



Review

Insect photoperiodism: Measuring the night

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ABSTRACT

In studies of photoperiodic induction of over-wintering diapause, independent variation of the light (L) and dark (D) components of the daily (LD) cycle shows, with few exceptions, that the duration of the night (D) is more important than that of the day (L). Extensions of D to give cycle lengths up to 3 days or more in so-called Nanda–Hamner (NH) experiments suggest that night length is measured repeatedly in the extended night, with peaks of high diapause incidence occurring at intervals close to 24 h. This indicates a circadian involvement in night length measurement. The circadian oscillation revealed in NH experiments is shown to take its principal time cue from the beginning of the night – at a phase close to Circadian time, CT 12 – in series of such experiments with increasing light (L) components, in a manner comparable to other circadian oscillations such as that controlling the adult eclosion rhythm. It is considered that the photoperiodic circadian oscillation is *causally* involved in the discrimination between short (summer) and long (autumnal) nights, although further 'downstream' actions of the circadian system on the outcome of time measurement are also likely. Therefore Bünning's original hypothesis – or development of it – is considered to offer the most likely explanation for the photoperiodic mechanism.

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1. Introduction

Photoperiodic induction of seasonal phenomena such as over-wintering diapause, or seasonal morph determination in aphids, is generally thought to include a linked series of events from (1)

photoreception, through (2) a central event of time measurement evaluating day or night length (or both), (3) accumulation of the effects of successive photoperiods by a 'counter' mechanism, to (4) the final regulation of the endocrine signals controlling the appropriate and alternative developmental pathways (Saunders, 2002). Thus, long days (or short nights) of summer lead to continuous or nondiapause development, whereas short autumnal days (or lengthening nights) lead to a state of arrested development. This

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review focuses attention on the central events of time measurement and the photoperiodic counter, events that operate during a restricted photoperiodic 'sensitive period' either during the instars leading up to the diapause or – in some cases – during the parental generation. It also examines the long-standing controversy whether or not the central events of photoperiodic time measurement in insects are a function of the circadian system.

2. Ideas and models

Ideas and models concerning photoperiodic time measurements have been reviewed recently (Saunders, 2011). Some of the earliest ideas proposed that time measurement was accomplished by a linear (i.e. non circadian) hourglass-like device beginning at light-on (dawn) and measuring the duration of the light component of the cycle, or – more commonly – an hourglass-like timer beginning at light-off (dusk) and measuring the night. In 1936, however, the German plant physiologist Erwin Bünning proposed, initially for plants, but later for insects, that photoperiodic time measurement was a function of the system of circadian oscillations now known to regulate numerous daily rhythms of behaviour and physiology (Bünning, 1936). This model, commonly referred to as Bünning's hypothesis, and more recent developments arising from it, have been extensively described in a number of papers and reviews (Vaz Nunes and Saunders, 1999; Saunders, 2002, 2011); these will not be described here in detail. Suffice it to say that two of the more robust models are 'external coincidence' and 'internal coincidence' (Pittendrigh, 1966, 1972; Saunders, 2011). External coincidence supposes that there is a circadian oscillation phase-set (entrained) by the daily light–dark cycle in such a way that a particular light-sensitive phase falls in the latter part of the night (at the end of the critical night length). In long autumnal nights this phase falls in the dark, leading to diapause, but under short summer nights the dawn transition of the daily light component 'tracks back' to illuminate the photoinducible phase, and development proceeds along the nondiapause pathway. In external coincidence, therefore, light has a dual role: entrainment and photoinduction (Saunders, 2012). In internal coincidence, on the other hand, it is proposed that two or more circadian oscillators are involved. In one version of this model some of the oscillators take their principal time cue from light-on (dawn) and others from light-off (dusk). In internal coincidence light may thus have only a single role – that of entrainment – whereas induction of alternate diapause or nondiapause responses is the result of different phase relationships between the constituent oscillators.

Experimental evidence for a circadian role in photoperiodic time measurement, based upon the known properties of circadian oscillations and their entrainment by cycles of light and temperature, have been extensively reviewed (Saunders, 1978, 2010a); these include experiments designed as tests for internal or external coincidence (Saunders, 2011). For many species these experiments strongly suggest that the insect circadian system plays an important role in photoperiodic time measurement, either in the 'core' process of time measurement itself or elsewhere in the chain of events between photoreception and diapause determination.

As a theoretical alternative to the two coincidence models outlined above, Pittendrigh (1972) also suggested the possibility that night length could be measured by a timer – either circadian-based or perhaps hourglass-like – with the effects of this timer being modulated by proximity to 'resonance' within the multioscillator circadian system (see Section 8, below). The essence of this concept has been extended in models for photoperiodic time measurement in the red spider mite, *Tetranychus urticae* (Vaz Nunes and Veerman, 1982) and in the pitcher plant mosquito, *Wyeomyia smithii* (Bradshaw and Holzapfel, 2010). In *T. urticae*, Vaz Nunes

and Veerman developed this concept as the "hourglass clock: oscillator counter" model. Application of this model to experimental data provided close agreement between theory and observation, but many of its precepts have been found to be explainable in terms of a circadian-based night length measuring system (Saunders, 2010b) using a combination of such features as subjective light intensity (i.e. photoreceptor sensitivity), circadian phase response curve 'amplitude' and responses to light of different wavelengths. In *W. smithii*, Bradshaw and his colleagues (Emerson et al., 2008) have proposed a model in which a day interval timer is modulated by the circadian system, presumably at some point downstream of this hourglass-like time measurement. This proposal is critically examined in the present review.

3. Night length or day length measurement?

The relative importance of the light (L) and dark (D) components of the daily cycle have been investigated on a number of occasions by independently varying L and D in overall cycle lengths (T h) close to 24 h in duration. In most published cases night length appears to be crucial. For example, working with the oriental fruit moth *Grapholitha molesta*, Dickson (1949) showed that diapause incidence was maximal when D was >10–11 h, but the greatest incidence occurred at a combination of LD 10:13 ($T=23$ h), close to the period of the natural day. In the knot grass moth *Acronycta rumicis* the dark period had to be in excess of 9 h (Danilevskii and Glinyanaya, 1949), in the silkmoth *Antheraea pernyi*, >11 h (Tanaka, 1951) and in the small cabbage white butterfly *Pieris rapae*, >12 h (Barker and Cohen, 1965). The central importance of night length was also seen in data for the flesh fly *S. argyrostoma* (Saunders, 1973a) in which the incidence of pupal diapause was very low in cycles containing a *short* night (e.g. LD 12:8 and LD 16:8) but approached 100% in cycles containing a *long* night (e.g. LD 12:12 and LD 16:12), regardless of the duration of the accompanying light component.

Working with the European corn borer *Ostrinia nubilalis*, Beck (1962) studied the effects of 10, 12 and 14 h of light in combination with a wide range of dark periods. Maximum incidence of larval diapause (>90%) was observed in cycles containing 10–14 h of darkness. Dark periods of this duration, however, produced the highest incidence of diapause when coupled with a wider range of light (5–18 h) indicating that the duration of the dark was of greater importance than that of the light. This relationship was further illustrated by an 'isoinduction surface' calculated from Beck's data by Pittendrigh (1966, 1972) in which the percentage of larval diapause was plotted for different combinations of L and D, and points of equal diapause incidence were presented as 'contours' of a three-dimensional surface. This type of plot clearly showed that night length was more important than day length, but also that maximum diapause induction occurred at about LD 11:12 ($T=23$ h), close to the period of the circadian system. These data thus indicate the central role of night length and – in some cases – a role (causally or as a modulator) for the endogenous circadian system.

In the spider mite *Panonychus ulmi*, Lees (1953) found that night length was also of central importance, but his data indicated that a dark-period hourglass or interval timer was in operation. An hourglass-like type of night length timer was also indicated in the green vetch aphid *Megoura viciae* (Lees, 1966, 1968). Nevertheless, when considering Dickson's (1949) data for *G. molesta* (see above) Lees concluded that in some species "the mechanism of control is here linked closely with the natural 24-h cycle of light and darkness" (Lees, 1955, p 22).

In a minority of cases, experiments, including the independent variation of L and D, have suggested the operation of a timer

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