least during the 31 days of the experiment. However, from experiments A–H in Table 2 it appears that the effect of long-night cycles is not accumulated; otherwise an intensification of diapause would have taken place making it more difficult for the 7 short-night cycles to terminate diapause the more long-night cycles the mites had “seen” before. This is apparently not what happens, according to the results shown in Table 2. This means that long nights are probably capable of maintaining the state of diapause at a certain depth for some time but are not capable of increasing the intensity of diapause in these mites. This conclusion is in accordance with the results presented in Tables 1 and 2, which show that long-night cycles may maintain diapause if given before the short-night cycles, but are not capable of reversing the effect of the short nights if experienced afterwards. Therefore there is no antagonistic effect of long and short nights in the photoperiodic maintenance of diapause, as it is the case in the photoperiodic induction of diapause in these mites.

From Fig. 1 it may be concluded that the speed with which diapause development proceeds strongly depends on photoperiod. In view of the fast and synchronous termination of diapause in short nights the short-night regime apparently actively terminates diapause (“activation” in Hodek’s, 1983 terminology). The fact that the activating effect of continuous light is almost as strong as that of short nights is surprising and rather puzzling, as it was shown in an experiment with contrasting signals (a short day combined with a short night and a long day with a long night) that scotophase length is more important for the photoperiodic termination of diapause than photophase length; the photoperiodic clock involved appears to be a nightlength timer, similar to the one involved in diapause induction in these mites (Koveos *et al.*, 1993b). However, from the fact that diapause maintenance was less in LD 17:17 than in LD 7:17, it could be concluded that the duration of the light phase affects the termination of diapause independently from the more prominent effect exerted by the scotophase length as measured by the photoperiodic clock (*cf* Koveos *et al.*, 1993b, Table 2).

Possibly short-night cycles (and to a lesser degree continuous light) actively release some kind of inhibition maintained by the long-night regime; another explanation for the observed effects might be the active synthesis or release of some development-promoting substance by short nights. However, any speculation on the physiological mechanism of diapause development and termination, on the basis of the present experiments, seems premature. The fast and synchronous termination of diapause by short nights is the more remarkable as

this response will not occur in nature; the photoperiodic maintenance of diapause by long nights takes place during autumn and early winter, but has probably already ended by mid-winter (Veerman, 1977b; Gotoh, 1986).

The effect of continuous light in the photoperiodic termination of diapause differs greatly from its effect on the photoperiodic induction of diapause. Continuous light was found to have only a slightly reversing effect on diapause induction if applied after a series of long-night cycles; it appeared to be more or less neutral (i.e. neither reversing nor promoting diapause induction) if it preceded the long-night cycles (Veerman and Vaz Nunes, 1987). The effect of continuous darkness on diapause termination as shown in Fig. 1 can probably be seen as the “spontaneous” progress of diapause development at the prevailing temperature, neither actively maintaining diapause, like long nights do, nor actively terminating diapause, like short nights and continuous light appear to do.

The threshold for diapause termination by short nights, expressed as the number of cycles required for 50% diapause termination, was found to become lower the more southern the origin of the strain of mites (Fig. 2). This parallels other latitudinal trends found in these mites, such as the critical daylength for diapause maintenance, and diapause intensity (Koveos *et al.*, 1993a,b).

Summarizing it may be stated that the effect on diapause termination of successive short-night cycles is accumulated in a way comparable to cycle summation during diapause induction, whereas the effect of long-night cycles is not summated. Short nights and long nights seem to act independently from each other, the former accelerating diapause development (“activation”), the latter slowing down diapause development (“diapause maintenance”). No antagonistic effect of long and short nights was found on the photoperiodic maintenance of diapause, in the sense that the effect of short nights might be diminished or reversed by long nights, and *vice versa*, as found in photoperiodic induction of diapause in *T. urticae*. Therefore it seems unlikely that a counter mechanism is involved in the photoperiodic maintenance of diapause which in any respect would be comparable with the counter involved in the photoperiodic induction of diapause in these mites.

REFERENCES

- Andrewartha H. G. (1952) Diapause in relation to the ecology of insects. *Biol. Rev.* **27**, 50–107.
- Gotoh T. (1986) Termination pattern of diapause in the two-spotted spider mite, *Tetranychus urticae* Koch (Acarina: Tetranychidae) in Sapporo. *Appl. ent. Zool.* **21**, 480–481.
- Hodek I. (1983) Role of environmental factors and endogenous mechanisms in the seasonality of reproduction in insects diapausing as adults. In *Diapause and Life Cycle Strategies in Insects* (Eds Brown V. K. and Hodek I.), pp. 9–33. Junk Publishers, The Hague.

- Koveos D. S., Kroon A. and Veerman A. (1993a) Geographic variation of diapause intensity in the spider mite *Tetranychus urticae*. *Physiol. Ent.* **18**, 50–56.
- Koveos D. S., Kroon A. and Veerman A. (1993b) The same photoperiodic clock may control induction and maintenance of diapause in the spider mite *Tetranychus urticae*. *J. biol. Rhythms* **8**, 265–282.
- Numata H. (1992) Temporal variation in the photoperiodic induction and termination of adult diapause in the bean bug, *Riptortus clavatus*. *J. Insect Physiol.* **38**, 447–452.
- Tauber M. J., Tauber C. A. and Masaki S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York.
- Vaz Nunes M. and Veerman A. (1982) Photoperiodic time measurement in the spider mite *Tetranychus urticae*: a novel concept. *J. Insect Physiol.* **28**, 1041–1053.
- Vaz Nunes M., Koveos D. S. and Veerman A. (1990) Geographical variation in photoperiodic induction of diapause in the spider mite (*Tetranychus urticae*): a causal relation between critical nightlength and circadian period? *J. biol. Rhythms* **5**, 47–57.
- Veerman A. (1977a) Aspects of the induction of diapause in a laboratory strain of the mite *Tetranychus urticae*. *J. Insect Physiol.* **23**, 703–711.
- Veerman A. (1977b) Photoperiodic termination of diapause in spider mites. *Nature* **266**, 526–527.
- Veerman A. (1985) Diapause. In *Spider Mites: Their Biology, Natural Enemies and Control, Vol. 1A* (Eds Helle W. and Sabelis M. W.), pp. 279–316. Elsevier, Amsterdam.
- Veerman A. and Koveos D. S. (1989) Separation of photoperiodic and circadian effects on the termination of diapause in the spider mite *Tetranychus urticae*. *Experientia* **45**, 1143–1146.
- Veerman A. and Vaz Nunes M. (1984) Photoperiod perception in spider mites: photoreceptor, clock and counter. In *Photoperiodic Regulation of Insect and Molluscan Hormones* (Eds Porter R. and Collins G. M.), pp. 48–64. Ciba Foundation Symposium 104, Pitman, London.
- Veerman A. and Vaz Nunes M. (1987) Analysis of the operation of the photoperiodic counter provides evidence for hourglass time measurement in the spider mite *Tetranychus urticae*. *J. comp. Physiol. A* **160**, 421–430.