

# 1

## General Introduction

Conditions vary seasonally almost everywhere that insects live; and this variation is matched by a remarkable diversity of insect adaptations to control seasonal development. Especially at higher latitudes, many species pass seasonally adverse periods in a state of arrested development or dormancy. We now know that the single term “dormancy” conceals many adaptive possibilities.

This book reviews insect adaptations to seasonal events, with the aim of providing a useful conceptual framework for these adaptations. Such a framework can be provided only if the life cycle is considered from a broad ecological orientation, for such an approach yields generalizations that are not possible when particular aspects of seasonal control, such as photoperiodic responses or biological clocks, are considered alone. Although the literature on dormancy is very extensive, there has been no previous extended treatment from the perspective taken here.

### History of studies on seasonality

Seasonal activity and development of animals and plants is well known, but because development was correlated with clear seasonal changes in temperature it was long assumed to be due to that factor. In the early twentieth century several investigators began to document experimentally the fact that daylength was responsible for seasonal development in plants. Klebs (1913) was the first to realize that light could probably act on plants as a “catalytic” as well as a “nutritive” (= photosynthetic) factor; in later terminology, that it was a token stimulus or cue. Garner and Allard (1920, 1923) coined the terms photoperiod and photoperiodism, and soon investigators had discovered similar phenomena in insects (Marcovitch 1923; Sabrosky *et al.* 1933; Kogure 1933; cf. Müller 1960*a*) and birds (Rowan 1926), and later in other vertebrates and invertebrates as well as in algae, mosses and ferns.

These findings were extended to show that photoperiod could control an extraordinary range of features, including sexual activity, migration, change of pelage or plumage, dormancy, and metamorphosis in animals, and vegetative growth, flowering, seed production, leaf colouration and fall, and seed, tuber and bud dormancy in plants. Indeed, taxonomic confusion was produced in some cases by the different seasonal morphs of the same species (see Saunders 1982*a*, pp. 144–149 for examples). Photoperiodism captured the imagination of the scientific world, and the study of dormancy in insects has since been dominated by the study of photoperiodism and of the clock mechanisms required by organisms to interpret photoperiodic information.

The demonstrated dominance of photoperiodic signals in the control of seasonal events was not surprising. Later work which analyzed the climatic background to

the response confirmed the general pervasiveness and reliability of photoperiodic cues. At the same time, physiologists sought mechanisms by which seasonal events were controlled inside the insects; and in particular the discovery by Williams (1946, 1952) that pupal diapause in the silkworm *Antheraea pernyi* was due to the suppression of hormones launched a period of intensive study of the neuroendocrine basis of diapause (other references are cited in Chapter 13). More recently, broader aspects of diapause, such as evolutionary and genetic perspectives, have been discussed (e.g. Tauber and Tauber 1981a), together with the evolution of insect life cycles in general (volumes edited by Dingle 1978a; Denno and Dingle 1981; Dingle and Hegmann 1982; Brown and Hodek 1983).

Although the work on insects was extensive, it nevertheless stayed largely separate from work on parallel adaptations in plants and other animals. There was significant overlap only in the area of "biological clocks". As a result, a common terminology has not developed, and the term "diapause" applied to many insect adaptations is seldom applied to plants, for which the term dormancy is normally used. In addition, marked arrests of development during the life cycle were detected in a wide range of organisms besides insects and vascular plants, for example nematodes (see Michel 1974; Schad 1977; Horak 1981 for reviews), and even fish (e.g. Wourms 1972; Matias 1982), though the control mechanisms such as photoperiod were not always understood.

These investigations of dormancy were prompted in part by curiosity; by the wish to understand the natural world. But in part, too, ways in which this knowledge might find practical use were considered, just as the early horticulturalists were able to modify flowering by the judicious use of artificial lighting. For example, the outbreak status of the sawfly *Neodiprion pini* depends on voltinism in a given year, which in turn is controlled by the conditions influencing diapause (e.g. Eichhorn 1982). Many investigations sought merely to describe the phenology of pests, so that control measures could be instituted. For example, insecticide sprays could be timed to kill insects before the diapause generation appeared (e.g. Sterling and Adkisson 1966). It was suggested that photoperiod could be manipulated (as by artificially illuminating fields) to eliminate diapause and therefore increase winter mortality (e.g. Hayes *et al.* 1970b; Schecter *et al.* 1971; Sáringner 1983). Other practical implications concerned natural enemies. Parasitoids introduced for biological control can succeed only if their diapause responses are appropriate (e.g. Legner 1979) or can be modified in the laboratory before release (Tauber and Tauber 1979). Predators that enter diapause when populations of their prey are active allow the prey to build up (e.g. Focks *et al.* 1980), and parasitoids may behave similarly (e.g. Schlinger 1960). Other inferences were drawn for pest dynamics. For example, the type of diapause determines breeding rate and buildup, the likelihood of reinfestation, resistance to pesticides, and other parameters in *Trogoderma* species infesting stored grain (Burges 1962b, p. 617; Howe 1962). The origin of pest species has also been assessed through their diapause response, as inferred for the weevil *Listronotus bonariensis* introduced into New Zealand (Goldson and Emberson 1980, as *Hyperodes*). In this species, the critical photoperiod for the induction of diapause resembles that of South American source populations, and is not adaptively appropriate to New Zealand, indicating that the weevil is a relatively recent introduction. Such applications (see also Chippendale 1982) gave further impetus to the study of insect diapause.

As knowledge about diapause accumulated, many attempts were made to review the increasingly complex information collected, for example by Andrewartha (1952), Lees (1955, 1968), Fuzeau-Braesch (1961), Harvey (1962), De Wilde (1962*a*, 1970), Way (1962), Danilevsky (1965), Abeloos (1965), Beck (1968, 1980), Danilevsky *et al.* (1970), Müller (1970), Mansingh (1971), Tauber and Tauber (1973*b*, 1976*c*, 1981*a*), Ushatinskaya (1973, 1976), Saunders (1976*c*, 1982*a*), Masaki (1980), Philogène (1983), Ratte (1985), Tauber *et al.* (1986) and Denlinger (1986). Among recent reviews, those by Beck (1980) and Saunders (1982*a*) are especially useful, because they figure or tabulate many relevant facts. Nevertheless, most attempts have treated information from one particular viewpoint, usually photoperiodic responses. Therefore, questions that were addressed related to only part of the total response, and the complete range of adaptations involved often was not viewed in a full variety of appropriate biological contexts.

### The diversity of adaptations

The seasonal adaptations of insect populations reflect interactions with a wide range of environmental conditions. Moreover, different conditions occur in different habitats, and behavioural adaptations allow certain conditions to be avoided. In addition, the timing of development influences not only survival during cold winters or hot summers, but also coincidence with food supplies (e.g. Shapiro 1971 for a butterfly restricted to a spring herb; several herbivores on temperate trees, such as the gypsy moth *Lymantria dispar*, that must synchronize egg hatch with bud-burst of the host plant; Kennedy *et al.* 1975 for insects parasitic on migrant vertebrates), synchrony of adult emergence (e.g. Corbet 1964), avoidance of competition, and other features. Therefore, adaptations that time the active, feeding, or reproductive periods in relation to available food resources or other factors can be linked in a variety of ways with those aimed at withstanding a season that is too hot or too cold. Many different sets of responses to a given set of conditions are therefore possible.

So many different aspects of the insect life cycle can be adjusted that an overwhelming diversity of adaptations has evolved in response to these seasonal pressures. Many insects from mid-latitudes are strictly univoltine, but in other species there may be several generations per year, or several years per generation, sometimes with successive dormancies in the same or different stages that live in the same or different habitats. Differences between related species are commonplace even in the same habitat. Not only can different qualitative or quantitative environmental signals or controls be used to mediate these responses at different times or stages, but the developmental responses themselves can take place in one or more of several stages (such as the egg, various larval instars, pupa, pharate adult, adult), and can vary from slight adjustments in the rate of growth to prolonged and intense developmental arrests. Occasionally, these arrests occupy the greater part of the life cycle. In cold temperate areas as in Canada, arrested development associated with winter survival is most evident — but there are many similarities between reactions to seasonal drought or heat (aestivation) and cold (overwintering) (e.g. Mansingh 1971); between the responses of forms from northern and southern hemispheres (e.g. Roberts and Warren 1975); and between insects and a wide range of other arthropods such as mites (e.g. Hoy 1975*a*, *b*) and crustaceans (e.g. Stross 1971). Certainly, therefore, diapause

has often evolved independently (Lees 1955, p. 6). Farner (1961, p. 71) concluded that dormancies, and photoperiodic mechanisms, have evidently evolved more than once independently within orders, families, and even genera. "Recognition of this probability", he wrote, "will prevent overzealous generalization."

Diapause responses of many of the species that have been especially well studied because they are of economic importance are very complex within the species, varying from one region to another and even among the individuals of one regional population. Many of these well-studied pest species, such as the moths *Pectinophora gossypiella*, *Ostrinia nubilalis*, and *Cydia pomonella* (references cited in later chapters), are wide-ranging "weedy" forms, and the potential complexity of their seasonal responses might require or result from this characteristic. However, diapause responses might be very complex more generally in species with a wide range of other characteristics, but the full extent of the complexity has been adequately described only in species (such as those pests) that have been studied in detail. Another set of examples confirms the latter view. The polymorphism of aphids has been especially well studied (Hille Ris Lambers 1966; Lees 1966a). Considerable differences in form found both within and between species have been attributed chiefly to the need to respond to the heterogeneity of aphid host plants and habitats. Such complexities to solve problems of survival in time and space support the expectation that comparable complexities occur, in this and other groups, to solve similar problems by means of dormancy and allied responses.

The resulting variety of adaptive "options" makes their analysis very difficult. Jungreis (1978, p. 47) concluded that "the study of insect dormancies is a study of misstatements and misunderstandings." Part of this misunderstanding has stemmed from a preoccupation with particular features associated with seasonal control of the life cycle. In particular, the biological clock through which seasonal position can be interpreted has been emphasized at the expense of the ecological relevance of the total response. A realization that the variety of adaptive modes is so wide perhaps allows these features to be viewed in a wider context. Establishing that context is the aim of this book.

#### **Outline and theme of the book**

First described here are attempts to classify dormancy (Chapter 2) and to characterize both dormancy (Chapter 3) and uninterrupted development (Chapter 4). The timing of arrests in development is then considered (Chapter 5). Chapters on the seasonal, especially climatic, basis for cues that control diapause (Chapter 6), and on responses to those cues (Chapters 7 and 8) treat the external control of diapause; but internal programmes (Chapter 9) interacting with these cues also contribute greatly to diapause responses.

Those chapters provide a basis for a broader view of the control of the life cycle developed in Chapter 10. To present such a view of dormancy is the reason for this book, and the basis of this approach can be introduced as follows.

Insect life cycles are timed so that active stages coincide with favourable conditions, and so that periods that do not provide the requirements for development can be passed safely. Poikilotherms are greatly affected by adverse conditions of temperature (and related changes in water relations), and often respond by dormancy, in winter

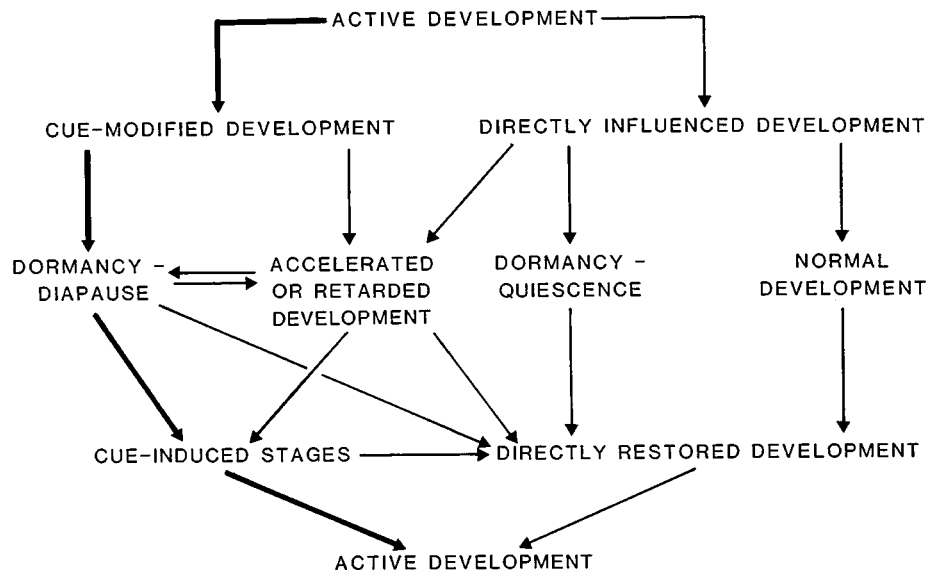


FIG. 1. Some developmental options during the life cycle of an insect (one or more periods of active development can take place in one generation). Bold arrows indicate the alternative that has been most emphasized in the past.

or summer according to species. An alternative to dormancy is displacement or migration, to avoid rather than withstand the seasonal adversity. Therefore, individual insects make alternative “choices” during development, for example either continuing or ceasing to grow, leaving the area or staying, and this is indeed one way in which the life cycle is controlled. Less obvious, but no less important, are options that might be referred to as gradual responses: for example modifying the rate of continuing growth, or modifying subsequent responses to environmental signals.

The particular pathway that development takes in a given member of the population can be programmed in advance, subject to the conditions experienced during development, or both. The most obvious alternative routes of development are diapause and non-diapause, but there are many other possible means to modify development and so control life cycles. Variables that effect this seasonal control (the subject of Chapters 3-9) therefore do not act in isolation, but are integrated throughout development.

The life cycle of an organism can thus conveniently be viewed as a pathway along which it may make a series of “either-or” choices, but at the same time continuously adjust its rate of development. Figure 1 illustrates these developmental alternatives in pointing out that most previous work has emphasized only one extreme exception to continuous development: diapause (a suppression of development cued by environmental signals that are not themselves limiting). In fact there are several other options, used alone, in combination (for example, retarded development in individuals destined to diapause, see Chapter 10), or successively through the life cycle.

Internal mechanisms for control, such as cue receptors (Chapter 11), timing systems (Chapter 12), and neuroendocrine systems (Chapter 13) are reviewed in only enough

detail to define some features of significance to such a general understanding of diapause as a component of ecological adaptation. The concluding part of this book treats the structure, assessment, and evolution of dormancy responses. Chapter 14 outlines ways in which future experimental work on diapause can be made more profitable, based on the lesson, derived from much past work, that too simple a perspective prevents complex phenomena from being assayed in a useful way. The final chapter (Chapter 15) gives a brief synopsis of the structure of dormancy responses, and attempts to set diapause in a broader, albeit largely speculative, evolutionary context. Some general conclusions are drawn from these sources. They reinforce the central concept that diapauses are best regarded as parts of complete life-cycle systems interpreted from an ecological perspective.