JOURNAL OF FOREST SCIENCE, *49*, 2003 (6): 252–258

Diapause of *Cameraria ohridella* Deschka et Dimic and its impact on the species population dynamics

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ABSTRACT: *Cameraria ohridella* Deschka et Dimic is a polyvoltine species which can complete under suitable conditions the development of as many as three generations a year. In the Czech Republic, however, the third generation suffers from high mortality due to the shortage of food and later also unfavourable weather. If the third generation is not completed the population continuity is ensured by diapausing pupae occurring in each generation. The number of diapausing pupae is determined by the actual abundance of the species and thus also by the actual damage to the horse chestnut (*Aesculus hippocastanum* L.) foliage. Relationships of the parameters were investigated in the first generation of *C. ohridella* and their intensity was studied by methods of regression analysis.

Keywords: *Cameraria ohridella*; *Aesculus hippocastanum;* diapause; pupa; regression analysis

In the central-European region, we encounter *Cameraria ohridella* Deschka et Dimic already for a period of more than ten years. For the period, mines in leaves of attacked horse chestnut (*Aesculus hippocastanum* L.) trees and premature leaf-fall became an inherent event nearly throughout Europe. A number of findings has been obtained both on the distribution of *C. ohridella* (TOMICZEK 1997; SZABÓKY 1997; LIŠKA 1997; SIVICEK et al. 1997; AVTZIS 2002; AUGUSTIN, GUICHARD 2002; TOMOV 2002a, etc.) and on the species bionomy (PSCHORN-WALCHER 1997; SKUHRAVÝ 1998; KALINOVÁ, SVATOŠ 2000; SAMEK 2001; FREISE, HEITLAND 2002, etc.). Data were obtained on some mortality factors of the species (LETHMAYER, GRABENWEGER 1997; STOLZ 1997; ČAPEK 1999; SAMEK et al. 2000; GRABENWEGER 2002; TOMOV 2002b; KEHRLI, BACHER 2002, etc.) and in recent years also on its harmfulness (LIŠKA 2000; MERTELÍK et al. 2000; SAMEK 2002, etc.). However, there are always some aspects of the biology of *C. ohridella* which deserve increased attention.

In addition to the exceptional tolerance of attacked horse chestnut trees, the potential of *C. ohridella* to cope with consequences of actual food-destructive activity is particularly good for remark.

Although in the course of the development of *C. ohridella*, the amount of available food decreases and the species mortality increases, the fact has no effect on its population dynamics. Population continuity is ensured by diapausing pupae which are a reliable insurance against the population collapse in consequence of the exhaustion of food sources. The diapause of *C. ohridella* pupae is a key for expansion and the successful existence of the species on occupied localities and, therefore, it is also an interesting objective of research from forestry and game management aspects. Horse chestnut is not only an ornamental species but in many hunting districts a producer of valuable feed and in regions of autochthonous occurrence, it is also a production species.

Part of pupae of each generation enters the diapause and these individuals hatch in the following year. The size of the proportion of diapausing pupae of the total number of pupae differs in particular generations and in comparison with the first generation, the proportion increases in next generations. There are also significant differences in the number of diapausing pupae between particular localities, parts of crowns and even particular leaves of the same tree. The aim of the study was, therefore, to quantify the proportion of diapausing pupae of *C. ohridella* in various samples of leaves of a host and to reveal causes of the different number of the pupae. In individuals of the first generation, a hypothesis was verified that the number of diapausing pupae of *C. ohridella* was primarily determined by the actual population density of the species and thus by the actual damage to the host foliage.

MATERIAL AND METHODS

At the beginning of July 2002 when the development of the first generation of *C. ohridella* was completed at localities in Brno and its environs, 12 samples at 20 compound leaves of horse chestnut were collected. The leaves were selected in such a way to represent all degrees of

Table 1. Localization of sampling the compound leaves of horse chestnut

Sampling place	Specification	Sample number	Locality
Crown circumference	–	4	Brno, Špilberk castle
	–	12	Sokolnice, game preserve
Crown storey	2 m	1	Brno, Mendel square
	6 m	2	Brno, Mendel square
	9 m	3	Brno, Mendel square
	2 m	9	Modřice, Pod kaštany
	6 m	6	Modřice, Pod kaštany
	9 m	5	Modřice, Pod kaštany
Cardinal point	west	7	Dolní Heršpice, Havránkova
	south	8	Dolní Heršpice, Havránkova
	north	11	Dolní Heršpice, Havránkova
	east	10	Dolní Heršpice, Havránkova

their damage. Samples were obtained from selected trees either from the whole crown circumference and the lowest crown storey or from various crown storeys or from particular cardinal points (Table 1). Following data were determined in the samples:

– The proportion of mines from the total area of leaves representing independent variable *X*. The method of mine outline redrawing was used and reading the area on a millimetre paper. According to determined values, the samples were classified into categories of damage graduated at 20% each.
– The proportion of diapausing pupae of *C. ohridella* from the total number of pupae representing dependent variable *Y*. Diapausing pupae were determined according to the character of pupal cocoons. While in cocoons of diapausing pupae, a greaseproof cap of silvery colour is always present, in pupae which do not diapause the cap does not occur.

Through regression analysis a hypothesis was verified that the proportion of diapausing pupae of *C. ohridella* in the first generation was positively rectilinearly dependent on the actual number of the species and thus on the actual damage to the host foliage. Determined values of dependent and independent variables were plotted into correlation diagrams and their relations were studied by means of the MS Excel supplement *Analysis of data.* The following relations were studied:

– The course of a linear regression function expressed by a regression line.
– Intensity of the dependence expressed by correlation index *I*. Square of *I* specified (in percentage) how dependent variable is conditioned (determined) by an independent variable.

Repeated examinations were carried out at the beginning of July 2002 on the sample of 28 individual leaves of horse chestnut. At the Horní Heršpice, Havránkova locality, one tree was selected and leaves representing all degrees of damage were taken from its western cardinal point and height 2 m above ground. The proportion of mines was determined in leaves from the total leaf area and the proportion of diapausing pupae of *C. ohridella* from all pupae. Relationships of the variables were studied by the method mentioned above.

The number of diapausing pupae of *C. ohridella* in the second generation was studied at the Modřice (Sokol

Table 2. Damage to compound leaves of horse chestnut by feeding and the proportion of diapausing pupae of *C. ohridella* in the first generation

Category of damage (%)	Sample number	% of mined leaf area	% of diapausing pupae
0–20	1	9	4.5
	2	11	12.7
	3	13	1.4
	4	14	3.8
21–40	5	26	8.4
41–60	6	41	13.1
	7	53	49.6
	8	60	44.1
61–80	9	63	59.3
	10	71	55.9
	11	76	54.7
81–100	12	84	37.1

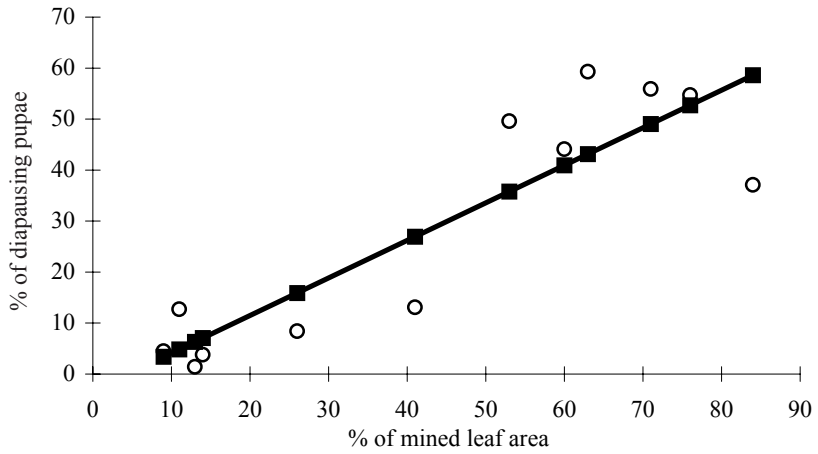

Fig. 1. Dependence of the number of diapausing pupae of *C. ohridella* on the intensity of damage to compound leaves of horse chestnut. Correlation index 0.88, determination 77.4%
○ *Y*, ■ expected *Y*, ▬ linear expected *Y*

house) and Sokolnice (game preserve) localities. At each of the localities, one full-grown horse chestnut tree was selected and at a height 2 m above ground, one skeletal branch was selected. From leaves of the branches, all diapausing pupae of *C. ohridella* of the first generation which cannot be differentiated from diapausing pupae of next generations were removed at the beginning of July 2002. In mid-August 2002, the proportion was determined of diapausing pupae in the second generation of all pupae.

RESULTS AND DISCUSSION

Study of compound leaves

The proportion of diapausing pupae of *C. ohridella* in the first generation rather differed in samples of compound leaves ranging in the interval from 1.4 to 59.3% of all pupae. The leaf damage reached a value of 9 to 84% of the total leaf area of samples. In the category of damage 0–20, 21–40, 41–60, 61–80 and 81–100% 4, 1, 3, 3 and 1 samples occurred, respectively (Table 2).

Using a regression function in the original point field of a correlation diagram, measured values (*Y*) were replaced by calculated values (*linear expected value Y*) and thus, evaluation was facilitated of the dependence of studied quantities. The steeply rising course of a regression line indicates that the number of diapausing pupae of the first generation *C. ohridella* is positively rectilinearly dependent on the actual population density of the species and thus on the actual damage to the host foliage (Fig. 1). With the increasing number of *C. ohridella* individuals in leaves of horse chestnut and thus with the increasing damage to the leaves the number of diapausing pupae also increases.

Correlation index *I* which can range in the interval <0; 1> reached a value of 0.88 so that the dependence approached a value of close dependence ($I = 1$). Through squaring the correlation index it was found that in studied samples of leaves the proportion of diapausing pupae of *C. ohridella* of the first generation was determined (affected) from 77.4% just by the number of *C. ohridella* and thus by damage to the host leaf area. Other influences determine the proportion from by 22.6%.

Study of individual leaves

Also in particular leaves of a selected tree of horse chestnut, the proportion of diapausing pupae of *C. ohridella* in the first generation was rather different ranging from 0 to 77% of all pupae. The proportion of mines from the total leaf area of particular leaves reached a value of 25–90% (Table 3). Also in particular leaves it was demonstrated that the number of diapausing pupae of *C. ohridella* in the first generation was positively rectilinearly dependent on the number of individuals in the leaves and thus on their actual damage. The steeply ascending course of a regression line was noticed and correlation index *I* equal to 0.87 was calculated. Determination reached 75.7% (Fig. 2). Through other effects, the proportion of determined diapausing pupae of *C. ohridella* of the first generation amounted to 24.3%.

The study of both compound and individual leaves revealed nearly identical values of the correlation index and determination of examined quantities. It follows that the *C. ohridella* pupae diapause is closely related to the actual number of the species individuals in leaves of a host and thus the actual damage to the leaves. These factors accounted for about 75% of all impulses affecting the number of diapausing pupae of the first generation.

Both investigations corroborated a hypothesis on the dependence of the number of diapausing pupae of *C. ohridella* in the first generation on the actual abundance of the species and thus damage to the host leaves. Increase in the number of diapausing pupae represents the logical response of a population on the increasing abundance of the species and resulting decrease in the amount of available food.

The diapause of *C. ohridella* is, however, not only a remarkable adaptation on the consequences of actual food-destructive activities but shows also another impact. With respect to the fact that under conditions of the Czech Republic the development of the third generation is not

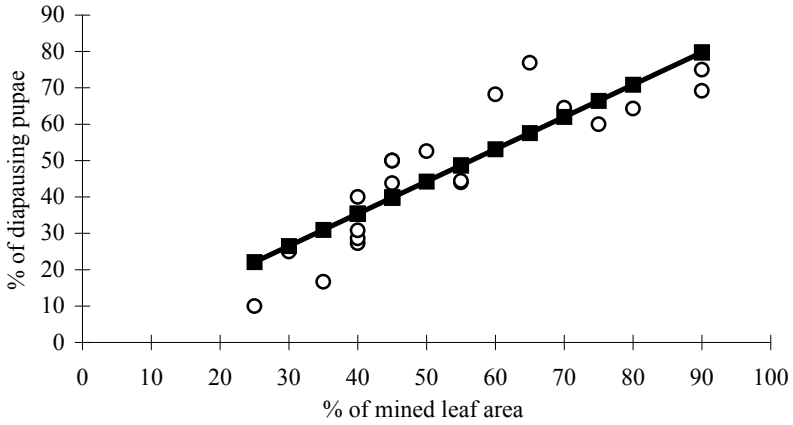

Fig. 2. Dependence of the number of diapausing pupae of *C. ohridella* on the intensity of damage to individual leaves of horse chestnut. Correlation index 0.87, determination 75.7%
○ *Y*, ■ expected *Y*, ▬ linear expected *Y*

often completed, the diapausing pupae represent also an insurance against the population collapse. Hatching of imagoes from the pupae occurs in the spring of the next year, i.e. in a period which is most favourable both from trophic and climatic aspects.

While hatching the *C. ohridella* imagoes of the first generation occurs from mid-June diapausing pupae of this generation remain in their cocoons in leaves. The diapause first happens in trees and after leaf fall on the ground where pupae finally hibernate. The finding is, however, in contradiction with the statement of some authors which assume that hibernating pupae of *C. ohridella* are members of only later generations. SKUHRAVÝ (1998) mentions that a pupal cocoon which is necessary for wintering is formed by larvae of the third generation from the end of August to mid-October. Also KALINOVÁ and SVATOŠ (2000) state that larvae of the third and later generations create a cocoon before pupating and overwinter in it. Investigations mentioned above, however, demonstrate that diapausing (and finally hibernating) pupae appear already in the first generation.

The number of diapausing pupae of *C. ohridella* is further increased at the turn of July and August when pupae of the second generation occur. The leaf system of the majority of horse chestnut trees is considerably damaged and the most damaged leaves already begin to fall off at that time. Diapausing pupae appear also in this generation. Through preliminary investigations carried out at the Sokolnice (game preserve) or Modřice (Sokol house) localities, the proportion of the pupae was 71 or 64% of all pupae, respectively. These proportions exceed values found by the study of compound leaves of horse chestnut trees at the end of the development of the first generation being evidently a result of the increase in the damage to the host leaves. Although the previously studied relationship was not verified at the generation its existence can be supposed with respect to the continuing decrease in food.

Table 3. Damage to individual leaves of horse chestnut by feeding and the proportion of diapausing pupae of *C. ohridella* in the first generation

Leaf number	% of mined leaf area	% of diapausing pupae	Leaf number	% of mined leaf area	% of diapausing pupae
1	25	0	15	45	44
2	25	10	16	45	50
3	30	0	17	45	50
4	30	0	18	45	50
5	30	25	19	50	53
6	35	0	20	55	44
7	35	17	21	55	44
8	35	0	22	60	68
9	40	0	23	65	77
10	40	27	24	70	65
11	40	29	25	75	60
12	40	31	26	80	64
13	40	40	27	90	69
14	45	0	28	90	75

The third generation of *C. ohridella* established in August suffers usually from considerable mortality in the Czech Republic. Owing to damage to the leaf area of host trees by previous feeding, frequent egg-laying occurs on necrotized leaf tissues and dying out the eggs. Due to the lack in food considerable part of caterpillars dies as well so that only a fraction of the generation enters the stage of a pre-pupa. With respect to the already advanced season, retardation or cessation of the development of remaining individuals occurs as a result of low air temperatures and thus, in the majority of localities in the Czech Republic, the third generation of *C. ohridella* is not completed. To the contrary, all pupae of the generation start to diapause.

At the beginning of the winter period, diapausing pupae of *C. ohridella* enter the stage of hibernation. During the stage, the diapausing pupae mortality of various intensity occurs. The proportion of died hibernating pupae of *C. ohridella* can reach almost 40% of their original number at the end of wintering. Adult emergence from hibernating pupae and establishment of the first generation occur in spring of the next year, under conditions of southern Moravia usually in April. Imagoes of *C. ohridella* hatch after 9 to 10 months from diapausing pupae of the first generation while in pupae which do not diapause the metamorphosis into imagoes is completed after 10 days. FREISE and HEITLAND (2002) mention that some pupae show a possibility to remain in diapause at least for three years. Thus, a fact has been explained that from the moment of the species appearance in 1985, a collapse has not been noticed in the pest populations although at the end of the second generation, the total depletion of food sources occurs yearly. The potential of the diapause prolongation in *C. ohridella* pupae was not noticed in the course of the study and, therefore, I could not corroborate it.

CONCLUSION

The proportion of diapausing pupae of *C. ohridella* from the total number of pupae in the first generation is not constant and can rather differ. In Brno and its environs in 2002, it was found that in samples of compound leaves from various localities and various parts of horse chestnut crowns, the proportion reached a value ranging from 1.4 to 59.3%. In samples of particular leaves of a selected tree, the proportion ranged between 0 and 77%. At the same time, significant differences were noticed in the area of damage to studied leaves caused by feeding. In compound leaf samples or individual leaves, the proportion of damaged leaf area reached a value of 9 to 84% or 25 to 90%, respectively.

By means of regression analysis, it has been found that there is a close relationship between the number of diapausing pupae and actual damage to leaves of a host. With the increasing number of individuals of *C. ohridella* in leaves and thus increasing damage to leaf area, the number of diapausing pupae of the first generation also increases. The phenomenon means a logical response of a population to the decrease in the amount of available food due to previous feeding. With respect to the existing decrease in food even in the next period it is possible to suppose the relationship also in other generations of *C. ohridella*.

Through the determination of close relationships of studied quantities, basic data are given for the more detailed knowledge of the population dynamics of *C. ohridella*. Findings obtained make possible to anticipate more exactly the following development of the abundance of particular developmental stages of the species and thus to facilitate the prediction of damage to horse chestnut by feeding.

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Received for publication March 1, 2003
Accepted after corrections April 24, 2003

Diapauza klíněnky jírovcové (*Cameraria ohridella* Deschka et Dimic`) a její dopad na populační dynamiku druhu

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ABSTRAKT: Klíněnka jírovcová (*Cameraria ohridella* Deschka et Dimic`) je polyvoltinní druh, dokončující za vhodných podmínek vývoj až tří generací v roce. V České republice však třetí generace v důsledku nedostatku potravy a později i nepřízně počasí trpí vysokou mortalitou. Není-li třetí generace dokončena, zajišťují populační kontinuitu diapauzující kukly, vyskytující se v každé generaci. Množství diapauzujících kukel je determinováno aktuální početností druhu a tedy i aktuálním poškozením listového aparátu jírovce maďalu (*Aesculus hippocastanum* L.). Závislost těchto veličin byla zkoumána v první generaci *C. ohridella* a její intenzita byla studována regresní analýzou.

Klíčová slova: *Cameraria ohridella*; *Aesculus hippocastanum;* diapauza; kukla; regresní analýza

Na vybraných lokalitách v Brně a okolí byla v roce 2002 studována diapauza kukel klíněnky jírovcové (*Cameraria ohridella* Deschka et Dimic`) a byl dokumentován význam tohoto jevu pro populační dynamiku druhu. Na začátku července, po ukončení vývoje první generace *C. ohridella*, byly ze zvolených jírovců maďalů (*Aesculus hippocastanum* L.) získány vzorky listů. Mezi zkoumanými vzorky byly zjištěny významné rozdíly jak v množství diapauzujících kukel *C. ohridella*, tak v poškození listové plochy žírem. Ve vzorcích složených, resp. jednotlivých listů se podíl diapauzujících kukel pohyboval v intervalu od 1,4 do 59,3 %, resp. od 0 do 77 % všech kukel. Podíl žírem poškozené listové plochy dosahoval v těchto vzorcích hodnot od 9 do 84 %, resp. od 25 do 90 % celkové listové plochy. Zjištěné údaje byly zaznamenány prostřednictvím korelačních diagramů a dále zkoumány regresní analýzou. Pomocí průběhu regresních přímek, hodnot indexu korelace (*I*) a hodnot druhé mocniny *I* bylo zjištěno, že mezi studovanými veličinami existuje těsná vazba. Byla zaznamenána pozitivní přímočará závislost množství diapauzujících kukel *C. ohridella* v první generaci na počtu jedinců a tedy na poškození listového aparátu hostitele. Nárůst množství diapauzujících kukel představuje logickou odezvu populace na rostoucí početnost druhu a z toho plynoucí pokles množství disponibilní potravy.

Diapauza *C. ohridella* je však nejen pozoruhodnou adaptací na důsledky vlastní potravně-destruktivní činnosti, ale má také další dosah. Vzhledem ke skutečnosti, že v podmínkách České republiky není často dokončena

třetí generace, představují diapauzující kukly současně pojistku před zhroucením populace. K líhnutí imag z těchto kukel totiž dochází až na jaře dalšího roku, tedy v období troficky i klimaticky nejpříznivějším. Pro populační dynamiku *C. ohridella* má proto diapauza zásadní význam a je jednou z příčin úspěšné existence druhu na nově obsazených lokalitách.

Zjištěné poznatky lze mj. využít jako podklady pro přesnější odhad vývoje početnosti *C. ohridella* a predikci vývoje poškození hostitelských stromů žírem.

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