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COLD-HARDINESS OF THE CABBAGE BUTTERFLIES *PIERIS BRASSICAE* L. AND *PIERIS RAPAE* L.

The problem of the cold-hardiness of cabbage butterflies was for the first time dealt with in detail by I. Kozhanchikov (1936). When analyzing the distribution area of *Pieris brassicae* L., he established the fact that the January isotherm —20 °C forms the northern boundary of the distribution of cabbage butterflies in eastern Europe and in Siberia. However, absolute minimum winter temperatures at the northern points of the distribution area of *Pieris brassicae* fall considerably lower, being —38.4° at Tula, —39.6 at Ulyanovsk, —40.8 in Moscow, —41.9 at Akmolinsk, —42 at Perm, —46.4 at Solikamsk and even —50.5 at Narym. Severe frosts of —30 to —35° occur quite regularly in these regions. Hence, according to I. Kozhanchikov, it follows that the cold-hardiness of *Pieris brassicae* should be within the limits of —30 to —35°. The distribution area of *Pieris rapae* L. in Siberia extends much farther north, and this shows that this species of butterflies should obviously possess a greater degree of cold-hardiness.

It is only in the last few years that experimental data on the cold-hardiness of cabbage butterflies have begun to be published in greater numbers. The supercooling point of diapausing pupae of *Pieris brassicae* has been reported by A. Danilevsky (1961) to be —22.5° in Leningrad and by L. Sømme (1967) —24.6 to —26.5° in Norway, depending on storage conditions.

Although cabbage butterfly pupae do not tolerate a freezing of tissues, it is not enough to know their supercooling point to establish their resistance to cold. In the case of exposures of long duration, a marked mortality of insect populations has been caused by temperatures considerably higher than the supercooling point (Salt, 1950; MacPhee, 1961; Goryshin, 1966).

The aim of the present investigation was to establish the seasonal changes in the supercooling points of cabbage butterfly pupae and their dependence on the duration of exposure.

Materials and methods

Experiments were conducted in the winters of 1968/69 and 1969/70. The mature larvae of cabbage butterflies were collected in the fields located in the vicinity of the town of Tartu, Estonian SSR, and raised in insectaria up to pupation. The pupae were stored in Petri dishes on cotton wool under conditions resembling those in nature, with the only difference that temperatures below —20° were avoided.

The supercooling points were measured with a copper-constantan thermocouple at a cooling rate of 0.5° per minute. The determinations of the average supercooling points were performed on 10 to 20 specimens in each series of runs.

The effect of the duration of exposure to constant low temperatures on mortality was studied in Dewar flasks in ethanol which was cooled by dry ice. Temperatures varied within the limits of ±0.1°. The freezing of pupae was registered by a recording potentiometer of the type MCP-1-08 and a resistance thermometer.

Results and discussion

1. Seasonal changes in the supercooling points

The course of the seasonal changes in supercooling points as well as the particular values of the temperatures at different points of time are very similar in both the species (Fig. 1). The larvae of the second generation of cabbage butterflies pupate in the first

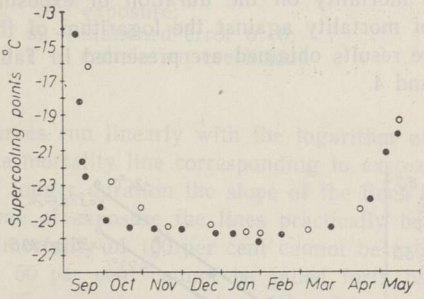

Fig. 1. Seasonal changes in supercooling points of the cabbage butterfly pupae ● — *Pieris brassicae*; ○ — *Pieris rapae*.

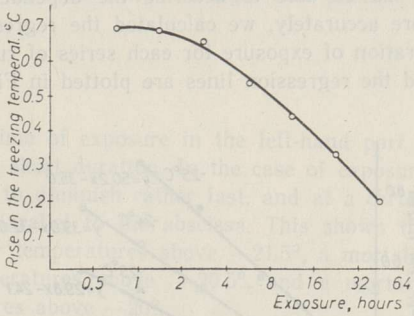

Fig. 2. Effect of the duration of exposure on the rise in the freezing temperature of the hibernating pupae of *Pieris brassicae*.

half of September. The sharpest rise in cold-hardiness proceeded in two weeks during pupation and after it. Thus, the mean supercooling point of the prepupae of *Pieris brassicae* on September 10 was —14.2±1.4°, that of the non-chitinized pupae on September 11 was —18.0±1.3° and on September 12 —21.6±0.8°; the supercooling points of the pupae with chitinized integuments were as follows: September 19 —24.5±0.3°, October 3 —25.0±0.3° and October 23 —25.5±0.3°. Thus the pupae attained cold-hardiness in October, i. e. a long time before the arrival of frosts. During the following winter months the cold-hardiness of the cabbage butterflies increased by 1°, at the most (—26.2±0.1° in the middle of January).

In spring, cold-resistance begins to diminish in April. Thus, the supercooling points were on April 27 —23.8±0.4° and on May 13 (i. e. in the last days of the pupal stage) — 20.3±0.4°.

There were no statistically significant differences in the winter supercooling points of the two species of cabbage butterflies.

Comparing the supercooling points of *Pieris brassicae* established by our experiments with those found in the literature, there appears to be a striking coincidence with the data published by L. Sømme (1967).

2. Effect of continuous constant low temperatures on the mortality of the hibernating pupae of cabbage butterflies

A certain amount of mortality in insect populations may also be brought about by sublethal temperatures, owing to their interference with the course of physiological processes. This cause plays a small role in the winter killing of the pupae of cabbage butterflies. Only 6 per cent of the 700 pupae of *Pieris brassicae* were killed in our

hibernation experiments carried out at sublethal temperatures during exposures of 5 months.

The chief cause of death, after all, was the freezing of pupae. Freezing increases as the temperature falls and the period of exposure lengthens. There are several methods for describing and forecasting the mortality caused by winter frosts of various duration. When studying the cold-hardiness of the wheat stem sawfly *Cephus cinctus* Nort., Salt (1966) came to the conclusion that the mean time of freezing doubles with each 0.53° rise in temperature. Having studied the effect of the duration of exposure in various species, E. Merivee and T. Hansen (1970) established the fact that over the range of exposure periods lasting from 0.25 min. to 16 hr. the mean supercooling point rises by 0.25° when the time of exposure is doubled. The drawback of the above-mentioned coefficients is their too high a degree of approximation, which is due to their strong dependence on the duration of exposure. In the case of *Pieris brassicae* pupae, this coefficient increased from 0.2 to 0.7 (Fig. 2) when the duration of exposure shortened from 2 days to 0.5 hr.

To be able to describe the dependence of mortality on the duration of exposure more accurately, we calculated the regression of mortality against the logarithm of the duration of exposure for each series of runs. The results obtained are presented in Table and the regression lines are plotted in Figs 3 and 4.

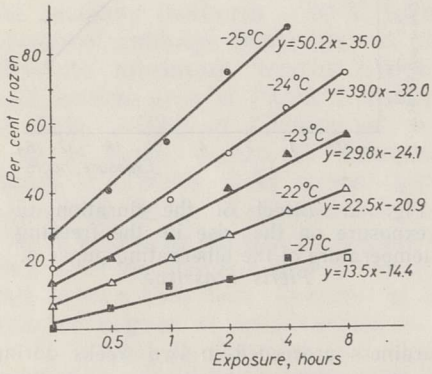

Fig. 3. Relation between percentage of *Pieris brassicae* hibernating pupae frozen and time of exposure at temperatures shown.

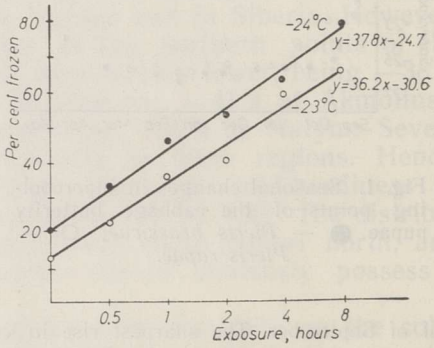

Fig. 4. Relation between percentage of *Pieris rapae* hibernating pupae frozen and time of exposure at temperatures shown.

Over the range of the times of exposure from 0 to 8 hr., a linear relationship was found to exist between mortality and logarithm of the time of exposure, which is shown by the exceedingly great values of the correlation coefficients (r=0.96 to 1.0). In all cases mortality begins by a certain period of time after the initial moment of a run (*a* values are negative), which can be explained by the great weight of the pupae of cabbage butterflies (they cool down slowly). The effect of the duration of exposure is more intense as the temperature of exposure approach the supercooling points — when approximating the latter, the slopes of the regression lines increase (cf. regression coefficient *b* in Table). When the duration of exposure is doubled, the mortality at an exposure to —25° increases by 15 per cent, whereas at —21° the increase is only 4 per cent.

Taking into account the very high correlation between mortality and the logarithm of the time of exposure, we extrapolated the obtained regression lines to longer periods of time. It can be assumed that a 100 per cent mortality is attained at —24° already after the 1.5 days, at —23° in about 11 days, and at —22° only after the seventh month. The curves presented in Fig. 5, with points where the regression lines shown in Fig. 3 cross the 100, 50 and 25 per cent mortality lines, make the matter even clearer. These

Data on the effect of time of exposure to various low temperatures on the mortality of cabbage butterflies *Pieris brassicae* and *Pieris rapae* pupae for exposure periods of up to 8 hours

Species	Temperature of exposure, °C	No. of pupae in test	a	b	s_b	r
Pieris brassicae	−21±0.1	30	−14.4	13.5	2.36	0.96
„ „	−22±0.1	30	−20.9	22.5	0	1.00
„ „	−23±0.1	30	−24.1	29.8	2.12	0.99
„ „	−24±0.1	30	−32.0	39.0	1.70	0.98
„ „	−25±0.1	30	−35.0	50.25	2.00	0.99
Pieris rapae	−23±0.1	15	−30.6	36.2	3.42	0.99
„ „	−24±0.1	15	−24.7	37.8	2.64	0,99

Test results are shown graphically in Figs 3 and 4.
b — linear regression coefficient of percentage mortality on logarithm of time of exposure;
s_b — standard error of b;
r — correlation coefficient.

curves run linearly with the logarithm of the time of exposure in the left-hand part of the mortality line corresponding to exposures of short duration. In the case of exposures of longer duration the slope of the lines begins to diminish rather fast, and at a certain time of exposure the lines practically become parallel to the abscissa. This shows that a mortality of 100 per cent cannot be evoked by temperatures above —21.5°, a mortality of 50 per cent cannot be called forth by temperatures above —20.5°, and a mortality of 25 per cent cannot be produced by temperatures above —20°.

If one compares the cold-hardiness of *Pieris brassicae* with that of *Pieris rapae,* one may note that the pupae of *Pieris rapae* at —23° and —24° show a higher mortality which is statistically insignificant.

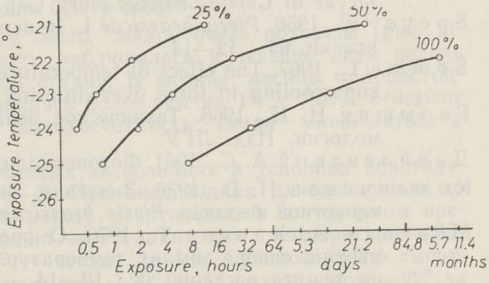

Fig. 5. Comparison of the time-temperature exposures to cause 25, 50 and 100 per cent mortality of *Pieris brassicae* hibernating pupae.

From the above we may draw the conclusion what the winter killing of the pupae of cabbage butterflies is due to temperatures approximating the supercooling points (below —20°). The effect of the duration of exposure is considerable only at exposures of short duration (of 1 to 8 hr.), at exposures of longer duration the effect of the duration of exposure approaches zero (Fig. 2). In nature, too, there occur minimum temperatures, owing to which the majority of insects perish in winter in a short time, sometimes within a few hours. Taking into consideration what has been said above, the authors are of the opinion that the 16-hr. critical temperature (i. e. the temperature at which 50 per cent of the specimens are killed) aptly describes the mortality of the insects hibernating above ground, on account of excessive frost. The critical temperature for *Pieris brassicae* is —22.3° (Fig. 5). Hence, under the conditions prevailing in Estonia, 100 per cent of the *Pieris brassicae* pupae hibernating exposed to low temperatures ought to perish every winter. The reasons for their winter resistance and for their large numbers must obviously be explained otherwise than by cold-hardiness.

In the case of *Pieris brassicae,* immigrations are one of the chief sources of their large numbers (Lederer, 1938, and others). Proof of this circumstance lies in the fact that in the whole of the European part of the Soviet Union there exists only a single large population of *Pieris brassicae* with a uniform photoperiodic response (Danilevsky,

1961). In addition, the first generation of *Pieris brassicae* is, as a rule, not numerous, not even when the numbers of parasites from the previous autumn were small and the larvae were numerously pupated (as in the years of 1966/67). It is obvious that a large part of the local *Pieris brassicae* population is winter-killed every year. Hibernation is possible only under the snow cover, but the mature larvae, after having completed their feeding, have a very strong negative geotaxis, on account of which hibernation under the snow is possible in exceptional cases, only. Thus, on North Sea islands, larvae of *Pieris brassicae* pupate on stalks of the sea sand-reed *Ammophila arenaria* (L.) Link. (Speyer, 1956). Their larvae, too, have a strong negative phototaxis because of which they often pupate on the inward sides of roofs of sheds and lofts, in halls and other kinds of buildings. It seems that *Pieris brassicae* is a rather synanthropic species. It is also synanthropy that makes it possible for a non-numerous and labile local population to exist.

The extensive distribution of *Pieris rapae* in Siberia cannot be explained by its greater cold-hardiness, either. The reason may rather lie in the peculiarity of the ecology of its hibernation. *Pieris rapae* pupae may often be found very near to the surface of the ground, even in the grass, on foundations of houses, etc. Nevertheless, when they hibernate under snow, the pupae are sufficiently cold-hardy.

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KAPSALIBLIKATE *PIERIS BRASSICAE* L. JA *PIERIS RAPAE* L. KÜLMAKINDLUS

Resümee

Kapsaliblikate nukkude suremust kestvates konstantsetes miinustemperatuurides uuriti Dewari anumast ehitatud külmtermostaadis kuiva lume abil jahutatavas piirituses. Temperatuuri kõikumised olid ±0,1 °C piirides. Allajahtumispunktid määrati vask-konstantaantermopaariga, jahutamiskiirus oli 0,5° minutis.

Allajahtumispunktide sesoonne muutumine oli mõlemal liigil väga sarnane (joon. 1). Külmakindlus suurenes kõige jõudsamalt paari nädala jooksul nukkumise ajal ja pärast seda. Talvekuudel suurenes kapsaliblikate nukkude külmakindlus maksimaalselt 1° võrra.

Pieris brassicae nukkude allajahtumispunkt oli jaanuari keskel —26,2°. Kevadel hakkas külmakindlus langema aprillis.

Andmed nukkude suremuse kohta kestvates konstantsetes madalates temperatuurides on esitatud joonistel 3—5. Kuni kaheksatunniste ekspositsioonide puhul valitses suremuse ja ekspositsiooniaja logaritmi vahel lineaarne sõltuvus. Ekspositsiooniaja kahekordistumisel suurenes suremus —25° puhul 15, —21° juures aga ainult 4%. —24° juures peaks sajaprotsendiline suremus saabuma 1,5 ööpäevaga, —23° juures 11 ööpäevaga, —22° juures 7 kuuga.

Kapsaliblikate nukkude talvist suremust põhjustavad allajahtumispunktile lähedased temperatuurid (madalamad kui —20°). Sealjuures on olulised ainult lühikesed, 1—8-tunnised ekspositsioonid. Pikemate ekspositsioonide korral läheneb ajafaktori mõju nullile (joon. 2). Avatalvituvate putukate pakasest tingitud suremust kirjeldab seepärast üsna hästi 16-tunnine kriitiline temperatuur. *Pieris brassicae* puhul on kriitiliseks temperatuuriks —22,3°. Selle liigi väikesearvuline ja labiilne kohalik populatsioon saab eksisteerida vaid tänu sünantroopsusele (talvitub hoonetes). *Pieris rapae* talvekindlust aitab selgitada tema talvitusökoloogia omapära: tema nukud talvituvad nimelt lume all.

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7. X 1970

ТИЙУ ХАНСЕН, ЭРМЕР МЕРИВЭЭ

ХОЛОДОСТОЙКОСТЬ КАПУСТНЫХ БЕЛЯНОК *PIERIS BRASSICAE* L. и *PIERIS RAPAE* L.

Резюме

Изучалась смертность капустных белянок при длительных константных низких температурах в сосуде Дюара в спирте, охлаждаемом сухим льдом. Температура колебалась в пределах ±0,1 °С. Точки переохлаждения (ТП) измерялись при помощи термопары медь-константан при скорости охлаждения 0,5° в минуту.

Ход сезонного изменения ТП оказался у обоих видов очень похожим (рис. 1). Самое интенсивное повышение холодостойкости наблюдалось в течение двух недель во время окукливания и в начале куколочной стадии. В зимние месяцы холодостойкость куколок капустных белянок не увеличивалась более чем на 1°. У *Pieris brassicae* в середине января ТП составляла —26,2°. Холодостойкость стала уменьшаться в апреле.

Данные о смертности куколок при длительных экспозициях в условиях константных низких температур приведены на рис. 3—5. При экспозициях длительностью до 8 *ч* наблюдалась прямолинейная зависимость между смертностью и логарифмом времени экспозиции. С каждым удвоением времени экспозиции при температуре —25° смертность повышалась на 15%, а при —21° — только на 4%. Стопроцентную смертность можно ожидать при —24° за 1,5 сутки, при —23° за 11 суток и при —22° за 7 месяцев. Зимнюю смертность куколок капустных белянок вызывают только температуры, которые незначительно превышают ТП (ниже —20°). Влияние фактора времени самое сильное при коротких экспозициях от 1 до 8 *ч*. При более длительных экспозициях оно приближается к нулю (рис. 2). Поэтому у насекомых, зимующих открыто, зимнюю смертность удовлетворительно можно прогнозировать на основе критических температур при 16-часовой экспозиции. У *Pieris brassicae* критической является температура —22,3°.

Малочисленная и лабильная местная популяция *Pieris brassicae* может существовать только благодаря синантропии (куколки зимуют в постройках). Зимостойкость *Pieris rapae* можно объяснить своеобразием его экологии зимовки (куколки зимуют под снеговым покровом).

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