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HIBERNATION PECULIARITIES AND COLD-HARDINESS OF THE GREAT SPRUCE BARK BEETLE, *DENDROCTONUS MICANS* KUG.

Winter frosts constitute very often the main reason for considerable losses in the population of insects and that is why in the conditions of temperate climate the adaption of insects connected with hibernation has a special importance in their life-cycle. The research work devoted to the specification of the biology of hibernation of the great spruce bark beetle (*Dendroctonus micans* Kug.) and the more detailed study of the physiology and biochemistry of different stages of hibernation started in Estonia in the second half of the 1970s after the population of *D. micans* had increased in Western Estonia and an outbreak of damage could be observed in young stands of Scotch pine (*Pinus silvestris* L.).

In the southern parts of its distribution area *D. micans* has a one-year generation, and it has been observed that it may hibernate in all the stages of development (Кобахидзе и др., 1969; Жарков, 1971). In the north of Scandinavia and in Yakutia the cycle of development of *D. micans* may last for three years and the larvae hibernate twice (Lekander et al., 1977; Аверенский, 1971). In the main part of the area *D. micans* has a two-year generation and hibernation takes place in the stages of larvae and beetles (Istrate, 1973; Коломиец, Богданова, 1978). In Estonia *D. micans* has also a two-year generation and mainly larvae of later instars and the beetles hibernate (Воолма, 1980). Sometimes after a cooler summer even younger larvae hibernate. According to the results of our observation in the winter of 1975—1976 82.1% of the total number of collected larvae (658) hibernated in the fifth instar and 17.9% in the fourth instar. Larvae of younger instars were not found. In the winter of 1977—1978 2247 larvae were analysed. According to their instars the distribution was: II instar 6.3%, III instar 17.0%, IV instar 27.5%, and V instar 49.2%. Hibernating eggs and larvae of the I instar were not found. There were a few single cases when we found pupa and newly emerging young beetles which were dead. In the more southern parts of the area hibernation is possible in the stages of young brown or yellow beetles, however, the mature black beetles prevail (Istrate, 1973). Consequently, in the conditions of Estonia *D. micans* hibernates, as a rule, in the stages of larvae of later instars and the mature beetle. Most evidently the other stages of development are less adapted to the survival in severe winter conditions.

The location of hibernation of *D. micans* depends on the host trees, site and especially on the climatic conditions of the region. In Scotch pine it inhabits only the lower part of the trunk (usually not higher than 30—40 cm) and big roots. This is the hibernation place of the pest, too. The beetles hibernate under the bark in the lower part of the trunk in the places of feeding, very often forming a chain in the passages in the compact frass. According to the data of our investigation carried out in the pine stands of Western Estonia the majority of beetles (80.3%) hibernate on the trunk not higher than 20 cm from the ground. As usual, the beetles hibernate lower than the line of snow cover. Hibernating larvae form groups lower than the feeding line. On some trees part of larvae (up to 30%) hibernate on roots, but sometimes they perish because of excessive humidity in autumn and spring. On Norway spruce (*Picea abies* (L.) Karst.) *D. micans* inhabits much higher parts of the trunk, the beetles and larvae may be found at the height of 10—12 metres, sometimes even higher. Larvae hibernate in the feeding place. Beetles usually leave the feeding galleries in autumn and gather at the foot of the trunk. They hibernate in groups in short galleries under the bark of the lower part of the trunk and thick roots. In the conditions of mild and normal Baltic winters they hibernate more sucessfully, but in severe frosts many specimens of *D. micans* perish. In the especially severe winter of 1978—1979 when the air temperature fell down to −42 °C, all the larvae and beetles which were hibernating above the line of snow cover froze. Long-lasting frosts and high mortality of *D. micans* also characterize the winter of 1986—1987.

The beetles and larvae of *D. micans*, as well as other bark beetles, inhabiting the tissues of trees, are supplied with feed all the year round. At favourable temperatures the cycle of generation of these insects can be uninterrupted. This speaks of the absence of an obligatory period of dormancy. The fact that in northern areas of distribution only certain stages of development can hibernate indicates that some stages are better adapted to hibernation than others. Namely, at these stages the formation of dormancy may be presupposed.

The investigation of dormancy of *D. micans* showed that dormancy takes place in quite a labile state, because hibernating specimens are reactivated at room temperature more rapidly: in autumn within 1—2 minutes; in winter, in December and January it is considerably slower — up to 20 minutes (Луйк, Воолма, 1980). A slow rate in metabolism of hibernating beetles appears at low temperatures. So at 0 °C developing beetles consume 90 mm^3 of oxygen per 1 g of body weight while hibernating ones consume only 30 mm^3. Hibernating specimens are characterized by the ability to acclimatize to the frost which appears in October and is well manifested in November and December and disappears irreversibly in spring, in April. Due to acclimatization both larvae and beetles develop a relatively high degree of cold-hardiness. If in August during freezing the supercooling point of the larvae of III instar was −15.7 °C, that of IV instar −16.4 °C, V instar −16.5 °C and beetles −12.2 °C, then in January the corresponding temperatures were −25.9, −26.9, −27.7 and −24.2 °C. In spring when the temperature rises cold-hardiness disappears. Specimens acquire and retain maximum cold-hardiness only when the temperature is below zero. When it is above zero, cold-hardiness decreases. In case of a mild winter the specimens do not even reach their maximum degree of cold-hardiness. For example, in the winter of 1974—1975 when the average monthly temperatures did not fall below zero, the supercooling point of beetles was only −10.7 °C. The same beetles are able to survive when they are exposed to quite lengthy periods of sublethal temperatures, so at −17 °C the critical exposure time (with mortality rate 50%) was 32 hours.

The curve of seasonal dynamics of the supercooling points runs parallel to the curve of changes in the average daily temperatures. The comparison of these indicators shows that both beetles and larvae are sufficiently cold-hardy for successful hibernation. The majority of the beetles and larvae hibernate under the snow cover which considerably mitigates the harm of the frosts. As our observation shows, during hibernation about 20% of the beetles perish. The mortality rate of larvae depends to a great extent on the place of hibernation — in the lower part of the trunk the mortality rate of larvae of IV and V instars does not usually exceed 5%, on the roots the mortality rate is higher because of abundant humidity. In the second half of winter the specimens may perish because on sunny days the temperature on the bark of the trees rises considerably and in turn brings along a decrease in the cold-hardiness of the insects. The frosts setting in after warmer days may become dangerous especially in the second half of the winter.

The increase of cold-hardiness of hibernating specimens is brought about by physiological and biochemical changes of the organism (Хансен и др., 1981). When the colder season sets in, the insects stop to consume feed and with the stoppage of feeding their cold-hardiness increases. So in our experiment of 4-day starvation the supercooling point of *D. micans* rose by 2.5 °C. Biochemically the cold-hardiness of larvae and beetles is based on the restructuring of water balance, as well as the accumulation of fats, glycogen and glycose. Biochemical changes are less clearly expressed in the larvae of II and III instars, but in the larvae of IV and V instars and beetles the changes are much more evident. With the coming of winter the water content of the larvae of the later instars decreases by 20% (from raw mass) reaching 59% of the body weight, in beetles it reaches even 50%. At the same time the content of glycogen in beetles increases gradually from 0.46% in September to 15.9% in November, the content of glycose grows correspondingly from 0.4% to 4.3%. From the end of November when the temperature of the environment falls below zero, the concentration of both substances decreases gradually, and this can be explained by the consumption of glycogen and glycose as energy substratum. Glycose, evidently, plays a leading role in the reactions of cold-hardiness of *D. micans*.

This way *D. micans* hibernates in a special state of winter dormancy, the course of which is controlled by the temperature of the environment. Similar reactions of cold-hardiness during hibernation characterize many other species of xylophagous (Merivee, 1978; Gehrken, 1984; Луйк, 1986; Хансен, 1986). The increase of cold-hardiness is achieved either by the formation of thermal hysteresis factors or by the accumulation of polyhydroxy alcohols and sugars (Zachariassen, 1985). For example, in the adults *Ips acuminatus* Gyll. the supercooling point falls from −17.0 °C in October to −22.9 °C in November thanks to thermal hysteresis, but the further fall to −33.8 °C is connected with the formation of ethylene glycol which takes place under the influence of subzero temperatures (Gehrken, 1984). The formation of antifreeze compounds is preconditioned by an earlier accumulation of reserve substances, primarily of glycogen on the basis of which it is possible to synthesize corresponding substances. As it became evident, considerable reserves of glycogen are accumulated in autumn. The signalling factors for neuroendocrinological systems of bark beetles might be photoperiodical or thermoperiodical conditions. According to Schopf (1985) the beetles *Ips typographus* generated in short day periods supercooled at −11.2°C, the long day beetles at −8.7°C. According to our data (Луйк, 1980), thermoperiodical treatment of bark beetles *Ips typographus* L. during more than 30 days conduced the formation of the ability of cold-hardiness of the specimens brought up both in the conditions of the short as well as the long day regimes. A prolonged thermoperiodical influence appeared to be even more efficient — after a 60-day period of using diurnal thermorhythms (10 hours at 17 °C and 14 hours at 6 °C) and the following acclimation at −3 °C during 35 days *Ips typographus* had almost maximum winter cold-hardiness of −24.8 °C. In an analogous way we may suppose that autumnal thermorhythms may play an inducive role in the accumulation of glycogen in autumn in the hibernating stages of bark beetles. The further formation of frost-protective substances is determined by the activization of the corresponding enzymes affected directly by low temperatures. As Hayakawa and Chino (1982) have shown, the activation of glycogen phosphorylase, preconditioning the synthesis of trehalose from glycogen, takes place namely at 2 °C, but when the temperature rises up to 20 °C, the resynthesis of glycogen takes place.

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HIIDÜRASKI (*DENDROCTONUS MICANS* KUG.) TALVITUMISE ISEÄRASUSED JA KÜLMAKINDLUS

Hiidüraski talvitusbioloogilisi uuringuid alustati 1970. aastate teisel poolel, pärast kahjustuskollete kujunemist Lääne-Eesti männinoorendikes.

Eestis kulub hiidüraski põlvkonna arenguks kaks aastat. Talvituvad enamasti viimaste kasvujärkude vastsed ja mardikad. Mändidel asustab hiidürask alumist, 30—40 cm kõrgust osa, juurekaela ja pindmisi juuri, kus ta ka talvitub. Kuuskedel võivad asustused paikneda ka tüvel kuni 10—12 m kõrgusel.

Talvituvate isendite puhkeseisund on labiilne, mistõttu toatemperatuuril nad reaktiveeruvad kiiresti. Ainevahetuse depressioon ilmneb ehedalt vaid madala temperatuuri puhul. Tänu külmaaklimatsioonivõimele, mis on hästi välja kujunenud oktoobrist detsembrini, saavutavad isendid edukaks talvitumiseks märkimisväärse talvise külmakindluse — vastsed keskmiselt −25,9 ... −27,7 °C, valmikud −24,2 °C.

Külmakindlus tagatakse biokeemiliste muutustega organismis. Talvituvatel isenditel väheneb vaba vee hulk, suureneb glükogeeni ning glükoosi sisaldus. Talvise puhkeseisundi kujunemine sõltub väliskeskkonna temperatuuritingimustest.

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ОСОБЕННОСТИ ЗИМОВКИ И ХОЛОДОУСТОЙЧИВОСТЬ КОРОЕДА-ДЕНДРОКТОНА (*DENDROCTONUS MICANS* KUG.)

Исследования по уточнению биологии перезимовки короеда-дендроктона начались в Эстонии во второй половине 1970-х годов, после того как в Западной Эстонии повысилась численность вида и появились очаги повреждения в сосновых молодняках.

В условиях Эстонии дендроктон имеет двухлетнюю генерацию. Зимуют в основном личинки старших возрастов и жуки. На сосне дендроктон заселяет только нижнюю часть ствола (обычно не выше 30—40 см), корневую шейку и большие корни. Там же проходит и зимовка насекомого. На ели поселения дендроктона обнаружены и на более высоких частях стволов (10—12 м).

Зимовка личинок и жуков дендроктона проходит в лабильном состоянии. При комнатной температуре зимующие особи быстро активируются. Депрессия обмена веществ проявляется при низких температурах. Благодаря осенне-зимней холодовой закалке личинки и жуки дендроктона достигают довольно высокой зимней холодостойкости — в среднем —25,9 ... —27,7 °С у личинок и —24,2 °С у жуков.

Повышение холодостойкости у зимующих особей достигается биохимическими перестройками в организме. С наступлением холодного сезона насекомые заканчивают питание, постепенно уменьшается содержание воды в организме и повышается количество гликогена и глюкозы. Протекание зимнего покоя контролируется температурой среды.