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SOME ASPECTS OF LIFE HISTORY AND POPULATION DYNAMICS OF *PISSODES PINIPHILUS* HRBST. (*COLEOPTERA*, *CURCULIONIDAE*)

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Abstract. The survival of *Pissodes piniphilus* was investigated on 60-year-old Scots pines with both healthy-looking and damaged crowns. As the weevils are primary stem attackers, the viable trees kill them in the phase of the eggs or young larvae. They produce new generations only on more weakened trees where the larval mortality is determined not only by the host tree but also by intraspecific competition caused by a high colonization density and entomophages, out of which were more frequently occurent specimens from genera *Eubazus*, *Lonchaea*, *Medetera*. On stems mostly the second- and the last-instar weevils larvae hibernate; their winter dormancy is quite easily terminated by high temperature, but they also acclimate to cold, and this guarantees a sufficient midwinter cold-hardiness of up to −34.5 °C. The population increase of *P. piniphilus* in Estonia is mainly caused by a weakness of the pine stands and temperatures that have been favourable for *P. piniphilus* development.

Key words: *Pissodes piniphilus*, *Pinus sylvestris*, larval survival, host tree influence, entomophages, dormancy, larval cold-hardiness.

Pissodes piniphilus Hrbst. (*Coleoptera*, *Curculionidae*) is a small weevil, which damages the Scots pine of the age of 20 to 80 years in many parts of Europe and Asia (Kohh, 1939; Ebert et al., 1978; Богданова, 1985; Шелухо, 1991). Damage to the trees is caused by both adults and larvae. The adult weevils, biting the smooth bark of the trunks for the maturation feeding and oviposition, and larvae developing under the bark cause further weakness of pines. The impact of *P. piniphilus* has risen in Central Europe in many forest ecosystems under the influence of some forest—weakening factors such as pollution (Krol, 1980; Harabin et al., 1981, Chlodny, 1982; Bychawska, 1983; Chlodny and Styfi-Bartkiewicz, 1984; Oppermann, 1985) and unfavourable weather conditions (Führer and Kerck, 1978). As the weevils maturation feeding and their mating occurs on the bark, the dry and hot spring-summer periods — which at the same time are stressful for host trees — are conductive to the species' development. At the end of the 1930s, under the influence of such conditions lasting for several years, big outbreak areas of this species developed in Southern Estonia. The climatic changes as well as considerable cutting of colonized trees brought along the decrease of *P. piniphilus* population (Kohh, 1939). In the following years some localized outbreak areas survived mainly in the stands damaged by *Heterobasidion annosum* (Riis, 1975). By the beginning of the 1990s, very big outbreak areas covering many thousands of hectares appeared in Southern Estonian *Cladina* and *Vaccinum vitis-idaea* site types pine stands (Fig. 1) (Luik, 1992). Nowadays *P. piniphilus* is the most distributed stem inhabitant in Estonian pine forests. For understanding the population dynamics of the species it is important to know its biology in details. There are very few data about the development of *P. piniphilus* and no data on the success of the species hibernation. Beetles hibernate in the forest litter, but the larvae on the trunk below the bark are accessible to the frost. For the sake of understanding the factors causing larval mortality, the aim of the present study was to determine the colonization density and the larval survival of *P. piniphilus* in two different populations — in a chronically damaged area at Kiidjärve and in the borderland of the outbreak area — Orava, where the stands were coweakened by the pine looper (*Bupalus piniarius* (L.). Also, the larval winter dormancy was investigated and their cold-hardiness was determined. The investigation was carried out from September 1990 until May 1992.

MATERIAL AND METHODS

Characteristics of damaged pine stands, the selection and analysis of the test trees. All South-Estonian stands damaged by *P. piniphilus* are growing on poor acidic (pH_{KCl} 3.3) sandy soils where the root damage by *Heterobasidion annosum* is very common. There the ground water is deeper than 3 meters and in arid times the waterstress is usual. As *P. piniphilus* prefers to colonize 60-year-old pines in *Cladina* site type, and even aged stands (Kohh, 1939) — the investigation was carried out in stands of such age where species inhabits 30% of stems (Fig. 1).

For the study of the population density of *P. piniphilus* pines from two stands were chosen. The Kiidjärve stand (average height 14.9 m) is the area chronically damaged by *P. piniphilus*. In the Orava stand (average

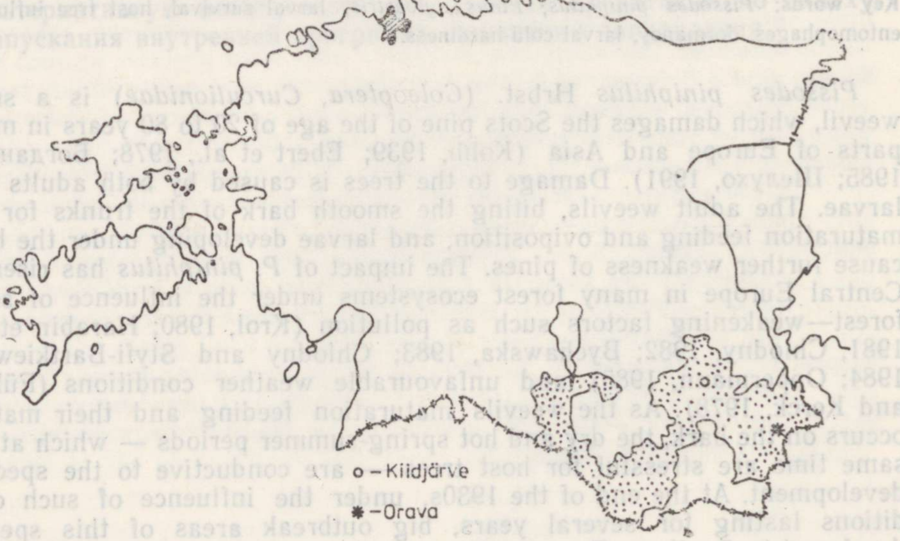

Fig. 1. The outbreak area of *P. piniphilus* in Estonia.

height 13.8 m) the pine looper also damages in some spots up to 90% of crowns. In both places the trees with different states of crowns colonized by *P. piniphilus* were analysed. 18 trees with green healthy-looking crowns (9 in both places) and 11 trees with yellowish tops from Kiidjärve and 10 trees with the 60 to 80% damage of crowns caused by the pine looper were investigated. The trees were felled and analysed in late autumn—November. On the trunks, starting from the root collar at every odd meter, 50 cm-wide sections around the stems were studied. All sections were measured, followed by a careful removing of the bark, and the bites, larval galleries and the larvae of *P. piniphilus* were counted; the associating species were also determined. Proceeding from these data, the average number and standard deviations of bites, larval galleries and living larvae per m² at different heights of the test trees were calculated.

For the examination of the colonization of *P. piniphilus* on felled stems 5 uninhabited pines were cut down in the middle of June in Kiidjärve and they were observed during June and July.

Also, the observations of weevils' larval development and colonizing the trees with other species of beetles were made in forest conditions in Kiidjärve.

Laboratory investigation. The headcapsules of the hibernating larvae (N=2471) were measured under the microscope in order to explain the different instars.

For the observation of the development ability of the hibernating larvae the colonized 50 cm-long pine logs (4 logs each time) were brought into the laboratory conditions (+21°C) at different times — at the end of August, in September and in March. Before this, the bark on these logs was removed from 10 cm-wide belts for the establishment of *P. piniphilus* development rate. The logs were taken from the trees with features of drying in their crowns. The logs were kept in laboratory conditions until weevils emerged. The behaviour of emerged adults was observed in the spring period.

In order to determine their cold-hardiness, the supercooling points of the last-instar larvae were measured thermoelectrically by using copper-constantant thermocouple in the middle of each month during the winter session 1990/91. The larvae were brought into the laboratory directly from the field conditions before each measuring. The series consisted of at least 20 to 25 specimens. The supercooling rate was 1 degree per minute.

For explaining the ability of cold acclimation, the larvae were exposed on logs at 2°C during different times from the middle of September to April.

RESULTS

The colonizing density of *P. piniphilus* on trunks is higher in the chronically damaged pine stand in Kiidjärve than in the borderland of the outbreak area in Orava (Fig. 2, 3). The inhabitation started immediately on the parts of the smooth bark and, in case of our test trees, at the height of 3 m, increasing towards the top.

The pines with healthy-looking crowns in both research areas were very densely bitten (Fig. 2). The adults of *P. piniphilus* bite the smooth bark of pines for the maturation feeding and oviposition. In a chronically damaged area, the biting rate was very high on the upper part of crowns — more than two thousand bites per m², on branches even up to 3000 bites per m². In the Orava district, the injured level of trees was lower. Typically, the number of bites prevailed many times the number of larval galleries,

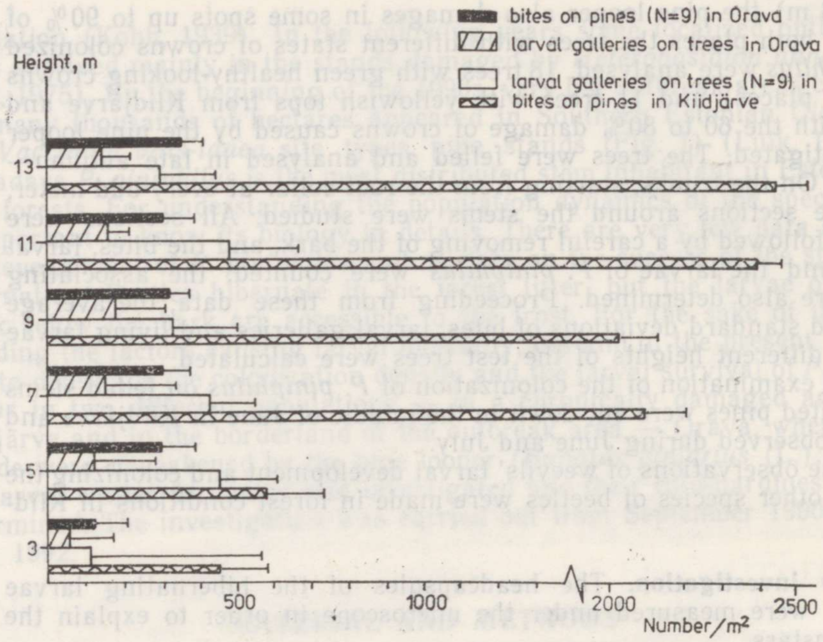

Fig. 2. The number of beetle bites and larval galleries of *P. piniphilus depending* on the different height of pines with healthy-looking greenish crowns.

which were short (1 to 3 cm long) and were filled with resin. There were found no living larvae or associate species. Three trees from Kiidjärve were only bitten and did not have any traces of larval galleries. The lower — one-meter-high — parts of all these trunks were not inhabited. But in the next spring trees of such kind of pathology were heavily attacked by *Tomicus piniperda* and *T. minor*, as it was shown in the analysis of trees with similar pathology.

On the pines with damaged crowns the number of bites was smaller than the number of larval galleries (Fig. 3). Larvae were also to be found on these trees. More living larvae were found on the lower parts of the trees in Orava damaged by the pine looper, whereas in the Kiidjärve pines the percentage of larval survival was higher in the upper part (Fig. 3). The larval survival rate was higher in the trees which were having more features of drying. The colonization density on the trunks in a chronically infested area was several times higher here than in Orava.

The lower parts of 30% of the test trees were colonized by *T. piniperda* with 9.8 egg galleries per m^2 on an average at the height of 1 m, and 24 at the height of 3 m. 20% of test sections of the heights of 9 to 13 m were coinhabited by *T. minor* with 25 egg galleries per m^2 on an average.

In these more weakened test trees entomophages in larval galleries were present (Table 1). In 2% of test sections appeared parasitic hymenoptera from genus *Eubazus*; *Coeloides* with parasitism rate of 5.3 to 37.5% appeared on several logs. Dipterous predators — *Lonchaea*, *Medetera* — occurred quite numerously in the trees having more features of drying, where timber under the bark was already stained blue. On the contrary, the entomophages of *Hemiptera*, *Coleoptera* and *Raphidioptera* were very few. The impact of entomophages seems to increase in the conditions of drying trees as it was seen in the case of the newly-felled trees. On the trees cut in the middle of June, *P. piniphilus* began maturation feeding at the beginning of July, and active mating on the stems took place in the

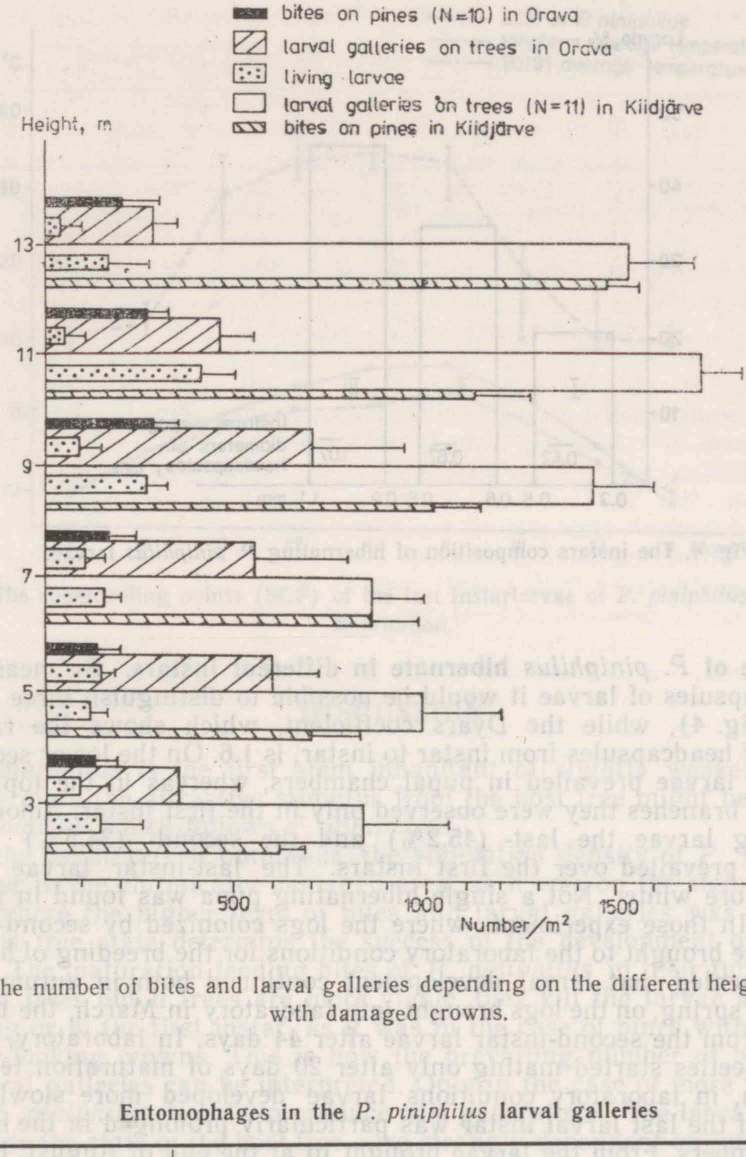

Fig. 3. The number of bites and larval galleries depending on the different height of pines with damaged crowns.

Table 1

Entomophages in the *P. piniphilus* larval galleries

Order	Genus
Hemiptera	*Anthocoris confusus*, *Scolopostethus* sp.
Coleoptera	*Phloeopora* sp.; *Thanasimus* sp.
Raphidioptera	*Raphidia* sp.
Hymenoptera	*Eubazus* sp.; *Coeloides* sp.
Diptera	*Medetera* sp.; *Lonchaea* sp.

middle of July. In September the larvae inhabiting the part of the trunk lower than 9 m already formed the pupal chambers, but in the top part there were only younger feeding larvae. The parasitism rate of larvae was 11.3 to 15.7% on different test sections, and they were mainly parasitized by *Eubazus* sp.

In the case of standing trees, beside insect entomophages woodpeckers also kill larvae and pupae, as it was already reported by Kohh (1939).

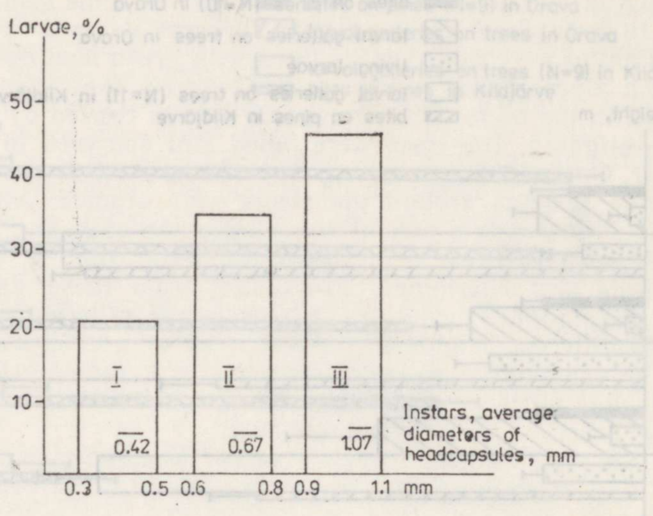

Fig. 4. The instars composition of hibernating *P. piniphilus* larvae.

The larvae of *P. piniphilus* hibernate in different instars. By measuring the headcapsules of larvae it would be possible to distinguish three larval instars (Fig. 4), while the Dyars coefficient, which shows the rate of increase of headcapsules from instar to instar, is 1.6. On the lower sections, last-instar larvae prevailed in pupal chambers, whereas in the top parts and in the branches they were observed only in the first instar. Among the hibernating larvae the last- (45.2%) and the second- (34.5%) instar specimens prevailed over the first instars. The last-instar larvae never pupate before winter. Not a single hibernating pupa was found in any of the trees. In those experiments where the logs colonized by second-instar larvae were brought to the laboratory conditions for the breeding of beetles, it was revealed that larval development continued both in autumn and spring. In spring, on the logs brought into laboratory in March, the beetles emerged from the second-instar larvae after 44 days. In laboratory, newly emerged beetles started mating only after 20 days of maturation feeding. In autumn, in laboratory conditions larvae developed more slowly; the duration of the last larval instar was particularly prolonged in the formed pupal chambers. From the larvae brought in at the end of August, beetles developed during 58 days, whereas from the second-instar larvae brought in at the end of September, beetles developed during 88 days. Consequently, in autumn the larvae had their dormant state and this particularly in their last instar, but the favorable temperatures quite easily terminated this. The dormant state guarantees for larvae the ability for cold acclimation. If the last-instar larvae had their supercooling point (SCP) −10.1 °C in September, then after being kept for 30 days in the conditions of 2 °C, they supercooled to −20.5 °C. At the same time in the natural conditions SCP of larvae fell only to −11.5 °C (Fig. 5). The SCP of first-instar larvae was only −6.2 °C in September and they were not able to acclimate to cold. Thanks to the ability of cold acclimation, the supercooling ability of the last-instar larvae fall, and with this their cold-hardiness rose parallel to the lowering of the temperature of the environment (Fig. 5). In midwinter larvae have high cold-hardiness — −34.5 °C on an average. But the larvae lost this cold acclimation ability in spring. A 20 days' exposure to 2 °C of larvae the SCP of which was in April −10.9 °C did not change their SCP.

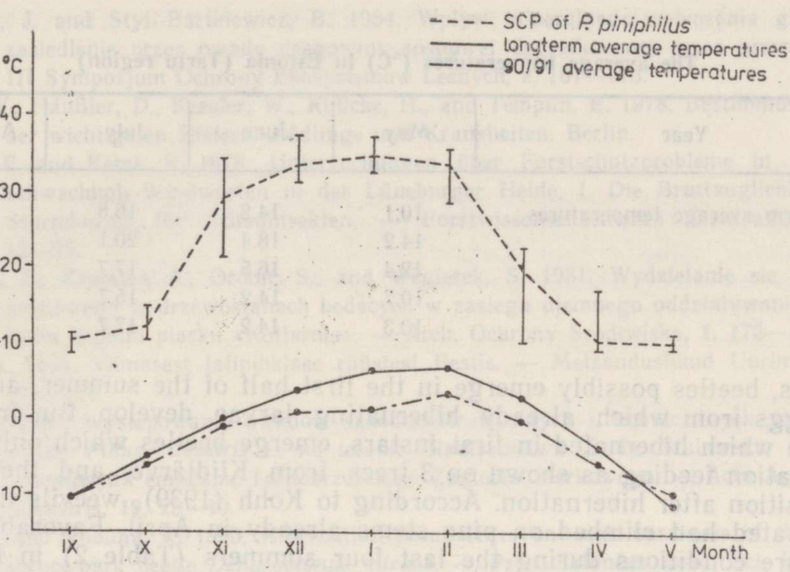

Fig. 5. The supercooling points (SCP) of the last instarlarvae of *P. piniphilus* during the hibernation.

DISCUSSION

P. piniphilus is the first stem inhabitant of slightly weakened pines and therefore the attractive stimulus from the host tree might be different from *Tomicus* which follows *P. piniphilus*.

In the conditions of outbreaks, the population density of *P. piniphilus* is higher in the chronically damaged area, as it was on the stems in Kiidjärve, where the higher level of bites and larval galleries was observed. The host tree state determins the success of the development of *P. piniphilus*. The maturation feeding bites of *P. piniphilus* in their turn weaken the host trees but if trees are more viable, they kill the larvae already at hatching or in the first instar, as it was in the case of pines with greenish healthy-looking crowns. This is how the prevailing number of bites upon the larval galleries can be interpreted. Only in the case of more weakened trees *P. piniphilus* is able to produce new generations. The larval survival is, beside the state of the host tree, also strongly dependent on intraspecific competition. In Kiidjärve there was already less than 10 cm² of the bark surface per larvae, which explains a rather high larval mortality on more weakened trees in the area. Comparing the larval survival in Kiidjärve to that in Orava where the intraspecific competition is lower (Fig. 3) than in the latter, it can be seen that the larval mortality was also very high. This is mainly explainable by the condition of the host tree, as many larval galleries were filled there with resin.

The increase of weevils' population density indicated that the stands contained quite a big number of sufficiently weakened pines for the weevils' development. With the drying of the host tree the role of entomophages rises. Usually pines successfully colonized by *P. piniphilus* die in the summer following their colonization; and by this time all the specimens have already emerged.

As larvae hibernate in different instars, in the next summer beetles emerge at different times, and start maturation feeding which lasts in natural conditions, perhaps for a shorter period than in the laboratory conditions. From the larvae which hibernated in the second and last

Table 2

The average temperatures (°C) in Estonia (Tartu region)

Year	May	June	July	August
Longterm average temperatures	10.1	14.2	16.8	14.9
1988	14.2	18.4	20.1	15.2
1989	12.4	16.5	17.7	17.0
1990	10.7	14.2	15.7	15.3
1991	10.3	14.2	17.7	17.1

instars, beetles possibly emerge in the first half of the summer, and they lay eggs from which already hibernating larvae develop. But from the larvae which hibernated in first instars, emerge beetles which only make maturation feeding as shown on 3 trees from Kiidjärve, and they start oviposition after hibernation. According to Kohh (1939), weevils that had hibernated had climbed on pine stems already in April. Favorable temperature conditions during the last four summers (Table 2) in Estonia (which were warmer than usual) promoted the mating and increased the speed of larval development. At the same time, as the winters were very mild without snow and frosts, all larvae (also in the first instar) were able to overwinter successfully.

The hibernating larvae have a dormant state characterized by the formation of the ability of cold acclimation due to which the second- and the last-instar larvae acquire high cold-hardiness — −34.5 °C — for midwinter. Usually such cold-hardiness level guarantees a successful hibernation for specimens. Only hard frosts could reduce the population. Apparently, one of the leading reasons why the weevils' populations reduced at the end of the 1930s was a very frosty winter in 1939/40 when the temperature fell down to −40 °C. The winter dormancy of *P. piniphilus* seems to be mainly an adaptation to the temperature, and the temperature controls its seasonal course. The similar dormant state also characterizes many other species of xylophagous (Zachariassen, 1985; Luik and Voolma, 1990). The increase of cold-hardiness under the influence of low temperatures is generally achieved either by the formation of the factors of thermal hysteresis, or by the accumulation of polyhydroxy alcohols or sugars.

On the basis of all these data it is possible to conclude that the increase of the population density of *P. piniphilus* in Estonia has been mainly caused by the weakness of pine-trees and due to favorable temperature conditions for the development of the insects.

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LATIPIHKLASE (*PISSODES PINIPHILUS*) ARENGU JA POPULATSIOONI DÜNAAMIKA MÕNINGAID ASPEKTE

Anne LUIK

Latipihklase vastsete suremust uuriti nii kahjustustunnustega kui ka tervete kroonidega 60-aastaste mändide tüvedel. Kuivõrd pihklane on esmane tüvede asustaja, siis hukkavad elujõulisemad puud pihklase juba kas muna või noore vastsena. Uus pihklase põlvkond suudab arengutsükli läbida vaid nõrgestatud puudel, kus populatsiooni tihedust reguleerivad peremeespuu kõrval ka tugev liigisisene konkurents ning entomofaagid. Viimaste hulgas on arvukamalt esindatud perekondade *Eubazus*, *Lonchaea* ja *Medetera* liigid. Haudepuude koore all talvitub *P. piniphilus* vanemate kasvujärkude vastsetena, kes aklimatiseerumisvõime tõttu saavutavad südatalveks märkimisväärse külmakindluse −34,5 °C. Vastsete talvine puhkeseisund on arenguks soodsates tingimustes kergesti ületatav.

Pihklase arvukuse tõus viimastel aastatel on tingitud eelkõige pihklasele soodsate haudepuude rohkusest ning arengut soodustavast temperatuurist.

НЕКОТОРЫЕ АСПЕКТЫ РАЗВИТИЯ И ЧИСЛЕННОСТИ СОСНОВОЙ ВЕРШИННОЙ СМОЛЕВКИ

Анне ЛУЙК

Смертность личинок смолевки изучалась на стволах 60-летних сосен как со здоровыми кронами, так и со знаками повреждения. Так как смолевка примарно атакует ствол сосны обыкновенной, то более жизнеспособные деревья уничтожают смолевку либо на стадии яйца, либо молодой личинки. Новое поколение успешно развивается только на ослабленных деревьях, где численность регулируется внутривидовой конкуренцией и энтомофагами, из которых наиболее распространенными являются представители родов *Eubazus, Lonchaea, Medetera.* Под корой кормовых деревьев смолевка перезимовывает на стадии личинки старшего возраста. Благодаря холодовой закалке в зимний период личинки достигают высокой холодостойкости — 34°С. Состояние зимнего покоя они легко преодолевают в условиях, благоприятных для развития.

Повышение численности сосновой вершинной смолевки в сосняках Эстонии обусловлено преимущественно обилием кормовой базы и благоприятными температурами развития смолевки.