Analysis of the operation of the photoperiodic counter provides evidence for hourglass time measurement in the spider mite Tetranychus urticae

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Summary. Photoperiodic induction of diapause in the spider mite Tetranychus urticae is the net result of at least two processes: time measurement (the photoperiodic ‘clock’) and the accumulation of the photoperiodic information contained in a sequence of light-dark cycles (the photoperiodic ‘counter’). In this paper an analysis is presented of the operation of the photoperiodic counter in the spider mite.

1. Mites which experienced a sequence of long-night cycles during their entire sensitive period showed 100% diapause; no diapause was observed in continuous darkness. When an increasing number of long-night cycles was applied to the mites against a ‘background’ of continuous darkness, diapause incidence was found to rise steadily: only 3 cycles sufficed to induce diapause in about half the population, whereas a minimal number of 6 cycles was required for 90–100% diapause to be attained. At the test temperature of 18.5°C the sensitive period lasted 11–12 days, comprising the complete post-embryonic developmental period, up to the final moult. Photoperiodic sensitivity was found to vary slightly over the whole sensitive period of the mites, the highest sensitivity being observed around days 3–6.

2. Short-night cycles were also shown to be accumulated, but with an effect opposite to that of long-night cycles. If the mites received a number of short-night cycles before being transferred to a long-night regime, the effect of the short-night cycles had to be levelled first by a number of long-night cycles, before the accumulation of the diapause-inducing effect of the long-night cycles was started.

3. Special attention has been given to the effect of the aperiodic signals continuous light and continuous darkness. It could be shown that continuous light has a slightly reversing effect on diapause induction if applied after a series of long-night cycles; continuous light is more or less ‘neutral’ (i.e. neither reversing nor promoting diapause induction) if it precedes the long-night cycles.

4. In experiments in which the effects of continuous light and continuous darkness were compared it could be shown that continuous darkness is equivalent to one long night: the minimal number of long-night cycles required for diapause induction was found to be one more if the long-night cycles were given after the mites had received continuous light instead of continuous darkness during the first part of the sensitive period.

5. A critical test, based on the photoperiodic counter principle and devised to discriminate between single and repeated nightlength measurements (using nights of 12 h and 36 h long), showed that all nights are counted only once, irrespective of their lengths: all nights longer than the critical nightlength were found to be about equally inducive. This shows that the photoperiodic clock in the spider mite does not operate according to oscillator kinetics: a clock of the oscillator type resets itself in longer dark phases and would have performed two consecutive acts of time measurement in a night of 36 h long. Consequently, the photoperiodic clock in T. urticae is either an hourglass or an instantly damped circadian oscillator, the kinetics of either of which would produce the results observed in the experiments reported here.

Introduction

It is generally recognized that photoperiodic responses in insects and mites involve a ‘clock’ which
is used to determine the qualitative difference between ‘long’ and ‘short’ nights (i.e. longer or shorter than a critical nightlength) and a ‘counter’ mechanism which accumulates successive long and/or short nights quantitatively, up to an internal threshold at which induction is complete (Tyszchenko 1977; Beck 1980; Saunders 1982a; Veerman and Vaz Nunes 1984). Although the requirement of a number of inductive cycles has been established already in the older literature on insect diapause (e.g. de Wilde 1962), the concept of a temperature-compensated photoperiodic ‘counter’ as an integral part of the photoperiodic mechanism has been expounded only more recently by Saunders (1966, 1971, 1981) and Goryshin and G.F. Tyszchenko (1970, 1972, 1973) and Goryshin and V.P. Tyszchenko (1974). In Sarcophaga argyrostoma induction of diapause was found to be effected by an interaction of the sensitive period and the ‘required day number’ (RDN), i.e. the number of long nights needed to raise the proportion of diapause to 50%. These two components have different temperature coefficients, with the latter showing a high degree of temperature compensation (Saunders 1971, 1975a).

An important aspect of the counter or ‘memory link’, as it is called in Russian literature on insect diapause, is that photoperiodic ‘information’ is not only accumulated but also stored, sometimes for long periods of time after the sensitive period has come to an end. The unknown entity which is summated has variably been called a ‘packet of photoperiodic information’ (Goryshin and G.F. Tyszchenko 1973; Goryshin 1977), the ‘diapause titre’ (Gibbs 1975) and the ‘induction sum’ (Vaz Nunes and Veerman 1982). Some insects were found to ‘add up’ only long nights (e.g. Mamestra brassicae (Goryshin and G.F. Tyszchenko 1973)), some only short nights (e.g. Megoura viciae (Lees 1972)), while others were found to collect both long and short nights (e.g. Acronyeta rumicis (Goryshin and G.F. Tyszchenko 1970)). The photoperiodic information accumulated during the sensitive period is presumably compared with an internal threshold value; diapause ensues if an individual’s ‘induction sum’ exceeds its threshold (cf. Gibbs 1975; Veerman and Vaz Nunes 1984). According to Beck (1980), there is abundant experimental evidence suggesting that diapause induction thresholds are normally distributed around a population mean.

Formal models have been proposed for the photoperiodic counter of S. argyrostoma (Gibbs 1975; Bradley and Saunders 1986), Tetranychus urticae (Vaz Nunes and Veerman 1982) and Papilio machaon (Shimada 1985). At this moment the nature of the stored information is still completely unknown. The ‘induction sum’ might represent, in concrete terms, an increase in a substance or state with time, or a decrease in something which promotes development. In Saunders’ view, the photoperiodic counter may comprise a chain of events, some stimulatory, some inhibitory (Saunders 1981).

In experiments devised to delimit the sensitive period of the spider mite T. urticae diapause incidence was found to increase with an increasing number of long-night cycles. It was also found that the diapause-inducing effect of a series of long-night cycles could be reversed by a series of short-night cycles, applied later during the sensitive period. Since the opposite effect was found as well, it was concluded that long-night cycles and short-night cycles both possess the capability of reversing the effect of the opposite regime and may do so with about equal ‘strength’ (Veerman 1977). Based on these results a model for the photoperiodic counter in T. urticae was developed, in which the ‘induction sum’ (S), the total amount of photoperiodic information collected by the mites during their sensitive period, is calculated as the difference between the number of long-night measurements ($\sum H^L$) and the number of short-night measurements ($\sum H^T$) experienced by the mites. Diapause is expected to occur if, at the end of the sensitive period, S surpasses a certain minimum value, the ‘diapause threshold’. An upper and lower threshold were introduced, respectively defining the 100% level and the 0% level of diapause incidence, as in the model for the photoperiodic counter proposed by Gibbs (1975) for S. argyrostoma. This rather simple model has been applied successfully in attempts to explain the results of very diverse photoperiodic experiments with T. urticae (Vaz Nunes and Veerman 1982, 1984, 1986a, b, 1987; Veerman and Vaz Nunes 1984).

In recent years emphasis in our work with spider mites has been laid predominantly on photoperiodic time measurement. However, in view of the importance of the photoperiodic counter as an integral part of the photoperiodic mechanism, we found it opportune to analyse various aspects of the counter in T. urticae in more detail. In this paper the summation and interaction of long- and short-night cycles is described, as well as the differential effect of a ‘background’ of continuous light vs continuous darkness. Knowledge of the operation of the counter in the spider mite also proved useful in enlarging our understanding of the kinetics of the photoperiodic clock in a newly developed