DOI: 10.2478/frp-2014-0035

Leśne Prace Badawcze (*Forest Research Papers*),
December 2014, Vol. 75 (4): 375–383

ORIGINAL RESEARCH ARTICLE

Survival and growth of the *Melolontha* spp. grubs on the roots of the forest's main tree species

Danuta Woreta, Lidia Sukovata*

Forest Research Institute, Department of Forest Protection, ul. Braci Leśnej 3, Sękocin Stary, 05–090 Raszyn, Poland.

* Tel. +48227153832; e-mail: L.Soukovata@ibles.waw.pl

Abstract. The survival, weight and relative growth rate (RGR) of the *Melolontha* spp. grubs feeding on roots of *Quercus petraea, Q. robur, Fagus sylvatica, Betula pendula, Larix decidua, Alnus glutinosa* and *Pinus sylvestris* were examined.

Overall, the youngest grubs, L1, were the most affected by food quality. The mortality of the grubs feeding on the roots of *A. glutinosa* changed most rapidly and, consequently, LT50 was the shortest (25.9 days), whereas the slowest changes in mortality with the highest LT50 values were observed on the two oak species (54.9 and 44.9 days on *Q. robur* and *Q. petraea*, respectively). The RGRs of the L1 grubs were the highest on oaks, *F. sylvatica* and *B. pendula*. The overall rate of survival of the older grubs was high (66.7-100%). It was the lowest on the roots of *B. pendula* (L2 grubs) and *L. decidua* (L3 grubs), which at the same time displayed the highest RGRs.

The interpretation of the results is difficult due to the lack of basic knowledge on the potential effects of food quality and other factors on grub metamorphosis. There is no doubt, however, that among the seven tested tree species the roots of *A. glutinosa* are the least favorable for the *Melolontha* grubs' performance.

Keywords: *Quercus robur, Quercus petraea, Fagus sylvatica, Betula pendula, Larix decidua, Pinus sylvestris, Alnus glutinosa*, relative growth rate, mortality, food quality

1. Introduction

The common cockchafer *Melolontha melolontha* (L.) and the forest cockchafer *M. hippocastani* F. (Scarabaeidae) are extremely harmful forest insect pests in Poland. Their larvae feed on the roots of trees and shrubs, causing die-off of forest plantations and delaying reforestation.

In Poland, after the World War II, there was an urgent need to afforest large areas of different types of unused or low-productive agricultural lands that had already been infested by cockchafer grubs (Woreta and Skrzecz 1996). The use of highly efficient chemical pesticides (DDT, HCH) to control these pests caused a substantial decrease in the area of grub occurrence to less than 500 ha in 1980-1993 (Woreta 1994). Over time, environmentally toxic plant protection chemicals were replaced with new pest control products, potentially less harmful to ecosystems. These products (e.g., from the group of pyrethroids), were highly efficient in the control of imagines (Woreta 1999). However, the European Parliament has introduced legal regulations banning the insecticides recently used to control grubs (e.g. Regulation (EC) No 1107/2009 of the European Parliament and of the Council of 21 October 2009) due to environmental concern. The lack of efficient plant protection products has resulted in the increase of forest regeneration areas threatened by *Melolontha* spp. grubs. Tree saplings damaged by cockchafer grubs often die and need to be replaced by new ones, and sometimes the entire area needs to be reforested once again. In 1966-2005, the percentage of the area which required supplementary reforestation was below 21%, whereas after 2005, it ranged from 26% to 53%. As a result of the long lasting outbreak of *Melolontha* spp., permanent outbreak foci appeared all over the country, where reforestation has

Received 22 May 2014, accepted after revision 18 July 2014.

become extremely difficult due to repeated damage of tree sapling roots.

The limited use of insecticides has led to increasing interest in non-chemical methods of plant protection, including silvicultural, agrotechnical and biological ones. The present study was aimed to examine the effects of food type (saplings of different forest tree species) on survival and body weight of cockchafer grubs. The results could be helpful in selecting species composition for reforestation/afforestation in the areas threatened by *Melolontha* spp.

2. Study objects and methods

Study objects

The *Melolontha* spp. grubs at all three instars: L1, L2, and L3, were used in the study. The instars were distinguished based on the width of a grub head capsule (Śliwa 1993). Precise identification of grub species was not possible due to the lack of reliable methods (Krell 2004). However, it could be stated with some probability that most of L2 and L3 grubs used in the study belonged to *M. hippocastani* (the surviving individuals emerged as *M. hippocastani* imagines).

The saplings of the following forest tree species were used to feed the grubs: pedunculate oak (*Quercus robur* L.), sessile oak [*Q. petraea* (Matt.) Liebl.], common beech (*Fagus sylvatica* L.), silver birch (*Betula pendula* Roth.), black alder [*Alnus glutinosa* (L.) Gaertn.], European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.).

Experimental design

Growth and survival of cockchafer grubs feeding on saplings of selected tree species were studied in 2011-2012, in the greenhouse of the Forest Research Institute (FRI).

The experiment with the L2 grubs was set up in 2011, and lasted from May 20 to September 29. The grubs were collected in the territory of Kozienice Forest District (Regional Directorate of the State Forests (RDSF) in Radom) by searching in the soil to the depth of about 20-30 cm. The grubs were fed with two-year old tree saplings obtained from tree nurseries of the following Forest Districts: Grójec and Chojnów (RDSF in Warsaw), Ostrowiec Świętokrzyski (RDSF in Radom) and Pniewy (RDSF in Poznan).

In 2012, the grubs that molted into L3 grubs in the middle of 2011 in the previous experiment and overwintered in the greenhouse were used in the experiment with the L3 grubs. The grubs were fed on the roots of two-year old saplings obtained from tree nurseries of the Forest Districts: Pniewy, Chojnów and Grójec between April 20 and June 27.

The experiment with the L1 grubs collected in the territory of Lubartów Forest District (RDSF in Lublin) was set up also in 2012. The L1 grubs were fed on the roots of one-year old saplings from the container nursery in the Jabłonna Forest District (RDSF in Warsaw). The study lasted from May 28 to September 18.

The grubs were placed into pots with garden soil (Agrohum, Łomianki, Poland) and saplings of the tested tree species (1 sapling/pot). There were two L1 grubs or one grub of either L2 or L3 instar in each pot. There were 15 replications for each tree species in the experiment with the L2 grubs, and 10 replications in the experiments with the L1 and L3 grubs. The L3 grubs were placed into the pots with the same tree species they were reared as the L2 grubs in 2011.

Before releasing into soil, the grubs were weighed individually with an accuracy of 0.001 g on an AD 300 scale (Axis Ltd., Gdańsk, Poland). Grubs survival and weight were assessed every 2–3 weeks. During each assessment as well as when dead saplings were found, the plants were replaced with new ones.

Mathematical and statistical analysis

The Generilized Linear Model (GLZ) with binomial distribution of the dependent variable and probit link function was used to estimate the mortality rate of the grubs at different instars feeding on the roots of tested tree species and to calculate the lethal time required for 50% of the individuals to die (LT50). The GLZ was also used for the paired comparisons of dynamics (changes in time) of survival and body weight of the grubs feeding on different tree species – paired with each other. The body weight had a normal distribution and the link function was log: in case of the L1 grubs, and the identity function in case of L2 and L3 grubs. The maximum likelihood method was used for model building (Stanisz 2007). The time from the beginning of the experiment to successive assessments of survival and body weight was calculated in days, and the survival was described by the number of live (code 0) and dead grubs (code 1).

The grub growth was assessed based on the relative growth rate (RGR) calculated as follows (Lazarević et al. 2002):

$$RGR = \frac{M_t - M_0}{T_{t-0} \times M_0}$$

where:
M_o and M_t – initial and final insect body weight (g),
T_{t-o} – the number of days between initial and final weight measurements (d).

Each year, RGR values were estimated for the period from the beginning of the experiment to the second half of August. Later on, the grubs start to prepare for overwintering and feed less intensively, leading to the loss of body weight.

The mean RGR values of the grubs feeding on the roots of various tree species saplings were compared using one-way ANOVA. When the ANOVA assumptions were violated, the Kruskal–Wallis non-parametric test was used, followed by ranks comparison.

The statistical analyses were performed using Statistica 10 (StatSoft, Inc. 2011) with the significance level set at α = 0.05.

3. Results

First instar grubs

Survival

Overall vitality of the L1 grubs collected in the territory of Lubartow Forest District in spring of 2012 was low. Substantial mortality was observed already at the initial phase of the experiment (Fig. 1A). Only 11.4% of the grubs survived between 28 May and 18 September, and the highest survival was observed among the grubs feeding on the roots of *Q. robur* (25%) and *Q. petraea* (20%). The grubs feeding on these two species also had the highest LT50, 54.9 and 44.9 days, respectively (Table 1). In the other grubs, the LT50 varied from 25.9 to 35.4 days. The high values of the LT50 in the grubs feeding on both oak species indicated the slow mortality dynamics, which differed significantly from the mortality dynamics in the grubs feeding on *L. decidua* and *A. glutinosa*, and in the case of the grubs feeding on *Q. petraea* it was also significantly slower than in the grubs feeding on *B. pendula* (Table 2). The mortality of the grubs feeding on the roots of *A. glutinosa* reached 100% already on 10 July, and its dynamics was significantly different from that of the grubs on all other tested tree species (Fig. 1A, Table 2).

Body weight

The changes in the mean body weight of the L1 grubs feeding on the sapling roots of different tree species

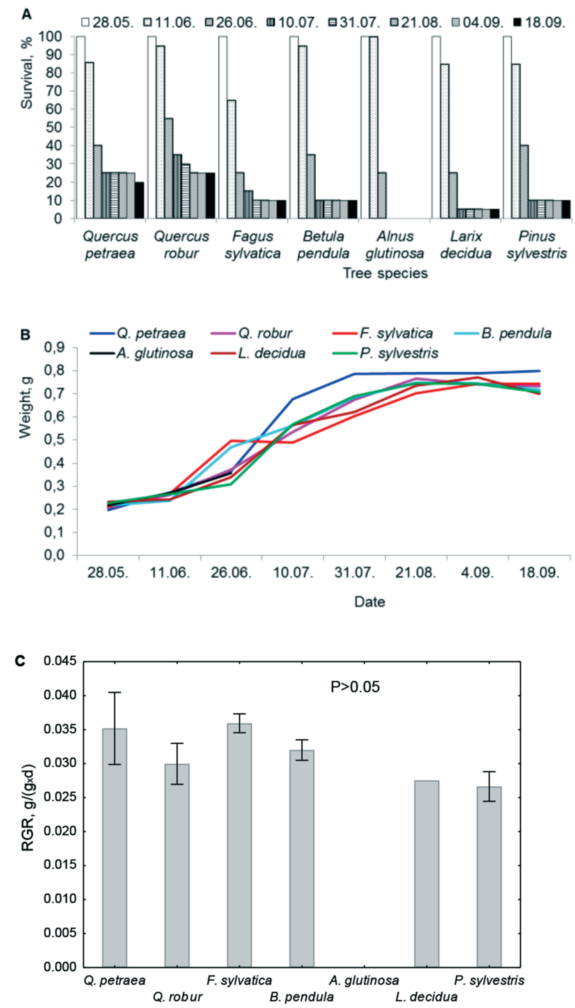

Figure 1. Survival (A) and changes of the body weight (B) of the L1 *Melolontha* spp. grubs feeding on the roots of saplings of various tree species in the period of 28 May–18 October 2012 and relative growth rate (RGR, mean ± SE) reached before 21 August (C)

were similar (Fig. 1B). In June, the body weight was changing more in individuals developing on *F. sylvatica* and *B. pendula* saplings, and in July – on *Q. petraea* saplings. However, the differences in the grub body weight dynamics were not statistically significant ($P > 0.05$).

The RGRs of the grubs feeding on tested tree species before August 21 had positive values and they did not differ significantly between tree species, even though in some cases the differences were almost two-fold. The lack of statistically significant differences can be explained by the high variability of RGRs obtained by the grubs on different tree species. The highest RGR values were found in the grubs feeding on the roots of *Q. petraea* and *F. sylvatica*, whereas the lowest ones – in the grubs feeding on *P. sylvestris* and *L. decidua* (the grubs feeding on the alder saplings were not considered in the comparison, because they lived only until July 10) (Fig. 1C). After August 21, a decrease of the body weight in the grubs feeding on the roots of *P. sylvestris*, *B. pendula* and *Q. robur* was observed, and the same process was observed after September 4 in the grubs developing on the roots of *L. decidua* (Fig. 1B).

Table 1. The results of building the generalized regression model describing the dependence of the L1 *Melolontha* spp. grubs mortality on time and calculated values of LT50

Tree species	df	Log likelihood	χ^2	*P*	LT50, days
Q. petraea	1	-89.32	40.13	<0.0001	44.9
Q. robur	1	-87.21	47.29	<0.0001	54.9
F. sylvatica	1	-72.06	53.01	<0.0001	26.2
B. pendula	1	-67.27	72.64	<0.0001	35.4
A. glutinosa	1	-11.88	166.18	<0.0001	25.9
L. decidua	1	-55.43	82.90	<0.0001	27.9
P. sylvestris	1	-68.83	68.26	<0.0001	34.0

Table 2. Comparison of mortality dynamics of the L1 *Melolontha* spp. grubs feeding on the roots of 7 tree species (the analysis was done for each pair of tree species; the results are presented only for the pairs, for which the interaction of tree species with time was statistically significant)

Pairs of compared tree species	df	Log likelihood	χ^2	*P*
Q. petraea vs *B. pendula*	1	-156.59	4.00	0.0456
Q. petraea vs *L. decidua*	1	-144.75	8.45	0.0037
Q. petraea vs *A. glutinosa*	1	-101.20	66.50	<0.0001
Q. robur vs *L. decidua*	1	-142.64	6.48	0.0109
Q. robur vs *A. glutinosa*	1	-99.09	62.87	<0.0001
A. glutinosa vs *F. sylvatica*	1	-83.94	55.35	<0.0001
A. glutinosa vs *B. pendula*	1	-79.15	48.29	<0.0001
A. glutinosa vs *L. decidua*	1	-67.31	38.90	<0.0001
A. glutinosa vs *P. sylvestris*	1	-80.71	49.90	<0.0001

Table 3. The results of building the generalized regression model describing the dependence of the L2 *Melolontha* spp. grubs mortality on time and calculated values of LT50 (n.s. – the result is not statistically significant at $\alpha = 0.05$)

Tree species	df	Log likelihood	χ^2	*P*	LT50, days
Q. petraea	1	-41.75	6.92	0,0085	195.0
Q. robur	1			n.s.	-
F. sylvatica	1	-46.77	4.37	0.0366	222.5
B. pendula	1	-52.18	12.90	0.0003	147.1
A. glutinosa	1	-46.94	10.98	0.0009	161.4
L. decidua	1			n.s.	-
P. sylvestris	1			n.s.	-

Second instar grubs

Survival

The survival of the L2 grubs feeding on the roots of all studied tree species was high, but the highest rate (100%) was observed in the grubs feeding on the roots of *Q. robur* and *P. sylvestris* (Fig. 2A). In contrast, the highest mortality was observed in the grubs reared on the roots of *B. pendula* and *A. glutinosa*, 33.3% and 26.6%, respectively. These individuals also had the shortest LT50, 147.1 and 161.4 days, respectively, i.e. about 5 months, whereas the LT50 for the grubs feeding on the roots of *F. sylvatica* reached 222.5 days (Table 3), i.e. more than 7 months, which is longer than the real time of their development during one growing season. Dynamics of the grub mortality on tested tree species did not differ significantly ($P > 0.05$). Overall, the high mortality was observed during grubs molting from L2 to L3 instar, i.e. in July.

Body weight

The grub body weight was changing more rapidly in the first two months of the study (Fig. 2B). The body weight dynamics in the grubs feeding on the roots of tested tree species did not differ significantly. However, the RGR of the grubs feeding on the roots of *B. pendula* saplings in the period prior to August 17 was significantly higher than the RGR of the grubs feeding on the roots of *A. glutinosa* (Fig. 2C). The RGR values for the L2 grubs were positive, regardless the tree species they were reared on.

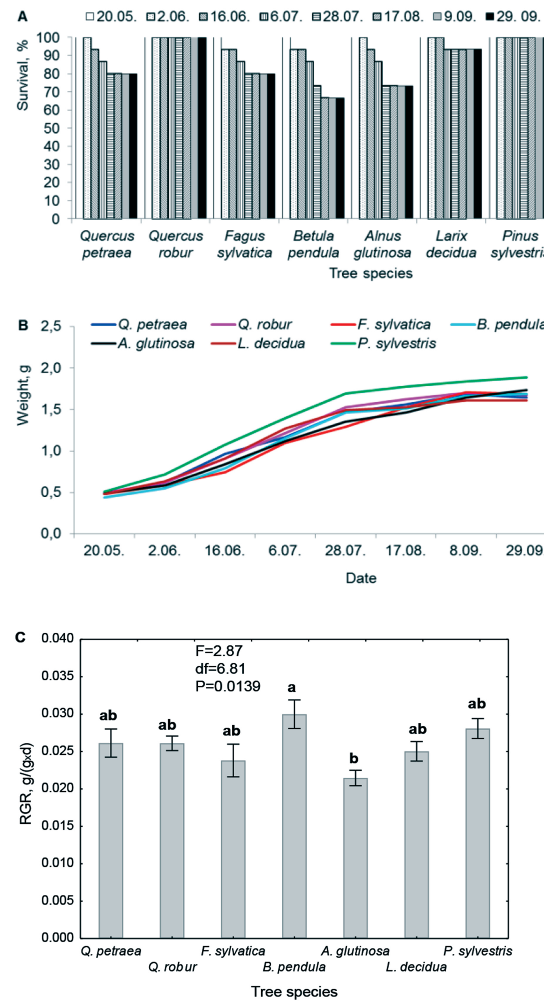

Figure 2. Survival (A) and changes of the body weight (B) of the L2 *Melolontha* spp. grubs feeding on the roots of saplings of various tree species in the period of 20 May–29 September 2011 and relative growth rate (RGR, mean ± SE) reached before 17 August (different letters indicate statistically significant differences at $\alpha = 0.05$) (C)

Third instar grubs

Survival

The survival of the L3 grubs was high. At the end of June 2012, it was between 70% for the grubs reared on the roots of *L. decidua* and *A. glutinosa* and 100% for the grubs reared on *Q. petraea* saplings (Fig. 3A). Tree species did not have a significant effect on the grub mortality dynamics ($P > 0.05$). The highest mortality was observed in the period of molting from L3 instar into a pupa.

Body weight

The mean body weight of the L3 grubs feeding on the roots of *P. sylvestris* was higher than that of the grubs feeding on other tested tree species (Fig. 3B). This could be a result of the highest increase of their body weight in the previous year (2011). In April and May 2012, the body weight changed only slightly, and the least changes were observed in the grubs reared on the roots of *L. decidua* and *B. pendula*. In contrast, the body weight of the grubs feeding on the roots of *Q. petraea* and *A. glutinosa* started to decrease already in late April. In the other grubs, the weight loss was observed only in June. By the end of June all the grubs were already in pupal chambers. The body weight changes in the grubs feeding on the roots of *L. decidua* saplings was significantly slower than the changes in the grubs reared on the roots of *Q. petraea* and *Q. robur* (Table 4). A significant difference was also found between the body weight dynamics in the grubs feeding on *Q. petraea* and *B. pendula*.

Tree species did not have a significant effect on the RGR. However, it should be pointed out that the RGR values were positive in the grubs developing on the roots of four out of seven tested tree species: *L. decidua*, *Q. petraea*, *B. pendula* and *P. sylvestris* (Fig. 3C). The RGRs were negative in the other cases and the smallest values were found in the grubs feeding on the roots of *F. sylvatica* and *Q. robur*.

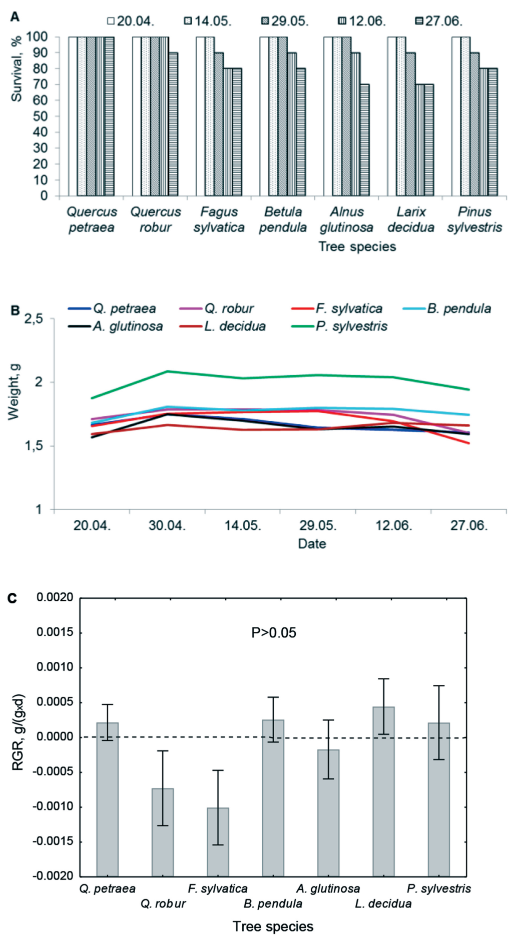

Figure 3. Survival (A) and changes of the body weight (B) of the L3 *Melolontha* spp. grubs feeding on the roots of saplings of various tree species in the period of 20 April–27 June 2012 and relative growth rate (RGR, mean ± SE) reached before 27 June (C)

4. Discussion

The *Melolontha* spp. grubs feed on the roots of many different plant species. However, it does not mean that food quality has no effect on their growth. In literature, there are only few examples of negative effects of herbaceous plants – e.g. the buckwheat (*Fagopyrum esculentum* Moench) and Tartary buckwheat [*F. tataricum* (L.) Gaertn.] from the Polygonaceae family, common wild oat (*Avena fatua* L.) and quackgrass [*Elymus repens* (L.) Gould.] from the Poaceae family, and common lambsquarters (*Chenopodium album* L.) from the Amaranthaceae family – on the grub density and growth (Satkowski 1899; Rożyński 1926; Ulatowski, 1932; 1933; Hauss and Schütte 1976; Malinowski et al. 2001). Moreover, the most of reported results were not based on detailed studies. The effect of woody species on the *Melolontha* grubs has received even less attention and to our knowledge is reported only in two papers. In the study with the *M. hippocastani* grubs, Gur'ânova (1954) showed that *B. pendula* was the most beneficial for the growth of the L1 grubs, whereas *P. sylvestris* was the most advantageous for the L2 grubs. In both cases, the grubs were heavier than those feeding on the roots of *Q. robur*. Moreover, their bodies contained the highest number of fat cells increasing their chances to survive in adverse environmental conditions. The L2 grubs were additionally subjected to 40-day starvation, and this experiment revealed that the survival of the grubs previously reared on the roots of *P. sylvestris* and *B. pendula* was 75 and 62.5% , respectively, whereas on the roots *Q. robur* – only 37.5%. Berezina (1957) studied the development of the *M. hippocastani* grubs on the roots of 7 tree and shrub species and suggested that the increase in the body weight was related to the high content of sugar and the low content of total nitrogen in the roots of

Table 4. Comparison of weight dynamics of the L3 *Melolontha* spp. grubs feeding on the roots of 7 tree species (the analysis was done for each pair of tree species; the results are presented only for the pairs, for which the interaction of tree species with time was statistically significant)

Pairs of compared tree species	df	Log likelihood	χ^2	*P*
L. decidua vs *Q. petraea*	1	26.11	8.52	0.0035
L. decidua vs *Q. robur*	1	21.01	4.14	0.0419
Q. petraea vs *B. pendul*a	1	22.52	4.39	0.0361

tested plants. However, this dependence was not regular, as mentioned by the author herself, as well as it was not tested statistically. The positive effect of increasing N:C ratio on insect growth is commonly known (White 1984; Lincoln et al. 1993; Awmack and Leather 2002). Although sugars are an important source of energy, fast growing insects may require lower intake of energy than insects characterized by slower growth and higher activity (Schoonhoven et al. 2005). The *Melolontha* spp. grubs developing three years and requiring a significant amount of energy for their movement in soil may be included to the latter ones.

In the present study, the largest mortality of the grubs was observed at the time of their molting and transition to the subsequent developmental stages. This could be related to the effect of, among others, food quality on hormone activity such as juvenile and prothoracic hormones, which are responsible for arthropod growth and molting (Lee et al. 2012; Andersen et al. 2013; Nijhout et al. 2014; Sangsuriya et al. 2014). The L1 grubs had the lowest vitality, which was probably due to the presence of pathogens in the population they were sampled from (the high mortality of the grubs was observed already during their transfer from the field to the laboratory). Only for the L1 grubs, we found a significant effect of food quality (tree species) on mortality rate, that could be the outcome of interaction with a weakened grub immunity (DiAngelo et al. 2009). The grubs feeding on the roots of *A. glutinosa* saplings were dying the most rapidly, whereas those feeding on the roots of *Q. robur* and *Q. petraea* – the most slowly. The survival of the L2 and L3 grubs was relatively high (66.7%–100%) on all tested tree species. The highest survival (100%) was observed among the L2 grubs feeding on the roots of *P. sylvestris* and *Q. robur*, and among the L3 grubs reared on *Q. petraea*.

The highest body weight increase was observed in the L1 and L2 grubs. In the period from May 28 to September 18, the body weight of the L1 grubs increased by approximately 300%. The body weight of the L2 grubs in four month period changed by approximately 250%. Schwerdtfeger (1939) found that shortly before pupation the *M. hippocastani* and *M. melolontha* grubs reach the weight of 1670 mg and 3190 mg, respectively. In our study, the average body weight of L3 grubs on 12 June was about 1750 mg, which indicated that they were *M. hippocastani* grubs. It was confirmed by the emergence of imagines of this species in the pots after the grubs passed through the pupal stage.

The food quality did not have a significant effect on the body weight dynamics of the L2 grubs, however the grubs feeding on the *B. pendula* saplings had significantly higher RGR than the grubs feeding on *A. glutinosa*. At the same time, a very interesting observation related to the body weight changes in the L3 grubs was made. The mean body weight increased only slightly, mainly in the grubs feeding on *L. decidua* roots, whereas the weight of the grubs feeding on *Q. petraea* and *A. glutinosa* started to decrease already at the end of April. The weight of sapling roots of different tree species was not estimated, thus it is difficult to say whether it could have any effect on the weight gain of the grubs. However, the root system of 2-year-old *P. sylvestris* saplings is less developed than that of *F. sylvatica* and *A. glutinosa* saplings (personal observations), but vital characteristics of the grubs feeding on the roots of these species did not reflect these differences. The increase in the body weight during the last larval instar usually lasts until reaching the so-called critical weight (Davidowitz et al. 2003, 2004). Then, the larvae stop feeding and begin seeking a suitable place to pupate. At that time, larvae lose their weight (Nijhout et al. 2014). This may explain a decrease in the body weight of the L3 grubs, and the specimens feeding on the roots of *Q. petraea* and *A. glutinosa* probably achieved their critical weight earlier than others. Surprisingly, only two grubs pupated relatively early, i.e. in late May-early June, whereas the other grubs pupated one month later, i.e. in late June-early July. The duration of the period of searching for pupation site depends on the concentration of juvenile and prothoracic hormones. Before pupation, the concentration of juvenile hormone drops down and the concentration of prothoracic hormone increases gradually, but its secretion depends on photoperiod (Truman 1972; Truman and Riddiford 1974; Cymborowski 1984). In the case of the cockchafer grubs developing in soil, away from the light, the course of these processes is likely to depend on the other, genetically encoded factors that prevent early pupation and subsequent emergence of adult insects.

The dependence of the body weight changes and tree species found in our study only partially supported the results presented by Gur'ânova (1954) and Berezina (1957). The grubs of all instars feeding on the roots of *B. pendula* had the largest or one of the largest RGRs, and the body weight dynamics in the L3 grubs was significantly different from that of the grubs feeding on *Q. petraea* saplings. However, survival of the grubs was generally lower than the survival of grubs feeding on the roots of both oak species. The RGR of the grubs reared in pots with *P. sylvestris* saplings was quite high, but only in case of the L2 and L3 grubs it was higher than that of the grubs reared on *Q. robur*.

The effect of food quality, and particularly the content of nitrogen (proteins) and sugars, on the grub development is not fully understood. On one hand, sugars provide energy for the grubs to move in such harsh environment, as is soil, in searching for food. Sugars have also been known as phagostimulants for many insect species (Johnson and Gregory 2006). The study of herbaceous plants showed a significant positive effect of the root sugar content on grub body weight gain and the percentage of the L1 larvae, which successfully molted (Sukovata et al. in print). On the other hand, larval growth generally depends on the amount of amino acids derived from proteins available in food, and their deficiency significantly retards their growth and causes an increase in larval mortality (Lee et al. 2012; Andersen et al. 2013). Physiological processes in the body of grubs during their growth as well as the effect of food quality and other factors on these processes certainly require further research, from both scientific and practical perspective.

5. Summary

The present study was aimed to assess the survival and growth rate of *Melolontha* spp. grubs at different instars feeding on the sapling roots of 7 forest tree species: *Q. petraea*, *Q. robur*, *F. sylvatica*, *B. pendula*, *A. glutinosa*, *L. decidua* and *P. sylvestris*.

The highest susceptibility to the food type, expressed by the high mortality, was observed in the youngest grubs (L1). The mortality rate was the highest among the grubs feeding on *A. glutinosa* roots, whereas the lowest mortality was observed among the grubs feeding on both oak species. In addition, the grubs feeding on oaks, but also on *F. sylvatica* and *B. pendula* had the highest RGR. The survival of the older grubs was relatively high (66.7–100%). The highest mortality was, like in the L1 grubs, in rearing on *A. glutinosa*, followed by *B. pendula* (among the L2 grubs) and on *L. decidua* (among the L3 grubs). Despite relatively high mortality, the L2 and L3 grubs feeding on two latter species reached the highest RGRs.

Interpretation of the results of our experiments is rather difficult due to the lack of basic knowledge on the processes involved in grub metamorphosis, especially in the last larval instar. The effects of the factors such as food quality and environmental conditions on these processes remain poorly understood. However, it is clear that among seven tested forest tree species, the roots of *A. glutinosa* are the least beneficial food for the development of *Melolontha* spp. grubs. Such information should be taken into account when planning silvicultural measures in the permanent cockchafer outbreak foci.

Acknowledgements

We would like to express our deep appreciation to Sławomir Lipiński and Robert Wolski for their help with laboratory experiments.

The study was conducted within the framework of the project financed by the National Centre for Research and Development (contract No NR12-0096-10/2010).

References

Andersen D.S., Colombani J., Léopold P. 2013. Coordination of organ growth: principles and outstanding questions from the world of insects. *Trends in Cell Biology* 23(7): 336–344.

Awmack C.S., Leather S.R. 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47: 817–844.

Berezina V.M. 1957. Ličinočnoe pitanie vostočnogo majskogo hrušča. *Trudy Vsesojuznogo Instituta Zascity Rastenij* 8: 37–74.

Cymborowski B. 1984. Endokrynologia owadów. Warszawa, Państwowe Wydawnictwo Naukowe, p. 260. ISBN 83-01-04700-3.

Davidowitz G., D'Amico L.J., Nijhout H.F. 2003. Critical weight in the development of insect body size. *Evolution and Development* 5: 188–197.

Davidowitz G., D'Amico L.J., Nijhout H.F. 2004. The effects of environmental variation on the mechanism that controls insect body size. *Evolutionary Ecology Research* 6: 49–62.

DiAngelo J.R., Bland M.L., Bambina S., Cherry S., Birnbaum M.M. 2009. The immune response attenuates growth and nutrient storage in *Drosophila* by reducing insulin signaling. *Proceedings of the National Academy of Sciences of the United States of America* 106: 20853–20858.

Gur'ânova N.I. 1954. Vliânie sostava pišči na fiziologičeskoe sostoânie vostočnogo majskogo hrušča (*Melolontha hippocastani* F.). *Trudy Vsesojuznogo Instituta Zascity Rastenij* 6: 31–37.

Hauss R. von, Schütte F. 1976. Zur Polyphagie der Engerlinge von *Melolontha melolontha* L. Pflanzen aus Wiese und Ödland. *Anzeiger für Schädlingskunde, Pflanzenschutz Umweltschutz*, 49: 129–132.

Johnson S.N., Gregory P.J. 2006. Chemically-mediated host-plant location and selection by root-feeding insects. *Physiological Entomology* 31: 1–13.

Krell F.-T. 2004. Bestimmung von Larven und Imagines der mitteleuropäischen *Melolontha*-Arten (Coleoptera: Scarabaeoidea). *Laimburg* 1: 211–219.

Lazarević J., Perić-Mataruga V., Stojković B., Tucić N. 2002. Adaptation of the gypsy moth to an unsuitable host plant. *Entomologia Experimentalis et Applicata* 102: 75–86.

Lee K.P., Kwon S.-T., Roh C. 2012. Caterpillars use developmental plasticity and diet choice to overcome the early life experience of nutritional imbalance. *Animal Behaviour* 84: 785–793.

Lincoln D.E., Fajer E.D., Johnson R.H. 1993. Plant-insect herbivore interactions in elevated CO_2 environments. *Trends in Ecology and Evolution* 8: 64–68.

Malinowski H., Augustyniak A., Łabanowska B.H. 2001. Nowe możliwości ograniczania populacji owadów żerujących na korzeniach roślin. *Progress in Plant Protection/ Postępy w Ochronie Roślin* 41: 175–181.

Nijhout H.F., Riddiford L.M., Mirth C., Shingleton A.W., Suzuki Y., Callier V. 2014. The developmental control of size in insects. *WIREs Developmental Biology* 3: 113–134.

Rożyński F. 1926. W sprawie walki z chrząszczem majowym (*Melolontha vulgaris*). *Przegląd Leśniczy* 7: 32–38.

Sangsuriya P., Phiwsaiya K., Pratoomthai B., Sriphaijit T., Amparyup P., Withyachumnarnkul B., Senapin S. 2014. Knockdown of a novel G-protein pathway suppressor 2 (GPS2) leads to shrimp mortality by exuvial entrapment during ecdysis. *Fish and Shellfish Immunology* 37(1): 46–52.

Satkowki K. 1899. Przyczynek do środków tępienia pędraka. *Sylwan* 17: 52–54.

Schoonhoven L.M., van Loon J.J.A., Dicke M. 2005. Insect-Plant Biology. Second Edition. New York, Oxford University Press, p. 421. ISBN 978-0-19-852594-3.

Schwerdtfeger F. 1939. Untersuchungen über die Wanderungen des Maikäfer-Engerlings (*Melolontha melolontha* L. und *Melolontha hippocastani* F.). *Zeitschrift für Angewandte Entomologie* 26: 215–252.

Stanisz A. 2007. Przystępny kurs statystyki z zastosowaniem STATISTICA PL na przykładach z medycyny. Tom 2. Modele liniowe i nieliniowe. Kraków, StatSoft Polska Sp. z o.o., s. 868. ISBN 978-83-88724-30-5.

StatSoft, Inc. 2011. STATISTICA (data analysis software system), version 10. www.statsoft.com.

Śliwa E. 1993. Szkodniki korzeni drzew i krzewów. Warszawa, Oficyna Edytorska „Świat", p. 53.

Truman J.W. 1972. Physiology of insect rhytms. I. Circadian organization of the endocrine events underlying the molting cycle of larval tobacco hornworms. *The Journal of Experimental Biology* 57: 805–820.

Truman J.W., Riddiford L.M. 1974. Physiology of insect rhytms. III. The temporal organization of the endocrine events underlying pupation of the tobacco hornworm. *The Journal of Experimental Biology* 60: 371–382.

Ulatowski W. 1932. Przykład walki z pędrakiem. *Echa Leśne* 9 (1): 5–6.

Ulatowski W. 1933. Pędrak chrabąszcza (*Melolontha vulgaris*) i jego zwalczanie. *Sylwan* 51 (7/8/9): 251–252.

White T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63: 90–105.

Woreta D. 1994. Zmiany występowania szkodników korzeni drzew i krzewów leśnych w latach 1961–1993 [Changes in the occurence of pests of forest trees and bushes roots]. *Sylwan* 5: 37–41.

Woreta D. 1999. Aktywność owadobójcza insektycydów przeznaczonych do ograniczania liczebności owadów doskonałych chrabąszczy (*Melolontha* spp.). *Prace Instytutu Badawczego Leśnictwa* 2: 61-74.
Leśnictwa, 20: 90–92.

Woreta D., Skrzecz I. 1996. Szkody wyrządzane przez owady w uprawach leśnych na gruntach porolnych i możliwości ich ograniczania. *Postępy Techniki w Leśnictwie* 58: 34–42.

Translated by: Adam Kaliszewski