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S. R. Leather, K. F. A. Walters and J. S. Bale
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Introduction

Although most insects in temperate climates spend a large proportion of their life in an overwintering stage (the small willow aphid, *Aphis farinosa* (Gmelin) (Homoptera: Aphididae), for example, spends 75 per cent of the year as an egg) the study of insect overwintering has, in many cases, been surprisingly neglected. Perhaps this is a reflection of the fact that many entomologists, like the majority of the insects they study, spend the long cold winter months carefully insulated from the outside world!

Why study overwintering?

The vast majority of the prodigious amount of literature concerning insects, and particularly the literature concerning those insects of economic importance (with which this book is mainly concerned) details investigations of the summer stages of the life cycle. This is, of course, understandable – the insects are present in large numbers during the summer (generally in the multiplicative stage of the life cycle) and this is, in general, the time when the damage to the crop becomes apparent. In addition, the majority of control measures are applied at or just before this time of the year. However, it is a sometimes forgotten fact that the size of the insect populations entering the overwintering stages, and the subsequent survival of these stages, play a major part in determining the population levels encountered in the following spring and summer. Although it has been stated that the literature on overwintering is extensive (Danks 1978), it has too often been of a superficial nature or confined to one specific area, generally that of cold-hardiness. Further, relatively few attempts have been made to correlate the ecological information gained from field studies with the results of physiological and biochemical investigations normally conducted in the laboratory. This is a serious fault and should be remedied.

Recent work within allied groups, e.g. red spider mite, and within insect groups such as the Aphidoidea, has highlighted the advantages, in terms of control and prediction, to be gained from a detailed knowledge of overwintering habits. For example, the number of overwintering eggs of the aphids *Aphis fabae* Scopoli. and *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) can be used to forecast the summer populations of these species developing on field beans in England and on cereals in Finland, respectively (Way *et al*. 1981; Leather 1983). In addition, the spread of potato leaf roll virus can be predicted from a knowledge of the overwintering habits of its aphid vectors (Turl 1983). In the field of forest entomology, the numbers of overwintering pupae of the pine beauty moth, *Panolis flammea* (D & S) (Lepidoptera: Noctuidae), and the pine looper moth, *Bupalus piniaria* (L.) (Lepidoptera: Geometridae), can be used to predict the need for control measures in the coming season (Stoakley 1977; Bevan and Brown 1978). There are many other similar examples, and these will be dealt with in greater detail later (see Chapter 6). There are also many examples where a knowledge of the overwintering biology of an insect would be advantageous, and some of these are pointed out. The study of insect overwintering habits is thus of great importance to entomologists.

What is overwintering?

This may at first seem a relatively simplistic question to pose, and one that may be answered just as simplistically as 'the way that an organism passes the winter'. However, this does not get us very far. Many different definitions of overwintering have been suggested, illustrating the complexity of the subject. Mansingh (1971) considers overwintering in his discussion of dormancy under the heading of hibernation. He defines insect hibernation as 'a physiological condition of growth retardation or arrest, primarily designed to overcome lower than optimum temperatures during winter or summer'. He goes on to point out that overwintering insects also have to contend with the other adversities associated with winter conditions. The main difference between hibernating insects and active ones is that the optimum body temperatures of the former are lower, which leads to torpidity and other metabolic changes. Under the heading of hibernation there are several subclassifications – after all, not all insects respond to winter conditions in the same way – some remain active throughout most of the winter, others cease activity completely, and many species adopt a mixed strategy depending on the daily weather patterns. These subclassifications have been defined by Mansingh as:

1. *Quiescence*. This is the response of individual insects to a sudden unanticipated, non-cyclic and usually short duration deviation of normal weather conditions. This is probably a phenomenon confined to early winter or to winter active insects, and only results in growth retardation.
2. *Oligopause*. This is seen in species inhabiting areas of moderate winter where there is a fixed period of dormancy in response to a cyclic and rather longer term climatic change. These species show a greater and longer retardation in growth than quiescent insects and growth arrest often occurs. Nutritional reserves are required, although periodic feeding does occur during the winter.
3. *Diapause*. This is the most highly evolved system of dormancy for overcoming cyclic, long term extremes in environmental conditions. The main differences between diapause and the two systems described above are that in diapause: (i) there is a definite preparatory phase, usually initiated by a temperature-independent factor, e.g. photoperiod, which involves metabolic changes; (ii) the insect does not feed during the winter; and (iii) the return of favourable conditions does not terminate diapause immediately. Rather, a complex series of events, e.g. the accumulation of heat units or critical photoperiods, is required before the insect terminates diapause and begins to emerge from its overwintering state.

Advantages and disadvantages of overwintering

This must be looked at in two ways – first in comparison to insects in tropical climates and secondly as compared to those insects that, although in temperate or extremely cold climes, remain active. It is important to recognise that temperate and polar species have to overwinter and that any advantages or disadvantages follow from this requirement.

The main advantage of overwintering for a temperate or polar insect, compared to a tropical insect showing a continuous uninterrupted life cycle, is that overwintering in a sufficiently cold-hardy state allows species to survive in inconstant environments that are not favourable for continuous reproduction and normal metabolic functions. A spin-off advantage from this is that predation by winter active animals, e.g. birds, is

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reduced because the resistant overwintering stages are generally more difficult to locate than the active feeding stages. Overwintering also has an advantage, not often recognised, that in strongly, but not entirely, parthenogenetic species, the production of overwintering eggs provides an opportunity to reproduce sexually without sacrificing too much of the rapid multiplicative phase of their life cycle (Ward *et al.* 1984). In addition, overwintering insects in full diapause are often more resistant to cold than those remaining active during the winter and do not have to face the danger of starvation, which can be a major mortality factor of winter active insects (Mansingh 1971). Some tropical insects respond to adverse conditions, e.g. extreme heat or drought, in a similar fashion, i.e. they aestivate, or go into summer diapause (Tauber *et al.* 1986).

There are, however, certain disadvantages accruing to overwintering insects. Although predation is reduced, once found, they are more vulnerable because they are usually non-mobile. This lack of mobility also means that the insect is unable to move from its overwintering site and so, if conditions become less favourable – drying out or waterlogging of the overwintering site being prime examples – they must be endured. There is thus often a high natural overwintering mortality rate underlying that imposed by predation, e.g. eggs of the bird cherry-oat aphid, *Rhopalosiphum padi*, decline by 80 per cent over the winter (Leather 1981) and overwintering pupae of the pine beauty moth, *Panolis flammea*, habitually suffer up to 40 per cent mortality (Leather 1984).

It can be seen that there are a number of points for and against overwintering and these will be discussed at greater length later.

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The overwintering locale – suitability and selection

Introduction

Overwintering insects can be exposed to extreme physical conditions and the choice of the site in which they spend the winter is often critical to their survival. By locating a suitable overwintering site before the onset of harsh conditions, insects can mediate the adverse effects of low temperatures, rapidly changing temperatures, the chilling effect of wind, desiccation, lack of oxygen in aquatic environments and other similar hazards.

The differences in suitability, both between and within winter habitats can best be understood by considering those factors affecting the conditions experienced in a particular habitat. Clearly, the general conditions that have to be contended with, depend on the regional climate, which is determined partly by latitude, partly by altitude and partly by proximity to the seas, lakes and mountains. These general conditions are modified by local effects, such as inclination and aspects of slopes, vegetation, the nature of the ground surface and snow cover (Flohn 1969).

Temperature, of both macro- and microhabitats, is a useful factor with which to compare insect overwintering sites (Danks 1978) and will be used to illustrate how both regional climate and local conditions affect the suitability of sites for winter survival of insects.

The winter habitat – regional climate

Climate on a regional scale is partly determined by continental position. Lower winter temperatures generally occur in the centre of large land masses, well away from large bodies of water and less severe winter conditions are found in areas nearer the sea. This is because land surfaces heat up and cool down more rapidly than the surface of water. The faster relative rate of heating and cooling of land surfaces also results in a much greater variability in daytime and night-time temperatures.

This difference in the rates of heating and cooling in the two habitats is largely due to differences in four physical properties of land and water (Strahler 1963). Firstly, water has a higher specific heat than soil or rock. Secondly, because of the mixing of warmer surface layers with cooler layers at greater depth heat is distributed more quickly in water than on land. Thirdly, evaporation from water surfaces prevents temperatures from rising as high as they otherwise would and, finally, as water is transparent, it allows the transmission of solar radiation to a depth of several metres. (Solid ground surfaces absorb all the energy in their top few centimetres.) Thus, the proximity of the overwintering habitat to large bodies of water determines in part the severity of the conditions experienced by an insect during the winter.

The effect of position in large land masses can be modified by advection, a process involving the transfer of heat by the horizontal movement of air. Thus, a coastal site in which the prevailing winds bring air from a continental interior will have more of a continental-type temperature cycle than one where the winds come from the sea. Wind also has a chilling effect on exposed overwintering sites and is thus a factor to be considered on both a regional and local scale.

Latitude

Latitude exerts a major influence on both the average temperature throughout the year and the seasonal extremes of summer and winter. These differences occur because of variations in the annual cycle of incoming solar radiation. At the equator there is relatively small variation in insolation throughout the year. However, at higher latitudes insolation reaches a peak in midsummer and minimum levels occur in the coldest month, January. As latitude increases, values for insolation during the winter period drop very rapidly until, north of the arctic circle, and south of the antarctic circle there is a total lack of incoming solar radiation for a period of up to 6 months (Strahler 1963).

Such variations in the severity of winter at different latitudes can frequently be related to differing adaptation shown by individuals of the same species. For example, it has been suggested that nymphs and adults of the cereal aphid, *Sitobion avenae* (Homoptera: Aphididae), survive the relatively mild winters of the southern part of Britain but that at more northerly latitudes the species relies to a greater extent on the more cold-resistant egg stage (Walters and Dewar 1986). Responses other than those related to temperatures have also been linked to latitude. The larvae of the pitcher plant mosquito, *Wyeomia smithii* (Diptera: Culicidae), spend the winter in a state of developmental arrest that is evoked, maintained and terminated by photoperiod. The critical photoperiods are strongly related to latitude, this factor accounting for 80.5 per cent of the observed variation (Bradshaw 1976).

Altitude

Altitude also affects the winter conditions experienced by insects. As the greenhouse effect is less pronounced at higher altitudes, high altitude overwintering sites usually have both lower average air temperatures and larger daily temperature ranges than low altitude sites. For example, the critical period for the initiation of developmental arrest in *W. smithii* is affected by altitude (Bradshaw 1976) as well as latitude. To account for geographic differences in the timing of such phenological events as insect emergence, Hopkins (1938) suggested that an increase of one degree of latitude is equivalent to a rise of about 122 m in altitude. This is still a generally accepted principle.

Terrain and overwintering success

Variations in topography can create significant differences in weather conditions in what might at first appear to be homogeneous habitat. For example, deep valleys that are invariably without cloud can lie next to ridges or hill tops that are rarely without cloud. On a smaller scale, a footprint in a lawn can be a frost hollow, whereas the rest of the lawn can be frost-free. Thus, the influence of terrain in the overwintering locale of insects should not be overlooked. The influence of terrain on insect population dynamics is discussed elsewhere (Wellington and Trimble 1984); we will confine our discussion to the influence of terrain on the suitability of overwintering locale and its effect on site selection.

Inversion effects and air mass stagnation

Observations of outbreaks of the moth *Epirrita* (= *Oporinia*) *autumnata* (Lepidoptera: Geometridae) in northern Sweden (Tenow 1975) have shown that some groups of birch trees were unaffected, although trees

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surrounding them were completely or partially defoliated – the so-called ‘green island’ effect. This was attributed to the fact that these trees were in cold-air ‘pools’ or ‘lakes’ that accumulated during wintertime inversions. The overwintering eggs of *E. autumnata* on trees in these cold air ‘lakes’ were killed, while trees above the surface of the ‘lake’ were defoliated to a greater or lesser extent depending on their degree of immersion. After a particularly severe winter, these ‘green islands’ joined together and reached uphill to the top of the inversion as temperatures below that level had fallen sufficiently to kill all the eggs present. When the supercooling points of the eggs of *E. autumnata* during various stages of winter were compared with the profiles of minimum temperatures experienced, a very good correlation between the horizontal and vertical extent of undamaged forest was found (Tenow and Nilssen 1990).

A similar situation is seen in the black pineleaf scale, *Nuculaspis californica* (Homoptera: Diaspididae), on Douglas fir, *Pseudotsuga menziesii*, in the western United States. In normal circumstances the overwintering scale on the needles is cold conditioned before freezing occurs and it persists without significant winter mortality. However, in some of the valley systems cool air from the higher surrounding areas drains into the lower valleys. If the mouths of the valley are narrow enough to prevent outflow, this cool air accumulates in the valley bottom. When the regional weather is near freezing, temperatures in such valley bottoms soon fall well below freezing point and kill all the scales, only those further up the slope surviving. In some years, if the regional air is not so cold, cold conditioning occurs in the valley bottoms and it is the up-slope scales that suffer the greatest overwintering mortality (Fig. 2.1) (Edmunds 1973).

The lodgepole needle miner, *Coleotechnites starki* (Lepidoptera: Gelechiidae), also shows a similar pattern of overwintering mortality in the Canadian Rocky Mountains. However, in this case the localised freezing conditions are caused by a combination of prolonged air mass stagnation caused by two opposing airflows meeting and continual radiant cooling from the surface layer of the air mass. This results in temperatures in the valley bottoms falling as low as −50 °C while up-slope temperatures only a few hundred metres away may be only −10 °C. Unless insulated by snow, the needle miners will inevitably die. Only the up-slope individuals near the top of the inversion within the warmer temperature zone have a chance of survival under these conditions (Henson *et al.* 1954; Stark 1959a,b).

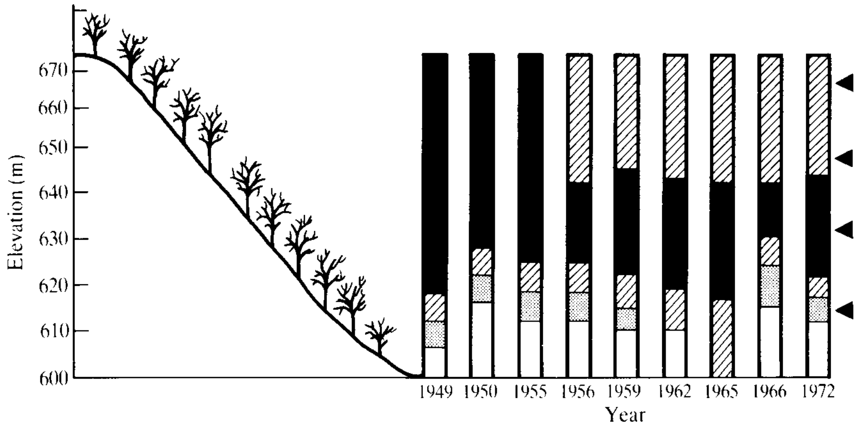

Fig. 2.1. Infestation of the black pine leaf scale, *Nuculaspis californica*, on Douglas fir in Spokane County, Washington, USA, showing the annual variation in population size resulting from the effect of frequent rapid freezing below 610 m, episodic rapid freezing between 610 and 620 m and above 640 m, and annual cold conditioning before freezing between 620 and 640 m. ■ scale severe killing trees, ▨ scale moderate – damage light, ░ scale rare, ☐ scale absent, ▶ elevations at which measurements were made (after Edmunds 1973).

Storm fronts and jet streams

Those insects that adapt the foliage of their host plants as shelters against predators and weather during their larval life often use the same shelters as winter hibernacula. The spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), is such an insect and although the greenhouse effect of these shelters is ideal during the growing period of the larvae, they can become detrimental to overwintering pupae in areas where winter sunshine is at a premium. Early snow cover kept in place on the conifer branches by continuing cool weather provides the best overwintering conditions for spruce budworm, but in some regions repeated rapid thawing and freezing of snow can be brought about by the frequent frontal storms. Under such conditions the local terrain can markedly influence the effect of the continental storm track and its associated jet stream, and thus exert a considerable influence on winter survival. Thus, insect populations will often remain small unless a climatic release occurs in a region where suitable forest is available (Wellington *et al.* 1950; Wellington 1952, 1954a,b).

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Effects of local habitat

The effects of the severity of the general regional climate during winter can be modified by insects both by the stage in which they overwinter (see Chapter 5) and by careful selection of the overwintering site. There are great differences between sites, which may be above or below the surface of the ground or near or under water, and insects exploit all such sites as overwintering habitats.

Soil

During the winter, soil generally offers both a warmer environment and one with a more stable temperature than the air above and is frequently utilised by overwintering insects. Soil temperatures can be influenced by a number of factors such as depth below the surface, the physical characteristics of the soil, moisture content and the presence and depth of a snow covering, all of which influence insect survival.

Soil depth and soil type

Heat transfer in the soil is by conduction. However, as mineral matter is not a particularly good conductor of heat the effects of surface heating and cooling die out rapidly with depth. Hence, the range of daily temperature variations decrease with increasing depth thus providing a more stable temperature environment during winter. Among the insects that take advantage of this stable environment is the grasshopper, *Melanoplus bivittatus* (Orthoptera: Acrididae), which overwinters in the Canadian prairies. The egg pods of this species are laid in the soil at a depth of approximately 5 cm. The soil temperature at that depth during a normal winter is significantly higher than air temperatures and although the mortality of eggs will increase with a decrease in soil temperatures, the temperatures which cause substantial mortality (−15 °C or lower) do not usually occur (Mukerji and Braun 1988).

The poor ability of soil to conduct heat can also offer other potential advantages to overwintering insects. During the cold winters of the continental interiors in northerly latitudes, the period of solar radiation is short and there is little warming of the soil surface. As cooling of the surface layers may occur for up to 18 hours in every 24 in such locations, the soil also becomes warmer with depth during the winter period (Fig. 2.2). Many overwintering insects take advantage of the higher temperatures to be found in deeper soil layers. However, because of the increased