Over-wintering of the Colorado potato beetle (*Leptinotarsa decemlineata* Say) in field conditions and factors affecting its population density in Estonia

K. Hiiesaar, L. Metspalu, J. Jõudu and K. Jõgar

Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Kreutzwaldi St. 64, 51014 Tartu, Estonia; e-mail: kylli.hiiesaar@emu.ee

Abstract. The adaptation of Colorado potato beetles (CPB) (*Leptinotarsa decemlineata* Say) to low temperatures has been the basis for the formation of a local permanent population in Estonia. The number of this pest fluctuates in different years on a large scale. The hibernation of the beetles in field conditions during the years 2000–2005 was observed and some factors influencing the beetles' mortality was discussed in this study. Soil with a lighter texture - loamy sand proved better for the hibernation of CPB than clay loam soil with a heavier texture. 30 cm confirmed to be more suitable depth for hibernation than 50 cm, demonstrating lower mortality rate. Every autumn CPB populations were differently prepared for hibernation: part of the beetles burrowed themselves into the soil considered to be ready for over-wintering, and there were more survivals than among the beetles staying on the soil surface: that could not complete their maturation feeding. The temperature may become lethal for a majority of the hibernating population only during extreme winters when the temperature falls to -30°C for a longer period of time. During our observation period, it happened only once: in 2002/2003. In more mild winters there were no problems with over-wintering: about two third of the beetles survived in clay sand and about a half in loamy clay soil. It is difficult to predict the annual damage caused by CPB because the Estonian population consists of adapted over-wintered beetles and beetles migrated from southern regions. In some years we have had a great number of immigrant beetles and, in some years, no immigration has occurred.

Key words: Colorado potato beetles, overwintering, soil type, mortality

INTRODUCTION

The history of the Colorado potato beetle (CPB) (*Leptinotarsa decemlineata)* in Europe is not long. The beetles reached Europe from the North America for the first time at the end of 19th century and established here only in 1922 (Roman & Radcliffe, 1992). The potential northern limit of their distribution area was considered 54–56° north latitudes. As environmental conditions, especially low temperatures, which are the main hindrance for their survival and spread, determine the borders of the beetle's distribution; CPB further spread to northwards was restricted. However the CPB has great ability to adapt to variable environmental conditions. Despite all predictions, the area of its distribution has been expanding continuously, and the first findings of the beetles in Estonia, at 59° north latitudes, come from the year 1965 (Kuusksalu & Kangilaski, 1972; Kuusik, 1978). Due to application of eradication measures and susceptibility of the beetles to cold they were not established in the area at that time.

Newerless according to our inspections during the last decades, CPB has formed a permanent population in Estonia (Hiiesaar et al., 2001; 2005). Expansion of the beetles habitat has not finished yet and, at present time, it is suggested that the area of CPB could widen as far as potatoes can be cultivated.

There are a numerous factors influencing the value of the low temperature exotherm and survival of the beetles. CPB overwinter as adult in the soil in diapause state. In case of hibernating beetles, a direct relationship between diapause and cold tolerance has been established (Pullin, 1994; Sømme, 1999). By the termination of diapause and in the course of cold-hardening, initiated already in fall by low temperatures and a short photoperiod, supercooling ability and cold tolerance of CPB increase noticeably (Merivee, 1978; Hiiesaar et al., 2001).

Many insects are able to increase their cold tolerance seasonally, which also enhances their winter survival (Bale 1989). Acclimation, which suppresses the effect of lethal temperatures on the insect, is also important factor increasing cold tolerance (McDonald et al., 1997). Non-acclimated active CPB can tolerate temperatures only some degrees below zero (Ushatinskaya, 1974; Merivee, 1978), whereas after the acclimation the temperatures tolerated are lower (Sømme, 1996; Block et al, 1999; Hiiesaar et al., 2001).

Cold tolerance of many insects is characterised by their supercooling points (Bale, 1987). Different authors have obtained different results by measuring supercooling points of CPB: from -6°C to -17°C (Rodionova, 1969; Minder & Chesnek, 1970; Lee et al., 1994; Boiteau & Coleman, 1996; Hiiesaar et al., 2001). There can be several reasons for that, however, we consider one reason to be the fact that the supercooling ability of CPB populations in different geographic areas is largely different. Nevertheless, the SCP (supercooling point) of beetles should not be considered the only criterion of cold hardiness, as many freezing-intolerant insect die at temperatures above their supercooling point before they freeze (Bale 1993; Renault et al., 2002). The exposure periods shall be taken into consideration as well. The beetles can tolerate temperatures near the supercooling point for a very short time, for a longer period they can survive only on much higher temperatures (Mail & Salt, 1933; Sømme, 1996).

Since successful hibernation of insects does not respond only to temperatures but depends on many environmental factors, and, it is not possible to imitate in a laboratory all field circumstances like moisture, fluctuating temperatures, microclimate, etc., it is recommended to carry out some experiments directly in nature (McDonald et al., 1997).

The aim of this paper was to determine the mortality of CPB in different years through their over-wintering under field conditions and to analyse some factors influencing the formation of a permanent local population of CPB.

METHODS

In the 2000/2001 one preliminary experiment was carried out to establish the influence of the feeding rate and over-wintering depth of the beetles on their survival during hibernation.

CPB of mixed sexes were collected from potato fields in southern Estonia during late August and September. The collected field-fresh beetles were placed in 3 litre glass jars half filled with slightly moist Sphagnum peat and kept at room temperature for 24 hours.

The beetles were divided into two groups according to their behaviour: part of them immediately dug themselves into the soil and part of them remained on the surface. Then the beetles were put into string bags filled with peat and placed in a refrigerator at +5^{o}C for one month. In October the bags were dug into the soil in an open field at different levels in 30 cm and 50 cm depth. The lowest temperatures during the entire over-wintering period were registered with two special minimum thermometers placed at the same depths into the soil.

In the years from 2001 to 2005, the CPB overwintering experiment was repeated. To imitate natural conditions entirely, the beetles were not separated anymore according to their behaviour and feeding rate. The beetles collected in the fields in September were immediately transferred in 0.5 litre perforated plastic jars filled with loamy sand and clay loam, brought to the field and dug into the soil at 30 cm depth.

In the middle of May, the beetles were retrieved from the soil and their mortality rate was determined.

Three replicate experiments were carried out at each soil type and digging depth. The data were processed by using the *t*-test and one-way ANOVA.

RESULTS

Over-wintering depth. The beetles were kept at the hibernation site from October until May, i.e. during the same period as they do usually under natural conditions. 30 cm proved to be more suitable depth for hibernation: the mortality of the beetles was lower than at 50 cm depth (Fig. 2). There was significant difference in mortality between the over-wintering depth of beetles irrespective of their feeding rate (*t*-test, $P < 0.05$).

Feeding rate. Beetles gathered from the field differed in their behaviour: part of the beetles dug themselves into the soil within the first 24 hours. These beetles had completed their feeding and it was considered them to be in diapause and ready for hibernating. Part of the beetles stayed on the surface of soil and moved actively around during the first 24 hours at room temperature and also when they were taken to a refrigerator at +5^{o}C. These beetles had not managed to finish their maturation feeding and were not ready for hibernation. A post-hibernation analysis showed that the beetles that dug into the soil over-wintered more successfully than those who remained on the soil surface, the mortality rates being 52% and 76% at 50 cm depth and 32% and 61% at 30 cm depth, respectively (Fig. 2). There was significant difference between the mean mortality of different feeding rate of beetles (*t*-test, $P < 0,05$).

The lowest temperature of the winter in this experiment was recorded -7.0°C at 30 cm depth and -4.0°C at 50 cm depth.

Soil type. A soil with lighter texture, loamy sand, proved to be better for the hibernation of CPB: the mortality rate there was lower than in clay loam soil. A statistical analysis of the test results showed the dependence of the mortality rate on the soil type clay loam: $F_{(3;8)} = 120.6$; $P = 0.0000005$ and loamy sand $F_{(3;8)} = 54.3964$; $P = 0.00001$, ANOVA test (Fig. 3).

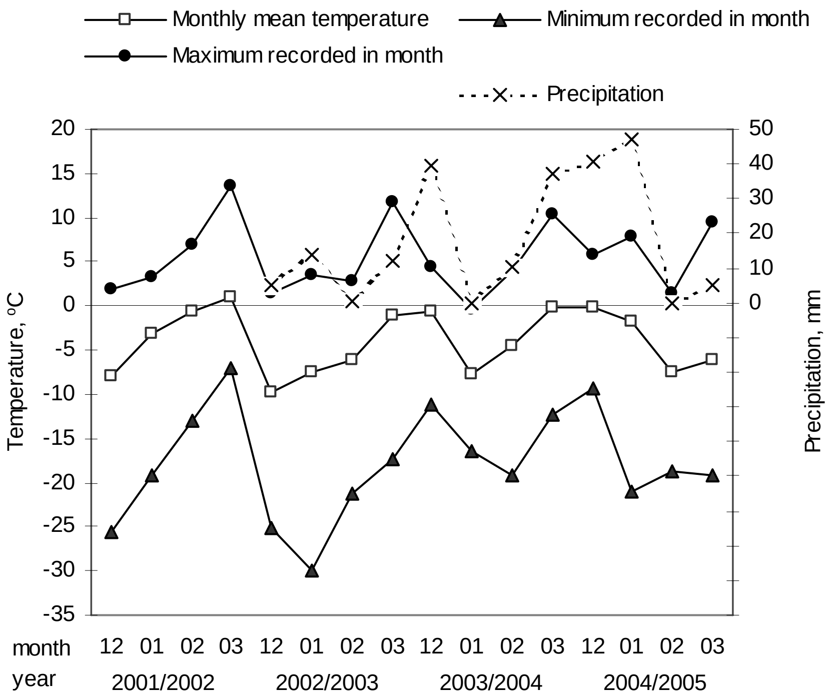

Fig. 1. Temperature data for 2001–2005 based on data provided by Tartu automatic weather station situated in Erika.

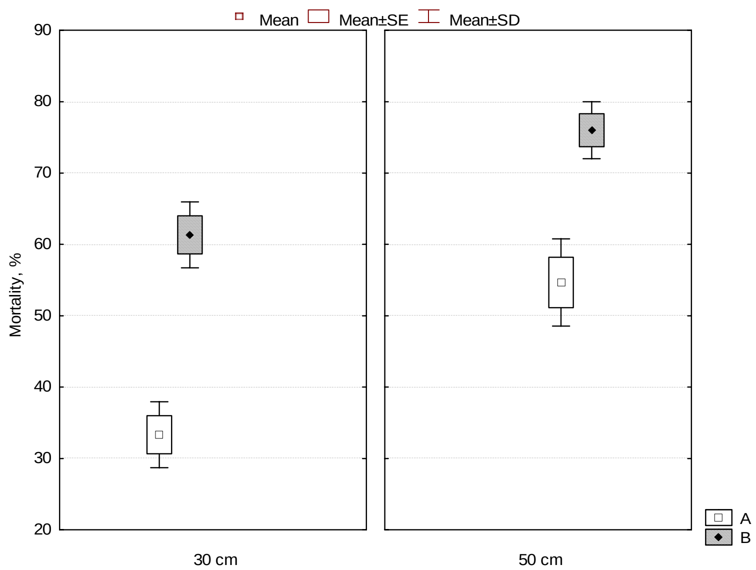

Fig. 2. Mortality of Colorado potato beetles by over-wintering in field conditions at different depth of soil. A. Beetles burrowed in the ground before overwintering; B. Beetles did not burrow in the ground before overwintering. Preliminary experiment of 2000/2001.

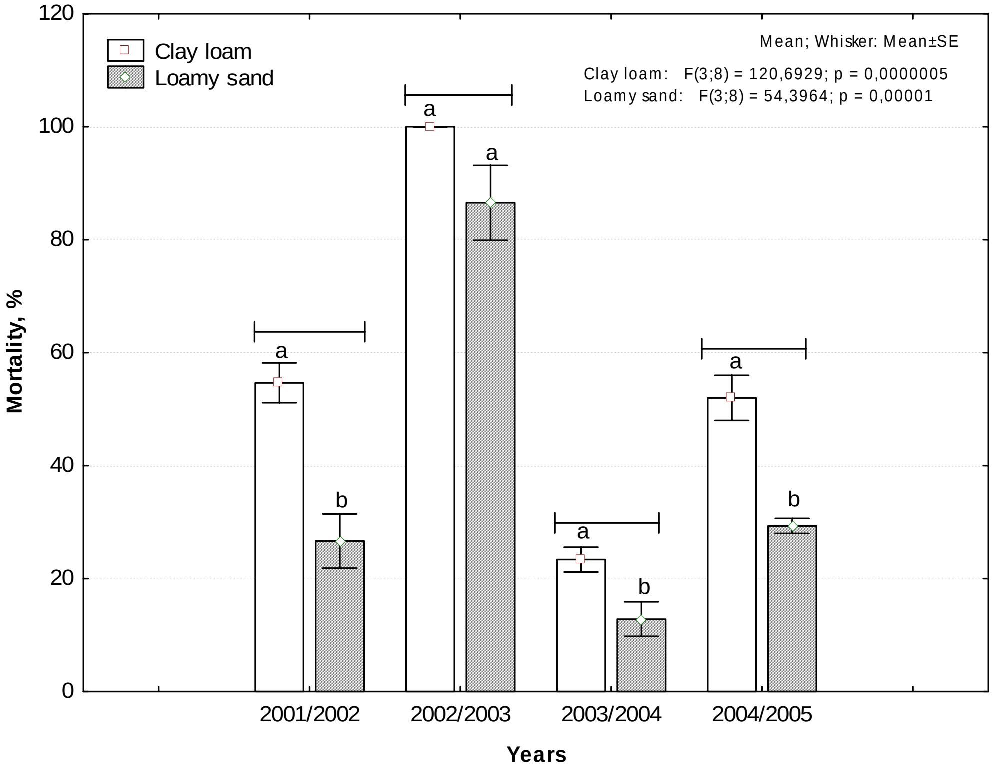

Fig. 3. The mortality of Colorado potato beetles overwintering in field conditions on different years in loamy sand and clay loam soil. Error bars indicate standard error of the mean. Mean values with same letters do not differ significantly (based on *t*-test). The horizontal bars mean that statistical comparisons are valid within the one and same winter.

Temperature and mortality of beetles. Estonian climate is highly variable in different years by temperatures and rainfall (Fig.1). The winter of 2001/2002 was not very cold but there were often long-term periods of thaw with a maximum temperature of up to +7.0°C (Fig. 1). During this period, more than a half of the beetles over-wintering in clay loam perished while only about one third died in loamy sand (Fig. 3).

The winter of 2002/2003 was extremely harsh, when temperature fell continuously near -30°C: then all the beetles hibernating in clay loam perished, however, about 12% of the beetles hibernating in lighter loamy sand survived (Fig. 3). The winters of the next two years were much milder.

The winter of 2003/2004 was the most favourable of the observation years. In that winter, the soil was frozen by December and there were no long periods of thaw. So in that year only about 12% of the beetles perished in loamy sand and over 20% in clay loam soil.

The minimum and average temperatures of the winter of 2004/2005 were somewhat higher than in the previous year, however, the mortality of the beetles was over twice higher than in the previous year: 32% in loamy sand and 57.6% in clay loam soil (Fig. 3).

DISCUSSION

Feeding. The success of the hibernation and formation of a permanent local population in northern regions depends on several factors influencing the survival of the beetles. One of the factors is the preparation for hibernation. Newly emerged CPB must be able to feed before going into soil for hibernation, because they require energy to survive long period at low temperatures. As our long-term observations show, in August and September, when most of young beetles emerge from the soil and begin feeding, potato plants in unsprayed fields have already perished due to late blight *(Phytophtora infestans*). However the chemical composition of food plants plays an important role in the formation of the beetle's diapause (De Wilde et al., 1959). This is the reason why all beetles have prepared differently for over-wintering by autumn. The beetles emerging earlier have enough time to feed sufficiently, their diapause has already been formed; beetles become positively geotactic and borrow into soil (de Wilde, 1969). The digging behaviour has been used as a criterion of the onset of diapause (Beck, 1968). Those beetles over-wintered better and their mortality level was relatively low. The beetles emerging later because of poor quality or lack of food could not store enough resources and kept wandering about in the field in search of food. They were not yet ready for hibernation and the mortality of these beetles was high.

According to some studies, the quality of the host plant has a great effect on development of CPB and the population growth (Voss et al., 1990). Healthy undamaged potato leaves contain the most well-balanced configuration of amino acids, which are the main components in synthesis of proteins (Cibula et al., 1967). If leaves have been destroyed by diseases, the beetles start eating potato stems and even the tubers on the ground, however, this does not provide them with all necessary nutrients, and over-wintering potential of the beetles is in danger (Ushatinskaya, 1981). Not only completion of maturation feeding of newborn beetles is important for successful hibernation. Development conditions of the earlier stages, like the temperature and the quality of food, which determines the weight of the adults, are also important. According to our research, beetles weighing less than 100 mg are not able to survive the winter (Hiiesaar et al., 2005).

Soil quality. In northern regions, where insects are subject to low subzero temperatures for a long time, temperature and behaviour adaptations are necessary for the occurrence and survival of species (Block, 1990). Continuous gradual declining of temperature fosters the acclimation, intensifies the diapause and increases the cold tolerance of beetles (Sømme, 1982). To avoid to be killed by frost, CPB burrow themselves in the soil where the fluctuation of temperature is lower than in the air and the temperature does not drop too low, especially when a snow layer covers the soil. The soil type, its physic-chemical attributes like structure, texture, water potential etc. play also an important role in overwintering of CPB. Hibernation was compared in two soil types most common in central and southern Estonia: loamy sand and clay loam soil. Loamy sand with better aeration and no excessive water proved to be the more suitable for CPB (Figure 3). There are data in literature suggesting that the mortality of the beetles may be 7–8 times lower in loamy sand than in clay loam

(Ushatinskaya, 1973). We, however, did not find such great differences. In lighter soils rich in organic substance, the beetles may penetrate to a depth of up to 60–80 cm, without any risk of oxygen lack (Kuusik et al., 2001). In heavier clay loams, the beetles penetrate only to a depth of 20 cm, however, there the outflow of melt-water is an obstruction and the beetles may easily suffer due to lack of oxygen. Ushatinskaya (1973) considers one of the main reasons for the lethality not directly freezing, as soil and snow cover create a considerably good insulation layer, but a lack of oxygen. Under such conditions, the beetles are often attack by several diseases caused by pathogenic micro-organisms (Sandner & Stanuszek, 1968; Minder & Tshesnek, 1970). An analysis of our material showed more often occurring fungal- and bacterial diseases while over-wintering in clay loam. Even if the disease does not kill the CPB, it reduces their cold- hardiness (Lee et al., 1994).

Winter temperatures. Mortality of several species can be predicted by winter temperatures (Bale, 1993). However, perishing in natural conditions is not always entirely consistent with the temperatures. Estonian winters can be highly variable: temperatures ranging from -30°C in one year and almost +10°C in another winter at the same time are not unusual. Low temperatures were considered a possible limiting factor in the northern spread of the CPB (Mail & Salt, 1933). Indeed, after their arrival in Estonia, CPB could not hibernate here. After first findings of the beetles in 1965, there followed many years with this pest absent (Kuusksalu & Kangilaski, 1972). Regular exposure to low temperatures may increase the frost tolerance of the beetles by lowering their supercooling points (Bale, et al., 2001). Due to their good adaptation ability the CPB has increased its cold hardiness continuously (Merivee, 1978) and adapted to over-wintering here. The temperature that can be survived by CPB (low temperature exotherm (LTE) is not a constant indicator. According to Boiteau and Coleman (1996), it is -11.7° C for the over-wintering beetles, but the value obtained by Ushatinskaya (1966) is only -7°C. Salt (1933) and Mail & Salt (1933) have obtained even higher values. According to our observation the supercooling point of CPB in diapause reached -14 to -17°C in mid-winter (Hiiesaar et al., 2001). Those records illustrate differences in LTEs of both spatially and temporally different populations but not their actual hibernation ability. CPB cannot survive long exposure to such low temperatures because their metabolic functions may be disrupted even at higher temperatures (Danks, 1987). In New Brunswick, 50% of over-wintered CPB adults survived only 3-h exposure to -7°C (Boiteau & Coleman, 1996). In our observations, also -7°C was measured the actual minimum temperature in the beetles' hibernation at 30 cm depth in 2000/2001, however, then only a third of the over-wintered beetles perished. It may be assumed that the beetles had to endure such a temperature for a longer period, which confirms the greater cold tolerance of Estonian CPB population. On the depth of 50 cm, the minimum temperature was measured -4.0°C, but the mortality of the beetles was higher, about 50%.

Thus the survival of CPB is not attributed only to one factor, low temperature, but there are other factors determine overwintering mortality in field conditions. Some authors consider that during long-term exposure to low temperatures the organisms may die from the exhaustion of energy supplies even if the insect does not freeze (Renault et al., 2002), and unfrozen individuals can be injured in above and below 0°C (Danks, 1996). Our perennial field experiments showed that temperature may become lethal for a big part of hibernating population only during extreme winters for instance in 2002/2003 when the air temperature was about -30°C for a longer period of time. Then all beetles perished in clay loam, however, the one tenth who successfully hibernated in lighter soil let us assume that CPB has established in Estonia permanently. The real mortality of CPB over-wintering freely in nature may be lower as their priority is their free choice of the hibernation sites. Part of the individuals leave the fields and go to the forest edges which are better protected from unfavourable climatic conditions: trees act as a barrier to snow and the places are rarely under water.

Summer immigration. In summers following a very harsh winter there can be predicted a low period for the local population, however, it is difficult to predict immigration from the southern regions. This depends primarily on weather conditions and prevailing wind directions, due to which, in some years, most of the fields have been infested with immigrant beetles but, in some years, no immigration has occurred. With thunderstorm air flows, large CPB swarms can be carried hundreds of kilometres in distance (Presman, 1968). Due to frequent south and south-east winds in 2002, we had abundant migration and outbreak of CPB that year. Much of adult beetles can be dispersed over long distances floating in sea water too. According to our laboratory experiments (unpublished data), the beetles could survive in sea water at least for 10 days, and some of specimens even longer.

Conclusion. The adaptation of CPB to low temperatures has been the basis for the formation of a local permanent population in Estonia. However, unfavourable climate of northern regions should be considered to be the limiting factor of the pest population. The beetles surviving over-wintering at low temperatures have functional changes in their organism like disorders of heart activity, metabolic disturbance etc. (Minder, 1969). Low temperatures during the vegetation period, spring-summer night frosts and lack of quality food affect through the preimaginal stages, the weight of the beetles and, as a result, also the success of their hibernation, later their fertility and therefore the population density (Hiiesaar et al., 2005). However CPB has so far been the only insect pest of potato in Estonia that requires application of chemical control measures from time to time.

ACKNOWLEDGEMENTS. The study was supported by Estonian Science Foundation grant No 6722.

REFERENCES

Bale, J.S. 1987. Insect cold hardiness: freezing and supercooling – an ecophysiological perspective. *J. of Insect Physiol.* **33**, 899–908.

Bale, J.S. 1989. Cold hardiness and overwintering of insects. *Agricultural Zoology Review* **3**, 157–192.

Bale, J.S. 1993. Classes of insect cold hardiness. *Functional Ecology* **7,** 751–753.

Bale, J.S., Worland, M.R. & Block, W. 2001. Effect of summer frost exposures on the cold tolerance strategy of sub-Antarctic beetle. *J. Insect Physiol.* **47,** 1161–1167.

Beck, S. 1968. *Insect Photoperiodism*. Academic Press, New York, London, 288 pp.

Block, W. 1990. Cold tolerance of insects and other arthropods. *Philosophical transactions of the Royal Society of London.* (B)326, 613–633.

Boiteau, G. & Coleman, W. 1996. Cold tolerance in the Colorado Potato beetle, *Leptinotarsa decemlineata* (Say) (Coleopter: Chrysomelidae). *Can. Entomol*. **128**, 1087–1099.

Cibula, A.B., Davidson, R. Fisk, F.W. & Lapidus, J.B. 1967. Relationship of free amino acids of some solanaceous plants to growth and development of *Leptinotarsa decemlineata* (Say) (Coleoptera:Chrysomelidae). *Ann. Ent. Soc. Am.* **60**(3), 626–631.

Danks, H.V.1987. Insect Dormancy*: An Ecological Perspective. Biological Survey of Canada (Terrestrial Arthropods),* Ottava, Ont., 439 pp.

Danks, H.V. 1996. The wider integration of studies on insect cold-hardiness. *Eur. J. Entomol.* **93,** 383–403.

De Wilde, J. 1969. Diapause and seasonal synchronisation in the adult Colorado potato beetle (*Leptinotarsa decemlineata* Say), In S*ymposium of the Society of Experimental Biology* **23.** Dormancy and Survival. Cambridge University Press, Cambridge, UK, pp. 263–284.

Hiiesaar, K., Kuusik, A., Jõudu, J., Metspalu, L., Hermann, P. 2001. Laboratory experiments on cold acclimation in overwintering Colorado potato beetles, *Leptinotarsa decemlineata* (Say). *Norw. J. Entomol*. **48,** 87–90.

Hiiesaar, K., Metspalu, L., Jõudu, J., Jõgar, K. 2005. Influence of low temperatures on development of preimaginal stages of Colorado Potato beetles *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). *Egipt. J. Agric. Res.* **83**(2), 707–718.

Kuusik, A. 1978. *Kartulimardikas. Bioloogia ja tõrje*. Valgus, Tallinn, 119 lk. (in Estonian).

Kuusik, A., Metspalu, L., Hiiesaar, K., Hermann, P., Harak, M. 2001. Anaerobioos kartulimardikal *Leptinotarsa decemlineata* Say. *EPMÜ Teadustööde kogumik* **213**, 89–95.

Kuusik, A., Hiiesaar, K., Metspalu, L., Hermann, P. 2001. The physiological characteristics of the perennial diapause in the Colorado potato beetles. *Transactions of the Estonian Agricultural University* **212,** 161–166.

Kuusksalu, R. & Kangilaski, E. 1972. Kartulimardikas. *Kartulikasvatuse päevaprobleeme* **2,** Tallinn, 261–265 (in Estonian).

Lee, R.E., Jr., Costanzo, JP., Kaufman, P.E., Lee, M.R. & Wyman, J.A. 1994. Ice-nuceating active bacteria reduce the cold-hardiness of the freez-tolerant Colorado potato beetle (Coleoptera; Chrysomelidae) *J . Econom. Enomolt.* **87**(2), 377–381.

Mail, G.A. & Salt, R.W. 1933. Temperature as a possible limiting factor in the northern spread of the Colorado potato beetle. *J. Econ. Entomol*. **26**, 1068–1075.

McDonald, J.R., Bale, J.S. & Walters, K.F.A. 1997. Low temperature mortality and overwintering of the western flower thrips *Francliniella occidentalis* (Thysanoptera: Thripidae). *Bull. Entomol. Res.* **87,** 497–505.

Merivee, E. 1978. Cold-hardiness in insect. Acad. Sci. Estonian SSR, Tallinn, 188 pp.

Minder, I.F. & Tšesnek, S.I. 1970. Зависимость холодоустоичивости колорадского жука от времени наступления диапаузы. *Зоол. Журнал* т. **49** стр. 855–861 (in Russian).

Minder, I.F. 1969. Холодоустоичивость колорадского жука. Периодичность индивидуального развития насекомых. М. Наука, стр. 99–29 (in Russian).

Presman, A.C. 1968. Электромагнитные поля и живая природа. М. Наука 288 стр. (in Russian).

Pullin, A.S. 1994. Evolution of cold hardiness strategies in insects. *CryoLetters,* **15,** 6–7.

Raman, K.V. & Radcliffe, E.B. 1992. Pest aspects of potato production. Insect pest. In Harris P.M.(ed.): *The potato crop. The scientific basis for improvement.* Chapman & Hall, London-New York-Tokyo-Melbourne-Madras, pp. 477–497.

Renault, D., Salin, C. Vannier, G. & Vernon, P. 2002. Survival at low temperatures in insects: what is the ecological significance of the supercooling point? *CryoLetters* **23,** 217–228. CryoLetters, c/o Royal Veterinary College, London NW1 0TU, UK

Rodionova, L.Z. 1969. Cryoprotective reactions in ovewintering Colorado potato beetles (*Leptinotarsa decemlineata* Say). In Arnoldi, K.V. (ed.): *Periodicity of Individual Development in Insect.* Nauka Publishers, Moscow, pp. 131–139.

Salt, R.W. 1933. Some experiments on the freezing and Hardening of the Adults of the Colorado Potato Beetle, (*Leptinotarsa decemlineata* Say. M.Sc. thesis, Montana State College, Bozeman, MT, 82 pp.

Sandner, H. & Stanuszek, S. 1968. Natürliche Regulationsfaktoren und biologische Bekampfung des Kartoffelkäfers (*Leptinotarsa decemlineata* Say). *Pflanzenschutzberichte* **38,** 12, 177–187.

Sømme, L. 1982. Supercooling and winter survival in terrestrial arthropods. *Comp. Biochem. Physiol. (*A) **73**, 519–543.

Sømme, L. 1996. The effect of prolonged exposures at low temperatures in insects. *CryoLetters* **17**, Wooton Way. Cambridge CB3 9 LX.U.K., pp. 341–346.

Sømme, L. 1999. The physiology of cold hardiness in terrestrial arthropods. *Eur. J. Entomol*. **96,** 1–10.

Ushatinskaja, R.S. 1966. Prolonged diapause in Colorado beetle and conditions of its formation. In Arnoldi, K.V. (ed.): *Ecology and Physiology of Diapause in the Colorado Beetle,* New Dehli, 357 pp.

Ushatinskaja, R.S. 1973. Диапауза насекомых и ее модификации. *Журнал общей биологии* **34,** 194–215 стр. (in Russian).

Ushatinskaja, R.S. 1974. Эколого-физиологическая приспособенность kолорадского жука (*Leptinotarsa decemlineata* Say) к периодичности абиотических факторов внешней среды. В кн. *Вопросы экологической фигзиологии беспозвоночных*. М., 5–44 (in Russian).

Ushatinskaja, R.S 1981. Colorado Potato Beetle, *Leptinotarsa decemlineata S*ay. Nauka Publishers, M., 375 pp.

Wilde, J.de, Duintjer, C. S. & Mook, L. 1959. Physiology of diapause in the adult Colorado beetle (*Leptinotarsa decemlineata* Say). The photoperiod as a controlling factor. *J. Insect Physio*l. **3,** 75–85

Voss, R.H. & Ferro, D.N. 1990. Phenology of flight and walking by Colorado potato beetle (Coleoptera:Chrysamelidae) adults in Western Massachusetts. *Environ. Entomol*. **19,** 117–122.