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REGULATION OF ADULT DIAPAUSE IN *COCCINELLA SEPTEMPUNCTATA SEPTEMPUNCTATA* AND *C. SEPTEMPUNCTATA BRUCKI* FROM TWO REGIONS OF JAPAN (A MINIREVIEW)

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In similar climatic conditions of central/northern Europe and Hokkaido, Japan, both subspecies of *Coccinella septempunctata* L. have similar life-cycles: long-day photoperiodic response ensures the induction of winter diapause. In the mild climate of Honshu, Japan, *C. s. brucki* Mulsant shows a different life cycle: short-day photoperiodic response leads to the induction of summer diapause while overwintering is quiescence. All populations show an important variation in photoperiodic response.

KEY-WORDS: *Coccinella septempunctata septempunctata, Coccinella septempunctata brucki*, diapause, quiescence, photoperiodic response.

Initially the claims about the life history of *Coccinella septempunctata* L. were far from realistic, *e.g.*, Smee (1922) reported 3-4 generations in England. In the same year, however, Th. Dobzhansky (Dobrzhanskii, 1922a, b) published an important study, which reported that beetles from around Kiev (Ukraine), had 2 generations with a genetically fixed sequence of reproducing 1st and diapausing 2nd generation. After this preliminary experimental study by Dobzhansky there has been no further analysis of diapause regulation in *C. septempunctata*. Jöhnssen (1930) reported univoltine cycle in central Europe and the possibility of a second generation under favourable climatic conditions.

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This is also indicated by our findings (Hodek, 1962). In September most adults are dormant in their hibernation quarters but some are still actively feeding on aphids, especially those on *Carduus* and umbelliferous weeds. Dissections of these active females, particularly when reared under long day conditions, indicate a tendency to bivoltinism. In dormant beetles, there are no traces of vitellinization in the ovaries, while 13-20% of sampled active females have one or more vitellinized oocytes or even eggs. If these beetles are kept for three weeks under long-day conditions, about 85-90% of the dormant females remain without any vitellinization, while the ovaries of about 90% of the active females collected on plants have vitellinized oocytes.

Also the dissections of females collected in sugar-beet fields in central Bohemia in summer indicate a strong tendency to univoltinism: 84-93% of the females enter diapause. Even in the warm region of S Slovakia, close to the Hungarian plains, in a warm year when the adults emerged as early as mid-May (and lived thus for about one month under long-day conditions; last dissection 21 June) the incidence of diapausing females ranged between 66 and 90%, with an average of 79% (n = 184) (Hodek, 1973, p. 181).

In studies in which non-diapause was selected for (Hodek & Čerkasov, 1960, 1961; Hodek, 1962) a gradual decrease in diapause incidence was achieved. In spite of favourable conditions (*i.e.* long-day conditions of 16L:8D or 18L:6D, a constant 25°C, an excess of essential aphid food), the incidence of diapause was high in the first generation; between 60 and 90%. The variability is related to certain conditions: e.g. the number of specimens used to start a culture, and the locality from which the beetles had been collected. A progressive decrease in diapause incidence was obtained within the first three generations. To achieve little or no diapause in later generations it is essential that the coccinellids are reared under optimal conditions (an excess of food, clean conditions, and a population density not exceeding 25 pairs in a cage of about 8 l). These results are not exceptional as it is assumed that multiple genes control the tendency to diapause (Tauber *et al.,* 1986; Danks, 1987).

The effect of environmental factors inducing diapause was studied using selected beetles of the generations beyond the fourth or the fifth, when all or nearly all beetles oviposited under long-day conditions (Hodek & Čerkasov, 1961). The response to short-day conditions was considerably modified by temperature. At the low temperatures of 18- 20°C, the incidence of diapause reached about 90%. An increase in temperature led to a marked decrease in the incidence of diapause; at temperatures fluctuating between 24-25°C (night) and 27-28°C (day) it was only 10%.

It is possible that diapause can be prevented by a succession of long-days after short days. Such a response was reported for populations from northern Europe (Semyanov, 1978; Zaslavsky & Semyanov, 1983).

OTHER POPULATIONS OF *C. S. SEPTEMPUNCTATA*

Although the climate around Paris is different from that of central Europe, the incidence of diapause there is similar (Bonnemaison 1964); 85-95% of the progeny of hibernants enter diapause despite favourable conditions. By selection one can produce a culture that consists solely of non-diapausing coccinellids by the sixth generation. In SE France (Basses Alpes, ca. 44° NL), *C. septempunctata* is reported to be univoltine or partly bivoltine (Iperti, 1966).

In northern Europe most authors report a univoltine cycle (Banks 1954, England; Sundby 1968, Norway; Semyanov 1978, N Russia). Surprisingly beetles from a population from Helsinki, Finland, all reproduced in the first generation when reared under constant long day conditions, i.e. they responded as if potentially multivoltine (Hämäläinen & Markkula, 1972). Such a response has never been found in central or western Europe, and may have been produced by rearing young adults (or larvae) under short days before the culture at long-day conditions.

In central Turkey, in the region of Ankara, Bodenheimer (1943) reported a univoltine cycle with an aestivo-hibernation diapause. In the coastal plain of Israel the beetle has one complete and one partial generation in spring and the same in autumn. One may conclude from Bodenheimer's (1943) observations that hibernation in *C. septempunctata* is quiescence rather than diapause in coastal Israel, while aestivation is a diapause. If so, this type of dormancy regulation in *C. s. septempunctata* is similar to that observed for *C. s. brucki* in central Japan (see below).

Preliminary studies on populations from the Thessaloniki region of N Greece, and from the Sevilla region of S Spain, reveal they have a much weaker photoperiodic response

(Hodek *et al.*, 1989; Hodek & Okuda, 1993). In the region of Athens and in S Greece, there is winter dormancy, at least in a proportion of the population (Hodek *et al.*, 1989). A detailed study has recently been made in this region by P. Katsoyannos (see this volume).

The first reports on the life cycle of *C. septempunctata* in the Nearctic region, New Jersey, USA, indicate it is almost entirely univoltine there with an occasional female producing a second generation (Angalet *et al.*, 1979). This might indicate that the colonizing population originated from western or northern Europe, where the populations are univoltine (see above). Obrycki and Tauber (1981) also found a univoltine cycle in New York state, where the predicted number of generations, based on the sum of effective temperatures, would be three.

In studying the incidence of tendency to multivoltinism in populations of *C. septempunctata* we face two problems. (1) The origin of the sample — the proportion of "obligatory" univoltine and potentially multivoltine individuals in a population differs between localities and most probably also between years. (2) It is diffcult to define the "optimal" or "ideal" experimental conditions for the maximum expression of potential multivoltinism.

Diapause induction in *C. s. brucki* Mulsant from Honshu

Two populations from the central Honshu regions of Nagoya and Tokyo have a life cycle strategy which is the reverse of that shown by *C. s. septempunctata* in Europe. The conditions on the Nagoya plain are suitable for reproduction and development of larvae in spring, from mid-April to late June, and again in autumn, in September and October. The active periods alternate with periods of developmental arrest, a "deep" aestivation in summer and a "weak" hibernation in winter (Sakurai *et al.*, 1981). There are morphological and physiological indications that only aestivation can be considered as diapause, while hibernation is quiescence (Sakurai *et al.*, 1982, 1983, 1986, 1987 a,b; Okuda & Chinzei, 1988).

Experiments on the beetles from the Nagoya and Tokyo regions indicate that short days and low temperature can prevent diapause (Hirano *et al.*, 1982; Niijima & Kawashita, 1982). The Nagoya population of *C. s. brucki* is heterogeneous in its response to photoperiod (Okuda & Hodek, 1983; Hodek *et al.*, 1984) like *C. s. septempunctata* in central and western Europe. Short day conditions prevent diapause, although not of all the individuals in a sample. Photoperiod and temperature similar to the autumn conditions or the Nagoya plain (13.5L:10.5D, 18°C) stimulated 62% of females to come into reproduction within 36 days, whereas only 5% oviposited within 50 days when kept under long day conditions (18L:6D) and a high temperature (25°C). Beetles in another sample responded similarly to shorter day conditions (12L:12D) even when combined with a high temperature (25°C): 79% of the females oviposited within 30 days while in the control (18L:6D, 25°C) only 36% of females were non-diapausing.

Thus all experiments indicate that *C. s. brucki* from central Honshu is a short-day insect.

Diapause development and termination in *C. s. brucki* from central Honshu

The short-day type of photoperiodic response also operates during the development and termination of diapause. Adults collected in September from aestivation sites in the Nagoya region were activated by autumn-like conditions (13.5L:10.5D, 18°C) with 36% of the females ovipositing within a fortnight and 77% within 80 days. Under a long day and a high temperature (18L:6D, 25°C) only 18 and 29% of the control females oviposited within 14 and 80 days, respectively (Hodek *et al.*, 1984).

In contrast to hibernation, aestivation diapause in insects in general is often terminated by environmental factors (Masaki, 1980). The aestivation of *C. s. brucki* seems thus to be terminated in the usual way. However, this should be verified by observations in the field as the laboratory results may reflect only one of the many ways by which diapause is terminated and another pathway may be followed under natural conditions. Hibernation diapause is often terminated by photoperiodic activation in the laboratory, but this usually is not the case in nature where diapause ends spontaneously around the winter solstice (Hodek, 1971; Tauber & Tauber, 1976).

C. SEPTEMPUNCTATA BRUCKI FROM SAPPORO, HOKKAIDO

A long day photoperiod combined with high temperature prevents diapause in the Sapporo population. This is revealed both by the relatively fast activation of the entire autumnal sample and by the incidence of reproductive females in the F_1 progeny. In long days of 16L:8D and 25°C all females collected in early September start to oviposit within 32 days. Short days of 12L:12D combined with 20°C, however, inhibited the reproductive activity of most females, with only 10% ovipositing after 10 weeks. In the F_1 generation 37 and 63% of the beetles did not go into diapause, when kept at a long-day photoperiod of 16L:8D and a temperature of either 25 or 30°C. Under short days of 12L: 12D and 20°C the beetles of the F_1 generation aggregated after a short period of feeding and did not begin to oviposit, even up to 68 days, when the experiment was discontinued (Okuda and Hodek, 1994).

The results strongly indicate that the Sapporo population of *C. septempunctata brucki* shows the long-day photoperiodic response in contrast to the short-day photoperiodic response of the populations from central Honshu. In this respect, *C. s. brucki* from Hokkaido is similar to *C. s. septempunctata* from central Europe (Hodek & Čerkasov, 1961; Hodek & Růžička, 1979) and some other parts of Europe (Bonnemaison, 1964; Hämäläinen & Markkula, 1972; Hodek *et al.*, 1977; Semyanov, 1978). This similarity in photoperiodic response is appropriate to regulate similar life cycles, i.e. to induce winter diapause in both climatically similar regions where the insects face long harsh winter. An intriguing question still remains to be solved: what happens in the transition zone between the two populations in northern Honshu.

RÉSUMÉ

Régulation de la diapause des adultes de *Coccinella septempunctata septempunctata* et de *C. septempunctata brucki* dans deux régions du Japon

Dans des conditions climatiques similaires en Europe centrale et en Europe du nord d'une part et à Hokkaido (Japon) d'autre part, les deux sous-espèces de *Coccinella septempunctata* présentent des cycles biologiques similaires : la réponse photopériodique aux jours courts entraîne l'induction d'une diapause hivernale. Sous le climat doux de Honshu, Japon central, *C. s. brucki* Mulsant présente un cycle de développement différent : la réponse photopériodique aux jours longs provoque l'induction d'une diapause estivale alors que l'hivernation correspond à un état de quiescence. Toutes les populations montrent une variation importante dans leur réponse photopériodique.

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