

# Insect Diapause: A Review

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**Abstract:** Diapause is defined as a period of suspended development in insects and other invertebrates during unfavorable environmental conditions. Diapause is commonly confused with term “quiescence” as both are dormant development stages. Here this paper aimed to review the research work done on different aspects of diapause. Attempt was made to explain definitions of diapause, incidence, stages and termination of diapause, genetic control, factors affecting diapauses, including temperature, photoperiod, moisture and food, etc..

**Key words:** Diapause, quiescence, diapauses theory, stages of diapauses, genetic control, biotic and abiotic factors, insects.

## 1. Introduction

Diapause is an important adaptation in many insect species enabling them to sustain in regions which would otherwise be unfavorable for permanent habitation, and to maintain high numbers in an environment which might otherwise support only a low population [1]. The term “diapause” was applied by Wheeler [2] to egg stage of grasshopper, *Conocephalus ensiferum* at which its development was ceased. Later the scope of diapause widened into various stages of insects as “periods of arrest in ontogenetic (origin and development of organisms) development” by Henneguy [3]. Diapause process is a splendid chance for insects to survive a great deal of seasonal changes in the environment.

Diapause can be categorized according to seasonal variations as aestivation (summer diapause) or hibernation (winter diapause); or according to life stages as an egg (embryonic), larval, nymphal or adult (imaginal, reproductive) diapause; or according to the influence of environmental factors as obligatory and facultative diapause. Depending on the species, diapause can occur at different stages, such as

embryonic, larval, pupal or adult stages. For example, silkworm moth (*Bombyx mori*) overwinters in embryo stage, just before segmentation. The gypsy moth (*Lymantria dispar*) enters diapause as a fully formed larva with hatching occurring immediately after diapause ends. Obligate diapause is often universal, resulting in strictly univoltine life cycle with every individual in every generation experiencing diapause, irrespective of any possible environmental variations. On the other hand, facultative diapause occurs due to environmental variations and results in a multivoltine life cycle. In this life cycle, one or more generations in which few individuals enter diapause alternate with a generation in which all or nearly all the individuals enter diapause. But in a particular environment (usually near the limit of geographic distribution of a species), facultative diapause may result in a virtual univoltine life cycle in which most individuals in every generation enter diapause.

According to physiological and ecological mechanisms of its incidence and termination, diapause can be classified into three types: parapause (an obligatory hereditary arrest of development or activity arising in every generation at a species specific instar), oligopause (an arrest of development or activity with control of its induction, maintenance and termination,

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similar for all these periods) and eudiapause (a facultative arrest of development or activity with different controlling mechanisms of induction and termination, e.g., through photoperiod and chilling, respectively) [4].

Diapause is not a physiological process; rather it is brought about by token stimuli that presage a change in the environment. It is highly important in temperate zone insects that overwinter. Most of the insects enter diapause at a single species-specific stage in their life cycle. Usually, diapause occurs in that stage of the life cycle which is highly adapted to resist the hardness of the climate. Below the definitions, intensity and incidence of diapause along with different phases of diapauses, theories of diapause, factors affecting diapause, diapause termination and genetic control of diapause have been detailed.

## 2. Definitions of Diapause

Many definitions of diapause have been proposed by scientists and some of them are given below: “a stage in the development of certain animals, during which morphological growth and development are suspended or greatly decelerated” [1]. According to Beck [5], “state of arrested development in which the arrest is enforced by a physiological mechanism rather than by concurrently unfavorable environmental conditions”. Although diapause is not maintained directly by environmental factors, but it is induced, and also terminated in many species, in response to environmental stimuli. Tauber et al. [6] mentioned that “diapause is hormonally mediated state of low metabolic activity associated with reduced morphogenesis, increased resistance to environmental extremes and altered or reduced behavioral activity”. Tauber [7], again defined this term as “diapause is a neurohormonally mediated, dynamic state of low activity that occurs during a genetically determined stage(s) of metamorphosis, usually in response to environmental stimuli that precede unfavorable conditions”. Definitions of diapause have been framed

in various ways from the basic ideas of processes including delayed response to growth, interference with development indirectly due to environmental factors and prolonged arrest of development, growth or reproduction, etc..

## 3. Incidence of Diapause

Diapause may occur in any stage of the life cycle of insects, such as eggs, larvae, pupae or adults. The stage at which diapause occurs is highly characteristic for each species. Moreover, there is no case known in which diapause occurs in more than one stage in the same life cycle. At the egg stage, it may begin when the embryo is still very young (e.g., *Gryllulus*, *Austroicetes*); when embryo is half-grown (e.g., differential grasshopper, *Melanoplus difflerentialis*); or when embryo is fully grown and apparently almost ready to hatch (e.g., red-legged grasshopper, forest tent caterpillar). In nymphs and larvae, diapause may occur more often in the last instar than other instars. The incidence of diapause may be quite variable, not only from species to species, but also between different populations of the same species.

## 4. Intensity of Diapause

Diapause is also immensely variable in its intensity; duration of diapause can be taken as a measure of intensity. Diapause lasts for 9-10 months in the temperate zones, and may persist for a year or more in less common cases. During diapause, most insects do not feed at all or, in the case of some larvae and adults, feed very little. This indicates that the insect must sequester sufficient food reserves in the pre-diapause phase to meet its metabolic needs during diapause and still have sufficient reserves remaining at the end of diapause to complete development and resume activity [8].

Diapause lasting more than a year is known as prolonged or extended diapause [9], and has been documented in 64 insect species. For example, yucca moth (*Prodoxus y-inversus*) adults emerge after 19

years of diapause as prepupae [10]. Another example, where larvae had been in soil up to three years followed by emergence of wheat-blossom midges (*Cantarinia tritici* Kirby), whereas larvae of wheat blossom midge (*Sitodiplosis mosellana*) overwintered for 12 years in the soil before adult emergence [11]. In some sawflies, diapause stage lasts for 3-4 years. Extra-long diapause may be achieved either by entering diapause exceptionally early (premature diapause) or by completing diapause exceptionally late (prolonged diapause). In both the cases, induction of diapause may be density-dependent or density-independent [12]. The physiological mechanisms of prolonged diapause are still incompetently understood [7].

## 5. Phases/Stages of Diapause

Insect diapause is a dynamic process consisting of several successive phases. In the literature, the conception and naming of diapause phases are ambiguous and unsettled. The phases of diapause were distinguished by Košťál [13]. The definitions of different phases are given below as suggested by Košťál (Fig. 1) [13].

### 5.1 Pre-diapause Phase

#### 5.1.1 Induction Phase

“Induction phase occurs during genotype specific ontogenetic stage(s) (sensitive period) when cues from the environment are perceived and transduced into switching the ontogenetic pathway from direct development to diapause when the token stimuli reach some critical level (the response may be modified by other environmental factors).”

#### 5.1.2 Preparation Phase

“Preparation phase occurs where the phases of diapause induction and initiation are separated by a period of direct development, during which the individual is covertly programmed for later expression of diapause. Behavioral and physiological preparations for diapause may take place.” Changes taking place

during this phase are food storage, behavioral changes and some changes in rate of development.

### 5.2 Diapause Phase

#### 5.2.1 Initiation Phase

“Direct development (morphogenesis) ceases, which is usually followed by regulated metabolic suppression. Mobile diapause stages may continue accepting food, building of energy reserves and seeking suitable microhabitat. Physiological preparations for the period of adversity may take place and intensity of diapause may increase.”

#### 5.2.2 Maintenance Phase

“Endogenous developmental arrest persists while the environmental conditions are favorable for direct development. Specific token stimuli may help to maintain diapause (prevent its termination). Metabolic rate is relatively low and constant. Unknown physiological process leads to more or less gradual decrease of diapause intensity and increase of sensitivity to diapause terminating conditions.”

#### 5.2.3 Termination Phase

“Specific changes in environmental conditions stimulate (accelerate or resume) the decrease of diapause intensity to its minimum level and thus synchronize individuals within a population. By the end of the termination phase, a physiological state is reached, in which direct development may overtly resume (if the conditions are favorable) or covert potentiality for direct development is restored but not realized (if the conditions are not favorable).”

### 5.3 Post-diapause Phase

“During Post-diapause quiescence, inhibition of development and metabolism was exogenously imposed, which follows the termination of diapause when conditions are not favorable for resumption of direct development.” It implies reorganization prior to full activity.

Insect diapause is centrally mediated at specific developmental stages, either in response to key stimuli

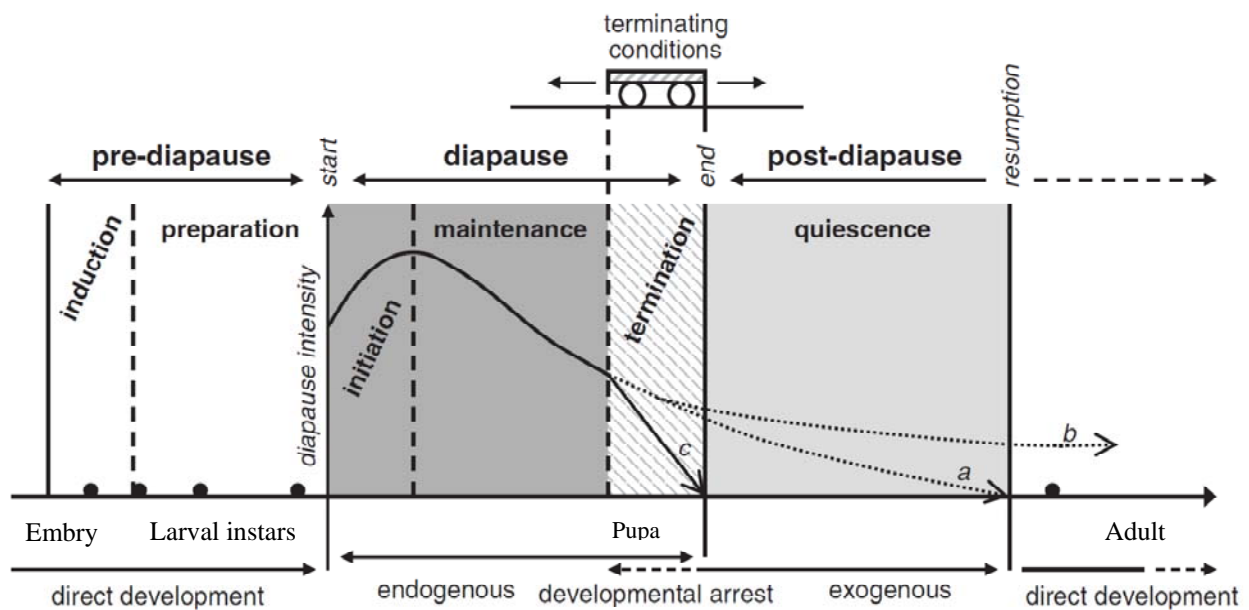


Fig. 1 Different phases of diapause reproduced from Ref. [13].

from environment (facultative diapause) or as a fixed component of ontogeny (origin and development of an individual organism from embryo to adult) (obligatory diapause). The maintenance of diapause itself is a physiologically dynamic and it changes over time in response to internal stimuli and environment [14].

### 6. Diapause vs. Quiescence

Dormancy is a generic term for any state of naturally occurring ecological or evolutionary adaptations of arrested development, and usually accompanied with metabolic suppression. Diapause and quiescence form two different types of dormancies in insects. In general, insects commonly confront two types of major environmental stresses. The first category includes unpredictable, irregular, temporary and localized stresses epitomized by short periods of seasonally high or low temperatures, food scarcity and drought. In this case, survival depends on appropriate and immediate response by insect. This type of response leads to quiescence or migration to favorable places. The second category of stress includes regularly occurring, seasonal fluctuations in temperature, humidity, food, natural enemies and other competitors over a wide geographic area. This

stress is kind of predictable pressure occurring in some specific pattern and insects take advantage of this predictability by responding through physiological and behavioral alterations for the forthcoming changes. These types of changes constitute diapause.

Diapause is quite distinct from quiescence, but at times it may be difficult to distinguish the two phenomena. Quiescence is common seasonal (phenological), long duration adaptation in the life cycles of many insects. Unlike diapause, quiescence is directly induced and terminated by surrounding environmental conditions, for example, low temperatures induce and high temperatures terminate the quiescence stage of insects. Extrinsic factors are involved in the onset and termination of quiescence, and these factors act directly on metabolic rate and that eventually results in either slow down or complete arrest of development. In univoltine species, normally only one stage of the life cycle enter quiescence with the onset of winter. On the other hand, in multivoltine species (e.g., blowfly in New Zealand), each life stage has a capability to survive in quiescence. Unlike quiescence, diapause is defined as a dormancy state with the characteristics including:

(1) Diapause is a seasonally specific adaptation, which persists for a certain minimum period of time, regardless of environmental fluctuations;

(2) Day length (photoperiod) and temperature have been reported to be involved in the timing and induction process of diapause;

(3) It occurs in only one species-specific stage in the life cycle of insects.

Diapause is not induced in direct response to unfavorable environmental conditions. It is “anticipatory”, which means that diapause occurs before the onset of winter while conditions still permit growth and development.

Above given postulates clearly demonstrate that in diapausing insect, an internally operating “clock” mechanism is involved, which can measure day length and hence the season can be discriminated. In addition to the above given facts, it can also be said that diapause is under complex hormonal control, whereas quiescence is a function of temperature acting on the metabolic rates. These points are helpful to some extent for distinguishing these two dormancy states [15].

## 7. Theories of Diapause

Many theories are out there to explain the process of diapause. There are different hypotheses for theories of diapause including hormone theory of diapause, ecological consequences of hormone theory, the stimulus which activates the neuro-secretory cells in species without diapause, evidence from ecology for the “food mobilization” hypothesis and the food mobilization hypothesis as discussed below.

### 7.1 Hormone Theory

#### 7.1.1 Hormone Theory of Diapause

Many hypotheses have been put forward in explanation of hormonal theory of diapause. According to the first hypothesis, accumulation of an inhibiting substance results in diapause and *vice-versa*. The inhibitors have been postulated as accumulated

waste products of metabolism causing auto-intoxication or “asthenobiosis” or “diapause factor”. According to the second hypothesis, deficiency of water in tissues is attributed to diapause stage. It was also found that diapausing organisms were heavier than those not entering diapause. The amount of water content tends to increase during post-diapause phase. This hypothesis explains that reduction in water content of tissues is so characteristic of insects in diapause that it is more likely to be an “effect” rather than a “cause”. The third hypothesis attributes diapause to the absence of a particular growth promoting hormone. The hormone theory is mainly concerned with the final stages of diapause. No explanation is available for how the neuro-secretory cells of diapausing individuals come to remain dormant while those of their non-diapausing counterparts are active; nor what ultimately causes the diapausing individuals to secrete the hormone.

#### 7.1.2 Ecological Consequences of Hormone Theory

In both obligate and facultative diapause, the pivotal physiological cause of diapause is the inactivity of the neuro-secretory cells. In diapausing individuals, the failure to produce hormone may be related to temperature, light, food and other diverse components of environment. The ultimate production of hormone may result from exposure (often prolonged exposure) to low temperature, light, etc..

#### 7.1.3 The Stimulus Which Activates the Neuro-Secretory Cells in Species without Diapause

Organisms which enter diapause usually consume more food than non-diapausing organisms. In non-diapausing organisms, the accumulation of a minimum amount of food may be a prerequisite for the completion of certain metabolic processes, which ultimately result in activation of the neuro-secretory cells. For example, the neuro-secretory cells in *Rhodnius* spp., are stimulated by one large meal not by two smaller ones [16]. It is well known that the food, which is being built up into reserves in the fat body and other tissues, is also concurrently in the

process of being broken down. These observations suggested that the neuro-secretory cells may be stimulated only after breaking down processes having reached a threshold value.

### 7.2 *The Food Mobilization Hypothesis*

The diapause is essentially the same phenomenon in whatever stage of the life cycle it may occur. This is imagined as the “clock”, which sets the production of the molting hormone at the critical time. In non-diapausing organisms, the mechanism is invoked automatically after a certain prerequisite amount of food has been ingested and metabolized. However in diapausing organisms, the mechanism fails due to the fact that the food that has been laid down in the fat body (or yolk) is unmanageable. It may be used only after an adequate exposure to low temperature, or in response to stimulus from environment.

### 7.3 “*Food Mobilization*” Hypothesis—Evidences from Ecology

#### 7.3.1 Quality of Food Ingested

The most evidences for this hypothesis come from the examples given below, where diapause is determined by the quality of the food ingested by the growing larva. For example, the larva of *Trichogramma* feeding on the yolk of the diapausing egg of *Cacaecia* (which contains only a very early-stage embryo) grows to maturity without prolonged delay, but fails to produce molting hormone which would induce pupation until after the winter. In other experiment, when same larva feeding on the contents of an egg from the same egg-mass which has already passed through a winter pupates without delay. It concludes that the growth of the *Cacaecia* embryo and the metamorphosis of the *Trichogramma* larva are both held up by the same intractable food supply, which in the latter case has been merely accumulated by the larva, but not adequately modified in the process. During exposure to low temperature, essentially, the same changes are required to render

this material available whether it is still egg-yolk or larval fat-body.

The linking of an embryonic diapause in one species with a larval diapause in another through a common food supply provides stronger evidence for the “food hypothesis” than cases in which only one species is concerned. But in these cases also, the larva grows either to maturity or to the end of a specific larval instar without prolonged delay on either type of food, but those reared on the poorer diet fail to produce the molting hormone except after a prolonged period of diapause development. But those reared on the more adequate diet complete development without interruption, the secretion of the molting hormone being stimulated without delay when the appropriate stage of the life cycle is reached.

#### 7.3.2 Correlation between Slow Growth and Diapause

Food, temperature and other components of the environment may be identical for all members of a population. But for those insects who are intended to go for diapause grow more slowly (often attaining a greater weight) than those who do not enter diapause. The correlation between diapause and slower growth seems to hold strong, irrespective of whether diapause has been determined by photoperiod (*Cydia*, *Lapeyresia*), genetic constitution (*Pyrausta*), maternal physiology (*Spalangia*) or other causes. This indicates a consistent difference between the diapausing and non-diapausing individuals with respect to food metabolism and building up of food reserves.

#### 7.3.3 Visible Differences in Fat Body or Egg Yolk

During the process of diapause, a sequence of striking changes occurs in the appearance of egg yolk. Appearance of fat body in diapausing and non-diapausing insects was found quite evident in beet webworm moth (*Loxostege* spp.). The fat body is generally creamy, fluid and without definite structure in the fifth instar larvae destined for diapause. However, the non-diapausing larval fat body is spherical bead-like substance of deep yellow to orange

color. Diapausing larvae are also heavier and drier containing on the average 0.038 g of dry matter and 38% of water compared to the non-diapausing larvae, which contains 0.020 g of dry matter and 72% of water. Higher protein content was found in diapausing larvae as 54% of the total dry matter compared with 22% in non-diapausing larvae [17].

#### 7.3.4 Delayed Manifestations of Diapause

In many species, diapause is also determined by “maternal physiology”. For example, in wasp (*Spalangia* spp.), diapause becomes obvious at the fifth larval instar, but it is determined in the females of the preceding generation while they are still larvae. The tendency towards diapause is transmitted to the next generation not in the genes but solely in the cytoplasmic contents of the egg. During development, the temperature experienced by the larval female influences the content of the cytoplasmic material (yolk cytoplasm associated enzymes), which she ultimately builds into the eggs that she lays. This helps in determining whether or not at the fifth instar the neuro-secretory cells will be stimulated to produce the molting hormone immediately or only after a prolonged period of diapause development at low temperature.

In insects, where diapause appears in the final larval instar after having been determined at an earlier stage, it is clear that whatever the mechanism, which results in the inactivity of the neuro-secretory cells at the critical stage, it has not interfered with the normal functioning of these organs during intermediate larval molts.

#### 7.3.5 Life Cycles of Internal Parasites in Multivoltine Hosts

It is usual to find the life cycles of parasitic Hymenoptera and Diptera synchronized with the life cycle of a multivoltine host. Many studies were done in past, but very little is known whether the parasite resumes activity before or after the secretion of the molting hormone by the host. If the parasite resumes activity before the molting hormone is secreted, then this clearly indicates that (1) changes sufficient to act

as a stimulus to the parasite occur in the tissues of the host in advance of the activation of the neuro-secretory cells; and (2) these changes are similar in species or strains of diapausing and non-diapausing generations.

## 8. Seasonal Changes: How Diapause Can Control Dormancy, Migration and Polyphenism

### 8.1 Dormancy

Dormancy is generally referred to as seasonally recurring period of suppressed growth, development and reproduction in the life of a plant or an animal. This suppressed period, which involves diapause, quiescence or both, provided the occurrence is regular on seasonal basis (as discussed earlier). Dormancy can be aestivation (summer), autumnal dormancy (fall), hibernation (winter) and vernal dormancy (spring) based on season in which it is occurring. Diapause occurs in response to token environmental cues, which is also called token stimuli. Token stimuli themselves do not directly affect growth and development, but act as messengers for changes in environment. Photoperiod, temperature, moisture and biotic factors act as token stimuli for seasonal changes (discussed in details in factors section). These stimuli are often perceived during stages preceding diapause rather than the diapause stage itself. Diapause is a suppressed stage of growth, development and reproduction even if conditions become favorable. Not all species undergo dormancy. Tropical cotton stainer (*Dysdercus* spp.) insects and large milkweed bug (*Oncopeltus* spp.) grow and reproduce all year round [18] and on arrival of unfavorable conditions, like scarcity of food or other requisites, these species shift to alternate food or migrate to new places and start normal growth and reproduction. During diapause, the expression of development may vary between species. Insects stop feeding and growth during diapause, but diapausing embryos (*Aulocara elliotti*)

may go through morphometric development [19].

### 8.2 Migration

Migration of free living insects from site of reproduction to another site to undergo dormancy is sometimes considered as diapause mediated seasonal migration. Depending upon species, migration may vary from few centimeters to thousands of kilometers. These movements occur in response to token stimuli and bring about physiological and behavioral changes [18, 20]. A typical example of seasonal migration is of monarch butterfly (*Danaus plexippus*) moving southward in most of the United States and Southern Canada [21]. Most of the southward migrating monarch butterflies in USA are in the state of reproductive diapauses, characterized by increased lipid content, undeveloped ovaries, reduced response to reproductive and vegetative stimuli and increased sensitivity to isomers of juvenile hormone [22].

Short range migration is reported in several insects that move from their reproductive sites to hiding places in nearby fields, abandoned lands and forest edges. The adult Colorado potato beetle (*Leptinotarsa decemlineata*) abandons the food plants, moves to field edge and burrows up to 25 cm in soil to hibernate. The movement of beetles during this period is guided by positive geotaxis and negative phototaxis [23].

### 8.3 Polyphenism

Diapause in insects also brings color or morphological changes to provide crypsis (ability of an organism to avoid detection by another organism) and protection against seasonal requirements [24]. These changes are referred as seasonal polyphenism. Polyphenism can be divided into two categories: seasonal and aseasonal. Seasonal polyphenism occurs in response to predictable, recurrent seasonal changes in environment. This type of response includes tightly spun cocoons versus coarsely spun cocoons, pupal cuticle with increased wax secretion, wings size, sexual versus asexual behavior, seasonal

color changes and hard versus soft egg shells. These types of polyphenism are usually induced by diapause inducing token stimuli due to environmental changes. Some of these form changes have been reported to be associated with hormonal changes [25]. Pre-diapause larvae of peach moths (*Carposina niponensis*) spin compact, tough, ball shaped cocoons as compared to coarse and elliptical cocoons of non-diapausing larvae [26]. Therefore, construction of ball shaped cocoons is highly specialized behavior associated with diapause. Similarly, small cocoons are spun by prediapausing larvae of spruce budworm (*Choristoneura* spp.) during hibernation, and these cocoons are different from those spun by non-diapausing larvae [27].

Aseasonal polyphenism is triggered by immediate, unpredictable or localized seasonal alterations in the environment. There is no long delay in growth or reproduction and the insects do not enter diapause. A typical example of this kind of polyphenism is non-diapausing summer pupae of butterfly (*Papilio polyxenes asterius*) where the color of the pupae is either green or brown depending on the substrate [28]. Similarly, sycamore aphid (*Drepanosiphum platanooides*) and lime aphid (*Eucallipterus tilliae*) show melanin pigmentation in asexual forms as a result of temperature, density, food quality and quantity [29].

## 9. Factors Affecting Diapause

There are number of environmental factors that can play a crucial role in completion of diapauses, such as temperature, photoperiod, light and water or moisture. Most studies on seasonal ecology of insects are mainly focused on temperature and photoperiod as major regulatory cues. Insect species exhibit distinctive characteristics that help them to go through diapause stage during unfavorable conditions. Sensitive period, insect stages, physiological expression and intensity are all species specific diapause inducing characteristics that are eventually



under the genetic control. Environmental factors affect expression of diapause which varies profoundly within each generation of an insect population. Based on this variation in expression, diapause is divided into two categories: facultative and obligatory (discussed earlier).

### 9.1 Photoperiod

Diapause induction is dependent on the actual number of hours of photoperiod phases and duration of scotophase (a dark phase in a cycle of light and darkness). During diapause, insects rely on photoperiod for a period of time [30], but varying temperature and other environmental factors modify photoperiodic effects on diapause. For example, European corn borer (*Ostrinia nubilalis*) is a long day insect and larval diapause is induced by naturally occurring photoperiods with scotophases of 10-14 h [5]. For more examples of diapause in insects affected by photoperiod check Table 1.

#### 9.1.1 Response Curves and Critical Photoperiod

Insects have evolved many ways to use photoperiod for regulation of diapause [31]. Insects are categorized according to the photoperiodic response (percentage) of population entering or terminating diapause under a series of stationary photoperiods. The photoperiod that induces response in 50% of the population is called critical photoperiod. For example, the photoperiodic range in lacewing (*Meleoma signoretti*) is between 15 h and 16 h of light/day for diapause induction and between 12 h and 14 h per day for diapause termination [6].

Two types of response curves have been proposed: the long day type and short day type. Long day type (Type I by Beck [31]) response is characteristic of insects that grow, develop and reproduce in long day conditions and go to diapause in short days. Short day response (Type II by Beck [31]) is less common and is shown in aestivating insects in response to long day conditions [32]. But exceptions to these generalizations occur in several species. In Chinese

tasar moth (*Antheraea pernyi*), critical photoperiod for diapause induction and termination are very similar [33]. While in other insects where natural populations were studied in field (*Meleoma signoretti* and mosquito (*Wyeomyia smithii*)), the two values of day length differed [30].

#### 9.1.2 Responses to Day Length

Limitation on the usefulness of the photoperiodic response curve is that it takes into account the stationary light-dark phases, which do not exist in nature because day length is considerably changing. Based on photoperiodic changes, insect responses can be categorized into four classes:

(1) Species where day length is not important. These species consider only the duration of day length in relation to critical photoperiod. For example, the mite, *Panonychnus ulmi* enters diapause under constant short day conditions. An increase or decrease in day length above critical photoperiods has no significant effect on diapause induction [6].

(2) Species that respond to day length across a critical photoperiod for induction or maintenance of diapause. In these species, stationary photoperiods (constant long or short days) cause reduction in incidence of diapause. However, if sensitive stage experiences decrease in day length from long to short days below critical period, diapause is induced. This type of response is called long day-short day response and is demonstrated in *Heliothis zea* [34] and red locust (*Nomadacris septemfasciata*) [35].

(3) Species that respond to day length across a critical photoperiod by averting or terminating diapause. In these species, stationary photoperiods (constant long or short days) response curve consists of an approximately straight line (100% diapause). However, if sensitive stage experiences increase in day length from short days (below the critical photoperiod) to long days below critical period, diapause is averted or terminated. This type of response is called short day-long day response. This kind of response is reported in several univoltine

insect species, including carabids, leafhopper, water strider and cricket [6].

(4) Species with response to changes in day length without a critical photoperiod. In above three categories, at least one critical photoperiod is involved for species to respond. Common green lacewing (*Chrysoperla carnea*) enters diapause, only if day length decreases abruptly. However, it is not clear whether this insect uses this ability to respond to changes in day lengths during natural diapause induction or termination [6].

#### 9.1.3 Effect of Photoperiod on Post-diapause Development

Photoperiod is known to affect pre-diapause and non-diapause development [36] and fecundity [6]. Some species are recorded with influence of photoperiod on post-diapause oviposition and re-inducing diapause after a period of oviposition [37]. Short day lengths can re-induce diapause after long period of oviposition in adult Colorado potato beetle [38] and these long lived adults can pass a second winter in diapause. Similarly, a species specific second diapause in spruce budworm (*Choristoneura* spp.) is influenced by photoperiodic conditions after completion of the first diapause [39].

## 9.2 Temperature

After photoperiod, temperature is considered as an important factor which influences dormancy in a number of ways: (1) temperature is a major diapause inducing factor in some species; (2) it can modify insects response to diapause inducing photoperiods to varying degrees; (3) in some species, it is important for diapause maintenance; (4) it can be an active stimulus in termination of diapause [5]. It plays a major role in regulating the rate of post-diapause growth (Table 2).

Hibernating insects have evolved a number of physiological and behavioral adaptations that help them tolerate extremely low temperatures. These adaptations are associated with diapause that helps

them protect from subzero temperatures. Two main physiological mechanisms which determine insect's overall tolerance to cold are: supercooling (resistance to freezing by lowering temperature of body below the freezing point of body fluids) and freezing tolerance (survival despite freezing of body fluids). Some insects have high supercooling points (poplar sawfly, *Trichiocampus populi*) which help them survive freezing at temperatures below supercooling point, while others with low supercooling points may be susceptible to subzero temperatures.

A study was conducted in the Inner Mongolian steppe, to determine the effects of six constant temperatures (15, 20, 25, 30, 35 and 40 °C) on the post-diapause embryonic development and hatching time in three grasshopper species: *Omocestus haemorrhoidalis*, *Calliptamus abbreviatus* and *Chorthippus fallax*. It was found that *O. haemorrhoidalis* adapted to hatch at a lower temperature range, *C. abbreviatus* to mid temperature range, and *C. fallax* at a higher temperature range. The results also indicated that *C. fallax* and *O. haemorrhoidalis* had a wider adaptive temperature range than *C. abbreviatus* [40]. High temperature is also reported to induce diapause in some insects during aestivation [32].

#### 9.2.1 Temperature as a Diapause Terminating Stimulus

It is apparent that temperature regulates rate of diapause development and is not a specific signal to terminate diapause. Although termination of diapause in laboratory is facilitated by low temperatures, as in giant silk moth (*Hyalophora cercopia*) [41], it is not necessary that "chilling" is a triggering signal in diapause termination. One well-studied example of high temperature termination is recorded in egg diapause of cricket (*Teleogryllus commodus*). In this case, egg diapause is not terminated even after long exposures (60-80 d) to cold conditions, while a brief exposure (3 d) at 20 °C or above results in termination of a second phase of diapause [42].

### 9.2.2 Effect of Temperature on Post-diapause Development

After termination of diapause, insects enter a phase of normal growth and development. At this point, when insect is given optimum nutrition, temperature is usually the primary environmental factor, which manages the rate at which the diapause characteristics (e.g., fat bodies) are lost and rate at which post-diapause growth and development occur [30]. As a result, temperature dependent thresholds and growth rates are often useful in predicting the timing of post-diapause events in field, especially in computer simulations of population trends in insect pest management programs.

### 9.2.3 Integrated Effect of Photoperiod and Temperature on Diapause

There are studies indicating integrated effects of photoperiod with temperature to induce diapauses [31]. In some insects, temperature drastically influences critical photoperiod. For example, noctuid moth (*Acronycta rumicis*) is short day diapausing insect for which critical photoperiod lengthens by 1.5 h with each 5 °C drop in rearing temperature. So the longer days are necessary to deter diapause at lower temperatures [43]. In long day insects, low temperature tends to promote diapause while high temperature tends to avert it. In muscoid fly (*Sarcophaga argyrostomata*), the critical day length is 14 h of light at 15 °C and 20 °C, whereas a rise in temperature to 25 °C produces no diapause at any photoperiod [44].

## 9.3 Moisture

Insects undergo periods of water stress during both hibernation and aestivation, as both high and subzero temperatures cause available water scarcity to the insects. Two main physiological mechanisms come into play during drought: resistance to desiccation and tolerance to water loss. For example, during aestivation, eggs of grasshopper (*Austroicetes cruciate*) showed both mechanisms. Desert species are mostly

drought hardy, but species inhabiting areas with seasonal droughts show adaptations to drought conditions mostly associated with diapause. Diapause in drought conditions needs resistance to desiccation, which comes from depressed metabolism, lowered water content, high fat accumulation during diapause and increased secretion of waxy coverings. Ground pearl (*Margarodes vitiumis*) is a significant example, where wax coated encysted nymph can survive for more than 10 years under dry conditions [45].

Impact of moisture on diapause development does not appear that simple from many studies done in the past, rather it is a complex issue to understand. Water and moisture have both positive and negative effects on diapause development. Flooding along with high humidity can endanger the development of offsprings and delay oviposition to post-rain season. Females of Mexican bruchid beetle (*Acanthoscelides obtectus*) spend April to November (wet period) in rolled dead leaves hanging from plants as in reproductive diapause phase. Due to positive effects of moisture, these beetles postpone their oviposition till mid-November to late-December, the time when rain fall is below 50 mm/month [46]. For details on examples of insects affected by moisture check Table 3.

Diapause development evidently initiates at dry conditions; however, wet conditions (rain, water or moisture) are must for restoration of development and pupation. The tropical borers are one of the most known examples of diapause termination by rains. Sorghum stem borer larvae diapause in dry stalks for 6-8 months, and pupate in spring after the onset of rain. It has been proven by series of experiments that previous exposure to drought is obligatory for the stimulatory effect of moisture. Okuda [47] also found that stimulation due to moisture is produced through drinking, rather than continuous contact with moist surface.

Both wet and dry conditions play an important role in diapause process. There are many examples (e.g.,

*Diabrotica* spp.) where complete diapause is followed by quiescence due to low moisture. Water content should be replenished to or above a critical level to resume post-diapause morphogenesis. After the temperature regulated diapause, larvae of wheat blossom midges (*Contarinia tritici* and *Sitodiplosis mosellana*) need high moisture for pupation [48]. In eggs of Australian plague locust (*Chortoicetes terminifera*), the development of “the second quiescent stage”, which is morphologically indistinguishable from diapause stage, can not start without replenishing with 10% moisture, which was lost in diapause stage [49].

#### 9.4 Food

Availability of food in nature can be an important seasonal cue for insects. Insects have evolved different ways to utilize alterations in food quality and quantity as factors governing dormancy [32]. Food has been observed as primary diapause regulating factor for insects, mostly in aestivating insects. It can be a primary diapause regulating factor or can play role in interaction with temperature and photoperiod. In two Australian species, a collembola (*Sminthurus viridis*), and a mite (*Halotydeus destructor*), the aestival diapause is influenced by food quality where maturity of host plant induces diapause [50]. In addition to aestivation, hibernating insects may also be influenced by food. Hibernating diapause is terminated in glassworm (*Chaoborus americanus*) [51] in response to prey and long day length, and in Indian meal moth (*Plodia interpunctella*) [52] in response to rice bran extract.

##### 9.4.1 Food as Modifier of Photoperiodic Responses

Food can modify photoperiodic response in insects by changing duration and incidence of diapauses [1]. Females of mite (*Panonychus ulmi*) laid diapausing eggs under favorable conditions of temperature and photoperiod only under the influence of bronzed foliage. Similarly, senescing potato leaves caused diapause in Colorado potato beetle (*L. decemlineata*) under normal long day conditions.

##### 9.4.2 Insect Density

Density may have significant effect on the diapause regulation in gregarious insects. Indian meal moth (*P. interpunctella*) has dual diapause systems: density dependent to avoid mortality under crowded conditions and density independent to avoid mortality due to seasonal variations [52]. Similar effects have been seen in planktonic crustaceans *Daphnia* spp. [53].

## 10. Evolutionary Aspects of Diapause

Species separated by geographic areas encounter a great variation in climate changes and thus leading to variation in their life cycles, like variable number of generations per year (univoltine, bivoltine, multivoltine and non diapausing strains). This phenomenon was first reported in Union of Soviet Socialist Republics (USSR) [43]. For example, in the Northern Great Plains of North America, populations of red-legged grasshopper (*Melanoplus sanguinipes*) are univoltine. Fisher [54] reported that eggs laid in the late summer and fall continues their embryonic development until diapause or cold temperatures terminate development. In alpine and high latitude environments, the growing season is short, which delays insect egg hatching sometimes up to two seasons, while areas with longer growing seasons support bivoltine insect populations [55]. Dean [56] showed that *M. sanguinipes* from Kansas produced a high proportion of non-diapausing eggs when parents were exposed to increasing photoperiods. Similarly, corn borer (*Pyrausta nubilalis*) is univoltine in northern states in U.S., while it is bivoltine or multivoltine in warmer states of Missouri and Kansas. Tobacco moth (*Ephesia*) is multivoltine in Florida and Caucasus [57] and is virtually univoltine in London [58].

Variations in intra-, continuous intra- and disjunct intra-populations are discussed below.

Phenotypic variations that help populations to adapt to unpredictable and heterogeneous environments play

an important ecological factor. During evolution, it serves as a building material for the diversification of periodic cycles of insect life and thus helps in adaptation [59]. Intra-population variations can be divided into two types: continuous intra-population and disjunct intra-population variations.

Continuous intra-population variations generally result in variability in the timing of phenological events. Variation in the timing of diapause initiation and pre-reproductive migration in milkweed bug is attributed to the genetic variability, which is maintained by seasonally fluctuating selection pressures and interbreeding between geographic populations [60]. This kind of variation sometimes results in some non-diapausing individuals or with short diapause periods as it is based on polygenic differences between individuals. Examples of this variation include non-diapausing laboratory populations of spruce budworm and gypsy moth.

In contrast to continuous variation, disjunct variation is not expressed in polymorphic system and it may lead to speciation [59]. This type of variation is expressed in populations with polymorphic expression at some stage in their seasonal cycle, such as diapause induction or termination. Most of these species live in regions of unpredictable environments, and polymorphism allows insect population to spread its risk along more than one line [32]. At unpredictable intervals (approximately 50 years) bamboo trees die synchronously after flowering due to the galls formation on bamboo buds by cecidomyid midge (*Hasegawia sasacola*). During this period of scarcity, portions of midge population go into prolonged diapause which helps maintaining population of this insect. Similarly, in spring, polymorphism occurs in predacious mosquito (*Chaoborus americanus*) in unpredictable periods of thawing and freezing [61]. During this period, larvae go into polymorphism. Early developing large and yellow morphs do well in mild spring, but exhibit high mortality if freezing periods interrupt spring.

Late developing small and pale morphs under cold climates perform well.

## 11. Ways to Prevent or Terminate Diapause

Diapause can be controlled by many ways including hormones, chemicals, wounding, alteration in chromosomes and modifications of environment factors, including moisture, temperature, photoperiod and oxygen.

### 11.1 Hormones

A hormone named 24-aa neuropeptide, also called as diapause hormone (DH) is known for regulating diapause in moths. Among members of the *Helicoverpa* complex of agricultural pests, DH prompts the termination of pupal diapause. Based on the structure of DH, several agonists were designed much more active than DH in breaking of diapause. One such agonist also been designed that when administered to larvae that are environmentally programmed for diapause prevents their entry into pupal diapause. In addition, the unique antagonist development strategy been designed by incorporating a dihydroimidazole (“Jones”) trans-Proline mimetic motif into one of the DH agonists, thereby converting the agonist into a DH antagonist that blocks the termination of diapause. These results suggest potential for using such agents or next-generation derivatives to dismay the success of overwintering in pest species [62].

### 11.2 Chemicals

In silkworm, hydrogen chloride (HCl) has been the most effective and primary method for the prevention of entry into embryonic diapauses, although another study in Japan showed dimethyl sulfoxide (DMSO) to do the same. The effect of diapause prevention was 78% with 100% DMSO concentration treatment, and the effect was comparable to that of the HCl treatment. DMSO analogs, such as dimethyl formamide (DMF) and dimethyl sulfide (DMS) did little preventive effect

against the diapause [63]. A study was carried out at Harvard University, and it was found that the diapause can be reversed in the flesh fly (*Sarcophaga crassipalpis*) by treating the third instar larvae with tropical application of juvenile hormone analogues (10 µg). Also, a 1 µg dose of cholera toxin, a stimulant of adenylate cyclase can prevent diapause in flesh fly, if the dose is injected into larvae 24 h prior to pupation [64].

### 11.3 Oxygen Level

In Japan, the effect of anoxia (a total depletion in oxygen level) on diapause development in leaf beetle (*Atrachya menetriesi*) was investigated to explain the role of oxygen in regulation of egg diapause. The effect of anoxia was temperature dependent; although anoxia alone had no effect on diapause termination, it decreased diapause intensity before chilling. Such an effect reached a maximum level when anoxia lasted for about 10 d. Diapause intensity was also reduced when anoxia was applied in pre-diapause stage. On the other hand, anoxia terminated diapause when the diapause intensity had been lowered by sufficient duration of chilling (50 d at 7.5 °C) [65].

### 11.4 Chromosomes Number

In UK, a study carried out in populations of the grasshopper (*Myrmeleotettix maculatus*) that were polymorphic (two or more clearly different phenotypes exist in the same population of a species called polymorphism) for the presence of B chromosomes. It was found that grasshoppers with two or more B chromosomes took longer time to develop from egg diapause to adult than those with one or no B chromosome [66].

### 11.5 Wounding

In addition to the above given examples, diapause can also be terminated by modifying factors, including temperature, photoperiod, day length and moisture (discussed in factors section). A number of examples

were cited in literature mentioning termination of diapause by wounding. This phenomenon is usually associated with relatively weak or indefinite diapause. The mobilization of the food reserves, which activates the neuro-secretory cells, is essentially a breaking down of the food laden tissues of the fat body and other tissues. Wounding, which involves the destruction of a small amount of tissue, might be expected to produce in small quantities similar substances to those which are associated in larger quantities with the larger destruction of tissues which precedes metamorphosis. It is significant that wounding is rarely effective with those species in which diapause would be classed as firm [1].

## 12. Genetic Control of Diapause

Understanding genetic basis for diapause is not simple [6] due to a wide range of factors influencing insect activities. For example, in cricket (*Allonemobius fasciatus*), variations can sometimes produce more than one pattern of voltinism within a population [67]. Diapause occurrence has been found to be heritable in several arthropods [68]. Following three types of genetic mechanisms can help understanding genetic control of diapause:

### 12.1 Polygenic Inheritance

Hybridization and speciation give substantial evidence for polygenic inheritance. The general characteristics for this inheritance are quantitative: length of critical photoperiod, duration of diapause and percentage population diapausing [69]. Wing dimorphism and diapause occurrence have been studied abundantly in insects [18, 70]. These two traits have a polygenic basis, making them relevant to the study of quantitative inheritance in nature. In insects like Knot grass (*Acronicta rumicis*) and white satin moth (*Leucoma salicis*) [43], tobacco hornworm (*Menduca sexta*) [71] and crab spider (*Philodromus dispar*) [72], polygenic inheritance related diapause appears to be sex linked.

### 12.2 Supergenic Inheritance

Polygenes controlling diapause in some insects appears to be closely linked. Such kinds of genes are called supergenes. Continuous latitudinal cline in photoperiodic responses in *Drosophila littoralis* is observed, but the elements controlling response to critical day length are segregated as single, autosomal Mendelian units. Allelic variation within the unit is sufficient to form a continuous cline in photoperiodic

reaction [73].

### 12.3 Mendelian Inheritance

Two sibling species of green lacewing (*Chrysopa* spp.) have demonstrated Mendelian inheritance of diapause [74]. This is the result of differences at two autosomal loci which leads to gross differences in seasonal characteristics of two species, that is, univoltine versus multivoltine life cycles.

**Table 1 Photoperiod plays a crucial role during diapause process in insect species.**

Insect	Order: family	Diapause induction	Country	Reference
<b>Egg stage</b>				
<i>Ochlerotatus campestris</i>	Diptera: Culicidae	Short day (< 14 h), 23 °C	Canada	[75]
<b>Larvae stage</b>				
<i>Chrysopa phyllochroma</i>	Neuroptera: Chrysopidae	Short day, induction incidence decreased from 25 °C to 30 °C	Russia	[76]
<i>Dendrolimus tabulaeformis</i>	Lepidoptera: Lasiocampidae	Short day, no difference at 24 °C and 28 °C	China	[77]
<i>Contarinia nasturtii</i>	Diptera: Cecidomyiidae	Short day (L:D = 10:14) at 12.8-16 °C	Canada	[78]
<b>Pupa stage</b>				
<i>Thyrassia penangae</i>	Lepidoptera: Zygaenidae	Long day (L:D = 15:9)	China	[79]
<i>Mamestra brassicae</i>	Lepidoptera: Noctuidae	Need alternate light and dark cycles regardless of length of photoperiod at 20 °C and 25 °C	Japan	[80]
<b>Adult stage</b>				
<i>Riptortus pedestris</i>	Heteroptera: Alydidae	Short day conditions	Japan	[81]
<i>Riptortus clavatus</i>	Heteroptera: Alydidae	Short day, critical daylength 13.5 h	Japan	[82]
<i>Dyscerus hylobioides</i>	Coleoptera: Curculionidae	Short day (L:D = 13:11 or L:D = 12:12) conditions required	Japan	[83]
<i>Drosophila auraria</i> complex	Diptera: Drosophilidae	Long day conditions, 15 °C	Japan	[84]
<i>Pissodes strobe</i>	Coleoptera: Curculionidae	Short day conditions (L:D = 8:16)	Canada	[85]

L:D = light:dark.

**Table 2 Temperature plays a crucial role during diapause process in insect species.**

Insect	Order: family	Diapause induction	Country	Reference
<b>Egg stage</b>				
<i>Scymnus camptodromus</i>	Coleoptera: Coccinellidae	15-20 °C, no effect of photoperiod	USA	[86]
<i>Bombyx mori</i>	Lepidoptera: Bombycidae	1-5 °C for even up to 400 d	Japan	[87]
<i>Locusta migratoria</i>	Orthoptera: Acrididae	25-30 °C, optimum 10 °C	Japan	[88]
<i>Aulocara ellioti</i>	Orthoptera: Acrididae	0-18 °C, optimum 7-8 °C	USA	[89]
<i>Tortix viridana</i>	Lepidoptera: Tortricidae	8 °C, no effect of photoperiod	France	[90]
<b>Larvae stage</b>				
<i>Chrysopa</i> spp.	Neuroptera: Chrysopidae	In thermo and cryophase temperature range of 33-24 °C and 24.5-5.5 °C; photoperiod dependent	Russia	[76]
<i>Melanoplus sanguinipes</i>	Orthoptera: Acrididae	22 °C for 30 d	USA	[91]

(Table 2 continued)

Insect	Order: family	Diapause induction	Country	Reference
<i>Chiasmia clathrata</i>	Lepidoptera: Geometridae	14 °C and low density	Finland	[92]
<i>Chymomyza costata</i>	Diptera: Drosophilidae	18 °C and short day	Czech Republic	[93]
<i>Lagria hirta</i>	Coleoptera: Tenebrionidae	5-30 °C	Germany	[94]
<i>Curculio sikkimensis</i>	Coleoptera: Curculionidae		Japan	[95]
Pupa stage				
<i>Coloradia pandora</i>	Lepidoptera: Saturniidae	5 °C	USA	[96]
<i>Delia antiqua</i>	Diptera: Anthomyiidae	24 °C, no effect of photoperiod	Japan	[97]
<i>Mamestra brassicae</i>	Lepidoptera: Noctuidae	5 °C	USA	[98]
Adult stage				
<i>Agropistes biplagiatus</i>	Coleoptera: Chrysomelidae	5 °C or 10 °C	Japan	[99]
<i>Dyscerus hylobioides</i>	Coleoptera: Curculionidae	25 °C, short day conditions required	Japan	[83]
<i>Pissodes strobe</i>	Coleoptera: Curculionidae	2 °C for four weeks	Canada	[85]

**Table 3** Moisture plays a crucial role during diapause termination process in insect species.

Insect	Order: family	Diapause termination	Country	Reference
Egg stage				
<i>Oedaleus senegalensis</i>	Orthoptera: Acrididae	1% soil moisture	Mali	[48]
<i>Stictophaula armata</i>	Orthoptera: Tettigonioidea	Water contact	Thailand	[100]
<i>Homichloda barkeri</i>	Coleoptera: Chrysomelidae	Wetting	Australia	[101]
<i>Deos flavopicta</i>	Homoptera: Cercopidae	Water contact	Brazil	[102]
Larva stage				
<i>Busseola fusca</i>	Lepidoptera: Noctuidae	Intensive rain	Republic of Cote d'Ivoire	[103]
<i>Coniesta ignefusalis</i>	Lepidoptera: Pyralidae	Continuous rain	Ghana	[104]
Pupa stage				
<i>Schausiella santarosensis</i>	Lepidoptera: Saturniidae	Rain, temperature decrease	Costa Rica	[105]
<i>Manduca dilucida</i>	Lepidoptera: Sphingidae	Rain	Costa Rica	[105]
Adult stage				
<i>Agabus disintegrates</i>	Coleoptera: Dytiscidae	Inundation	USA	[106]
<i>Stenotarsus rotundus</i>	Coleoptera: Endomychidae	100%	USA	[107]
<i>Zygogramma bicolorata</i>	Coleoptera: Chrysomelidae	Monsoon rains	India	[108]
<i>Diclodispa gestroil</i>	Coleoptera: Chrysomelidae	Rain	Republic of Madagascar	[109]
<i>Hypolimnas bolina</i>	Lepidoptera: Nymphalidae	Rain	Australia	[110]

### 13. Conclusions

Diapause is defined as a stage in the development of certain animals during which morphological growth and development is suspended or greatly retarded. This phenomenon is defined by many scientists in their own different ways; however the main idea remains the same. Diapause occurs at different life stages of insects, such as embryo, egg, larvae, pupae and adults. It is

quite distinct from “quiescence”, but sometimes it may be difficult to discriminate between the two phenomena. Various factors, including temperature, photoperiod, moisture, food and geographic location control the process of diapause. Different processes, such as dormancy, migration and polyphenism can be modified by diapause. Diapause termination can happen by means of chemicals, hormones, oxygen level, chromosome numbers, wounding and genetics.



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