Diapause in Insects

Many species of insects have evolved a strategy called **diapause**. Diapause is a suspension of development that can occur at the embryonic, larval, pupal, or adult stage, depending on the species. In some species, diapause is facultative and occurs only when induced by environmental conditions; in other species the diapause period has become an obligatory part of the life cycle. The latter is often seen in temperate-zone insects, where diapause is induced by changes in the photoperiod (the relative lengths of day and night). The day length when 50% of the population has entered diapause is called the **critical day length**, and it is usually quite sudden (Figure 1). Insects entering diapuse when the day length falls below this threshold are called long day insects. Those insects that develop normally when there are only a few hours of sunlight and that enter diapuse when exposed to longer days are called short-day insects. The critical day length is a genetically determined property (Danilevskii 1965; Tauber et al. 1986).

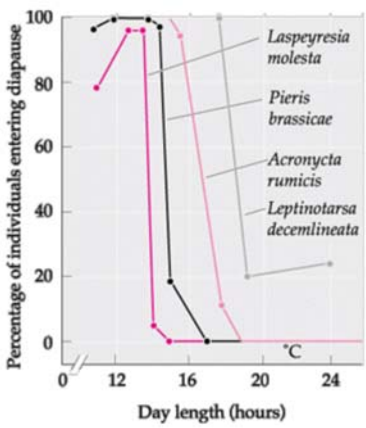

Figure 1 The photoperiodic response of long-day insects which are induced to enter diapause when the daylight hours falls below a certain level. The four species shown here, *Laspeyresia molesta, Pieris brassicae, Acronycta rumicis,* and *Leptinotarsa decemlineata* each leaves diapause when daylight is 14–17 hours. (After Danilevskii 1965).

Diapause is not a physiological response brought about by harsh conditions. Rather, it is brought about by token stimuli that presage a change in the environment. Diapause begins before the actual severe conditions arise. Diapause is especially important in temperate zone insects that overwinter. Embryos of the silkworm moth *Bombyx mori* overwinter as embryos, entering diapuse just before segmentation. The gypsy moth *Lymantia dispar* initiates its diapause as a fully formed larva, ready to hatch as soon as diapause ends. Other insects experience diapause as eggs, pupae, or even as adults.

In the silkworm *Bombyx*, embryonic diapause appears to be regulated by **diapause hormone**, a 24-amino acid peptide that is produced in the subesophageal ganglion (Fukuda 1952, Hasegawa 1952). This hormone acts on the maturing oocytes in the pupal stage and causes development to stop once the embryo has reached about 12,000 cells (Kitazawa et al. 1963). The regulation of the gene encoding the diapause protein has been seen to be induced by temperature (Xu et al. 1995).

While diapause in the embryonic stage appears to be regulated (at least in some species) by a diapause hormone, larval diapause appears to be controlled by the inhibition of PTTH production (see Chapter 18). This prevents the larvae from molting and entering pupation. In many butterflies, this inhibition of PTTH is due to a continued elevated titre of juvenile hormone. Similarly, the lack of PTTH and ecdysone secretion once pupation has occured will cause diapause during this part of development. Diapausing pupae can be reactivated by adding back 20-hydroxyecdysone. However, under nomal conditions, the brain of diapausing pupae (such as those of the moth *Hyalophora*) is activated by the exposure to cold weather for a particular duration. Moth pupae kept in warm conditions will remain in diapause until they die (see Nijhout 1994). The mechanism by which these temperature and day length changes regulate hormone production remains to be elucidated.

The ability to time one's development to season, temperature, or even tides is a critical property of many organisms. In some species, the timing of development has to take several ecological variables into account simultaneously. One sees such an example in the baroque life cycle of a small midge, *Clunio marinis*.

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