

## 2

# Definitions, Terminology, and Classifications of Dormancy

### Introduction

This chapter outlines previous attempts to name and define the types and stages of dormancy in insects, in order to arrive at a set of terms that can be used precisely and consistently in subsequent chapters.

Two main difficulties hinder attempts to define useful terms. Firstly, the actual events in an organism's developmental programme may not always be readily visible, so that the markers used to observe development or its cessation — such as emergence, oviposition, or hormonal levels — may not fully or accurately represent the sequence of events. Secondly, classifying complex patterns of adaptation may arbitrarily subdivide phenomena that essentially are continuous, for example with respect to the “depth” of dormancy or its dependence on particular environmental signals.

Arrested development during adverse seasons, known as heterodynamic development (Roubaud 1922), hypobiosis (Keilin 1959), torpor, rest, or most commonly dormancy (especially in plants), has been noted for many years in a wide variety of organisms. Three trends are most visible in the literature on dormancy: attempts to distinguish dormancy that stems from simple environmental controls from the programmed arrest in development most commonly, and especially in arthropods, termed diapause; attempts to name the temporal substages of diapause; and attempts to classify diapause into various types.

### Definitions of dormancy

The fact that dormancies in insects were not all merely inactivity due simply to low temperatures was indicated as early as 1869 by Duclaux for the eggs of the silkworm *Bombyx mori*. Wheeler (1893) applied the term “diapause” to a particular stage at which eggs of the grasshopper *Conocephalus* (as *Xiphidium*) *ensiferum* ceased development (see Chapter 5), and this usage was widened by Henneguy (1904) to include similar “periods of arrest in ontogenetic development” in various stages of insects in general.

Shelford (1929) recognized the key difference between stoppages of development due simply to currently adverse conditions, for example temperatures that were too cold for activity, and stoppages that appeared to be “spontaneous”. The responses were called *quiescence* and *diapause* respectively, and these terms are retained here. Several other terms have been coined to emphasize the distinction between the two

Table 1. A comparison of quiescence and diapause

Name and main features	Synonyms
Quiescence	Physical rest (Ushatinskaya 1976)
Immediate response	“Konsecutive Dormanz — Quieszenz”
Environmental factors directly limit development	(excluding oligopause) (consecutive dormancy) (Müller 1965, 1970)
Arrested development concurrent with adverse conditions	Torpidity (Ushatinskaya 1957, 1976) Pseudo-diapause (Roubaud 1930, 1953) (cf. non-specific arrested development of Horak 1981)
Diapause	Physiological rest (Ushatinskaya 1976)
Programmed (delayed) response	“Spontaneous” arrest (Shelford 1929)
Environmental factors indirectly modify developmental pathways	“Prospective Dormanz” (prospective dormancy) (Müller 1965, 1970)
Suppressed development lasts longer than adverse conditions	Auto-dormancy (Flanders 1944) Diapause vrai (Roubaud 1930, 1953) (cf. seasonal arrested development of Horak 1981)

types of response (see Table 1).

Definitions of diapause have been framed in various ways from these basic ideas. Most recent definitions emphasize that the response is programmed rather than direct, and that diapause (unlike quiescence) is thus centrally or “physiologically” controlled: for example, diapause is “a programmed arrest of growth, development, or reproduction, resulting in reduction of active physiological functions” (Sláma *et al.* 1974, p. 14); “a state of arrested development in which the arrest is forced by a physiological mechanism rather than by unfavourable environmental conditions” (Beck 1962). Subsequently, because “development” of a different sort goes on during diapause itself (see below), Beck (1968) modified his definition to refer to “suppressed” rather than arrested development.

A few authors have tried to narrow the meaning of diapause; for example, Shroyer and Craig (1980) confined use of this term to photoperiodically-induced delays in hatching of the eggs of *Aedes* mosquitoes, terming other hatching delays “latency”. Again, Philogène (1983) urged that the term diapause be limited to those organisms with an arrest in development characterized by “the intervention of photoperiod and temperature, the two principal factors which release an anticipated physiological regulation” and by “hormonal changes, which vary according to the stage thus interrupted in its development”. Tauber *et al.* (1984, 1986) chose to restrict the term to its physiological meaning. “A neurohormonally mediated, dynamic state of low metabolic activity” was included in their long definition (1986, p. 21). This restriction led to the new compound term “diapause-mediated dormancy” that was intended to contrast with diapause-mediated seasonal migration and seasonal polyphenism, and with nondiapause dormancy, etc. This restriction and proliferation of terms, which reverses long usage, is not adopted here. In particular, the degree of coupling between diapause and migration, phenism and other traits (as well as their “seasonal” components) varies widely, creating difficulties in assigning many cases (for example, migration in locusts and aphids, colour changes in some Lepidoptera, some forms

of seasonal synchronization without diapause) to one of the seasonal or aseasonal categories elaborated by Tauber *et al.* (1986).

“Classic” diapause responses prevent growth and development. However, cases have been discovered in which responses that are likewise programmed indirectly by the conditions experienced do not result simply in a complete and straightforward stoppage of activity. In some species, development continues, but its *rate* may be altered — often considerably — by cues such as photoperiod. Such responses are considered in Chapter 10. In other cases, growth continues, but *development* does not. For instance, larvae of *Wyeomyia smithii* continue to grow even though pupation is prevented (Bradshaw and Lounibos 1972) although these active-dormant larvae usually consume little food (e.g. Evans and Brust 1972). Other larvae remain active and may feed while “dormant” (e.g. Katiyar and Long 1961 for *Diatraea saccharalis*; Corbet 1956a for *Anax imperator*; Cobben 1967 (p. 292) for *Chiloxanthus pilosus*; Kisimoto 1959a for *Nephotettix cincticeps*; Wright and Venard 1971 for *Aedes triseriatus*; Sims and Munstermann 1983 for *A. geniculatus*; Fischer 1974, Ineichen *et al.* 1979 for *Chironomus plumosus*; Neumann and Krüger 1985 for *Clunio marinus*; Furunishi and Masaki 1983 for *Hagenomyia micans*; Oku 1984 for *Xestia c-nigrum*; Boyne and Rock 1985 for *Platynota idaeusalis*). As in “classic” diapause, these dormancies may be prolonged, presumably because they require specific conditions to end, or they may end “spontaneously” after shorter intervals. In such cases, metamorphosis is merely delayed. Philogène and Hammond (1984) and Roe *et al.* (1984, 1985) emphasized the distinction between the “diapause” of *Diatraea grandiosella*, which does not feed during dormancy, and the “delayed metamorphosis” of *D. saccharalis*, which does.

Delayed metamorphosis may result in observable morphological changes even though development to the next instar is prevented (e.g. Jenner and McCrary 1964 for *Toxorhynchites rutilus*). Some species continue to moult — within one life stage — during delayed development of this type (e.g. Usua 1970 for *Busseola fusca*; Burges 1962b for *Trogoderma granarium*), and may even add extra larval instars beyond the number typical for the species (e.g. Oku 1984).

In other cases, some form of activity continues, with or without feeding. Several tropical species take up water during diapause, as noted by Denlinger (1985, p. 251). Adults quite commonly are active during (reproductive) diapause. In a few cases, too, reproductive activity may be reduced rather than eliminated by token stimuli. Thus photoperiods of a length intermediate between those that allow and those that prevent reproductive diapause in males of the grasshopper *Oedipoda miniata* produce a low level of mating activity and an intermediate reproductive state (Pener and Orshan 1980, 1983).

These cases of arrested development thus range from total stoppages in activity to suppressed development with less extensive effects on growth (or reproduction) within a stage. This suggests that a wider definition of diapause that does not require growth arrests, but only definitive suppression of development, is most appropriate.

In summary, then, *dormancy* is a state of suppressed development, which is either: *quiescence*, an immediate direct response to a limiting factor, such as cessation of development if temperatures fall below the developmental threshold but immediate resumption of development if they rise above it; or *diapause*, a more profound interruption that routes the metabolic programme of the organism away from direct

developmental pathways and into a much more clearly organized break in development that is not controlled simply by the direct action of environmental factors, and which in nature precedes the advent of adverse conditions.

### Stages of diapause

Diapause, as just defined, has attracted the most attention in investigations of the control of seasonal development (cf. Fig. 1). Many authors have described the stages of diapause, as summarized in Table 2. The first column of the Table shows the terminology that is preferred here.

In classical cases of diapause ("eudiapause" or "teleodiapause" of authors), the programming for diapause during pre-diapause development includes (see Table 2) *induction* by internal and external factors acting on the *sensitive stage* of the life cycle, and *preparation* for the dormant period, for example by the accumulation of food reserves.

Table 2. Summary of the stages of diapause, and some terms used by various authors

Stage and manifestation	Synonyms
Pre-diapause development	
Preparation (food storage, behavioural changes, some changes in rate of development, etc.)	Preparatory phase (Mansingh 1971) Prediapause period (Tauber <i>et al.</i> 1986)
Induction [sensitive stage] (diapause programmed endogenously (incl. "obligate") or by exogenous factors (cues))	Part of diapause induction period (Tauber <i>et al.</i> 1986)
Diapause	
Entry [responsive stage]	Onset, initiation, beginning, start; part of diapause induction period, and diapause intensification (Tauber <i>et al.</i> 1986)
Diapause development (endogenous and/or cued development that restores ability to respond to permissive conditions)	Physiogenesis (Andrewartha 1952, Tauber and Tauber 1973 <i>b</i> ) Conditioning (Morden and Waldbauer 1980, Waldbauer 1978, Waldbauer and Sternburg 1978) Restoration period (e.g. Ushatinskaya 1976) Diapause development (Andrewartha 1952, Lees 1955, Tauber and Tauber 1976 <i>c</i> ) Refractory period (Mansingh 1971) Endogenous phase (Dobrinjević 1980) Acquisition of competence (Williams 1956) Évolution de la diapause (Thanh-Xuan 1975) Maturation (Agrell 1951 <i>b</i> ) Diapause processes (Zolotarev 1947, 1950 <i>a, b</i> ) Diapause-ending processes (Schneiderman and Horwitz 1958) Latent development (Agrell 1951 <i>b</i> ) Reactivation (Danilevsky 1965) (Re)activation process (Mansingh 1971) Breaking diapause [Diapause maintenance period (Tauber <i>et al.</i> 1986)]

Table 2. (concluded)

Stage and manifestation	Synonyms
End of diapause development (competence to resume activity if conditions are permissive)	Termination (Tauber and Tauber 1973 <i>b</i> , 1976 <i>c</i> ) Completion (Hodek 1964) Quiescent phase (Dobrinjević 1980) Termination or termination-phase of some authors (e.g. Hinton 1957, Mansingh 1971, Waldbauer and Sternburg 1973) Diapause broken Post-diapause transitional period — quiescence (Tauber <i>et al.</i> 1986)
Post-diapause development (reorganizations prior to full activity)	Morphogenesis (Andrewartha 1952, Tauber and Tauber 1973 <i>b</i> , 1976 <i>c</i> ) Reactivation included here by some authors Growth development (Andrewartha 1952) (see Read 1968) Post-diapause transitional period — morphogenesis (Tauber <i>et al.</i> 1986)
Completion (activity resumes)	“Reactivated” of Way 1962
Non-diapause development (uninterrupted development)	Continuous development

Individuals that enter diapause at the *responsive stage* of the life cycle will not respond immediately to conditions that normally allow growth and development; a period of *diapause development* must first take place, which restores developmental potentiality. In some species, characteristics of diapause, such as colour or low respiration rate, initially become more marked (“intensification” of Tauber *et al.* 1984, 1986), in accordance with an increase in the intensity of diapause. The period of diapause development has been given many alternative names (see Table 2). After this, the insect is “activated”, or diapause is “broken” (Beck 1980, p. 135, objects to these terms because the insect in diapause is not physiologically inactive) and development will recommence whenever suitable conditions return.

Although some authors have used the term (diapause-)termination for the *end of diapause development*, it is probably best to avoid this term because several other authors have equated termination with diapause development, or with the actual resumption of development, rather than the readiness to resume development. At least in nature, that readiness greatly precedes the return of permissive conditions for most species (see Chapter 8).

Before non-diapause metabolism and activity begin, there may be a period of metabolic changes (*post-diapause development*) that act as a transition between the diapause and non-diapause condition. Usually, this lasts for only a short time (e.g. 3 days in embryos of the cricket *Gryllus pennsylvanicus*: Rakshpal 1962*c*). Non-diapause and post-diapause states are therefore not equivalent (cf. Norris 1964, p. 59).

Most observations of development record simply the resumption of normal activity, without reference to any stages during diapause. The neutral term “*completion*” is

used for the return to normal activity, though Hodek (1964), Hodek and Honěk (1976), Collier and Finch (1983*a*), and others have used that term in passing as a synonym of the end of diapause development. Tauber *et al.* (1986, p. 61) defined criteria for the end of the post-diapause period.

In addition to the different meanings for “termination” that have been published, some other terms have been used in slightly different ways than those established in Table 2. “Induction” has been used both for the processes resulting from reactions to cues that lead to diapause (as in Table 2), and for the beginning of diapause itself. Moreover, a perfect coincidence between induction and preparation has sometimes been assumed, although no fixed linkage between the two is implied here.

### Classifications of diapause

Notwithstanding the complexity of diapause responses, some authors have attempted to classify diapause (see Table 3).

Table 3. Summary of some schemes for classifying diapause

Author/categories	Main features	Induced by	Ended by
<b>Classifications based mainly on requirements to induce and end diapause</b>			
<i>Müller 1970</i>			
Oligopause (quiescent oligopauses, typical oligopauses, diapausal oligopauses)	Appears and ends with a delay; duration limited	Suboptimum factor	Same factor re- entering optimum range
Eudiapause	Clear induction phase	Usually photoperiod	Factors other than the inducing one
Parapause (thermal parapause, hygric parapause, nutritive parapause, photoperiodic parapause)	No clear phase of induction	Obligatory	One, or two (double parapause), alterations in <i>one</i> environmental factor
<i>Witsack 1981</i>			
Oligopause	Appears and ends with a delay relative to conditions	Unfavourable conditions	End of unfavourable conditions
Eudiapause	Clear induction phase	Initiated by one factor	Ended by a different factor
Parapause		Normally initiated by optimal conditions	Ended by “unfavourable” conditions
Primary parapause	Prevented by exposure to unfavourable conditions		
Secondary parapause	Cannot be prevented		
Hyperpause	Obligate	Determined genetically	Determined genetically
[Superpause = high intensity diapause, included under above categories]			

Table 3. (concluded)

Author/categories	Main features
<b>Classifications based partly on seasonal constraints</b>	
<i>Mansingh 1971</i>	
Related to conditions	
Hibernation	Due to temperatures lower than optimum
Aestivation	Due to temperatures higher than optimum
Athermopause	Due to factors other than temperature
Related to depth	
Oligopause	Due to mild and long-term adversity; preparation shortly before adversity, short refractory phase
Diapause	Due to extreme and long-term adversity; preparation long before adversity, long refractory phase
Ateleodiapause	Low-intensity diapause
Teleodiapause	High-intensity diapause
<i>Ushatinskaya 1976</i>	
Aestivation	
Sleep	Daily relaxation of tension
Oligopause	Intermediate between sleep and diapause
Diapause	Deep and continuous diapause
Superpause	Diapause for more than one adverse season
Hibernation	
Sleep	
Oligopause	
Diapause	(See above)
Superpause	

One series of schemes, initiated by Müller (1965, 1970, 1976*a*, and see 1979) classifies diapause chiefly from differences in the patterns of environmental conditions that induce and end the diapause. Müller (1970) recognized quiescence (chiefly as defined above, but see below), oligopause (direct response to deteriorating conditions, but only after a delay), eudiapause (diapause induced only under certain environmental conditions, the inducing factor not the limiting one; the factor that ends diapause not the inducing one), and parapause (obligatory (developmentally fixed) diapause without environmental induction; ended by a change or changes in a single environmental factor).

Topp (1979) believed that Müller's categories formed a spectrum in the degree of response to environmental conditions, varying from quiescence (direct response) to "hyperpause" (no obvious influence of exogenous factors, even for ending the diapause). Based on a few of the species of staphylinid beetles that he studied, Topp (1979) added also the category of "allopause", in which induction was obligatory and diapause development not under environmental control — as in hyperpause — but in which successful development after physiogenesis (diapause development) required further specific outside conditions (such as short days) in addition to temperatures above the developmental limit.

Witsack (1981; and see 1985) extended Müller's scheme in three ways (see Table 3): by adding hyperpause (but not allopause), following Topp (1979), for diapause that is entirely controlled endogenously; by accepting, for any of the types of diapause

recognized, the term "superpause" as introduced by Ushatinskaya (1973, 1976) for diapause lasting more than one adverse season; and by slightly redefining parapauses and distinguishing primary and secondary parapauses within this category.

A second type of scheme was developed by Mansingh (1971), who distinguished dormancy responses in relation to the adverse conditions to which they were a response, "hibernation" (to cold), "aestivation" (to heat) and "athermopause" (to other factors). Mansingh then used the depth of dormancy as his primary orientation, distinguishing the sequence: quiescence (as defined above), oligopause (intermediate level of dormancy, including periodical feeding during the dormant period), ateleodiapause (diapause that can be terminated precociously) and teleodiapause, as involving progressively deeper dormancy and relating this to the ultimate selective force of the degree of seasonal climatic severity, expressed by latitude, geographic area, or its equivalent. Diapause itself was therefore subclassified "physiologically", on the basis of differences between the substages that he recognised (preparation, induction, refractory phase (absent in ateleodiapause), activated phase, termination phase). Yin and Chippendale (1979) adopted Mansingh's terms, and distinguished the stages in *Diatraea grandiosella* partly by "breaks" in the temporal pattern of juvenile hormone titre.

Ushatinskaya (1973, 1976) modified Mansingh's scheme by recognizing different depths of dormancy (sleep, oligopause, diapause, superpause) within each of the ecological categories "aestivation" and "hibernation" (Table 3); she believed that the distinction between ateleodiapause and teleodiapause was unjustified. Some other authors such as Falkovitch (1979) have also emphasized the association of developmental stages with particular times of year, attaching less importance to modes of reaction to external cues. Sometimes the terms "summer diapause" (Masaki 1980) and "winter diapause" have been preferred, though Masaki (1980, p. 3) was forced to exclude "tropical diapause" from summer diapause because in some tropical regions winter is the dry season. Although several authors have applied the term "hibernation" to insect diapause during winter, Philogène (1983) has pointed out that the term can properly be applied only to mammals, which are warm blooded.

Finally, some classifications have been made on a smaller scale by authors reviewing seasonal reproductive types in particular groups: for example carabid adults (Thiele 1977a) and mirid eggs (Cobben 1968) in diapause. Cobben (1968) wisely made the point that "The categories listed . . . are considered apart, without suggesting mutual relationships or progressions." Additional terms (e.g. hiemopausic, autopausic), but not additional ideas, were offered for Lepidoptera by Tilden (1976). Belozero (1973) referred to "behavioural diapause" (in ticks that would not feed aggressively) as distinct from morphogenic diapause, and such behaviour has been taken as a criterion of diapause (e.g. Wright 1971b).

Each of the different classifications just outlined has particular weaknesses, as a result of which some argument developed among proponents of particular schemes (e.g. Thiele 1973).

Classifications such as that of Mansingh (1971), based largely on north-temperate experience, interpret dormancy chiefly with respect to the broad climatic effects of latitude, suggesting that diapause has been selected most strongly (and is deeper or more intense) at higher latitudes. However, the origins of diapause may have been diverse, and abilities that now allow survival of some species during cold winters may

in fact have evolved in subtropical areas in response to drought, as Krysan *et al.* (1977) pointed out for *Diabrotica virgifera* (Chrysomelidae). Moreover, cases of diapause that are not attributable to the dominant role of seasonal climate through its effect on temperature are grouped by Mansingh in the heterogeneous category of “athermopause”.

Schemes such as those of Müller (1970) are less rigidly bound to the concept of the depth or intensity of dormancy as related to climate and geography. However, forcing diverse adaptive responses into defined categories based chiefly on how they are controlled also leaves equivocal cases. Oligopause in particular, as defined by Müller, appears to cover a wide range of different responses, including those intermediate between “diapause” and “development” in which metamorphosis is delayed but individuals continue to feed. Bährmann (1985) considered oligopauses in more detail, and even claimed to recognize trends of evolutionary development from oligopause.

Although Müller’s (1970) scheme was preliminary, he gave a diagnostic table to allow the types of diapause to be identified. As a result many authors, especially in Europe, “classified” diapauses encountered in their studies, sometimes by extrapolating rather slender results. This was not always a meaningful thing to do. For instance, some cases believed to belong to one category have been reclassified as a result of future study. The silkworm *Antheraea pernyi* was once believed to enter diapause in response to photoperiod but (like many other overwintering pupae) to depend on low temperatures for diapause development. This response to a different factor defines its arrest in development as “eudiapause” in Müller’s scheme, but in fact diapause development in this species can also be controlled by photoperiod, the same factor as for induction (Mansingh and Smallman 1967). Again, Philogène and Benjamin (1971*b*) reported that prepupae of the sawfly *Neodiprion swainei* might undergo one of two sorts of diapause, in addition to diapause for more than one year: a “short” diapause which ended independently of daylength or temperature, and a “long” diapause governed by these factors. Diapause of these two types of individuals would require different “Müllerian” definitions. Again, Hodek (1968) pointed out that different types of cues (cold treatment or long photoperiod) could end diapause in the bug *Pyrrhocoris apterus*, and these would accord in the one case with oligopause and in the other with eudiapause as defined by Müller (1965). Adults of some species respond continuously to photoperiod. Individuals kept as adults in short days enter diapause, those in long days develop eggs, and the programme can be reversed at any time by appropriate photoperiods. Such a state was called “photoperiodic quiescence” (Ferenz 1975*a*; Müller 1970; Thiele 1971, 1977*a*, etc.), but the term is inappropriate because it implies direct control by a cue that can act only indirectly (through the neurohormonal system) on the ovaries.

Unlike Mansingh (1971) who considered mainly climatically controlled dormancy, and especially overwintering, in larvae or pupae, Müller was concerned also with reproductive dormancy, including dormancy during part of the summer. Reproductive activity in insects is generally more sensitive to unsuitable conditions than is growth, and so might involve a wider variety of adaptive responses at a given latitude, especially to parameters other than climate; and although temporal programming of adult reproductive potential is an adaptive alternative to precise timing of the appearance of the reproductive stage itself, the control/response mechanisms may have been

selected in very different ways. Norris (1964), for example, noted that adult diapause in insects tends to be less firmly established than diapause in other stages, and the developmental processes respond more easily to changes in the environment.

Cases of adult diapause investigated by Müller (e.g. 1960*b*, 1976*b*) and Thiele (e.g. 1971) thus allowed recognition of the “obligatory” dormancy they termed parapauses, which requires environmental change for *development* (rather than diapause) to occur. “Obligate diapause” was also reported for eggs by Braune (1971, 1973), who tabulated yet another short classification of dormancy (1971) to accommodate his results. Thiele (e.g. 1977) believed that the strength of Müller’s (1970) scheme was that it clearly distinguished “obligatory” diapause requiring a change of conditions to end (“parapause”) from diapauses with a specific induction phase (“eudiapause”), and indeed this discovery (but not the classification as such) allows a broader understanding of the control of life cycles, because it demonstrates that either active development or stoppages in development can be specifically programmed (see Chapter 15). In other words, some programmes of development force diapause to start or continue unless special conditions are met; especially when the necessary conditions take time, the diapause has been termed obligate or obligatory. Diapause programmes that are specifically induced by outside conditions are easily observed by experiment to be “facultative”. Such a distinction between “obligate” and “facultative” diapause has not previously been perceived, although Tauber and Tauber (1981*a*) realized that obligate diapause was a catchall category including cases that had been insufficiently studied, and increasingly were revealed as facultative with more stringent laboratory tests, and they suggested that the terms be rejected. Philogène (1983, p. 307), however, took issue with this opinion, emphasizing several cases of obligatory diapause that had been adequately investigated (see Chapter 5), and stating that the ecological terms “univoltine” and “multivoltine” recommended by Tauber and Tauber (1981*a*) were not equivalent to “obligate” and “facultative” (see also Tauber *et al.* 1986, p. 112). Hodek (1981, and especially 1983) pointed out that diapause development could take place in two ways: by “ordinary” development at the standard rate as intrinsic inhibition gradually decreased — “horotelic processes”; and by development stimulated by outside influences at a faster rate — “tachytelic processes” (see Chapter 8). This is another example of the diversity of processes involved in “diapause”, and it makes the same point as the distinctions just discussed between primary programming of active development or of diapause.

The great diversity of developmental programmes, therefore, including responses that do not involve clear-cut arrests in development, greatly hinder all attempts to classify diapause. There is no single “correct” or easy classification, for “diapauses” are a series of cases in a continuum of adaptive responses to a variety of circumstances. Because classifications are static, most of them cannot discriminate between two or more possible routes to a given end product (cf. Tauber and Tauber 1978*a*).

Recognizing the complexity of response, authors such as Tauber and Tauber (1973*b*, 1976*c*) did not attempt to classify diapause but instead focussed attention on the different environmental conditions that can control it. This alternative approach to understand dormancy by elucidating the modes of proximate control may provide the necessary level of understanding more simply. From this perspective, the complexity of responses that makes classifications of dormancy difficult at the present time hopefully relies on relatively few control mechanisms.

### Introduction to other terminology

#### *Life stages of diapause*

Diapause can also be classified with respect to life stage. Arrested development within the egg is rarely a true “egg diapause”, because diapause at a very early stage of embryogenesis is unusual: *embryonic diapause* is often a better term. *Larval diapause* can be used very broadly: it is better to avoid the term nymphal diapause for larval diapause of exopterygotes, because the “nymph” of some European languages is the pupa. Little is known about substages in *pupal diapause*, but the term pupal diapause is generally satisfactory.

Because adults more often than larvae remain active during diapause, and because the key arrest in development in adults takes place in the ovaries, imaginal or *adult diapause* has commonly been called ovarian or *reproductive diapause*. This feature was emphasized by some earlier terms. “Gonotrophic dissociation”, first used by Swellengrebel (1929) for *Anopheles* mosquitoes, has been adopted for blood-feeding without egg production in mosquitoes by many subsequent authors (see the discussion of Washino 1977). Some other terms for reproductive diapause are seldom used, such as “phasic castration” (Flanders 1944), or “gonoinactivity”.

These terms were coined because of evidence from ovaries alone of a true diapause as defined above. However, direct limitation of reproductive maturity (e.g. by cold or lack of food) is reproductive quiescence, not diapause.

#### *Definitions based on experimental observations*

Several of the terms used in studies of diapause have arisen because certain experimental results are most conveniently summarized in particular ways. Two prevalent examples of this sort are briefly noted here. Many other terms relate to experiments on “biological clocks” and are treated in Chapter 12; see also the glossary provided by Saunders (1982a).

##### 1. Diapause intensity

Different individuals may require different conditions, or durations of conditions, for diapause to end. The term *diapause intensity* has been used to describe the time required under given conditions before some measure of the end of diapause is observed (usually completion such as emergence or reproduction). Animals that require a longer period under these conditions are said to have a greater intensity or depth of diapause.

Sometimes the “intensity” of diapause is difficult to recognize or define, since the amount of delay can vary so widely. Indeed, Dingle *et al.* (1980) found that in effect the variation between “diapause” and “non-diapause” in *Oncopeltus fasciatus* is continuous. Although diapause was defined in this species as a reproductive delay greater than 30 days, diapause intensity may actually vary from 0 (no diapause) to over 200 days. For further discussion of diapause intensity, see Chapter 8.

##### 2. Critical photoperiod

In typical experiments on responses to photoperiod, samples of insects are tested at different photoperiods and results expressed as the percentage of individuals that respond (diapause, develop) under given conditions.

The *critical photoperiod* (daylength, nightlength) is the photoperiod at which 50% of the individuals respond. The estimate of critical photoperiod, which in typical

laboratory experiments includes no twilight period, therefore depends on the sample size. Usually the population response is normally distributed, so that the cumulative response curve is sigmoid (e.g. Chapter 7, Fig. 16A–B). Fortunately, a small change in photoperiod normally produces a relatively rapid transition in the whole population from diapause to non-diapause, so that unless the sample is very small, sample effects introduce less error than might be expected. However, sometimes the response changes only gradually as photoperiod changes, or the response is incomplete (for example, the cumulative response curve for one group of *Pieris rapae* studied by Yata *et al.* (1979) levels out at about 60–70%; critical photoperiod was still taken as the 50% point; see also Chapter 7, Figs. 17B, etc.).

Although critical photoperiod was defined by Adkisson (1965) for *Pectinophora gossypiella* as the photoperiod at which diapause first occurs when insects are reared at successively shorter daylengths beginning with one that prevents diapause, this definition is no longer used. Adkisson's (1965) definition would emphasize extreme rather than median values, which are important in a different context. Additional terms related to the response to photoperiod and to other cues are considered in more detail in Chapter 7.

### Conclusions

Definitions and classifications of diapause have generally been deficient because they were built up piecemeal as knowledge accumulated. For example, early conceptions of diapause included no information from physiological studies, and attempts to incorporate such results led to revisions of the definition of diapause (e.g. De Wilde 1981*b*, p. 194). A more serious difficulty is that diapause is a relative conception, with various degrees (cf. Agrell 1951*b*, p. 288). Cobben (1968, p. 298) placed these degrees in perspective by recognizing that types of dormancy and their subdivisions are the manifold results of physiological, ecological and genetic adaptations, results that are therefore unlikely to fall neatly into simple discrete categories. Moreover, even arrests in growth or development that are incomplete can significantly modify life cycles; and the degree of retardation which constitutes an "arrest" in development is a value judgement made by the observer (Beck 1973, p. 897).

For all of these reasons, detailed definitions of different kinds of diapause are currently inappropriate. Existing classifications that attempt to recognize specific types of diapause are unsatisfactory, and no such terminologies are adopted in subsequent chapters. Terms that will be used here for the temporal stages of diapause are shown in the first column of Table 2.

At a general level, two deliberately broad terms within the category of dormancy are useful (see Table 1). *Quiescence* is the direct inhibition of development by adverse environmental conditions. *Diapause* includes all other cases in which morphological development is suppressed, whether or not growth ceases completely.