J Comp Physiol B (2016) 186:969–984
DOI 10.1007/s00360-016-1018-9

REVIEW

Physiological and molecular mechanisms underlying photoperiodism in the spider mite: comparisons with insects

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Received: 29 February 2016 / Revised: 28 June 2016 / Accepted: 9 July 2016 / Published online: 16 July 2016

Abstract Photoperiodism is an adaptive, seasonal timing system that enables organisms to coordinate their development and physiology to annual changes in the environment using day length (photoperiod) as a cue. This review summarizes our knowledge of the physiological mechanisms underlying photoperiodism in spider mites. In particular, the two-spotted spider mite *Tetranychus urticae* is focussed, which has long been used as a model species for studying photoperiodism. Photoperiodism is established by several physiological modules, such as the photoreceptor, photoperiodic time measurement system, counter system, and endocrine effector. It is now clear that retinal photoreception through the ocelli is indispensable for the function of photoperiodism, at least in *T. urticae*. Visual pigment, which comprised opsin protein and a vitamin A-based pigment, is involved in photoreception. The physiological basis of the photoperiodic time measurement system is still under debate, and we have controversial evidence for the hourglass-based time measurement and the oscillator-based time measurement. Less attention has been centred on the counter system in insects and mites. Mite reproduction is possibly regulated by the ecdysteroid, ponasterone A. Prior physiological knowledge has laid the foundation for the next steps essential for the elucidation of the molecular mechanisms driving photoperiodism.

Keywords Diapause · Photoperiodic response · Photoperiodism · Spider mite · *Tetranychus urticae*

Spider mites and photoperiodic regulation of diapause

Among arachnids, the Acari is the only group that feeds on plants. Approximately 7000 species of phytophagous mites are known, including the Tetranychidae, which is a large family with approximately 1300 species and 90 genera (Migeon and Dorkeld 2015). Species belonging to this family are termed 'spider mites' owing to their ability to produce silk webs. Spider mites are less than 1 mm in length and their life cycles include five developmental stages: egg, larva, protonymph, deutonymph, and adult. More than a hundred of these organisms are considered pests, and approximately ten are classified as major pests (Migeon and Dorkeld 2015). The most well-known and widespread of the pests is the two-spotted spider mite, *Tetranychus urticae*. This species attacks approximately 1100 species of plants (Migeon and Dorkeld 2015). In *T. urticae*, one generation is completed in less than 2 weeks when the temperature is between 21 and 23 °C and in only 7 days when the temperature is higher than 30 °C. Oviposition can begin within a few days after adult emergence. Each female may lay 100–180 eggs throughout her lifespan of a month (Tehri 2014). Because spider mites are economically important agricultural pests (Attia et al. 2013; Van Leeuwen et al. 2015), and owing to the simplicity and ease of rearing them in a laboratory, the biology of spider mites has been extensively studied. One of the topics that have been focussed on includes understanding the regulatory mechanism of diapause (Veerman 2001).

Diapause is the developmental arrest that occurs in recurring periods of adverse environmental conditions, and

Communicated by I.D. Hume.

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is most often observed in arthropods, especially in insects and mites. This is an adaptive strategy to synchronize the organism's life cycle with favourable biotic and abiotic environmental conditions for development, reproduction, and survival (Tauber et al. 1986; Danks 1987). Diapause has been described in a large number of tetranychid species, and both the hibernal and aestival types of diapause (winter diapause and summer diapause, respectively) have been reported (Veerman 1985). In each species of spider mite, diapause occurs only at a specific stage, either the egg (embryonic diapause) or the adult female (reproductive diapause or adult diapause). For example, females of *T. urticae* enter diapause as adult and arrest ovarian development by terminating the transcription of vitellogenin, a precursor of a yolk protein, vitellin (Kawakami et al. 2009). The fruit tree red spider mite *Panonychus ulmi* enters diapause as egg. While summer eggs continually develop and do not undergo diapause, the winter eggs enter diapause at the blastoderm stage (Lees 1953a).

Diapause invokes a number of behavioural, physiological, morphological, and molecular modifications. In general, diapause is characterized by suppression of metabolism, changes in behaviour, and increased stress tolerance, often caused by the synthesis of cryoprotectants (Veerman 1985). For example, females of *T. urticae* in diapause alter expression of genes involved in digestion and detoxification, cryoprotection, carotenoid synthesis and the organization of the cytoskeleton (Bryon et al. 2013), suppress metabolism leading to a significant reduction in most amino acids and TCA cycle intermediates (Kohdayari et al. 2013), move to dark hibernacula for overwintering owing to loss of attraction to visible light and tendency to avoid UV light (Suzuki et al. 2013), and enhance tolerance to multiple stresses, including exposure to cold, heat, desiccation, anoxia, acaricides, and gamma irradiation (den Houter 1976; Ghazy and Suzuki 2014; Kohdayari et al. 2012; Lester and Petry 1995; Lester et al. 1997; Suzuki et al. 2015). In addition, diapause females change their body colour from yellow-green to orange, due to the accumulation of ketocarotenoids, especially astaxanthin, in their body, which is different from nondiapause females (Veerman 1974; Kawaguchi and Osakabe 2014). Astaxanthin acts as a scavenger of reactive oxygen species (Naguib 2000) and its accumulation is believed to confer higher tolerance to UV exposure in diapause individuals (Suzuki et al. 2009). Eggs of *P. ulmi* and *Schizotetranychus schizopus* in diapause also appear to accumulate higher amounts of carotenoids (see Veerman 1974).

Although diapause occurs as an obligatory phase of individual development (obligatory diapause) or in response to biotic and/or abiotic cues (facultative diapause), in general, facultative diapause is common in short-lived and multivoltine species, including mites. In temperate regions, the photoperiod is the major cue controlling diapause induction and termination, i.e., photoperiodism (Tauber et al. 1986; Danks 1987). For example, *T. urticae* adult females enter diapause when they experience short-day conditions during preimaginal development, whereas females in long-day conditions avert diapause and start oviposition immediately after adult emergence (Kawakami et al. 2009; Fig. 1). Diapause can be terminated only after completion of a physiological process called 'diapause development', of which the physiological mechanisms are still largely unknown (Hodek 1996). Diapause development proceeds at a slow rate spontaneously, but it can be accelerated by several

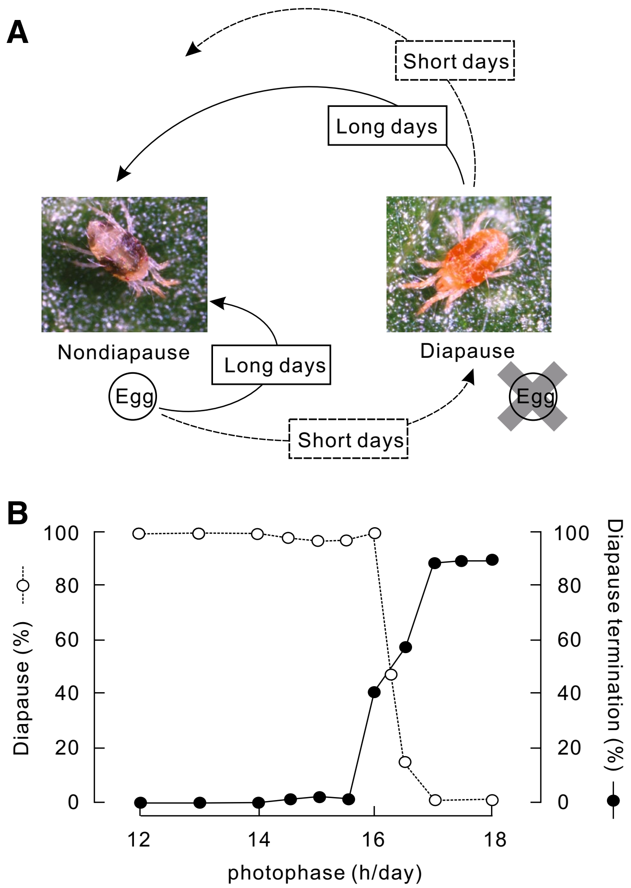

Fig. 1 Life cycle of *Tetranychus urticae* and its photoperiodism. **A** The life cycle of this species is regulated by photoperiod. Adult females enter diapause when they experience short-day conditions, whereas females in long-day conditions avert diapause and start oviposition. Diapause can be terminated spontaneously (horotelic process) in spider mites, but long-day conditions accelerate diapause development (tachytelic process). Thus, diapause can be terminated in a short period of time when diapause females were reared under long-day conditions, whereas it takes much longer time under short-day conditions. From Goto and Endo (2015). **B** Photoperiodic response curves of diapause induction (*open circles*) determined at 19 °C and diapause termination (*closed circles*) determined at 19 °C after cold storage at 4 °C, in the Leningrad (St. Petersburg) strain of *T. urticae* (Koveos et al. 1993)

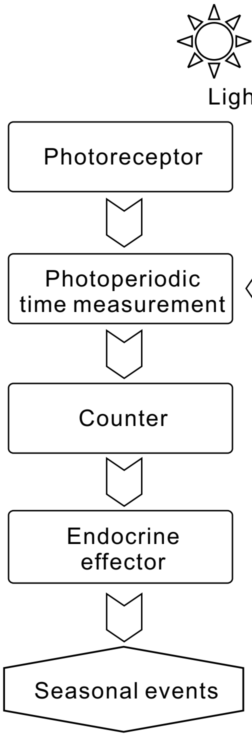

Fig. 2 Various modules establishing photoperiodism. Light/dark signals are received by photoreceptors for photoperiodism and the circadian clock, which may not be identical (Veerman and Veenendaal (2003)). The photoperiodic time measurement system measures the length of day or night and involves the circadian clock. The counter system counts the number of light–dark cycles. When the number of cycles exceeds an internal threshold in the counter, the release/restraint of endocrine effectors is triggered and seasonal events occur (Goto and Numata (2014))

environmental factors including photoperiod. For example, in *T. urticae* diapause development is accelerated under long-day conditions, but persists between several weeks to 2 or 3 months when mites experience short-day conditions (Koveos et al. 1993; Fig. 1).

A conceptual cascade involved in photoperiodism is shown in Fig. 2 (Saunders 2002). At the very beginning of the photoperiodic response, organisms must receive environmental light and/or dark signals through photoreceptors. The photoreceptors can be either retinal photoreceptors, a part of the visual system, or extraretinal photoreceptors, involved in the nonvisual system. The photic information is then sent to the photoperiodic time measurement system, which measures the length of day or night. A circadian clock is thought to play a pivotal role in the photoperiodic time measurement, which may rely on distinct photoreceptors. The counter system determines the number of light–dark cycles received and the endocrine effector directly regulates seasonal events, including diapause and seasonal morphs. The physiological mechanisms involved in these systems are reviewed in the following sections.

Photoreceptors

In insects, the photoperiodic signals can be received through retinal photoreceptors, extraretinal photoreceptors, or both, and there are no apparent phylogenetic constraints linked to their usage (Goto et al. 2010). For example, in the northern blow fly, *Protophormia terraenovae*, surgical removal of compound eyes from adult flies severely affected the induction of diapause in adults, underscoring the significance of retinal photoreceptors in this process (Shiga and Numata 1997). On the other hand, the urban bluebottle blow fly, *Calliphora vicina,* retained photoperiodic sensitivity for maternal induction of larval diapause even after removal of the optic lobe (a connective region between the central brain and compound eyes), indicating that their photoreceptors are extraretinal (Saunders and Cymborowski 1996). It should be noted that retinal and extraretinal photoreception are not mutually exclusive; in fact, the stink bug *Plautia stali* uses both for the photoperiodic induction of diapause (Morita and Numata 1999).

In mites, it has been suggested that extraretinal photoreception plays an important role in photoperiodism. This association has been made, for example, because the predacious eyeless mite *Amblyseius potentillae*, which does not possess eyes or ocelli-like structures, shows a clear photoperiodic response (McMurtry et al. 1976; van Houten and Veenendaal 1990). In contrast to eyeless phytoseiid mites, spider mites have distinct eyes on the dorsal side of the prodorsum. External morphology and internal structure of the eyes have been predominantly studied in *T. urticae* (McEnroe 1969; Mills 1973). Adult *T. urticae* possess two pairs of eyes (ocelli). The anterior eye faces dorsal-forward and the posterior eye faces dorsally. The anterior eye has a biconvex lens, whereas the posterior eye has a simple convex lens. Five or ten retinular cells form several rhabdomeres in the anterior and posterior eyes, respectively. Naegele et al. (1966) reported spectral sensitivity in the orientation and locomotor responses of *T. urticae*. Both these responses were demonstrated when mites were exposed to light with wavelengths ranging from 350 to 600 nm, but not to light >600 nm, with clear peaks observed in the spectral sensitivity in the UV region at 375 nm and green region at 525 nm. McEnroe and Dronka (1966, 1969) suggested that photoreception of UV and green light is performed by independent photoreceptor systems, and further concluded that the anterior eyes possess photoreceptors sensitive to UV and green light, whereas the posterior eyes possess photoreceptor sensitive only to UV light. However, physiological validation of these theories is still needed.

Hori et al. (2014) surgically removed the anterior and posterior eyes of *T. urticae* either bilaterally or unilaterally with a laser ablation system, to clarify whether the eyes play a role in the photoperiodic termination of diapause. A

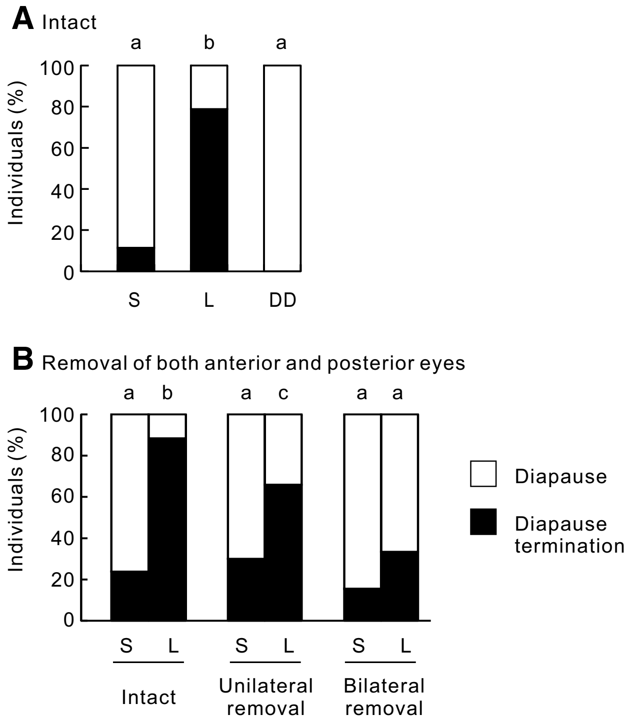

Fig. 3 Photoperiodic termination of diapause in *Tetranychus urticae* and the role of the eyes. Mites in diapause were chilled at 5 °C for 20 days and then transferred to short-day conditions (S), long-day conditions (L), or constant darkness (DD) at 17 °C. No significant differences were detected between treatments with the same letter (Tukey-type multiple comparisons for proportions, $P > 0.05$; Zar 2010) in each panel. **A** Intact mites. **B** Mites whose both anterior and posterior eyes were removed unilaterally or bilaterally (Hori et al. 2014)

dye laser (coumarin 440) effectively focusses on the screening pigment of the eye of diapause females, and therefore the internal structure of the eyes, beside the external structure, was destroyed. Females in diapause were exposed to low temperatures and transferred to an environment characterized by long-day conditions, short-day conditions, or constant darkness (Fig. 3). Intact females terminate diapause in response to long-day conditions, whereas they remain in diapause when exposed to short-day conditions or constant darkness. Thus, long-day signals are required to terminate diapause. Bilateral and unilateral removal of the anterior eyes did not affect photoperiodic discrimination (i.e. the females terminate diapause under long-day conditions, whereas they maintain diapause under short-day conditions). The same holds true for bilateral and unilateral removal of the posterior eyes. In contrast, bilateral removal of both anterior and posterior eyes significantly affected the termination of diapause. Mites without eyes failed to discriminate photoperiods and maintained diapause, irrespective of the photoperiod (Fig. 3). Thus, in *T. urticae*, both anterior and posterior eyes function as photoreceptors for the photoperiodic termination of diapause. However, it is still unknown whether this finding is generally applicable to other spider mite species, since even closely related insect species use distinct photoreceptors (Goto et al. 2010). It is also noteworthy that unilateral removal of both anterior and posterior eyes also significantly reduced the incidence of diapause termination under long-day conditions (Fig. 3). A similar effect of unilateral removal of photoreceptors on the photoperiodic response was shown in *P. terraenovae*, *P. stali*, as well as the crickets *Modicogryllus siamensis* and *Dianemobius nigrofasciatus* (formerly known as *Pteronemobius nigrofasciatus*) (Shiga and Numata 1996, 1997; Morita and Numata 1999; Sakamoto and Tomioka 2007). These results suggest that photoperiodic machinery resides in both hemispheres in the brain (specifically in the case of mites, the synganglion), and photoperiodic information from photoreceptors on both sides must be integrated to fully discriminate the photoperiod. It is known in *P. terraenovae* that the circadian clock located in each optic lobe is causally involved in the photoperiodic response (Shiga and Numata 2009). Involvement of the circadian clock in photoperiodism will be discussed later in this review.

Although not statistically significant, the incidence of diapause termination under long-day conditions was still higher than that under short-day conditions, even when both anterior and posterior eyes were removed bilaterally (Fig. 3). Although it is possible that the eye-removal was not complete in some mites, these results may indicate supplemental involvement of extraretinal photoreception in photoperiodic termination of diapause in *T. urticae*, in addition to the principal role of retinal photoreception, as was found in *P. stali* (Morita and Numata 1999).

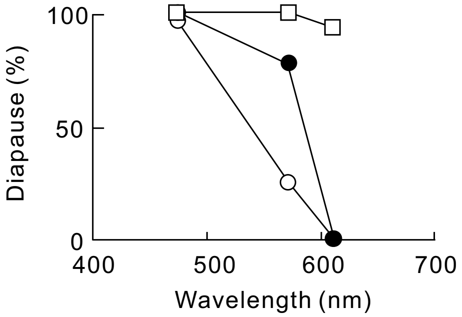

Fig. 4 Diapause induction in *Tetranychus urticae* in cycles of 8-h of monochromatic light and 16-h of darkness at 18 °C. Various wavelengths of light (blue, 475 nm; green 572 nm; orange, 612 nm) at various intensities (50, 500, and 2500 mW/m^2 for *open circles*, *closed circles*, and *open squares*, respectively) were used (Suzuki et al. 2008a)

Suzuki et al. (2008a) investigated spectral sensitivity and light intensity required for photoperiodic induction of diapause in *T. urticae* (Fig. 4). When monochromatic light was used as a light source in a 8-h light: 16-h dark (LD 8:16 h) and intensity of the light was changed, the threshold intensity to induce diapause in 50 % of the individuals was the lowest for blue light (475 nm), intermediate for green light (572 nm), and highest for orange light (612 nm). On the other hand, *T. urticae* had no ability to respond to red light (658 nm). Thus, *T. urticae* can receive a broad range of light wavelengths and is highly sensitive to light with short wavelengths. Lees (1953a) also reported that *P. ulmi* is able to respond to a broad range of light wavelengths from the near UV (365 nm) to blue-green light (540 nm) to avert embryonic diapause, with maximal sensitivity of the blue (425 nm) region. This species had no ability to respond to the orange, red and infrared light (longer than 550 nm).

Veerman (1980) investigated the photoperiodic response of four albino mutants isolated from wild *T. urticae* populations, in which uptake and oxidative metabolism of carotenoids were blocked. The original wild populations entered diapause in response to short-day conditions, whereas diapause incidence appeared to be lowered in the mutants. When a semisynthetic diet was used, no diapause was found in the albino mutant under short-day conditions on the standard diet. However, partial restoration of the photoperiodic response was obtained after addition of β-carotene to the diet, and full restoration was observed after the addition of vitamin A (Bosse and Veerman 1996). The significance of carotenoids in photoperiodic induction of diapause has also been clarified not only in the mites *A. potentillae* and *Amblyseius cucumeris* (Van Zon et al. 1981; Veerman et al. 1983; Overmeer et al. 1989), but also in several insect species (see Saunders 2012). Thus, vitamin A and its derivatives are prerequisites for the photoperiodic induction of diapause.

The requirement of vitamin A or its derivatives, and the broad range of the effective wavelength of light required for the photoperiodic response in *T. urticae,* is reminiscent of visual pigments. Visual pigments have been identified as photoreceptor molecules in various organisms, and comprised the opsin protein and a vitamin A-based pigment, which can be retinal or 3-hydroxyretinal. Each visual pigment generally exhibits a narrow range of spectral sensitivity; however, each species possesses multiple visual pigments with distinct spectral classes. Therefore, animals can perceive light across broad wavelengths (Henze and Oakley 2015). Tamaki et al. (2013) utilized RNAi to demonstrate that UV-, blue-, and long-wave-sensitive opsins are causally involved in photoperiodic photoreception in the nymphal diapause of *M. siamensis*. These results, together with those studies on mites, indicate that multiple types of visual pigments or a single type of visual pigment sensitive to a broad wavelength of light located in the anterior and posterior eyes function as photoreceptive molecules for the photoperiodic response in *T. urticae*.

Genome of *T. urticae* has been available as the first complete chelicerate genome (Grbić et al. 2011). Owing to the availability of next-generation sequencing methods, an increasing number of mite genomes and transcriptomes have been released in public database (Van Leeuwen and Dermauw 2016). In *T. urticae*, three putative opsin genes (tetur12g04340, tetur07g05150, tetur24g02280) and one peropsin gene (tetur04g04260) have been detected in the OrcAE database (Online Resource for Community Annotation of Eukaryotes; http://bioinformatics.psb.ugent.be/orcae/). Peropsin is a member of the opsin family and has characteristics of two functionally distinct opsin-groups, i.e. amino acid residues conserved among opsins involved in light-sensing and retinal-photoisomerase-like molecular properties. In a spider, peropsin is localized in nonvisual cells in the retina and acts as a photosensitive pigment with a nonvisual function (Nagata et al. 2010). In *P. ulmi*, five transcripts encoding putative opsin (GCAC01000911, GCAC01005648, GCAC01005363, GCAC01000911, GCAC01006475) and one transcript encoding putative peropsin (GCAC01001176) were found in the DDBJ/GenBank/EMBL database. Although the spectral sensitivity of these pigments in relation to the opsins and peropsin is still unknown, multiple opsin genes indicate that they are characterized by a broad sensitivity to light.

Photoperiodic time measurement and circadian clock

The relative importance of the light and dark components of the daily cycle have been investigated in various organisms by independently varying light and dark in overall cycle lengths close to 24 h in duration. It is now generally accepted that duration of the night is much more important than the duration of light not only in insects but also in mites (Saunders 2013). For example, Lees (1953b) combined various lengths of light and dark and found that diapause of *P. ulmi* is averted in photoperiods containing a night equal to or shorter than 8 h (e.g. LD 16:4 h, LD 24:4 h, LD 12:8 h, LD 16:8 h, and LD 24:8 h) but is clearly induced in photoperiods containing a night longer than 8 h (e.g. LD 4:12 h, LD 8:12 h, LD 12:12 h, LD 16:12 h), irrespective of the duration of the accompanying light component. Also in *T. urticae*, diapause incidence was low in photoperiods containing a short night (e.g. LD 12:8 h and 16:8 h) but approached 100 % in photoperiods containing a long night (e.g. LD 8:12 h and LD 12:12 h), regardless of the duration of the accompanying light component (Veerman 1977; Veerman and Veenendaal 2003). Nevertheless, terms focussing on day but not night, such as long-day conditions, short-day conditions and day length, have been commonly used in the literatures. These terms are used in this review.

Bünning (1936) first proposed the involvement of a circadian clock in photoperiodic time measurement.

Bünning's hypothesis posited that the 24-h circadian clock consisted of two 12-h half-cycles, which were termed the photophil and scotophil (light- and dark-loving phases, respectively). It also stated that short-day effects are observed when light is restricted to the photophil, while long-day effects are produced when light penetrates the scotophil. Although this idea is too simple to explain the range of photoperiodic responses, the basic concept of a circadian clock in photoperiodic time measurement is now widely accepted, not only in insects (Saunders and Bertossa 2011) but also in other organisms, ranging from fungi to mammals (Nelson et al. 2010).

Whether the circadian clock is involved in photoperiodic time measurement can be assessed by experiments revealing the known effects of environmental light pulses on the phase shifting and entrainment of circadian oscillations (Saunders 2002). For instance, a short-day photophase ranging from 10- to 12-h can be coupled with periods of scotophase varying from 4- to 72-h [known as the Nanda–Hamner protocol: Nanda and Hamner (1958)]. Alternatively, insects can be exposed to 48- or 72-h cycles consisting of a 12-h photophase with a light pulse systematically interrupting an extended period of perceived night [known as the Bünsow protocol: Bünsow (1960)]. In both types of experiments, these aberrant light cycles are repeated throughout the photoperiod-sensitive period, after which short-day effects are assessed for each condition. A circadian involvement is suspected when short-day effects occur in alternating peaks and troughs with an approximate 24-h periodicity in the extended scotophase. Conversely, the absence of this pattern is evidence of an hourglass-like timer, which is the case in the aphid *Megoura viciae* (Lees 1973). An hourglass is a mechanism that follows a set time course in darkness after being initiated at lights off and needs a minimum duration of light to restart the measurement process at the beginning of the next scotophase. This can be considered a non-circadian mechanism; however, it can also be considered a heavily dampened circadian oscillator, of which oscillation is easily dampened out below threshold in extended periods of darkness (Saunders 2010). Such dampened oscillator is able to measure only one night in the extended darkness, so that the accumulation of short-day information is lowered, so reducing the final incidence of diapause. This heavily dampened circadian oscillator has been shown to be important for photoperiodic timing even in *M. viciae* (Vaz Nunes and Hardie 1993). Thus, the functional role of a circadian clock in photoperiodic time measurement is now widely accepted, although some details are still under dispute (Bradshaw and Holzapfel 2007).

When *T. urticae* was reared in cycles consisting of 8-h of photophase and different durations of scotophase (the Nanda–Hamner protocol), peaks of high diapause incidence recurred with cycle lengths (duration of light plus dark) of approximately 24, 44, 64 and 84 h, which correspond to 16-, 36-, 56- and 76-h of scotophases, respectively. Diapause induction was completely averted in photoperiodic cycles consisting of 8-h photophase combined with scotophases ranging from 4 to 9, 24 to 28, 44 to 48 and 60 to 64-h (Veerman and Vaz Nunes 1980; Fig. 5). These results indicate a functional connection between the circadian system and photoperiodism in *T. urticae*. It is important to note that the resonance peaks are approximately 20-h apart. This indicates that period of the circadian clock involved in *Tetranychus* photoperiodism in the free-run state (free-running period) is 20-h.

Veerman and Vaz Nunes (1987) compared the response under a 12-h light:12-h dark (LD 12:12 h) with that from a 12-h light:36-h dark (LD 12:36 h) cycle. As the number of the light–dark cycles increased, diapause incidence increased in both conditions. However, the efficacy of diapause induction under the LD 12:36 h cycle was approximately half of that of LD 12:12 h, indicating that a night 36-h long in the environmental cycle of 48-h in LD 12:36 h is effectively one long night. If the clock measuring night length is an oscillator which is able to free-run under constant darkness, with a night 36-h long in an LD cycle of 12:36 h is measured as two long nights (Fig. 6). Thus, photoperiodic time measurement in the spider mite is either a true non-circadian hourglass or a heavily damping oscillator. Based on these results, Vaz Nunes proposed the double circadian oscillator model (Vaz Nunes 1998). This model assumes the presence of two independent circadian mechanisms where both play a role in the determination of the length of a night. One of the mechanisms is the long night (LN) system, which assigns scotophase a positive value when the night is long. The other is the short night (SN) system, which assigns scotophase a positive value when the night is short. The model successfully simulates the photoperiodic response in *T. urticae* with the assumption of a

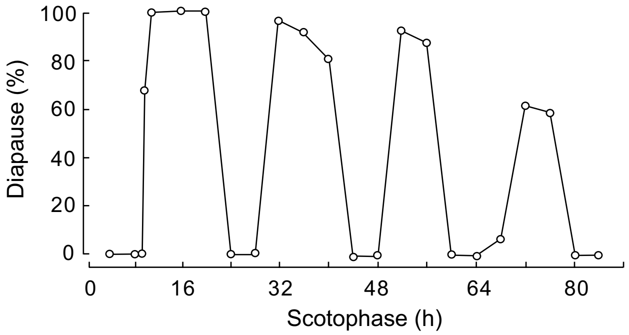

Fig. 5 Diapause incidence of *Tetranychus urticae* when exposed to cycles consisting of 8-h of light and various durations of scotophase (the Nanda–Hamner protocol) (Veerman and Vaz Nunes 1980)

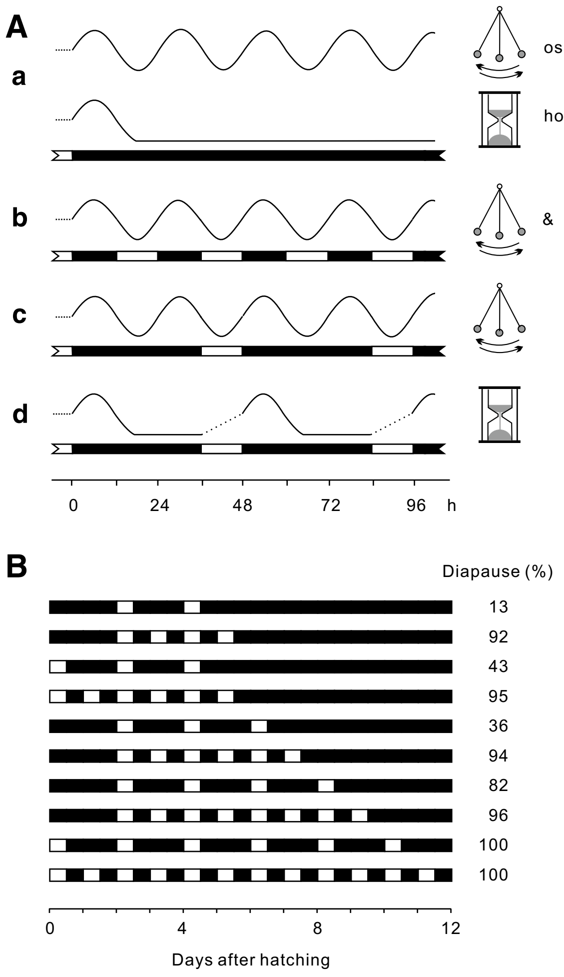

Fig. 6 Different kinetics of photoperiodic time measurement between an oscillator and an hourglass and diapause incidence of *Tetranychus urticae* under Veerman-Vaz Nunes light–dark cycles. *Open* and *closed horizontal bars* indicate photophase and scotophase, respectively (Veerman and Vaz Nunes 1987). **A** Clocks based on the oscillator principle oscillate even under constant darkness, whereas clocks based on the hourglass stop after a single time measurement (**a**). Both the oscillator and hourglass can measure length of night under light–dark cycles (**b**). The oscillator can perform two acts of time measurement in nights 36-h long (**c**), compared to only one measurement when using an hourglass (**d**). Consequently, twice as many 'inductive events' can be counted during the same number of light (L) and dark (D) 12:36 cycles if the clock is an oscillator, as in the case of hourglass time measurement. **B** Diapause incidence of mites exposed to either constant darkness, LD 12:12 h, or LD 12:36 h during their development

rapidly damping LN system and a non-damping SN system (Vaz Nunes 1998).

In insects, interlocked positive and negative feedback loops based on transcription and translation are the essence of circadian clocks, and major players of the loops include *period* (*per*), *timeless* (*tim*), *mammalian-type cryptochrome* (*cry-m*; also known as *cry2*), *cycle* (*cyc*) and *Clock* (*Clk*) genes (Tomioka and Matsumoto 2015). Some insect species possess another type of *cryptochrome*; i.e. *Drosophila-type cryptochrome* (*cry-d*; also known as *cry1*). Its protein product acts as a photoreceptor molecule to reset the circadian clock (Tomioka and Matsumoto 2015). Knocking down these clock genes using RNAi revealed their causal involvement in photoperiodism in some insect species, (Numata et al. 2015). For example, RNAi of *per*, *cry-m*, *cyc,* and *Clk* disrupted the photoperiodic induction of reproductive diapause in the bean bug *Riptortus pedestris* (Ikeno et al. 2010, 2011a, b, 2013). NAi directed against *per, tim*, and *cry-m,* and pigment-dispersing factor (*pdf*), a putative output gene of the circadian clock, also disrupts the photoperiodic response in the mosquito *Culex pipiens* (Meuti et al. 2015). *per* RNAi disrupted photoperiodic induction of larval diapause in the jewel wasp *Nasonia vitripennis* (Mukai and Goto 2016) and photoperiodic induction of nymphal diapause as well as circadian locomotor rhythmicity in *M. siamensis* (Sakamoto et al. 2009). A genetic variant found in nature also supports causal involvement of the circadian clock in photoperiodism. A genetic variant of the drosophilid fly, *Chymomyza costata*, which is named the non-photoperiodic diapause (*npd*), showed an abnormal photoperiodic response (Riihimaa and Kimura 1988) and an arrhythmic pattern of adult eclosion (Lankinen and Riihimaa 1992). Daily oscillations in *per* and *tim* expression were clearly observed in wild-type flies, whereas *per* was expressed arrhythmically at low levels and *tim* mRNA was completely absent in the variant (Košťál and Shimada 2001, Pavelka et al. 2003), due to a large deletion in a crucial *cis*-regulatory element and minimal promoter (Kobelková et al. 2010). A genetic linkage analysis mapped the gene responsible for the abnormal photoperiodic phenotype to the locus containing *tim* (Pavelka et al. 2003). These results provide evidence for the role of *tim* in the photoperiodic induction of diapause in *C. costata*.

These studies raise the question: does malfunction of circadian clock genes affect photoperiodism by altering clock function, or does malfunction of circadian clock genes directly affect diapause? This question is a focal point in the discussion concerning the molecular basis of photoperiodism, with some studies in *R. pedestris* supporting the former possibility after analysing results from knocking down all major clock genes (Numata et al. 2015). Recently, Pegoraro et al. (2014) focussed on the photoperiodic response in chill-coma recovering time (CCRt) in *D. melanogaster*. Wild-type flies maintained under short-day conditions exhibited significantly shorter CCRt than flies under long-day conditions. Arrhythmic mutant strains, *per*^{01}, *tim*^{01} and *Clk*^{Jrk}, demonstrated a disrupted photoperiodic response in CCRt. It is of interest to note that mutants with long free-running periods consistently showed short-day-type responses in CCRt under both long and short photoperiods, compared with mutants with short free-running periods. The results aligned with those expected under Bünning's hypothesis. In mutants with a long free-running period (where photophil is longer), various photophases consistently coincided with the photophil phase and were interpreted as short-day conditions (Pegoraro et al. 2014). The different photoperiodic phenotypes of the slow and fast clock mutants suggest a causative role for the circadian clock in the photoperiodic time measurement. Mohamed et al. (2014) focussed on the link connecting the circadian clock to a photoperiodic endocrine switch in the Chinese oak moth *Antheraea pernyi*, of which pupal diapause can be terminated by long-day conditions. Through employing RNAi, immunohistochemistry, radioimmunoassay (RIA) and radioenzymatic assay, they demonstrated that *N*-acetyltransferase (AA-NAT), a rate-limiting enzyme for the production of melatonin and one of the clock-controlled genes, regulates secretion of the prothoracicotropic hormone (PTTH), which stimulates the prothoracic gland to secrete ecdysteroids, and terminate diapause.

Although the causal involvement of the circadian clock in photoperiodism has been reported in these insect species, controversial evidence has accumulated in *T. urticae*. Veerman and colleagues focussed on the critical day length (CDL) to clarify the role of the circadian clock in photoperiodism in *T. urticae*. The CDL is the day length in which a half of population shows a long-day response with a distinct latitudinal cline (Goto and Numata 2014). Vaz Nunes et al. (1990) compared variation in CDL with variation in the free-running period of the Nanda–Hamner rhythm, which is involved in the photoperiodic response in *T. urticae*. If the circadian clock is indeed involved in the photoperiodic time measurement, there must be a correlation between them, as indicated by Pegoraro et al. (2014). However, only a very weak correlation between them was observed (Fig. 7), with little or no correlation between CDL and the circadian phenotype reported in *Drosophila auraria* (Pittencrigh et al. 1984), *Drosophila littoralis* (Lankinen and Forsman 2006), and the pitcher plant mosquito, *Wyeomyia smithii* (Bradshaw et al. 2003, 2006). Genetic analysis has also been completed in the spider mite. Reciprocal crosses were made between two strains of mites, which differed by 3-h in CDL and 2-h in the free-running period of the Nanda–Hamner rhythm. The crossing experiments showed that a short free-running rhythm is almost completely dominant over a long free-running rhythm, whereas CDL is inherited in an intermediate way (Vaz Nunes et al. 1990), indicating that these characteristics are governed by independent genetic elements. Moreover, in two strains of *T. urticae*, originating from the same latitude, CDL appeared to be the same, whereas the period of the free-running rhythm of the Nanda–Hamner experiments differed from 1 to 3-h among the strains, depending on temperature (Koveos and Veerman 1996). Veerman and Veenendaal (2003) revealed that the photoperiodic time measurement system is sensitive to light ranging from orange to red, whereas the Nanda–Hamner rhythm (of which free-running period is 20-h) is insensitive to the light, and therefore, it free-runs under the orange-red light photoperiod. These results do not provide evidence in favour of a circadian-based photoperiodic time measurement.

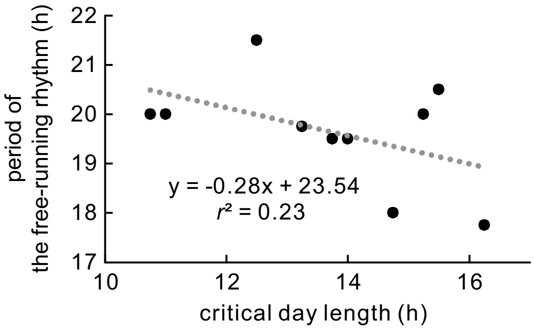

Fig. 7 Relationship of the critical day length for induction of diapause and the period of the free-running rhythm under the Nanda–Hamner protocol in 10 *Tetranychus urticae* strains (Vaz Nunes et al. 1990). The regression line and r^2 value are also shown

Based on these results, Veerman (2001) emphasized that a clock role for the circadian system in mite photoperiodism is highly unlikely and photoperiodic time measurement in mites most likely is a non-circadian hourglass mechanism. In his idea, positive Nanda–Hamner and Bünsow results indicate that some subsystem(s) other than the photoperiodic time measurement system is affected by the circadian system, resulting in the rhythmic responses observed. Indeed, a wide array of physiological processes in an organism is expected to be fallen under circadian control (Allada and Chung 2010). Currently, there is a debate regarding which of the concepts (hourglass timer vs. circadian clock) in *T. urticae* is based only on classic physiology, and therefore, understanding of this process is still highly conceptual. It would be beneficial for new approaches to address the point to be proposed.

Homologues of clock and clock-related genes are also found in *T. urticae* (*per*, tetur11g03490; *tim*, tetur27g02370; *cry-m*, tetur09g05920; *cyc*, tetur08g07430; *Clk*, tetur08g07600; *cry-d,* tetur16g02770). *pdf* gene has not been found in *T. tetranychus* genome, but its putative receptor (tetur04g08940) was detected (Veenstra et al. 2012). Also in *P. ulmi*, transcripts of putative *per* (GCAC01001617 and very short sequence of GCAC01025045), *cry-m* (GCAC01005533 and rather short sequence of GCAC01001108), *cyc* (GCAC01002042), and *Clk* (GCAC01003834) and 2 *cry-d* (GCAC01000428 and GCAC01007196) were found, but *tim* transcript was not. However, the roles of these clock genes in the circadian clock and also in photoperiodism have not been investigated in any Acari species.

Counter

The photoperiodic counter registers successive cycles during the sensitive period until an internal threshold is reached, which triggers a physiological response mediated by endocrine effectors. In one model of photoperiodic summation, organisms accumulate a hypothetical diapause-inducing substance under short-day conditions in the counter system after processing photoperiodic information in the time measurement system (Gibbs 1975). Thus, a short-day response is elicited upon exceeding the internal threshold, whereas a long-day response is induced at subthreshold values (Gibbs 1975; see also Tagaya et al. 2010). In *T. urticae,* Koveos and Veerman (1994) found that the threshold for diapause termination in long-day conditions, expressed as the number of light–dark cycles required for 50 % diapause termination, is lower in the southern strain than the northern strain (Fig. 8). In addition, considerable differences in the number of light–dark cycles required for diapause termination were also observed among strains. These inter- and intra-strain variations would be derived from variation in the synthesis rate of the hypothetical substance or the threshold. However, their molecular and neural bases are still largely unknown. In *A. pernyi*, it has been suggested that the photoperiodic counter is driven by mutual inhibition between the melatonin and dopamine pathways (Wang et al. 2015). AA-NAT increased in expression level in response to long-day conditions, whereas dopa decarboxylase (DDC), the rate-limiting enzyme for the production of dopamine, decreased in expression level in response to changes in the photoperiod. Wang et al. (2013) also found in *A. pernyi* that expression of one type of serotonin receptors (5HTR$_B$) decreases in response to long-day conditions, and RNAi directed against the receptor induces PTTH accumulation and results in early diapause termination. Injection of 5,7-dihydroxytryptamine (5,7-DHT), a pharmacological agent decreasing serotonin concentration, induces early emergence even under short-day conditions.

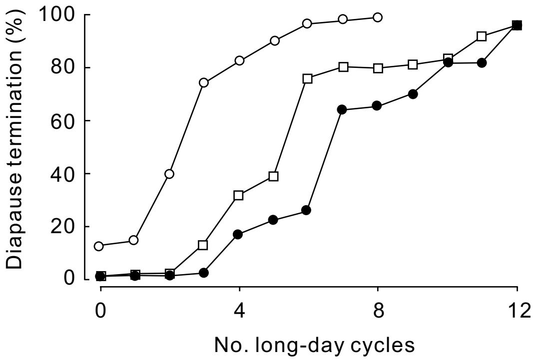

Fig. 8 Number of long-day (LD 17:7 h) cycles required for diapause termination at 19 °C in three *Tetranychus urticae* strains after cold exposure at 4 °C. After experiencing the indicated number of long-day cycles, mites were transferred to continuous darkness at 19 °C. Percentages of diapause termination were determined 12 days after removal from cold storage. *Closed circles* Leningrad (St. Petersberg); *open squares* Voorne; *open circles* Thessaloniki-II (Koveos and Veerman 1994)

At least five (tetur22g00750, tetur12g02440, tetur01g00420, tetur07g07500, and tetur247g00020) and two (GCAC01002910 and GCAC01007129) sequences showing high similarity to *DDC* have been found in *T. urticae* and *P. ulmi*, respectively. Several genes and transcripts showing high similarity to the serotonin receptor are also found in them. Although genes homologous to *AA-NAT* have not been identified in Acari (Hiragaki et al. 2015), its activity and the action spectrum for suppression of the activity have been investigated in *T. urticae* (Suzuki et al. 2008b). It is of interest to measure the levels of these biogenic amines and the expression levels of these genes in mites under diapause-inducing short-day conditions and diapause-averting long-day conditions. They are the candidates of the diapause-inducing substances hypothesized by Gibbs(1975).

Endocrine effector

Although there is no conclusive evidence, it is reasonable to assume that embryonic and reproductive diapause in the spider mite is hormonally regulated, as reported previously in insects. In insects, embryonic diapause is regulated by diapause hormone (DH) or ecdysteroids, whereas reproductive diapause is regulated by juvenile hormone (JH) or ecdysteroids (Denlinger et al. 2012). DH, a member of the FXPRL-amid peptide family, is a crucial factor that directly regulates embryonic diapause of the silk moth *Bombyx mori* (Yamashita 1996). Although downstream cascade of DH has also been elucidated in *B. mori*, there is no evidence to suggest that the regulatory mechanisms documented in the species is applicable to embryonic diapause in other insect species. Ecdysteroids, a specific family of sterol derivatives, are essential for controlling insect development, including moulting, metamorphosis, and also diapause (Lafont et al. 2012). Embryonic diapause of the Australian plague locust *Chortoicetes terminifera* and the migratory locust *Locusta migratoria* is considered to be induced by the absence of ecdysteroids (Gregg et al. 1987; Tawfik et al. 2002a), whereas that of the gypsy moth *Lymantria dispar* is induced by an elevated ecdysteroid titre (Lee and Denlinger 1997). Low titre of JH, a family of acyclic sesquiterpenoids, is well-known to induce reproductive diapause in many insect species, such as the Colorado potato beetle *Leptinotarsa decemlineata* (de Kort

1990), the Northern house mosquito *Culex pipiens* (Readio et al. 1999), and *P. stali* (Kotaki et al. 2011). On the other hand, absence of ecdysteroids is considered to be the key in reproductive diapause in *D. melanogaster* (Richard et al. 1998) and *L. migratoria* (Tawfik et al. 2002b).

Genome analysis revealed that *T. urticae* has no ability to produce JH due to a lack of the CYP15A1 gene, which encodes the enzyme introducing the signature epoxide of insect JHs. Instead of JH, *T. urticae* produces methyl farnesoate (MF) (Grbić et al. 2011). The role of MF in spider mite physiology has not been verified, but Regev and Cone (1976) reported that females of *T. urticae* treated topically with farnesol laid more eggs than females. This result implies some role of MF in their reproduction. MF is also the final product in crustaceans, but there is a debate regarding its role. Laufer et al. (1998) revealed in the crayfish *Procambarus clarkii* that administration of MF stimulates ovarian maturation. However, recent studies have indicated that MF has no effects on vitellogenin (Vg) gene expression in the hepatopancreas of shrimp (*Metapenaeus ensis*), lobster (*Homarus americanus*), and crab (*Charybdis feriatus*) (Subramoniam 2011). In contrast, Marsden et al. (2008) indicated an inhibitory role of MF in the late stage of ovary development in black tiger prawn *Penaeus monodon.* In ticks, 20-hydroxyecdysone (20E) is responsible for the initiation of Vg synthesis, and ecdysteroids secreted by the epidermis and converted into 20E by the fat body (Cabrera et al. 2009). Vg is synthesized primarily in the fat body and midgut, and to a lesser extent in the ovary (Rosell and Coons 1992; Thompson et al. 2007). However, the source of extraovarian Vg has not been clearly determined for any mite species and it remains to be addressed, because in contrast to ticks, most mites lack the fat body (Cabrera et al. 2009). In *Tetranychus,* the midgut has been suggested to be a source of Vg (Shatrov 1997, 2002). The *T. urticae* genome lacks two P450 genes, CYP306A1 and CYP18A1, which encode C25 hydroxylase and a C26 hydroxylase/oxidase involved in hormone inactivation, respectively. The absence of CYP306A1 indicates that the spider mite uses the ecdysteroid, ponasterone A, as the moulting hormone instead of the typical arthropod 20E, which was confirmed by biochemical analysis of spider mite extracts (Grbić et al. 2011).

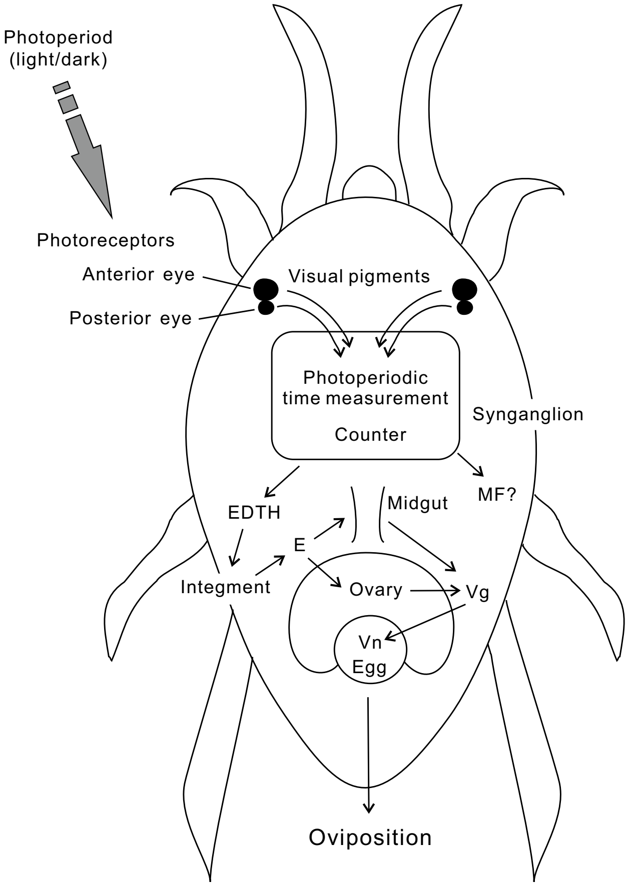

Fig. 9 Model summarizing current knowledge on regulation of ovarian development in *Tetranychus urticae.* Anterior and posterior eyes function as photoreceptors in *T. urticae*. Visual pigments, which comprised opsin protein and a vitamin A-based pigment, would be involved in photoreception. The physiological basis of the photoperiodic time measurement system and the counter system is still largely unknown. Reproduction is possibly regulated by the ecdysteroid (E), ponasterone A. Cabrera et al. (2009) proposed that the synganglion synthesizes an ecdysiotropic hormone (EDTH) that initiates the production of ecdysteroids in the epidermis. The ecdysteroid then induces vitellogenin (Vg) production in the midgut and ovary. After incorporation into oocytes, Vg is stored in a crystalline form as vitellin (Vn), a reserve food source for the future embryo. Some process regulating ponasterone A synthesis would be involved in diapause induction. The role of methyl farnesoate (MF) in spider mite physiology has not been verified

Cabrera et al. (2009) proposed a hypothesis to describe the regulation of vitellogenesis and female reproduction in Acari and theorized that ecdysteroids play an important role in acarine vitellogenesis. The synganglion synthesizes an ecdysiotropic hormone (EDTH) that initiates the production of ecdysteroids in the epidermis. The ecdysteroid then, possibly ponasterone A, induces Vg production in the midgut and ovary (Fig. 9). Reproductive diapause in mites is possibly induced and maintained by some process suppressing ponasterone A secretion. Kawakami and Numata (2013) found that topical application of a synthetic pyrethroid, cypermethrin (CyM), induces ovarian development in *T. urticae* undergoing diapause. In unengorged adult females of the soft tick *Ornithodoros moubata*, CyM induces Vg synthesis in the fat body and vitellin accumulation in the oocytes, whereas it does not induce oviposition (Chinzei et al. 1989; Taylor et al. 1991). Although the mechanism of action of the pyrethroid leading to the induction of vitellogenesis is unknown, Chinzei et al. (1989) suggested that the endocrinological steps required for vitellogenesis are induced by neurosecretory factors secreted artificially, due to the change in electrical activity of neurosecretory cells driven by the pyrethroid. In diapause adults of the beetle *Henosepilachna vigintioctopunctata*, pyrethroids also stimulate ovarian development and partially induce oocyte maturation and oviposition (Kono and Ozeki 1987). Diapause in mites is likely induced and maintained by suppression of neurosecretory secretion, although the identity of the neurosecretory factors remains unknown. Endocrinological mechanisms promoting embryonic diapause in spider mites are still unknown.

Future prospectives

Although we have accumulated much data on the physiological mechanisms of mite photoperiodism, the molecular mechanisms underlying it, especially those related to photoperiodic time measurement and the counter, are still largely unknown (see Fig. 9 for a summarising model). Since genomic information is available for *T. urticae* (Grbić et al. 2011), now it is easy to clone genes of interest. Gene silencing is possible in *T. urticae* by injecting or feeding the organism double-stranded RNA (Khila and Grbić 2007; Kwon et al. 2013), although its efficacy seems to be very low. Silencing candidate genes considered to be involved in the photoperiodic cascade (for example, those involved in light perception, the circadian clock, and hormone syntheses) would be a valuable method to dissect molecular mechanisms underlying photoperiodism.

Recently, it has become relatively easier to access high-throughput technologies, including next-generation sequencing platforms and microarrays. Bryon et al. (2013) investigated essential physiological processes in *T. urticae* in diapause by studying genome-wide expression changes, using a custom-built microarray. Analysis of this dataset showed that 11 % of the total number of predicted *T. urticae* genes was differentially expressed. Similar experiments focussing on differential gene expression in diapause and nondiapause individuals have also been performed in various insect species (for example, Kankare et al. 2010; Kumar et al. 2014; Poelchau et al. 2013; Qi et al. 2015; Wadsworth and Dopman 2015). However, use of a high-throughput approach during the photoperiod-sensitive stage has been limited (Le Trionnaire et al. 2009; Poupardin et al. 2015; Zhang et al. 2011). Huang et al. (2015) utilized powerful RNA-seq technologies to elucidate gene expression in *C. pipiens* during its photoperiod-sensitive stage. This study found upregulation of *tim*, *cry-d* and JH-inducible proteins and activation of two amino acid metabolic pathways in non-blood-fed females under diapause-inducing short-day photoperiods. These genes and proteins are the candidates of the players in the photoperiodic time measurement and counting. The photoperiod-sensitive stage for diapause induction in *T. urticae* is predominantly restricted to deuronymphs with some sensitivity observed at the larval and protonymphal stages (Suzuki and Takeda 2009). It would be very interesting to compare gene expression between deutonymphs maintained in short-day and long-day conditions.

Geographic variation in diapause potential has been reported in *T. urticae* (Gotoh and Shinkaji 1981; Takafuji et al. 1991; Koveos et al. 1993; Vaz Nunes et al. 1990). Genetic crosses revealed that variation in diapause potential could be attributed to various genetic systems including the presence of dominant alleles at multiple loci (Kawakami et al. 2010), a recessive allele at a single locus (Kawakami et al. 2010; Ignatowicz and Helle 1986), and incompletely recessive alleles at multiple loci (Goka and Takafuji 1990, 1991; So and Takafuji 1992). Although several genes responsible for natural variation in the diapause phenotype have been elucidated in the model insect *D. melanogaster* (Schmidt et al. 2008; Tauber et al. 2007; Williams et al. 2006), such loci or genes responsible for the phenotype have not yet been revealed in *T. urticae*. Mapping the location of causal mutations using genetic crosses has traditionally been a complex and multistep procedure, but next-generation sequencing now allows for the rapid identification of causal mutations at the single-nucleotide resolution level even in complex genetic backgrounds (Schneeberger 2014). Recent advances of this mapping-by-sequencing approach include methods that are independent of reference genome sequences, genetic crosses or any type of linkage information. Van Leeuwen et al. (2012) adopted this methodology (bulk segregant analysis mapping method with high-throughput sequencing technology) to verify the locus responsible for the resistant phenotype to the acaricide etoxazole in the field-collected *T. urticae* population. Finally, they clarified a single amino acid change in the chitin synthase 1 as conferring target site resistance to etoxazole. These approaches could shed light on the molecular mechanisms underlying not only photoperiodism but also other physiological processes in spider mites (Van Leeuwen and Dermauw 2016).

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