Contribution to the knowledge of development and harmfulness of imported willow leaf beetle (*Plagiodera versicolora*) (Coleoptera, Chrysomelidae)

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ABSTRACT: The paper deals with the occurrence, development and harmfulness of imported willow leaf beetle (*Plagiodera versicolora* Laich.) in riparian and accompanying stands of the Svratka and Svitava rivers in the region of Brno. *Salix fragilis* L. and *S.* × *rubens* Schr. are the most damaged species there. Imagoes leave wintering places usually at the beginning of May. During about a 60-day period, they damage ca. 23.3 cm² leaves of *S. fragilis* and lay 250 to 730 (on average 539) eggs. The whole egg-laying consists of 16 to 48 (on average 35.5) groups with 6 to 26 (on average 15.2) eggs. The fecundity of females hatched in the laboratory is minimally twice lower. Larvae hatch after 5 to 8 (in the laboratory after 4.3) days and damage about 282 mm² leaves. The development from laying eggs until hatching imagoes of the 1st generation takes about 21 (in the laboratory about 15) days. Imagoes of the 1st generation occur on trees from the end of May to mid-August and die after completing their reproduction. *Plagiodera versicolora* creates 3 to 4 (in the laboratory 4 to 6) generations during a year. The small part of imagoes of the 2nd generation, predominant part (or all) imagoes of the 3rd generation and under conditions of a tetravoltine development all imagoes of the 4th generation enter a diapause. In the course of the growing season, the food consumption of imagoes and larvae decreases and fecundity of females markedly decreases. *Schizonotus sieboldi* (Ratz.), *Medina melania* (Meig.) and *M. luctuosa* (Meig.) rank among main enemies of *Plagiodera versicolora*.

Keywords: *Plagiodera versicolora;* Chrysomelidae; occurrence; development; fecundity; enemies; economic importance

In connection with several episodes of excessively dry and warm weather at the end of the last and at the beginning of the present century, the marked activation of dendrophilous insect species occurred in the Czech Republic. Water deficit became evident in the decreased resistance of trees and increased fecundity and survival of insect. Heavy feeding to defoliation was also noticed in a number of species of Chrysomelidae on broadleaved species. Extreme weather and primary physiological weakening of willows caused by the weather stimulated the origin of the unique gradation of *Chrysomela vigintipunctata*

(Scop.) occurring in the CR only rarely yet. Excessive heavy feeding to defoliation in alder was caused by *Agelastica alni* (L.) and *Linaeidea aenea* (L.) and in rowan by *Gonioctena quinquepunctata* (F.).

Significant damages were also caused by *Phratora vitellinae* (L.) in willow and poplar, by *Lochmaea capreae* (L.) in willow and birch, by *Galerucella lineola* (F.) in willow and alder, by *Chrysomela populi* (L.) in poplar and by *Plagiodera versicolora* (Laich.) mainly in willow.

Gradations of Chrysomelidae became a suitable occasion to study their occurrence, bionomy and

harmfulness (Urban 1997, 1998a,b, 1999, 2000, etc.).

Some new findings were obtained in a biologically interesting and economically important imported willow leaf beetle (*P. versicolora*). It is one of about 50 species of chrysomelids living in Central Europe on forest tree species. It belongs not only to frequent pests of willows (mare rarely of poplars) but also to the most abundant species of Chrysomelidae at all. According to the markedly orbiculate shape of its body and irregularly dotted wing-cases, it is possible to differentiate the species from other blue to green salicicolous chrysomelids of the genus *Phratora* Chevr. (= *Phyllodecta* Kir.).

P. versicolora is a species of the holarctic distribution. It occurs on extensive areas extending from northern Africa through the whole Europe (including the European part of the former Soviet Union and the Caucasus), Asia Minor and Central Asia, Siberia, China and Korea as far as Japan (Arnoldi et al. 1955; Brovdij et al. 1974; Kimoto, Takizawa in Ishihara et al. 1999, etc.).

The species is harmful in countries with Mediterranean and continental climate in the interval of annual temperature isotherms 9 to 12°C which roughly corresponds to 30–52° northern latitude (Maisner 1974). According to Schaufuss (1916), it is more abundant in Central Europe than in southern and northern Europe or in Siberia.

The species occurs not only far in the north but also high in mountains (Escherich 1923). Its range of distribution in Fennoscandia (above all in Norway, Finland and Lapland) reaches nearly the utmost north (Hellén et al. 1939). In 1911, it was introduced to New Jersey in the USA (Hood 1940) and in 1942 to the province of Quebec in Canada (Lechevalier 1944).

Various species of willows (*Salix* spp.) and poplars (*Populus* spp.) (Reitter 1912; Kuhnt 1913; Fleischer 1927–1930; Lopatin 1960; Warchalowski 1973; Aslan, Ozbek 1999, etc.) are host plants of *P. versicolora*. Roubal (1937–1941) mentions the chrysomelid mainly in narrow-leaved willows and poplars, Schaufuss (1916) in willows and *P. alba* L., Gusev and Rimskij-Korsakov (1953) in willows and *P. tremula* L. and Calwer (1876) and Klapálek (1903) even in birch. According to Medvedev and Šapiro (1965) the species lives mainly on willows and less abundantly to rarely on poplars. It damages shrubby and arborescent *S. fragilis* L., *S. viminalis* L., *S. purpurea* L., *S. caprea* L., *S. alba* L. and *S. triandra* L., rarely poplars (Brovdij et al. 1974). Its host species in Turkey are willows and more rarely poplars (Aslan 2001). In the former Yugoslavia, in addition to willows it is also *P. tremula*, *P. × canadensis* Moench. and *P. nigra* L. var. *italica* (Kovačevič 1957). According to Hood (1940) in the USA it prefers *S. nigra* Marsh. and *S. alba* L. var. *vitellina*, however, it attacks also *S. babylonica* L., *S. lucida* Muehlb. and poplars.

Many authors mention the chrysomelid only in willows. For example, Pernersdorfer (1941) found the species in Germany on *S. alba*, *S. fragilis* and *S. purpurea*. In Russia on the coast of Baikal Lake, it colonizes shrubby and arborescent willows (Dubeško 1970). In Japan, it lives on willows, particularly on *S. sachalinensis* F. Schm., sporadically on *S. miyabeana* Seem. and *S. integra* Thunb. (Ishihara et al. 1999).

In laboratory tests of 19 species and cultivars of willows and poplars, larvae mostly preferred *S. caprea* and *S. matsudana* Koidz. *tortuosa* whereas *S. triandra*, *P. alba*, *P. tremula* and *P. × canadensis* were resistant. However, there were differences in the food preference of larvae and imagoes.

Through the study of the chemical composition of willow leaves it has been found that according to the content of secondary metabolites and the occurrence of trichomes willows can be divided at least to 2 groups (Hegnauer 1973). Leaves of some species (eg *S. fragilis* and *S. purpurea*) contain phenolglycosides whereas leaves of other species (eg *S. alba*, *S. caprea* and *S. cinerea*) contain mainly proanthocyanides and tannins. While leaves with phenolglycosides are usually glabrous, leaves with proanthocyanides are usually covered with trichomes. Soetens et al. (1991) etc. found that the food preference of chrysomelids corresponded to the type and content of secondary metabolites and to the density of leaf trichomes. Observations carried out in nature show that *P. versicolora* damages mainly *S. fragilis* which contains the high proportion of phenolglycosides (particularly salicin) in leaves. However, trichomes play even a more important role than secondary metabolites in the choice of host species. For example, trichomes on leaves of *P. alba* intensely repel larvae of *P. versicolora* (Bogatko 1990).

Stimulation and inhibition effects of secondary metabolites on the occurrence of the chrysomelid on *S. integra* was studied by Jassbi (2003). Tahvanainen et al. (1985) experimentally corroborated that phenolglycosides affected food selection of chrysomelids. Matsuda and Matsuo (1985) emphasize the role of salicin, populin and luteolin 7-glucoside in the food preference of *P. versicolora*. Stimulation effects on feeding show flavonoids quercitrin, rutin, quercetin, myricitrin, myricetin and morin

(Matsuda 1978). Ikonen et al. (2001) found that the chrysomelid did not prefer willows with the low content of hydrochlorid acid in leaves and that the acid did not provide effective protection to willows from herbivorous species even with unreasonably high concentrations. Through the detailed study of food preferences and the development of 4 species of chrysomelids including *P. versicolora* on *S. sericea* Marsh. and *S. eriocephala* Michx. and their hybrids it has been proved that species with phenolglycosides are more looked up by special willow herbivorous species whereas species without phenolglycosides are more suitable for general herbivores (Orians et al. 1997). Hallgren (2002) found the different content of phenolglycosides and tannins in *S. caprea*, *S. repens* L. and *S. aurita* L. and their hybrids. According to the author, herbivores are variously affected by interspecific hybridization and usually they damage more hybrids than parent pairs.

The development of *P. versicolora* is dealt with in many aggregate and specially oriented papers (eg Kaltenbach 1874; Schaufuss 1916; Escherich 1923; Hood 1940; Lechevalier 1944; Fatachov 1953; Arnoldi et al. 1955; Schnaider 1957, 1972; Wagner, Ortmann 1959; Maisner 1974; Wade, Breden 1986; Bogacheva 1998; McCauley et al. 1988; Stevens, McCauley 1989; Kokanova 1992; Ishihara et al. 1999; Aslan 2001, etc.).

Effects of nutrition and reserves of water in soil on the growth and content of proteins and phenolglycosides in leaves of *S. sericea* studied Lower et al. (2003). According to the authors, well supplied species have got the higher content of proteins which supports (in spite of the lower content of phenolglycosides) laying and production of eggs. Nitrogen fertilization affects not only chemical composition, growth dynamics and leaf dimensions of *P. deltoides* Bart. but also damage caused by *P. versicolora* (Wait et al. 1998, 2002). Therefore, *P. versicolora* and a number of other species of chrysomelids cause greater damages at lower localities with higher moisture, particularly in flooded or artificially irrigated places (Lopatin 1960).

The species always prefers leaves in a certain stage of development which is related to their localization and nitrogen supply. In contrast to the concentration of phenolglycosides the total content of nitrogen in leaves of *P. deltoides* increases due to shading and imagoes tend to prefer species growing in shade (Crone, Jones 1999).

In *P. versicolora*, imagoes consume younger leaves at a distance of several cm from shoot tops and lay eggs on somewhat older leaves. The development on younger and older leaves brings both advantages and disadvantages. Raupp (1985) found that during the consumption of older leaves of *S. babylonica* and *S. alba* imagoes considerably wore their mandibles. It reflects upon the reduction of consumed food and fecundity. However, in rearings carried out by King et al. (1998), females selected younger leaves not only for feeding but also for egg-laying regardless of their size and position. During feeding on younger leaves mandibles of larvae wear less and larvae develop more faster reaching higher weight. Expositions of acute doses of ozone (Jones, Coleman 1988; Coleman, Jones 1988) show positive effects on feeding and negative effects on oviposition. Relationships between the chrysomelid and *Melampsora alliifragilis* Kleb. on *S. × cuspidata* Schulz were studied by Simon and Hilker (2003). The pathogen caused increase in mortality, decrease in weight and prolongation of the development of larvae. However, the previous feeding of the chrysomelid did not affected mortality or duration of the development of larvae but significantly decreased their weight.

Larvae of *P. versicolora* live in aggregation in the first half of their development. Crowe (1995a,b) deals with ethology of larvae including effects of the group size on their growth and survival. In his laboratory experiments, larvae positively responded to siblings, however, their secretes and frass showed reaggregation effects. The number of larvae in a group did not affected their weight but significantly influenced their mortality. Larvae thrived best in groups of 16 members which corresponds to the average number of eggs (15.3) in a group in nature.

Effects of the number of larvae in a group and of cannibalism on the growth and survival of larvae were also studied by Breden and Wade (1985, 1987, 1989). According to the authors, individuals in larger groups show lower mortality and individuals feeding their own eggs and larvae develop faster.

A number of other partial problems of the biology of *P. versicolora* was also investigated. For example, Jones et al. (1993) studied systemic induction of the resistance of *P. deltoides* to the chrysomelid. Raupp and Denno (1984) and Raupp and Sadof (1991) dealt with effects of the previous damage to leaves on the growth, mortality, development and distribution of the chrysomelid on *S. babylonica* and *S. alba*. Positive effects of shelters in *S. miyabeana* made by caterpillars of Lepidoptera on the mortality of larvae were proved by Nakamura and Ohgushi (2003). Biosynthesis of defensive secretes of larvae is, eg dealt with by Daloze and Pasteels (1994) and Veith et al. (1994). Intraspecific and interspecific effects of larval secretes were, for example assessed by Grégoire (1988), Pasteels et al. (1988), Strauss

(1988), Hilker (1989), Sugeno and Matsuda (2002), etc. Effects of a photoperiod on the diapause of adults were studied, eg by Ishihara (2000) and Ishihara and Hayashi (2000). They have found that the start of a diapause induces a short light day and terminates a long light day.

Schizonotus sieboldi (Ratz.) (Jones 1933; Dowden 1939; Nikolskaja 1952; Fatachov 1953) and *S. latus* (Walk.) (Pteromalidae) (Džanokmen 1978; Ishihara et al. 1999) rank among natural enemies of the chrysomelid. *Coelopisthia rotundiventris* (Gir.) (Weiss, Dickerson 1917) and *Arthrolytus incongruens* Masi (Leonardi 1922) belong to parasitoids of the chrysomelid. *Anthomyiopsis nigrisquamata* (Zett.) (Leonardi 1922), *A. plagioderae* Mesn. (Ruffo 1938; Mellini 1957; Ishihara et al. 1999) and *Medina luctuosa* (Meig.) (Tachinidae) (Jolivet 1950) are rare parasitoids. Nematoda from the family Mermithidae (Siddikov et al. 1989) often parasitize in the chrysomelid. There are only few data concerning predators of the chrysomelid (Whitehead, Duffield 1982; Yamane 1990; Hamanishi 1996, etc.).

Numerous references can be also found in literature on the *P. versicolora* harmfulness and control. Kokanova (1992), Bogatko (1993), Czerniakowski (2000, 2002), Aslan (2001), etc. deal with the economically important damage to willows. Possibilities of using *Bacillus thuringiensis* Berl. to control the chrysomelid were studied by Bauer (1992) and Feng-Shu et al. (2000). Traditional and alternative methods and means of control were summarized by Allegro (1989).

Good effects of granulated systemic insecticides to control *P. versicolora* on poplars were demonstrated by Cavalcaselle (1972). The author, however, does not recommend their application with respect to high financial expenses. Jodal (1985) effectively killed larvae and imagoes in a poplar plantation using insecticides based on diflubenzuron and carbofuran. Xu and Wan (1990) found that mixtures of pesticides applied to control *P. versicolora* made possible to control more pests and so they were more effective than individual preparations.

MATERIAL AND METHODS

The majority of field observations of the occurrence, development and harmfulness of *P. versicolora* was carried out in riparian and accompanying stands along the Svratka and Svitava rivers in the region of Brno in 1995 to 2005. Along the Svratka river, a stand was studied differentiated from the aspect of species, age and space in the cadastre of town parts Brno-Komín and Brno-Jundrov at an altitude of 205 to 210 m. Mean annual temperature amounts to 8.4°C, mean annual precipitation 547 mm and the growing season about 168 days. In the rich species composition, *Salix fragilis*, *S. alba*, *S. × rubens* Schr. (= *S. alba × S. fragilis*), *Populus nigra*, *P. nigra* var. *italica*, *P. alba* and *P. × canescens* (Ait.) Smith. were abundantly represented. Inspections were carried out there during the growing season usually in week intervals. Along the Svitava river, a stand was checked in the section from Brno-Obřany to Adamov at an altitude of 218 to 250 m and a neighbouring stand along a small stream in Řícmanice. The stands occur in a similar climatic region showing also similar silvicultural-management aspects. *S. fragilis*, *S. alba*, *S. × rubens*, *S. viminalis*, *S. triandra*, *S. purpurea*, *S. × rubra* Huds. (= *S. viminalis × S. purpurea*), *S. caprea*, *P. nigra*, *P. nigra* var. *italica* etc. are abundantly represented in it. Inspections were usually carried out there in 2-week intervals. Occasionally, also some other localities were checked in central and southern Moravia.

During field trips, the occurrence was studied of particular developmental stages of *P. versicolora* on various species of willows and poplars. Attention was paid to the intensity of maturation and regeneration feeding of imagoes on leaves in various parts of tree crowns and to the localization of egg groups including the number of eggs in the groups. At the same time, the occurrence was studied of other important salicicolous species, particularly of *Chrysomela vigintipunctata* (Scop.), *C. populi* L., *Phratora vitellinae* (L.), *P. vulgatissima* (L.), *Lochmaea capreae* (L.) and *Galerucella lineola* (F.). The insect was caught by simple collection or by means of sweep nets for subsequent laboratory studies.

In the laboratory, *P. versicolora* was reared on freshly cut foliaged sections of shoots (particularly *S. fragilis*) and tentatively also on other species. Lower ends of shoots were put to small vessels with water and sealed with paper wool or covered with damp slips of paper wool. Shoots with imagoes, eggs and larvae or pupae were put into glass vessels of a diameter of 20 (or 10) cm and height of 10 (or 5) cm. Under such arrangement of rearing leaves preserved freshness for the period of several days. Moderately wilted or heavily damaged shoots were replaced by fresh ones in 2-week or 4-week intervals.

Imagoes were usually reared in mixed groups 3 to 30 adults each, namely from the beginning of their spring invasion to trees or from the time of their hatching. Throughout the growing season, damaged leaf area was measured using planimetry. The number of laid eggs and the number of partial egg-

laying (egg groups) on the abaxial and adaxial face of leaves was recorded. Copulation of imagoes and their period of life were monitored. In dead females, the number of unlaid eggs was determined by means of ovary dissection. The period of embryonic development was recorded. The size of eggs was measured using micrometry soon after their laying and near before hatching.

Larvae were reared in groups of 6 to 60 (on average 17) members. The period of feeding and leaf area damaged by larvae of the 1st to the 3rd instar were recorded. Instars were identified according to the width of head measured by micrometry and tentatively also according to the number of exuviae on leaves. Localization and dimensions of feeding marks on the adaxial and abaxial face of leaves were determined as well as the size of frass.

After completing the development of the last generation of *P. versicolora*, imagoes were placed in outdoor conditions and after undergoing their winter diapause back to the laboratory. Parasitoids of imagoes from the family Tachinidae were determined by dr. J. Čepelák (Nitra).

RESULTS AND DISCUSSION

Host tree species

In nature, *P. versicolora* was found most frequently on *S. fragilis* and *S. × rubens* and rather frequently also on *S. alba* var. *vitellina*, *S. viminalis* and *S. caprea*. In the comprehensive study of insect pests in 60 osier plantations in Moravia in 1969 to 1976 gradations of the chrysomelid were not noted. It occurred most abundantly in Pouzdřany (former district of Břeclav) on willows *S. × rubens* and *S. × basfordiana* Schl. (= *S. alba* var. *vitellina* × *S. fragilis*).
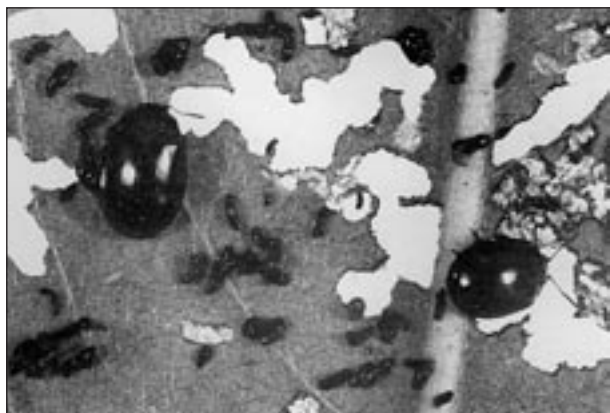
In laboratory rearings, imagoes consumed most willingly *S. fragilis* and *S. × rubens*. They damaged less intensively *S. viminalis*, *S. caprea*, *S. × smithiana* Willd. (= *S. viminalis* × *S. caprea*), *S. × rubra*, *S. purpurea*, *S. americana* Hoedt., *P. nigra* and *P. nigra* var. *italica*. If imagoes were in a position to select among some species mentioned above then they did not consume *S. daphnoides* Vill., *S. acutifolia* Willd., *S. triandra* and *P. alba* at all. They completely refused to consume leaves of *Betula verrucosa* Ehrh. and *Alnus glutinosa* (L.) Gaertn. and during 14 days they died. Larvae preferred *S. fragilis* and *S. × rubens* as compared with *S. viminalis*, *S. caprea*, *S. purpurea*, *S. × rubra* and *S. americana*. In the course of rearing, the order of popularity of species several times changed and, therefore, results of the tentative tests do not entitle to express definitive conclusions.

The occurrence and distribution of *P. versicolora* are dependent not only on chemical but also on physical properties of trees (Bogatko 1989; Soetens et al. 1991). According to Bogatko (1989, 1990) the chrysomelid shows the greatest trophic affinity to *S. fragilis* and *S. caprea*. The following willows rank among highly attractive species: *S. × rubens* (Soetens et al. 1991) and *S. × basfordiana*. According to Hood (1940), the chrysomelid preferentially damages also *S. alba* var. *vitellina*. Commonly, it develops on *S. americana* (Czerniakowski 2000, 2002) and on a number of other willow and poplars, eg on *P. nigra* and *P. nigra* var. *italica*.

According to Coleman and Jones (1988), Jones et al. (1993), Wait et al. (2002) etc., *P. deltoides* Marsh. and according to Kovačevič (1957) also *P. tremula* rank among its primary host plants. According to Bogatko (1989), eg *S. triandra*, *P. alba*, *P. tremula* and *P. candicans* Ait. belong to resistant species.

Fig. 1. Last year's imagoes of *Plagiodera versicolora* when perforating on the adaxial face of a leaf of *Salix fragilis*. Numerous frass occurs on leaves. Laboratory rearing, 8 June 1998

Fig. 2. A male and a female of *P. versicolora* including frass on the adaxial face of a leaf of *S. × rubens*. Brno-Komín, 14 May 1997

Fig. 3. Details of damage to a leaf of *S. fragilis* caused by an imago of *P. versicolora*. Laboratory rearing, 12 May 1995

Fig. 4. Lateral feeding of imagoes of *P. versicolora* on a leaf of *S. fragilis* including the group of eggs. Laboratory rearing, 15 May 1998

Fig. 5. Different appearance of damage to an old leaf of *S. fragilis* by imagoes of *P. versicolora*. Laboratory rearing, 30 May 1995

Hibernation and feeding of imagoes after wintering

Imagoes of *P. versicolora* winter on the soil surface under dry leaves, in bark fissures, in hollow stems of plants and in other ground-level and aboveground shelters. During low winter temperatures, they undergo a diapause and thus, in spring after increasing the temperatures they can continue in their development. In localities under study, they leave their winter habitats usually at the beginning of May, in the warmest areas of southern Moravia (the region of Břeclav) already at the end of April and in regions of central and northern Moravia in the first half of May. According to Heeger in Kaltenbach (1874), Dowden (1939), Pernersdorfer (1941), Arnoldi et al. (1955), Lopatin (1960), etc. imagoes colonize host species in May. Nüsslin and Rhumbler (1922), Mohr (1966) and Maisner (1974) mention leaving the hibernation shelters already in April. In Tadzhikistan, they are active even at the end of March and mainly at the beginning of April at a mean temperature of 14.7°C which usually coincides with the period of willow budbreak (Fatachov 1953). On the other hand, in Japan, imagoes begin to occur on trees only after the end of May (Ishihara et al. 1999).

Hungry and debilitated beetles start maturation feeding on freshly unfolded leaves immediately after reaching host trees. After about one-week feeding (in the laboratory already after 2 or 3 days), imagoes mostly mate for the first time. The copulation can be observed in nature throughout their occurrence on trees. Pernersdorfer (1941) allegedly observed a male copulating with a female of *Chrysomela saliceti* (Weise). According to Stevens and McCauley (1989), many females copulate repeatedly with more than one male, namely usually before their enter into a diapause. According to our observations, imagoes do not copulate with one another in late summer and early autumn and thus, usually unfertilized females enter the diapause. The are very wary responding to approaching danger by a fall to the soil surface.
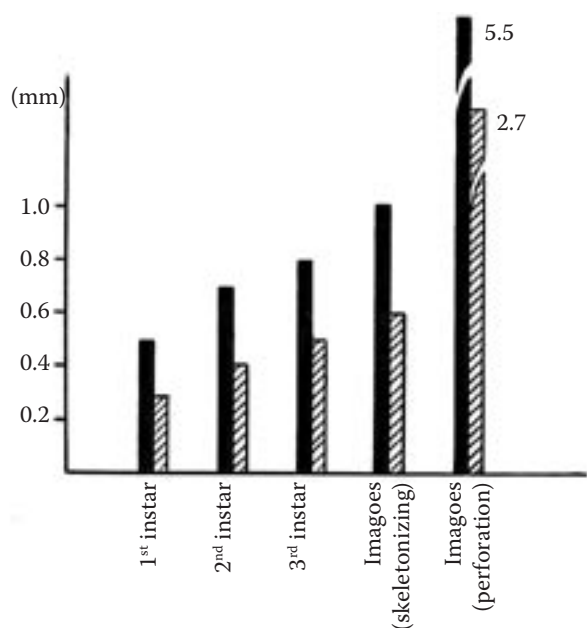

Fig. 6. The average length (dark) and width of feeding marks (dash line) of larvae of the 1st to the 3rd instar and imagoes of *P. versicolora* on leaves of *S. fragilis* (mm). Laboratory rearing, 1995 to 2004

Table 1. Ways of damage to leaves of *Salix fragilis* by imagoes of *Plagiodera versicolora* including their localization in feeding. Laboratory rearing, 1995 to 2004

Generation of imagoes	Way of damage		Localization		Note-peripheral feeding
	perforation (incl. peripheral feeding)	scratchy feeding (skeletonizing)	adaxial face of leaves	abaxial face of leaves	
After hibernation	90	10	90	10	often
1st	85	15	90	10	often
2nd	50	50	85	15	rather often
3rd	20	80	80	20	rarely
4th	15	85	80	20	rarely
5th	10	90	75	25	–
6th	10	90	75	25	–

Table 2. Length and width of frass of larvae of the 1st to the 3rd instar and imagoes of *P. versicolora* (mm)

Instar Stage	Length		Width	
	from–to	mean	from–to	mean
1st	0.11–0.28	0.21	0.07–0.14	0.10
2nd	0.25–0.54	0.40	0.14–0.25	0.19
3rd	0.46–0.89	0.61	0.18–0.32	0.25
Imagoes	0.54–1.32	0.84	0.18–0.32	0.25

Table 3. The average period of feeding of imagoes of *P. versicolora* on leaves of *S. fragilis* (days). Laboratory rearing

Year	Last year's imagoes (after hibernation)		This year's imagoes (from rearing) – generation					
	from nature	from rearing	1st	2nd	3rd	4th	5th	6th
1995	?	33	49	34	28	23	–	–
1998	60	34	39	38	37	25	–	–
1999	60	37	38	45	38	36	28	26
2001	?	?	38	39	35	30	–	–
Mean	(60)	(34)	(41)	(39)	(35)	(29)	(28)	(26)

Imagoes bite out irregular gaps into leaf blades (Figs. 1 to 3) or feed on leaves along their margins (Fig. 4). They also often damage lateral leaf veins. Somewhat older and thus also tougher leaves are perforated or skeletonized by imagoes, however, venation is usually not disturbed (Fig. 5). In laboratory rearing, leaves of *S. fragilis* were 90% perforated or browsed from leaf margins and only 10% skeletonized while venation or leaf epidermis were not damaged. Leaves were 90% fed from their adaxial face (Table 1). Bite out holes are on average 5.5 mm long and 2.7 mm wide. However, holes bite out in older leaves are only on average 1.0 mm long and 0.6 mm wide (Fig. 6). During feeding, imagoes produce considerable amounts of frass on average 0.61 mm long and 0.25 mm wide (Table 2). The frass is black, uneven on its surface, oval on one end and usually moderately elongated on the other end (Fig. 1).

Last year's beetles caught in nature at the beginning of the period of their activation took food about 60 days. Last year's beetles reared in the laboratory after wintering in outdoor conditions damaged leaves on average only 34 days and soon died (Table 3). Imagoes of the last generation reared in the laboratory lived after a diapause under outdoor conditions on average 300 days. The duration of living both of males and females was the same (Table 4, Fig. 7).

Last year's imagoes caught in nature in spring before the beginning of feeding damaged in rearings about 23.3 cm² leaves of *S. fragilis*. On the other hand, imagoes reared in the laboratory after the end
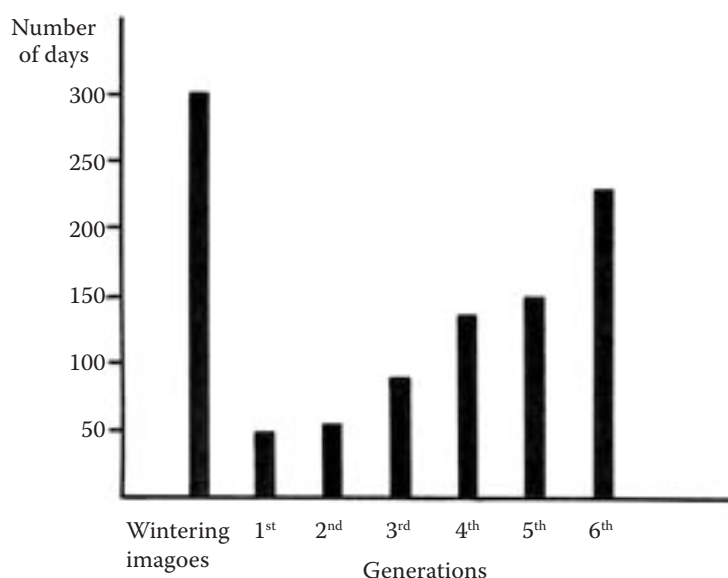
Fig. 7. The average time of living of imagoes wintering in nature and imagoes of the 1st to the 6th generation of *P. versicolora* (days). Laboratory rearing, 1995 to 2005

of a winter diapause damaged on average only about 10.7 cm² leaves of *S. fragilis* (Table 5). Last year's imagoes caught in nature near before the beginning of feeding lived in capture about 1.8× longer and damaged 2.2× larger leaf area than imagoes reared in the laboratory. Imagoes from nature consumed most food in the 2nd to the 5th week (imagoes from laboratory rearings already in the 1st week) after the beginning of feeding (Table 6). The intensity of feeding gradually decreased and in the 13th week (in imagoes from rearings already in the 7th week) the feeding ceased.

Egg-laying of the 1st generation

Eggs developed in ovaries of females as late as during the maturation and regeneration feeding. In rearings, females oviposited the first eggs after 4 to 6 days of feeding. In nature, the first eggs occur after about 7 days (according to Fatachov 1953, after 8 to 10 days) from the invasion to trees. In studied localities, eggs of the 1st generation of the chrysomelid were usually found in the period from the 7 May to the 25 June. In the period of the most intense feeding, females lay eggs nearly every day.

Table 4. The period of living of imagoes hibernating in nature and imagoes of the 1st to the 6th generation of *P. versicolora* in days (from–to and mean). Laboratory rearing, 1995 to 2004

Sex	Generation of imagoes						
	after wintering	1st	2nd	3rd	4th	5th	6th
Males	275–350 300	10–350 54	4–340 54	18–202 96	54–313 163	65–250 158	? (230)
Females	275–350 300	10–350 41	15–340 56	32–256 84	22–313 116	45–230 146	? (230)
Mean	275–350 300	10–350 48	4–340 55	18–256 90	22–313 137	45–250 149	? (230)

Table 5. The average area of leaves of *S. fragilis* damaged by imagoes of *P. versicolora* (cm²). Laboratory rearing

Year	Last year's imagoes (after hibernation)		This year's imagoes (from rearing) – generation					
	from nature	from rearing	1st	2nd	3rd	4th	5th	6th
1995	?	11.2	26.3	13.1	10.3	4.1	–	–
1998	21.1	11.0	13.0	10.2	10.0	11.2	–	–
1999	24.2	9.6	15.5	14.4	11.0	11.3	9.5	5.0
2001	?	?	19.2	10.8	7.3	6.0	–	–
Mean	(23.3)	(10.7)	(17.1)	(12.5)	(9.3)	(7.7)	(9.5)	(5.0)

Table 6. The average damage to leaves of *S. fragilis* by imagoes of *P. versicolora* (in % of the total damaged area) and the average total damaged area (cm²). Laboratory rearing, 1995, 1998, 1999 and 2001

Week	Last year's imagoes		This year's imagoes – generation					
	from nature	from rearing	1st	2nd	3rd	4th	5th	6th
1st	13.7	26.4	29.0	38.9	54.4	44.3	44.9	66.4
2nd	15.5	22.5	18.8	22.9	19.8	34.3	21.1	24.9
3rd	15.3	16.3	15.6	12.1	10.3	10.1	8.6	5.8
4th	14.5	14.1	13.3	9.6	6.6	3.7	5.9	2.1
5th	15.4	12.1	11.0	7.0	5.0	3.0	7.3	0.6
6th	10.5	6.0	5.4	4.2	1.9	1.6	4.6	0.2
7th	5.0	2.6	3.6	2.0	0.3	1.1	2.0	–
8th	4.8	–	2.0	1.8	–	1.0	2.6	–
9th	3.5	–	1.0	1.2	–	0.8	1.0	–
10th	0.7	–	0.3	0.3	0.7	–	2.0	–
11th	0.6	–	–	–	0.7	–	–	–
12th	0.3	–	–	–	0.3	0.1	–	–
13th	0.2	–	–	–	–	–	–	–
%	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
Area (cm²)	(23.3)	(10.7)	(17.1)	(12.5)	(9.3)	(7.7)	(9.5)	(5.0)

They place the eggs into groups on the abaxial face of leaves. In laboratory rearings, however, females oviposited on average 62.0% eggs (according to KING et al. 1998 about 70% eggs) on the abaxial face of leaves, 29.3% on the adaxial face of leaves, 8.4% on walls of glass rearing dishes and 0.3% on damp paper wool (Table 7). In nature, the majority (about 59%) of eggs is laid on the basal third of a leaf blade. About 28% eggs are oviposited on the central third of a leaf blade and about 14% eggs on the apical third of a leaf blade.

Eggs are oblong, cylindrical, round on both ends, lustrously yellow-white to yellow-orange (Figs. 9 and 10). Newly oviposited eggs are 0.93 to 1.11 (on average 1.02) mm long, according to FATACHOV (1953) about 1.2 mm. Their width is 0.40 to 0.46 (on average 0.44) mm. The length of eggs nearly does not change during the embryonic development, however, their width slightly increases and in the period before the eclosion of egg larvae, it amounts to 0.4 to 0.5 (on average 0.46) mm. Unlike chrysomelids from the genus *Phratora* spp. eggs are placed upright or obliquely on leaves, sporadically also in parallel with a leaf. Between neighbouring eggs in a group, there are mostly about 1 mm gaps an so eggs touch each other only rarely.
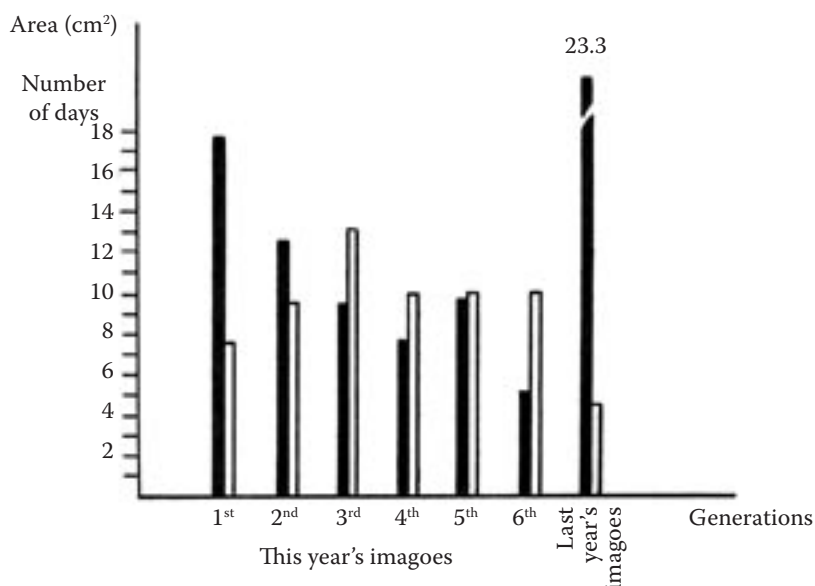

Fig. 8. The average area of leaves of *S. fragilis* (cm²) damaged by this year's and last year's imagoes of *P. versicolora* (dark) and the average time of feeding of females (days) till the beginning of oviposition (light). Laboratory rearing, 1995 to 2001

Table 7. Localization of eggs of *P. versicolora* on leaves of *S. fragilis* in nature (1st line) and in rearing plates (% of the total number of eggs). Bílovice nad Svitavou, Řícmanice and Brno-Komín, laboratory rearing, 1995 to 2004

Females	Leaves		Walls of glass rearing vessels	Moisten paper wool
	abaxial face	adaxial face		
Last year's (from nature)	100.0	–	–	–
Last year's (from rearing)	62.0	29.3	8.4	0.3
1st generation	58.9	21.9	18.8	0.4
2nd generation	49.7	37.6	12.7	–
3rd generation	47.3	43.7	9.0	–
4th generation	41.9	57.7	0.4	–
5th generation	44.0	56.0	–	–
6th generation	40.0	60.0	–	–

Table 8. The average number of eggs laid by females of *P. versicolora* obtained from nature and from rearing on *S. fragilis*. Laboratory rearing

Year	Last year's females (after wintering)		This year's females (from rearing) – generation					
	from nature	from rearing	1st	2nd	3rd	4th	5th	6th
1995	?	267.0	355.0	74.1	34.2	0.0	–	–
1998	412.0	250.0	151.7	57.5	32.0	11.5	0.7	–
1999	570.5	223.0	219.3	172.7	117.4	69.0	22.7	8.8
2001	?	?	192.0	33.6	16.9	0.5	–	–
Mean	(538.8)	(249.4)	(222.4)	(90.2)	(39.2)	(22.4)	(15.4)	(8.8)

Imagoes live in nature about 2 months. They ingest food, repeatedly copulate and lay eggs for a period of about 7 weeks. In total, they lay 250 to 730 (on average 539) eggs (Table 8, Fig. 11). The whole collection is placed in 16 to 48 (on average 35.5) groups (partial collections) of a mean number of 15.2 eggs. After the cessation of their feeding, they live even 2 weeks and die. The fecundity of females reared from eggs in laboratory conditions is much lower. In actual rearings, these females oviposited 120 to 456 (on average 249) eggs, ie 2.2× less than females in nature (Table 8, Fig. 11). Eggs were laid in 8 to 32 (on average 17.3) groups of a mean number of 14.4 eggs in a group. There is a direct proportion between the number of laid eggs and the consumption of food (Raupp 1985).

By means of microscopic dissections of naturally dead females no eggs were found in ovaries. It means that females always lay all eggs and thus the actual fecundity is equal to the number of eggs created

Fig. 9. The group of eggs of *P. versicolora* on the abaxial face of leaves of *S. fragilis*. The leaf was intensely damaged by imagoes. Laboratory rearing, 15 May 1998
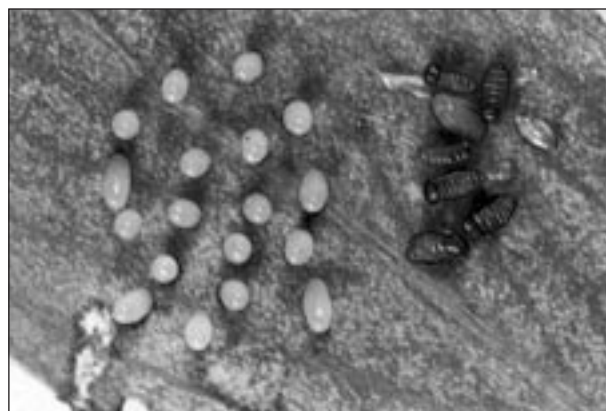

Fig. 10. The group of eggs and the group of larvae of the 1st instar of *P. versicolora* on the abaxial face of a leaf of *S. × rubens*. Brno-Komín, 27 May 1997
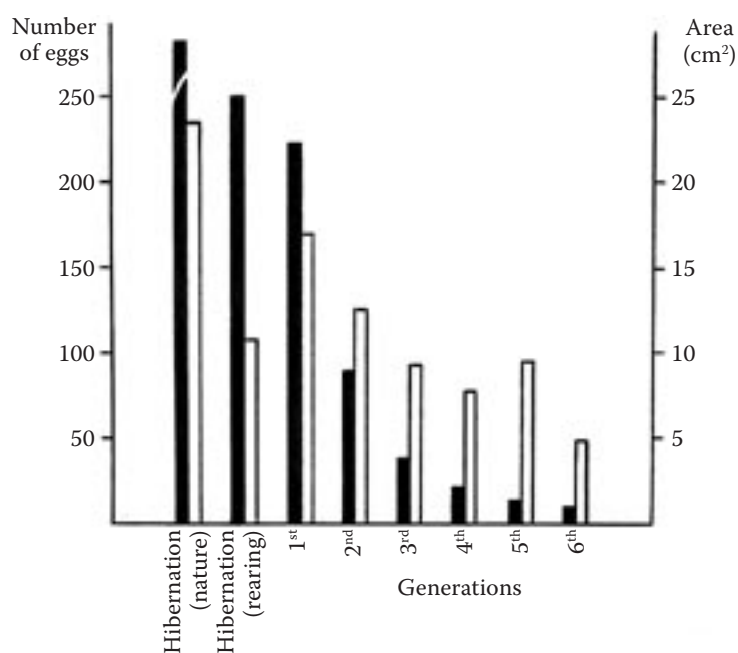
Fig. 11. The average number of eggs laid by females of *P. versicolora* (dark) and the average area of leaves of *S. fragilis* (cm²) damaged by male and female imagoes (1:1) (light). Laboratory rearing, 1995 to 2003

in ovaries. The average fecundity of females is also related to their size. The length of examined females amounted to 3.8–4.8 (on average 4.3) mm, the length of males 3.2–4.2 (on average 3.7) mm (Fig. 12). The fecundity of females of a below-average size was usually lower as compared with above-average females. In this context, it is necessary to mention that numerous literature sources (REITTER 1912; SCHAUFUSS 1916; MEDVEDEV, ŠAPIRO 1965; MOHR 1966, etc.) note the different length of imagoes (from 2.5 to 4.5 mm). Results of our measurements of the length of 152 males and 235 females correspond to findings of FATACHOV (1953). According to the author the length of imagoes ranges from 3 to 5 mm.

In egg groups of *P. versicolora* on leaves of *S. fragilis* in Bílovice nad Svitavou and Řícmanice, there were 6 to 26 (on average 15.2) eggs (Fig. 13). The similar number of eggs in groups (1 to 34 eggs, on average 14.4 eggs) occurred also in laboratory rearings (Fig. 14). In mass rearings of imagoes, it was

sometime rather difficult to determine the number of egg groups and, therefore, data in Fig. 14 are not quite exact. Based on Figs. 13 and 14, it is evident that the number of egg groups with the even number of eggs is significantly higher than the number of egg groups with the odd number of eggs. Table 9 demonstrates the marked numerical predominance of egg groups with the even number of eggs in nature as well as in the laboratory. In groups with the even number of eggs there were about 60% (in laboratory rearings about 59%) eggs. This interesting finding can be logically substantiated by the pair structure of ovaries of females and by the number of functional ovarioles in ovaries.

Literature data on the period of oviposition and their localization are not abundant and sometimes are rather different. Little findings have been obtained on the fecundity of females yet. For example, KALTENBACH (1874) mentions that females lay eggs on leaves in groups of 4 to 8 eggs in June. SCHNAIDER
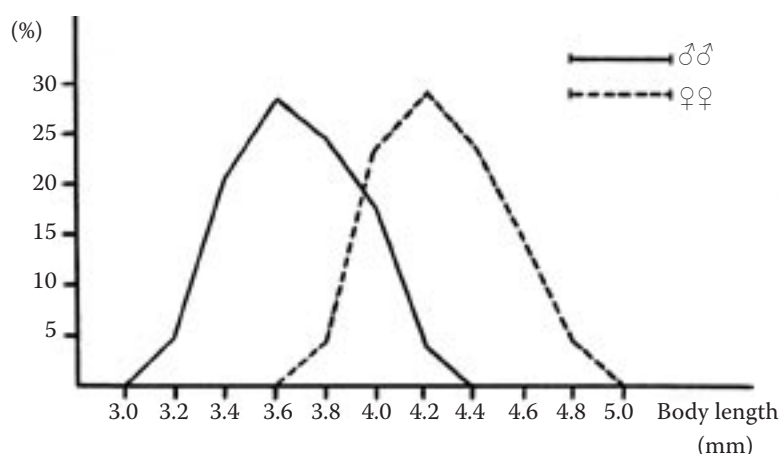

Fig. 12. The percentage of male and female imagoes of *P. versicolora* according to the body length (mm)
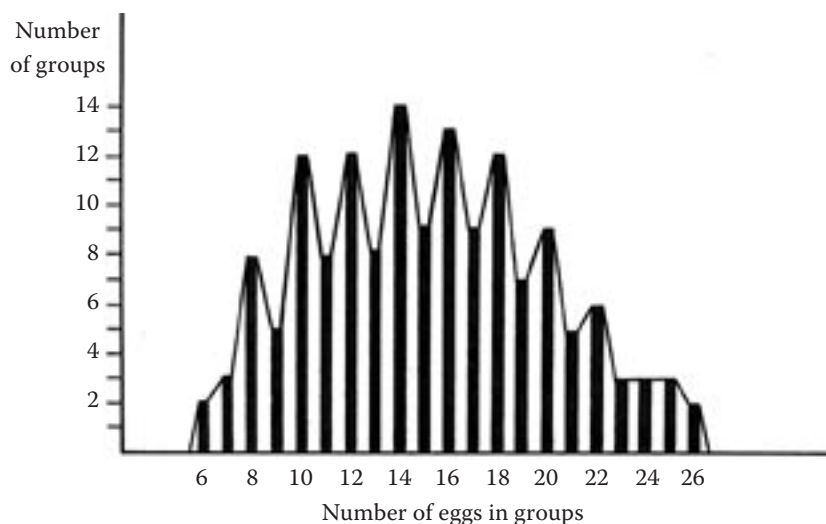
Fig. 13. The frequency of the occurrence of egg groups of *P. versicolora* of the even and odd number of eggs on *S. fragilis* and *S. × rubens*. Bílovice nad Svitavou, Řícmanice, Brno-Komín and Brno-Jundrov, 1995 to 2004

(1957) mentions laying the eggs on the lower side of leaves. According to the author, females can lay as many as 200 eggs. According to Fatachov (1953), females lay eggs from 10 April to 17 May (ie 37 days). During the period, they lay about 290 eggs in groups of 13 to 15 eggs each. Maisner (1974) notes that females lay about 350 eggs on the abaxial face of leaves in groups of 10 to 20 eggs each. The average number of eggs in groups (15.2) found by the author in nature on *S. fragilis* is identical with the number of eggs in groups on *S. nigra* and *S. alba* in the USA (Crowe

1995b) and on *S. sachalinensis* in Japan (Ishihara 2000; Ishihara, Hayashi 2000). On the island of Hokkaido (Japan), imagoes begin to colonize their host plants (mainly *S. sachalinensis*) as late as at the end of May. The proportion of females with mature ovarioles increases there till the beginning of June when the period of oviposition also begins (Ishihara et al. 1999; Ishihara 2000). In the USA, mother beetles occur on trees in April and May (Raupp, Sadof 1991) and lay eggs at the beginning of May (Wade, Breden 1986) or from mid-May (Dowden 1939).

Table 9. The number of egg groups, the number of eggs and the % of eggs of *P. versicolora* with the even and odd number of eggs in a group. Bílovice nad Svitavou, Řícmanice and Brno-Komín, laboratory rearing, 1995 to 2004

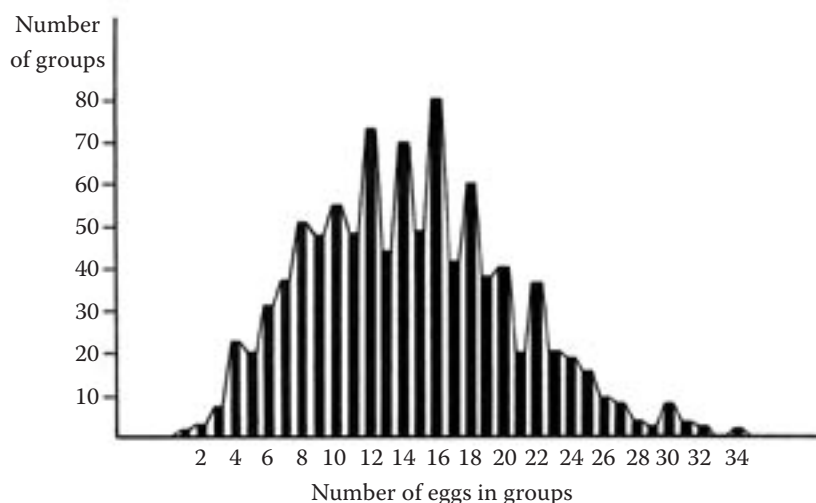| Number of eggs in a group	Nature			Laboratory		
	number of groups	number of eggs	%	number of groups	number of eggs	%
Even	93	1,396	60.1	567	8,266	58.9
Odd	60	928	39.9	405	5,775	41.1
Total	153	2,324	100.0	972	14,041	100.0
Mean	15.2		–	14.4		–

Fig. 14. The frequency of the occurrence of egg groups of *P. versicolora* of the even and odd number of eggs on *S. fragilis*. Laboratory rearing, 1995 to 2004

Table 10. The average period of development of *P. versicolora* on *S. fragilis* from oviposition to hatching the imagoes (days). The development of the 7th generation was not completed. Laboratory rearing, 1995 to 2004

Generation	Period of development (days)			
	embryos	larvae	prepupae and pupae	total
1.	4.3	6.8	3.9	15.0
2.	4.3	6.9	4.0	15.2
3.	4.3	7.0	4.0	15.3
4.	4.3	7.2	4.3	15.8
5.	4.3	7.3	4.4	16.0
6.	4.3	7.6	4.6	16.5
7.	?	?	?	?
Mean	(4.3)	(7.1)	(4.2)	(15.6)

The period of spring invasion to crowns of host trees coincides with the abundance of quality food at the beginning of the growing season.

P. versicolora belongs to specific phytophages preferring young leaves in the certain stage of development. In nature and in the laboratory, imagoes most preferentially consume fresh flushed (not flushing) leaves with completed (or nearly completed) growth. According to the author's observations, it always refers to sub-terminal leaves which are localized on shoots at least 5 to 10 cm from the apex. However, they lay eggs on somewhat older leaves in middle parts of annual shoots. In our rearings and in rearings of KING et al. (1998), imagoes selected young freshly unfolded leaves both for feeding and oviposition. As already mentioned in the paper introduction the trophic value of leaves (mainly the content of proteins) is mainly dependent on the content of available water and nutrients (eg nitrogen) in soil. Therefore, imagoes more often damage and lay eggs on species with the higher content of proteins in leaves (LOWER et al. 2003). In species growing on nutrient-rich sites, the chrysomelid usually has got better conditions for its development and also more frequently exhibits mass outbreaks.

The fecundity of females is also positively or negatively affected by some other factors. For example, RAUPP and DENNO (1984) found that females showed lower fecundity when they consumed leaves coming from naturally damaged shoots of *S. babylonica*. Similar results were obtained with females which were fed by leaves from artificially damaged shoots of *S. alba* Tristis. During the consumption of tough leaves, mandibles of imagoes are fast worn and thus, the consumption of food and the number of laid eggs decrease (RAUPP 1985).

The 1st generation development

In nature, egg larvae of *P. versicolora* hatch after 5 to 8 days, according to FATACHOV (1953) already after 4 to 5 days and according to MAISNER (1974) after 5 to 10 days from oviposition. In our own rearings, the embryonic development took on average 4.3 days (Table 10). Freshly hatched larvae are about 1.2 mm long, yellowish with a black head and legs. Their cranium is 0.36 to 0.46 mm wide (Fig. 15). In the course of several few hours larvae become dark. Then, they usually eat up egg coats and near the place of egg laying, they gradually line up and begin together to skeletonize
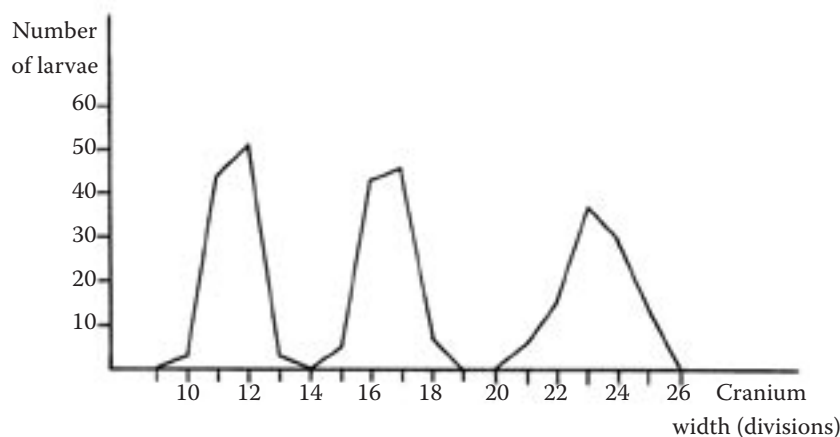

Fig. 15. The width of the cranium of larvae of the 1st to the 3rd instar of *P. versicolora* (1 division = 0.0357 mm)

Fig. 16. The frontal feeding of larvae of the 1st instar of *P. versicolora* on the abaxial face of a leaf of *S. fragilis*. Brno-Jundrov, 18 June 1998

Fig. 17. Growing up larvae of the 2nd instar of *P. versicolora* in feeding on the abaxial face of a leaf of *S. fragilis*. Brno-Jundrov, 18 June 1998
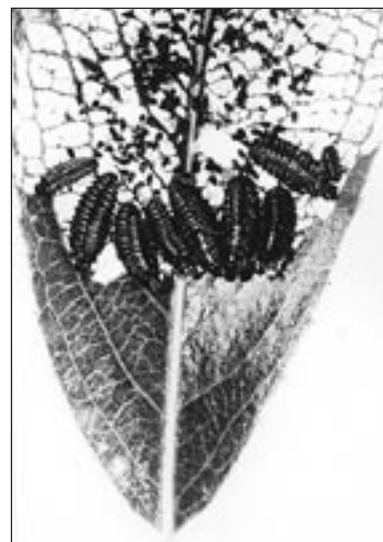

Fig. 18. Seven larvae of the 3rd instar and two larvae of the 2nd instar of *P. versicolora* in feeding on the abaxial face of a leaf of *S. fragilis*. Laboratory rearing, 4 June 1995

a leaf. They bite out small holes into the leaf blades leaving upper leaf epidermis and all venation undisturbed. The holes are of irregular oval shape on average 0.44 × 0.24 mm in size (Figs. 6 and 16). During feeding, the larvae produce black fusiform frass on average 0.2 mm long and 0.1 mm wide (Table 2). Larvae of the 1st instar damage on average 15 mm^2 leaf blade of *S. fragilis*. Between particular feeding marks and along veins they leave small remainders of undisturbed leaf tissues. Nevertheless, damaged parts of leaves become brown and die during several days.

After about 4 to 5 days (in the laboratory on average after 3.5 days) larvae moult for the first time. Newly moulted larvae of the 2nd instar are orange-yellow, however, they become dark after short time. Their head is markedly black (similarly as in other instars) and their cranium is 0.53 to 0.64 mm wide (Fig. 15). At first, larvae continue in the common skeletonizing of leaves from their abaxial face (Fig. 17). Later, they spread on leaves and eat in small groups rarely separately. Feeding marks reach up to the upper epidermis which remains together

Fig. 19. Feeding and frass of the 3rd instar of *P. versicolora* on the adaxial face of a leaf of *S. fragilis*. Laboratory rearing, 11 June 1998
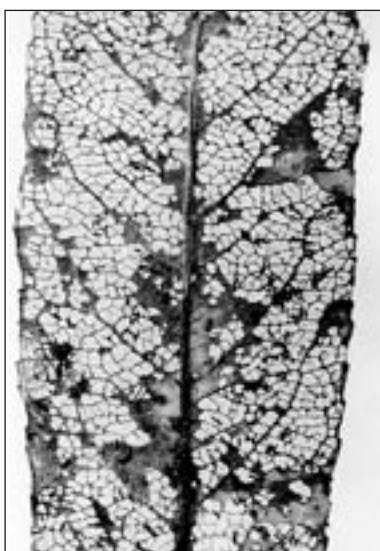

Fig. 20. The general appearance of a leaf of *S. fragilis* damaged by larvae of the 1st and 2nd instars of *P. versicolora*. Laboratory rearing, 24 June 1994

Fig. 21. Larvae of the 3rd instar of *P. versicolora* perforating a young leaf of *S. fragilis*. Laboratory rearing, 31 May 1995
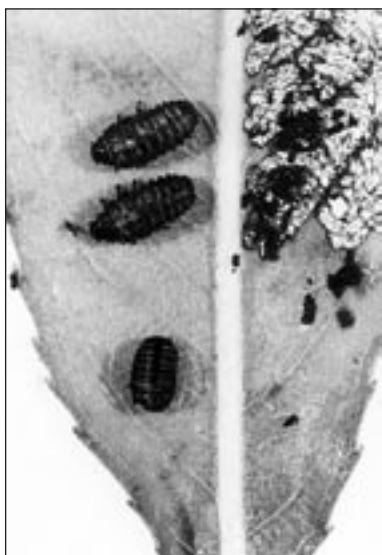
Fig. 22. Prepupae of *P. versicolora* on the abaxial face of a leaf of *S. × rubens*. Brno-Komín, 4 June 1998

Fig. 23. Newly hatched and older pupae of *P. versicolora* on the abaxial face of a leaf of *S. × rubens*. Brno-Komín, 8 June 1998

with venation undamaged. Particular feed marks are on average 0.7 mm long and 0.4 mm wide (Figs. 6 and 17). The frass is black, fusiform, on average 0.4 mm long and 0.2 mm wide (Table 2). As for their appearance, they do not differ substantially from feeding marks of larvae of the 1st instar. Larvae of the 2nd instar damage about 61 mm² of the leaf blade of *S. fragilis*.

Approximately after 2 days (in the laboratory after about 1.5 days), larvae on leaves moult for the second time. Larvae of the 3rd instar have got a cranium 0.75 to 0.89 mm wide (Fig. 15). They damage leaves in smaller groups or separately (Figs. 18 and 19). The chrysomelids usually skeletonize or perforate them (Fig. 20) while young leaves are always perforated (Fig. 21).

In laboratory rearings, larvae of the 3rd instar rather frequently skeletonized leaves (less frequently perforated) even on their adaxial face while the lower epidermis of leaves and venation were usually undisturbed. Particular feeding marks are on average 0.8 mm long and 0.5 mm wide (Fig. 6). Frass is black, fusiform being round on one or both ends or elongated on one end to a point (Fig. 19). On average, it is 0.61 mm long and 0.25 mm wide (Table 2). Leaves are usually damaged from their abaxial face, according to CORNELIUS (in KALTENBACH 1874) allegedly only from their adaxial face. After excretion, frass falls to the earth. Under conditions of minority feeding on the adaxial face of leaves frass sticks to leaves for a certain time until it is taken down due to climatic conditions (rain and wind) to the earth. Larvae of the 3rd instar in the 1st generation take food for about 3 days (in the laboratory only 2 days). They are 6 to 7 mm long and damage on average 206 mm² of the leaf blade of *S. fragilis*.

Larvae of all three instars develop for a period of 9 to 12 (according to SCHNAIDER 1957, 8 to 20) days, in the laboratory about 7 days. During the time, they damage on average 282 mm² leaves of *S. fragilis* (Fig. 25), ie 8.3× less than last year's imagoes after wintering. Grown up larvae firmly attach by the back part of their abdomen on the abaxial face of laves (Fig. 22) and only rarely on the bark of shoots. The body of larvae gradually shortens and arcuately turns to the ventral side. After several hours, the skin of prepupae moults. Newly hatched pupae are yellowish, however, characteristic dark spots soon occur on them (Fig. 23). Prepupae and pupae last in nature 5 to 8 days, in the laboratory 3.5 to 4.5 days. The whole development of the chrysomelid from oviposition till hatching the imagoes of the 1st generation takes about 3 weeks in the region of Brno, in the laboratory about 15 days (Table 10, Fig. 24). The same time of the 1st generation development (19 to 22 days) is given by FATACHOV (1953) in Tadzhikistan. Imagoes of the 1st generation occur on their host species from the end of May till mid-August and after completing their reproduction die.

The chemical composition of plants is a fundamental factor affecting the dietary behaviour of phytophages. Feeding of the chrysomelid can be stimulated not only by basic plant substances (carbohydrates, amino acids, fatty acids, sterols, vitamins, inorganic salts, etc.) but also volatile and non-volatile plant substances (eg phenolglycosides). Numerous observations show that the abundance of *P. versicolora* positively correlates with the content of phenolglycosides and negatively with the density of trichomes on leaves (BOGATKO 1989, 1990; SOETENS et al. 1991, etc.). An important role is also plaid by
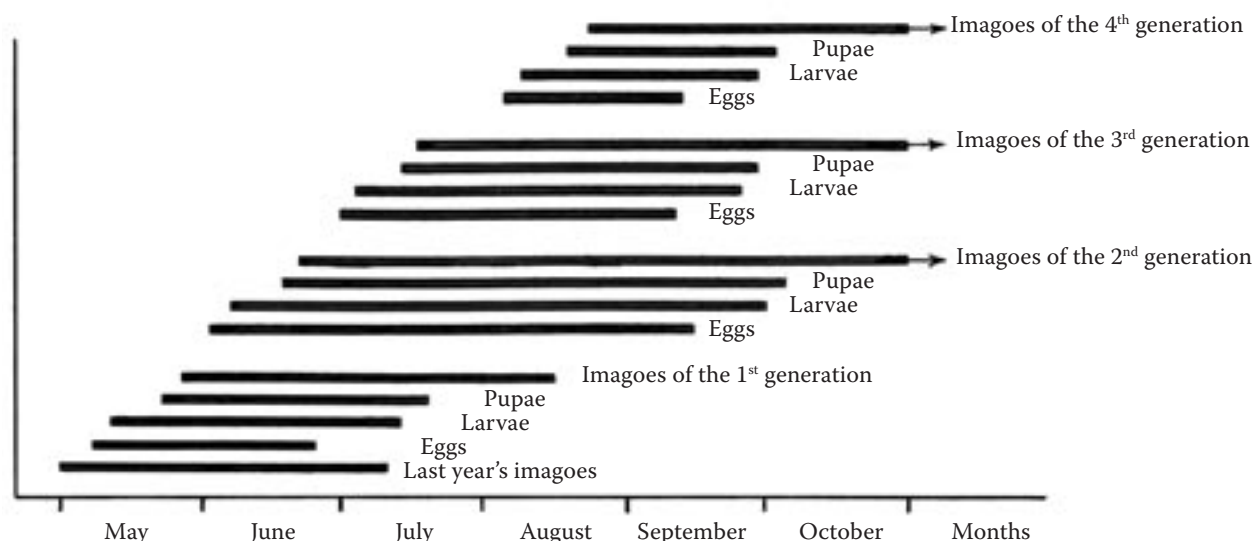
Fig. 24. The basic scheme of the tetravoltine development of *P. versicolora*. Laboratory rearing, 1995

the content of nitrogen, tannins and water including the toughness of leaves. In consuming tough leaves, mandibles of larvae are faster worn which results in the longer development and lower weight of larvae and also lower consumption of food (Raupp 1985; King et al. 1998, etc.). Larvae use phenolglycosides contained in leaves of willows and poplars as precursors of salicylaldehyde which they excrete in a defensive secret against predators and parasitoids (Pasteels et al. 1988, etc.). The transformation of plant glycosides to repellent substances occurs enzymatically in reservoirs of secrets of dorsal glands (Daloze, Pasteels 1994).

The development of larvae is negatively affected by pathogens, eg *Melampsora allii-fragilis* Kleb. or by the previous damage to host plants. The mortality of larvae on leaves of *S. × cuspidata* Schulz infected by the rust increases, their development is extended and their weight decreased. The previous damage significantly decreases the weight of larvae, however, the period of development and mortality are not affected (Simon, Hilker 2003). According to Raupp and Denno (1984), feeding on damaged leaves decreases the weight of larvae and extends their development. The quality of food is increased by the interspecific hybridization of willows (Hallgren 2002). The amount of consumed food and the weight of larvae are related to the species of a host plant. Differences in the total amount of consumed food in *Salix* spp. and *Populus* spp. are quite small (max. 10%). However, the average weight of larvae eg on *S. × smithiana* (9.6 mg) is nearly twice larger than on *P. tremula* (5.9 mg) (Bogatko 1993).

Larvae of *P. versicolora* are characterized by an active social behaviour from the earliest age till the 2nd instar. Their gregariousness obviously increases the defence

of individuals by the cumulative effect of toxins which are contained in the secret of dorsal glands (Grégoire 1988). Therefore, it is not surprising that socially living species of chrysomelids (*Chrysomela* spp., *Phratora* spp., etc.) are chemically protected. The chemical protection is created by defensive allomones contained not only in the secret of dorsal glands and the haemolymph of larvae but also in eggs and imagoes (Pasteels et al. 1988). In the protection of larvae against natural enemies the coloured polymorphism of a community created by the mixture of off-colour (ie light coloured) to dark individuals (Grégoire 1988) can also occur. According to the author, the group solidarity of larvae is supported by contacts and perhaps also by acoustic signals. The mutual contact inhibits the movement of larvae and supports feeding. Larvae in a group do not move and begin to eat soon whereas isolated larvae move as if aimlessly and feed only after the creation of a group. Substantial differences appear in the behaviour of young and growing up larvae. While 4-day live in nature in groups, 8-day larvae live separately (Crowe 1995a). The size of larval groups shows positive effects on the survival (mortality) and weight of larvae (Wade, Breden 1986). According to Crowe (1995b), however, the size of groups significantly affects only the mortality of larvae but not their weight. In larval communities, cannibalism can occur during the first 24 hours after hatching. Newly hatched larvae feeding eggs or siblings grow faster reaching higher weight (Breden, Wade 1987).

Generation conditions

Generation conditions of *P. versicolora* are rather complicated. Escherich (1923), Nejedlý (1950),

Schnaider (1957), Wagner and Ortmann (1959), Brovdij et al. (1974), etc. mention 2 to 3 generations per year. Three generations per year are mentioned eg by Arnoldi et al. (1955), Wade and Breden (1986) and Crowe (1995b) and 3 to 4 generations are noted by Breden and Wade (1987). According to Hood (1940), unfertilized females of the 3rd generation winter in the USA. If the females mate then they lay eggs even in the same growing season. On the other hand, Stevens and McCauley (1989) found that mostly fertilized females of the 3rd generation winter in the USA. According to them, only a very small number of females of this generation lays eggs before a diapause. Dowden (1939) mentions a trivoltine and partly tetravoltine generation cycle from the USA. According to the author, overlaps of generations occur in all developmental stages from June to September while always one stage is dominant at a certain time.

The development of *P. versicolora* is significantly modified by the occurrence of the summer diapause of imagoes which can continuously change to a winter diapause. The summer diapause induces extreme humidity and drought or high temperatures and seasonal changes in the quality of food. In Europe, these factors determine the number of 2 to 4 generations per year (Maisner 1974). Similarly as in many other insect species living in a wide geographical area, local adaptations occur in this chrysomelid manifested in its developmental cycle. Differences in voltinism are related to the quality of food and natural conditions given particularly by a temperature gradient within geographical latitude. Therefore, in southern parts of its range more generations occur while near the northern limit of distribution only one generation per year. On the island of Honshu (Japan), the chrysomelid creates 5 to 6 generations per year (Kimoto, Takizawa in Ishihara et al. 1999). On the other hand, on the island of Hokkaido it shows only 1 to 2 generations (Ishihara 2000) or 2 generations per year (Ishihara, Hayashi 2000). In the southern part of a sub-arctic zone in Siberia, it can create (as the only species of the family) the 2nd generation (Bogacheva 1998). A photoperiod exhibits a significant effect on the rate of development and induction of a diapause (Ishihara 2000; Ishihara, Hayashi 2000). During a long day, the development of the chrysomelid is shorter than during a short day and thus, imagoes have enough time for reproduction. In the course of short days in mid-September, all imagoes from leaves of host species disappear looking for winter places (Ishihara, Hayashi 2000). The diapause is finished in spring of the next year under conditions of a long light day.

In studied localities in Moravia, the chrysomelid usually creates 3(2) to 4 generation per year. In addition to all imagoes of the 4th generation also the predominant part of imagoes of the 3rd generation and the small part of imagoes of the 2nd generation enter a diapause. It refers always to individuals hatched in the second half of the growing season, ie particularly in August and at the beginning of September. The first and the second generation of *P. versicolora* consumes quality food during a long light day (in the 2nd half of spring and at the beginning of summer). In the 2nd half of the growing season, the proportion of imagoes entering the diapause increases with shortening the length of the light part of days and worsening the environmental conditions (particularly the food quality of leaves). Before the departure to wintering places, imagoes intensively take food for the period of 2 to 3 weeks but usually they do not mate and females do not lay eggs. Unlike findings of Stevens and McCauley (1989), it is possible to state that unfertilized females usually winter. Ovaries of females do not develop at all before the departure to winter places. The fast development of eggs occurs only after wintering, namely during maturation feeding in spring.

Under laboratory conditions, *P. versicolora* produced 4 to 6 generations per year (Fig. 24). In 1999, females of the 6th generation even sporadically laid eggs of the 7th generation. The eggs were not fertilized and, therefore, it was not possible to continue in rearing. During the growing season, the food value of leaves gradually decreases and their toughness increases. Thus, with the transition of the chrysomelid to higher generations the proportion of a leaf area damaged by perforation significantly decreases and the proportion of an area damaged by skeletonizing increases (Table 1). Last year's imagoes and imagoes of the first generation damaged 90% leaves from their adaxial face. From the 2nd generation, the proportion of imagoes on the adaxial face of leaves gradually decreased due to a summer diapause (Table 1). With the transition of the chrysomelid to higher generations the average time of feeding decreased (Table 3). Last year's imagoes obtained from nature took food for a period of about 2 months after the diapause. Imagoes of the 1st generation took food for a period of about 41 days. With the occurrence of next generations the average period of feeding gradually decreased mainly due to an increase in the proportion of imagoes entering the diapause. Last year's imagoes obtained from nature after their diapause lived for the longest time (about 300 days). On the other hand, imagoes of the 1st and the 2nd generation lived in the laboratory for the shortest time
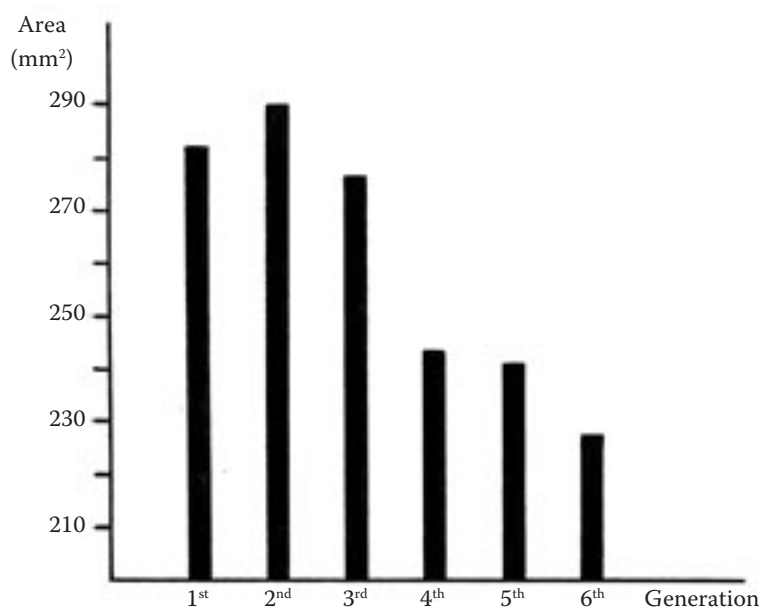
Fig. 25. The average area of leaves of *S. fragilis* damaged by larvae of the 1st to 6th generations of *P. versicolora* (mm²). Laboratory rearing, 1996 to 2003

(less than 2 months). Considerable part of imagoes of the 3rd generation did not reproduce and entered to a summer diapause which gradually converted to a winter diapause. With the increasing proportion of diapausing imagoes the average period of the life of imagoes increased (Table 4, Fig. 7). It has been proved that the average time of the life of males and females is the same (Table 4).

A period of the occurrence of imagoes on trees is related to the average size of damaged leaf area and the average number of laid eggs. Far most harmful is the spring feeding of last imagoes after a winter diapause (Table 5). These imagoes destroyed about 23.3 cm² leaves of *S. fragilis* during maturation and regeneration feeding. The average leaf area damaged by last year's imagoes reared in the laboratory was substantially lower (about 10.7 cm²).

Imagoes of the 1st generation damaged on average 17.1 cm² leaves and imagoes of the 2nd generation 12.5 cm² leaves. The average area of leaves damaged by imagoes of next generations gradually decreased. Imagoes of the last (6th) generation consumed on average 5 cm² leaves and nearly all then entered a diapause (Table 5, Fig. 8). The first eggs mature in ovaries of females during a several-day maturation feeding always in spring. For example, in a hexavoltine development, last year's females began to lay eggs only after 4.5 days of feeding. In females of the 1st generation, the first eggs matured after about 7.5 days of feeding and in females of the 2nd to 5th (6th) generations after about 11 days of feeding (Fig. 8). In a tetravoltine development, females of the 1st generation laid eggs only after one-week feeding. Females of the 2nd generation began to lay eggs only after a 10-day feeding and females of the 3rd generation only

after a 19-day feeding. Females of the 4th generation did not lay eggs and after a previous maturation feeding they went away to winter places.

Last year's imagoes caught in nature after a winter diapause (before the beginning of feeding) damaged leaves of *S. fragilis* most in the 2nd to the 5th week. From the 6th to the 9th week, intensity of feeding rapidly decreased and last traces of feeding were evident on leaves even in the 13th week. On then other hand, imagoes reared under laboratory conditions consumed food most already in the 1st week. During next weeks, intensity of their feeding gradually decreased till the 7th week when the feeding of imagoes ceased (Table 6, Fig. 26).

Interesting results were obtained by the comparison of the localization of eggs laid by last year's females (both from nature and laboratory rearings) and females of the 1st to the 5th generation. Last year's females from nature laid eggs always on the abaxial face of leaves. Last year's females from rearings laid about 62% eggs on the abaxial face of leaves. The proportion of eggs on the abaxial face of leaves in females of the 1st to 5th (6th) generations decreased from 59 to 44% and on the adaxial face of leaves increased from 22 to 56%. Females laid eggs rather frequently on walls of rearing vessels and sporadically also on damp paper wool (Table 7).

Evident worsening the living conditions during summer and at the beginning of autumn is related to the increasing proportion of diapausing imagoes and to the decreasing average number of eggs corresponding to 1 female. The highest fecundity (about 540 eggs) showed females which hatched and wintered in nature. Females reared from eggs in the laboratory laid on average 250 eggs after wintering and
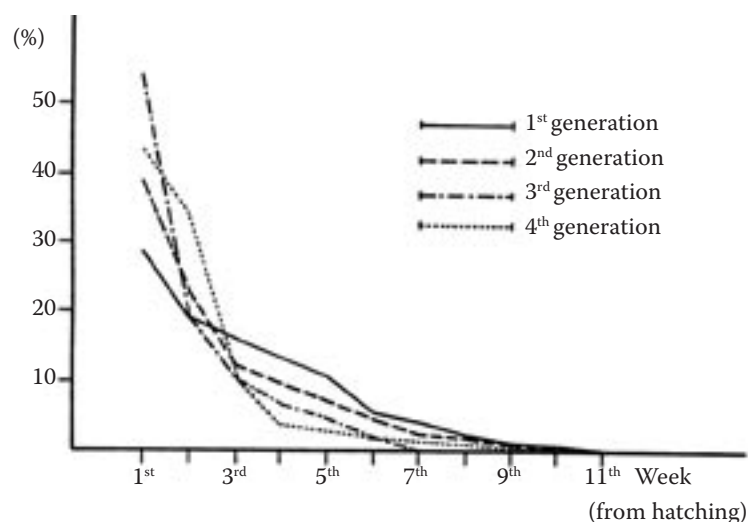
Fig. 26. Intensity of damage to leaves of *S. fragilis* by imagoes of the 1st to the 4th generation of *P. versicolora* (in % of the total damaged leaf area). Laboratory rearing, 1995 to 2001

Legend in figure:
— 1st generation
— 2nd generation
— 3rd generation
— 4th generation

females of the 1st generation about 222 (according to FATACHOV 1953 about 50) eggs. Females of the 2nd generation laid only about 90 eggs. A considerable decrease in the average number of eggs falling to 1 female was caused both by the decrease in fecundity of females and the increase in the proportion of diapausing individuals in a population. Both the facts are markedly reflected in the fecundity of females of the 3rd to the 6th generation (Table 8, Fig. 11).

It has been found that the period of the development of larvae, prepupae and pupae slightly extends in the course of the growing season. Larvae of the 1st generation developed on average 6.8 days whereas larvae of the 6th generation on average 7.6 days, ie nearly 1 day longer. Also the average period of the duration of prepupae and pupae gradually increased from the 1st generation to the 6th generation, viz from 3.9 to 4.6 days. However, the average period of the embryonic development in eggs of the 1st to the 6th generation was roughly the same throughout the growing season, namely 4.3 days (Table 11, Fig. 24). The extension of the period of development with shortening the light part of a day was also demonstrated by ISHIHARA (2000).

In the laboratory, larvae of the 1st instar destroyed about 15 mm² leaf blade of *S. fragilis*. Larvae of the 2nd instar destroyed about 55 mm² leaf blade and larvae of the 3rd instar about 190 mm². The proportion of larvae of the 1st, 2nd and 3rd instars in the total average damaged leaf area (260 mm²) was 5.8, 21.1 and 73.1%, respectively. The largest leaf area was destroyed by larvae of the 1st generation (about 282 mm²) and larvae of the 2nd generation (about 290 mm²). From the 3rd generation, an average area damaged by larvae gradually decreased and in the 6th generation of larvae, it amounted to only 227 mm² (Table 11, Fig. 25). Results rather positively show that with worsening the quality of food during the growing season the average consumption of the food of larvae decreases.

Southern and central Moravia belong to regions with very favourable conditions for the development of *P. versicolora*. Therefore, the 3rd and the 4th generation is created there in the course of a year (according to the present data only the 2nd and the 3rd generation). In consequence of the long period of leaving winter places, the very long period of oviposition and extraordinarily fast preimaginal development vari-

Table 11. The average area of leaves of *S. fragilis* damaged by larvae of the 1st to the 3rd instar of *P. versicolora* (mm² and % of the total damaged area). Laboratory rearing, 1995 to 2004

Generation of larvae	1st instar		2nd instar		3rd instar		Total	
	mm²	%	mm²	%	mm²	%	mm²	%
1st	15	5.3	61	21.6	206	73.1	282	100.0
2nd	15	5.2	60	20.7	215	74.1	290	100.0
3rd	15	5.4	55	19.9	206	74.7	276	100.0
4th	15	6.2	55	22.6	173	71.2	243	100.0
5th	15	6.2	50	20.8	176	73.0	241	100.0
6th	15	6.6	50	22.0	162	71.4	227	100.0
Mean	(15)	(5.8)	(55)	(21.1)	(190)	(73.1)	(260)	100.0

ous developmental stages of at least 2 generations of the chrysomelid occur at the same time. Therefore, from the beginning (or mid-June), it is possible to determine the generation of particular individuals only with difficulties. Complicated generation conditions are made difficult by a summer diapause the causes of which are not fully elucidated yet. The development of *P. versicolora* is undoubtedly affected by exogenous factors (abiotic, ie climate, soil etc. and biotic, ie food and inter-specific and intra-specific relations) as well as endogenous factors (morphological/anatomic, genetic etc.). Only due to the cooperation of all the factors/effects we can explain the different time of the start of a diapause in individuals reared together in the same rearing means.

Imagoes of *P. versicolora* undergo intensive feeding on leaves of host species before entering the diapause. Only then, they begin to look for suitable wintering places on trees in their vicinity. In nature, we can meet last imagoes even in the second half of September and exceptionally at the beginning of October (according to Dowden 1939; Maisner 1974 in August; according to Kaltenbach 1874; Arnoldi et al. 1955; Lopatin 1960; Mohr 1966; Ishihara et al. 1999 in September). By a departure to winter places, the developmental cycle of the chrysomelid is completed.

Natural enemies

Imagoes of *P. versicolora* are not well protected from extreme winter which can result in fatal effects for them (Hood 1940). A polyphagous species *Schizonotus sieboldi* (Ratz.) (Pteromalidae) is an important native parasitoid of pupae of the chrysomelid. In addition to *P. versicolora*, it attacks also other species of chrysomelids pupating on trees (eg *Chrysomela populi* L., *C. tremulae* F. and *C. vigintipunctata* Scop.). Its occurrence on *C. vigintipunctata* in Moravia describes Urban (1997, 1998b, etc.). Unlike chrysomelids of the genus *Chrysomela* pupae of *P. versicolora* occur during the predominant part of the growing season and so even 3 generations of the parasitoid can develop on them.

Of about 15% imagoes caught on 7 May 1995 in Bílovice nad Svitavou, a species *Medina melania* (Meig.) hatched in the laboratory from 15 to 20 May 1995. *M. luctuosa* (Meig.) (Tachinidae) parasitized in imagoes less frequently. A brief overview of some natural enemies is given in an introduction of the paper.

Harmfulness

Plagiodera versicolora is one of the most important leaf-eating pests of willows and less frequently also poplars (Arnoldi et al. 1955; Mohr 1966; Brovdij et al. 1974; Bogatko 1989, etc.). It causes the largest damages in osier plantations (Escherich 1923; Wagner, Ortmann 1959; Schnaider 1972; Czerniakowski 2000, 2002, etc.). The chrysomelid is also dangerous in nurseries and young forest and park plantings of willows and poplars (Maisner 1974; Vasiljev et al. 1975, etc.). In Bulgaria, it significantly participates in the defoliation of poplar plantations (Penev, Ovčarov 1992). In the Ukraine, it damages mainly on moist and artificially irrigated sites at lower locations (Lopatin 1960). It is considered to be an important salicicolous pest eg in Hungary (Györfi 1952), in the former Yugoslavia (Kovačevič 1957), Turkey (Aslan 2001) and North America (Dowden 1939; Hood 1940; Lechevalier 1944; Raupp, Sadof 1991; King et al. 1998, etc.).

At studied localities in Moravia, the beetles occur on their host plants usually from the beginning of May. During a week feeding on young leaves, they mature sexually and lay their first eggs on somewhat older leaves. Other eggs repeatedly mature in ovaries of females during a regeneration feeding. In the course of about 2-month feeding females lay about 539 eggs to about 35.5 groups of an average number of 15.2 eggs. After a week, larvae hatch from laid eggs. The larvae soon begin to skeletonize leaves in the vicinity of egg-laying. With the fast increase in the pest population density the degree of defoliation of young shoots increases. Owing to the very short (3 weeks) preimaginal development imagoes of the 1st generation occur already at the turn of May and June. The beetles begin to damage leaves soon after hatching and after one-week feeding they begin to reproduce. Damage to young leaves caused by imagoes increases. With the fast transition of larvae to higher instars and increase in their abundance more and more marked symptoms begin to occur of the larval damage to middle-aged leaves.

The quality of food sources for imagoes and larvae of the chrysomelid constantly deteriorates and the quantity diminishes during the growing season (and also due to various damage to leaves). Other conditions for the successful development of the chrysomelid also gradually deteriorate. Under conditions of the shortage of suitable food the beetles often eat fine bark and buds of terminal parts of shoots. Thus, in imagoes and larvae, the wear of mandible increases. The average consumption of food, average period of feeding and fecundity of females significantly decrease. From the 2nd generation, a summer diapause becomes increasingly evident in the pest

population. With the entrance of autumn, the diapause changes to a winter diapause. In the period of peak summer, the damage to trees culminates and ends in mid-September.

It has been found that imagoes of *P. versicolora* are much more harmful than larvae. In *S. fragilis*, eg, imagoes destroy on average 5 cm^2 leaves before their departure to wintering places and after wintering other 23.3 cm^2 leaves, ie in total 28.3 cm^2. Larvae of the 1st and the 2nd generation damage on average only 2.8 cm^2 leaves and larvae of the 3rd and the 4th generation even less. Thus, the total average consumption of food in larvae is 10× lower than that in imagoes. Negative impacts of the feeding of larvae on trees are also lowered by a fact that the larvae nearly always damage a little older leaves than imagoes. These leaves fulfilled their assimilatory function to a greater extent than just grown-up young leaves damaged by imagoes.

The chrysomelid undergoes outbreaks mainly on rich sites well supplied with water. Optimum conditions for its development occur particularly at warmer lowland locations along watercourses mainly during dry and warm years. During water deficits, supply of nutrients to leaves stagnates and thus also photosynthesis including the production of secondary metabolites. Due to the physiological weakening of trees their resistance to damage decreases. In case of outbreaks the pest causes heavy feeding to defoliation and in case of the lack of suitable food it often feeds on the youngest buds and fine bark at the end of annual shoots. Heavily damaged shoots (up to 50 cm long) die being replaced by lateral shoots in the next year thereby undesirable flowering occurs. In case of extraordinarily heavy damage even whole trees can die. Affected trees and young plantations (nurseries, poplar plantations, osier plantations etc.) look at the first glance like they would be damaged by late frosts or fire. It results in the marked decrease to cessation in the increment of trees and their technical debasement.

Possibilities of protection and control

In the past, beetle collection by means of sweep nets was recommended or shaking off beetles into vessels. In addition to portable shaking off devices also a more complicated special mobile equipment was constructed. Special brushes were used for the mechanical control of larvae on small areas. In nurseries and osier plantations, beetles wintering in fallen leaves were killed by raking up and burning the leaf litter. Where it was possible from technical aspects the pests were killed by long-term control-led artificial flooding in the spring period. Imagoes and larvae were sometimes controlled by chemical means (eg arsenates and later preparations based on DDT and HCH).

For example, JODAL (1985) dealt with chemical control with defoliators including *P. versicolora* in recent time. His application of Furadan G-10 (ai carbofurane) into holes at a dose of 60 to 100 g per a tree reliably operated for a period of 2 to 3 months. Poplar leaves treated by means of 0.05 to 0.1% Dimiline (ai diflubenzurone) caused 98 to 100% mortality of larvae. Imagoes survived after the dose, however, they did not reproduce any more. XU and WAN (1990) applied the mixture of several pesticide preparations which was more effective than in case of a separate use to control (both manual and aerial control) the chrysomelid. On the other hand, it was found that the pest was resistant to the infection of *Beauveria bassiana* (Bals.) (MAISNER 1974) and *Bacillus thuringiensis* Berl. (FENG-SHU et al. 2000).

At present, it is possible to control both imagoes and larvae by means of a number of modern insecticide preparations devised for ground or aerial spraying. In the Czech Republic, their list and the scope of allowed use are given in the *List of permitted preparations for forest protection*. For forestry, the list is compiled by the Forestry and Game Management Research Institute Jíloviště-Strnady on the basis of the *List of registered preparations for plant protection* and approved by the Ministry of Agriculture of the Czech Republic. It is necessary to carry out measures to control the chrysomelid at the beginning of the mass invasion of imagoes on host trees. Chemical control of larvae is more difficult with respect to their occurrence on the abaxial face of leaves.

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Příspěvek k poznání vývoje a škodlivosti mandelinky okrouhlé (*Plagiodera versicolora*) (Coleoptera, Chrysomelidae)

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ABSTRAKT: Práce pojednává o výskytu, vývoji a škodlivosti mandelinky okrouhlé (*Plagiodera versicolora* Laich.) v břehových a doprovodných porostech řeky Svratky a Svitavy na Brněnsku. Nejvíce je tam poškozována *Salix fragilis* L. a *S. × rubens* Schr. Dospělci zimoviště opouštějí obvykle začátkem května. Během asi 60denního období poškodí kolem 23,3 cm² listů *S. fragilis* a vykladou 250 až 730 (průměrně 539) vajíček. Celou snůšku tvoří 16 až 48 (průměrně 35,5) skupin se 6 až 26 (průměrně 15,2) vajíčky. Fekundita samiček vylíhlých v laboratoři je minimálně dvakrát nižší. Za 5 až 8 (v laboratoři za 4,3) dnů se líhnou larvy, které během 9 až 12 (v laboratoři 7) dnů poškodí kolem 282 mm² listů. Vývoj od vykladení vajíček až do vylíhnutí dospělců první generace trvá kolem 21 (v laboratoři kolem 15) dnů. Dospělci první generace se na dřevinách vyskytují od konce května do poloviny srpna a po skončení rozmnožování hynou. Mandelinka vytvoří během roku 3 až 4 generace (v laboratoři 4 až 6). Do diapauzy vstupuje malá část dospělců druhé generace, převážná část (nebo všichni) dospělci třetí generace a při tetravoltinním vývoji všichni dospělci čtvrté generace. Během vegetačního období se snižuje spotřeba potravy dospělců i larev a výrazně klesá fekundita samiček. K nepřátelům patří mj. *Schizonotus sieboldi* (Ratz.), *Medina melania* (Meig.) a *M. luctuosa* (Meig.).

Klíčová slova: *Plagiodera versicolora*; Chrysomelidae; výskyt; vývoj; fekundita; nepřátelé; hospodářský význam

Koncem minulého a začátkem tohoto století střední Evropu několikrát postihlo extrémně suché a teplé počasí. Anomální počasí se mj. projevilo ve výrazné aktivizaci řady lesních hmyzích škůdců. K nárůstu populačních hustot, spojenému se silnými žíry až holožíry, došlo i u celé řady druhů mandelinkovitých (Chrysomelidae). Rozsáhlé gradace byly v ČR zaznamenány u mandelinky dvacetitečné (*Chrysomela vigintipunctata* [Scop.]), bázlivce olšového (*Agelastica alni* [L.]), mandelinky olšové (*Linaeidea aenea* [L.]), mandelinky *Gonioctena quinquepunctata* (F.) aj.

Škodlivý výskyt byl na několika lokalitách na Moravě zjištěn také u biologicky zajímavé a hospodářsky významné salicikolní mandelinky okrouhlé (*Plagiodera versicolora* [Laich.]). Tato mandelinka náleží vzhledem k holarktickému rozšíření a ke své značné škodlivosti v mnoha zemích Starého i Nového světa k nejlépe známým druhům mandelinkovitých na vrbách a topolech. Nedávný nárůst její početnosti byl vhodnou příležitostí ke zpřesnění a doplnění dosud existujících údajů o jejím výskytu, vývoji a škodlivosti. Většina šetření byla vykonána v letech 1995–2005 na vrbách a topolech v břehových a doprovodných porostech kolem řeky Svratky a Svitavy na Brněnsku. Kontroly tam byly prováděny během vegetačního období v týdenních až dvoutýdenních intervalech. Souběžně byli dospělci i larvy mandelinky studováni v laboratorních podmínkách na listech *Salix fragilis* L. a orientačně i na jiných dřevinách. Testovala se trofická afinita dospělců k různým dřevinám. Vyšetřován byl mj. průběh jejich žíru a velikost poškozené listové plochy. Pozornost byla věnována kladení vajíček a fekunditě samiček jednotlivých generací mandelinky. Podrobně byl sledován vývoj larev jednotlivých instarů a pokolení včetně škodlivosti. Systematickým studiem výskytu, bionomie a škodlivosti mandelinky byly získány tyto hlavní výsledky:

1. V zájmové oblasti Moravy mandelinka *P. versicolora* osídluje hlavně *Salix fragilis* L. a *S. × rubens* Schr. (= *S. alba* L. × *S. fragilis*). Velmi hojná je na *S. alba* var. *vitellina*, *S. × basfordiana* Schl. (= *S. alba* var. *vitellina* × *S. fragilis*), *S. viminalis* L. a *S. caprea* L. V laboratorních podmínkách dospělci přednostně konzumovali *S. fragilis* a *S. × rubens*. Méně poškozovali *S. viminalis*, *S. caprea*, *S. × smithiana* Willd. (= *S. viminalis* × *S. caprea*), *S. purpurea* L., *S. × rubra* Huds. (= *S. viminalis* × *S. purpurea*), *S. americana* Hoedt., *Populus nigra* L. a *P. nigra* L. var. *italica*. Odmítali konzumovat *S. daphnoides* Vill., *S. acutifolia* Willd., *S. triandra* L. a *P. alba*. Larvy troficky preferovaly v podstatě stejné dřeviny jako dospělci. Pořadí oblíbenosti primárních a sekundárních hostitelských dřevin se v průběhu testů poněkud měnilo.

2. Dospělci zimují hlavně pod suchým opadlým listím nebo ve štěrbinách kůry. Na Brněnsku svá zimoviště opouštějí obvykle začátkem května, na jižní Moravě (Břeclavsko) již koncem dubna a na severní Moravě (Vsetínsko) v polovině května. Ihned po dosažení hostitelských dřevin přistupují k úživnému žíru na čerstvě vyrašených listech. Asi po týdenním (v laboratoři dvoudenním až třídenním) žíru se dospělci obvykle poprvé páří.

3. Dospělci listy děrují z adaxiální strany, řidčeji také ožírají od okrajů. Často přitom poškozují boční listové žilky. Vykousané otvory mají průměrnou délku 5,5 mm a šířku 2,7 mm. Poněkud starší listy dospělci z adaxiální strany často skeletují až k protější epidermis, kterou zpravidla neporušují. Jamky ve starších listech dosahují průměrné délky 1 mm a šířky 0,6 mm. Nejvíce poškozují čerstvě vyrašené listy lokalizované několik málo centimetrů od vrcholů výhonků. Během příjmu potravy produkují četné trusinky o průměrné délce 0,6 mm a šířce 0,25 mm.

4. Loňští dospělci během asi 50denního období poškodí průměrně 23,3 cm² listů *S. fragilis*. Dospělci vychovaní v laboratoři žili po diapauze průměrně 35 dnů a poškodili kolem 10,7 cm². Loňští dospělci ulovení v přírodě před počátkem žíru žili v zajetí 1,8krát déle a poškodili 2,2krát větší listovou plochu než dospělci vychovaní v laboratorních podmínkách.

5. Samičky *P. versicolora* kladou vajíčka zhruba po týdnu od počátku náletu na hostitelské dřeviny, v chovech již po 4–6 dnech. Na vyšetřovaných lokalitách na Brněnsku byla vajíčka nalézána obvykle od 7. května do 25. června, a to vždy na abaxiální straně listové čepele. V chovech samičky vykladly na tuto stranu listů pouze 62 % vajíček.

Dalších 29 % vajíček vykladly na adaxiální stranu listů a 9 % na stěny chovných misek. V přírodě se kolem 59 % vajíček vyskytovalo na bazální třetině čepele, 28 % na střední třetině čepele a 14 % na apikální třetině čepele. Na rozdíl od listů poškozovaných dospělci, které jsou vždy lokalizovány poblíž vrcholků výhonků, se vajíčka mandelinky vyskytují zpravidla na poněkud starších listech ve středních částech výhonků.

6. Loňské samičky (získané z přírody po ukončení zimní diapauzy) vykladly během asi 60 dnů 250 až 730 (průměrně 539) vajíček. Celá snůška byla rozdělena do 16 až 48 (průměrně 35,5) dílčích snůšek (vaječných skupin) se 6 až 26 (průměrně 15,2) vajíčky. Fekundita loňských samiček, které byly vychovány v zajetí, byla mnohem nižší. Tyto samičky vykladly celkem 120 až 456 (průměrně 249) vajíček do 8 až 32 (průměrně 17,3) skupin o průměrném počtu 14,4 vajíček ve skupině. V 60 % (v chovech v 59 %) vaječných skupin byl sudý počet vajíček. Početní převaha skupin se sudým počtem vajíček vyplývá z párové stavby ovarií a z rozdílů ve funkčnosti jednotlivých ovariol.

7. V přírodě se vaječné larvy líhnou za 5–8 dnů a v laboratoři průměrně za 4,3 dne od vykladení. Larvy 1. instaru mají cranium široké 0,36 až 0,46 mm. Po vylíhnutí obvykle nejdříve zkonzumují vaječné obaly. Pak začnou společně do listů vykusovat nepravidelné jamky o průměrné délce 0,44 mm a šířce 0,24 mm. Jejich trusinky jsou průměrně dlouhé 0,2 mm a široké 0,1 mm. Za 4 až 5 dnů (v laboratoři asi za 3,5 dne) poškodí kolem 15 mm² listů *S. fragilis* a na listech se poprvé svlékají.

8. Larvy 2. instaru mají cranium široké 0,53 až 0,64 mm. Mladší larvy tohoto instaru žijí vždy ve skupinách, starší larvy se někdy po listech rozlézají a žijí v menších skupinách, zřídka samostatně. Do listů vyžírají požerky o průměrné délce 0,7 mm a šířce 0,4 mm, které sahají až ke svrchní epidermis. Produkují trusinky o průměrné délce 0,4 mm a šířce 0,2 mm. Asi za dva dny (v laboratoři již za 1,5 dne) poškodí kolem 61 mm² listů *S. fragilis* a podruhé se svlékají.

9. Larvy 3. (posledního) instaru mají cranium široké 0,75 až 0,89 mm. Listy poškozují v menších skupinách nebo samostatně. Obvykle je skeletují a pomístně i děrují, poněkud mladší listy děrují. Požerky jsou průměrně 0,8 mm dlouhé a 0,5 mm široké. Trusinky jsou vřetenovité o průměrné délce 0,61 mm a šířce 0,25 mm. Během tří (v laboratoři během dvou) dnů poškodí kolem 206 mm² listů *S. fragilis.* Larvy všech tří instarů

se vyvíjejí 9–12 (v laboratoři kolem 7) dnů a poškodí průměrně 282 mm^2 listů, tj. 8,3krát méně než dospělci po přezimování. Po 5 až 8 dnech (v laboratoři již po 3,5–4,5 dnech) trvání předkukly a kukly se líhnou dospělci. Celý vývoj od vykladení vajíček až do vylíhnutí dospělců 1. generace trvá na Brněnsku kolem 21 dnů, v laboratoři kolem 15 dnů.

10. Na zkoumaných lokalitách na Moravě se dospělci 1. generace vyskytují na dřevinách od konce května do poloviny srpna a po skončení rozmnožování hynou. Během celého vegetačního období mandelinka vytvoří 3–4 generace. Malá část dospělců 2. generace (především ti, kteří pocházejí z nejpozději vykladených vajíček) a převážná část až všichni dospělci 3. generace včetně dospělců 4. generace vstupují po předchozím žíru do diapauzy. Během 2–3týdenního úživného žíru se dospělci obvykle nepáří. Ovaria diapauzujících samiček se vyvíjejí až na jaře během několikadenního (v chovech průměrně 4,5denního) období zralostního žíru. V laboratorních podmínkách mandelinka vytvářela 4–6 generací a minoritní část samiček zakládala dokonce 7. generaci. S přechodem mandelinky do vyšších generací se průměrná doba žíru zkracovala. Nejdéle (kolem 300 dnů) žili loňští dospělci získaní po zimní diapauze z přírody. Nejkratší dobu (necelé 2 měsíce) žili v laboratoři brouci 1. a 2. generace. S nárůstem letní diapauzy (která obvykle postupně přechází v zimní diapauzu) se doba života dospělců prodlužovala. Samečci žili průměrně stejně dlouho jako samičky.

11. Zhoršování životních podmínek během vegetačního období se promítá do postupného snižování spotřeby potravy dospělců i larev a do výrazného snižování fekundity samiček. Zatímco larvy 1. generace se v laboratoři vyvíjely průměrně 6,8 dne, larvy 6. generace jen 7,6 dne. Doba embryonálního vývoje však zůstávala přibližně stejná (kolem 4,3 dne). Larvy 1. a 2. generace poškodily kolem 286 mm^2 listů *S. fragilis*. Od 3. generace poškození postupně klesalo až na pouhých 227 mm^2 u larev 6. generace. Průměrná fekundita klesala od 538,8 vajíček (u loňských samiček ulovených v přírodě) (resp. od 249,4 vajíček u loňských samiček z chovu) přes 222,4 vajíček (u samiček 1. generace) až k pouhým 8,8 vajíčkům (u samiček 6. generace).

12. Mandelinka *P. versicolora* má četné přirozené nepřátele. Na kuklách hojně parazituje polyvoltinní kovověnka *Schizonotus sieboldi* (Ratz.) (Pteromalidae). Parazitoid vytváří na jižní a střední Moravě obvykle tři generace v roce. V dospělcích se často vyvíjí polyfágní kuklice *Medina melania* (Meig.) a řidčeji *M. luctuosa* (Meig.) (Tachinidae).

13. V přírodních podmínkách Moravy mandelinka *P. versicolora* škodí hlavně ve vrbových, případně topolových plantážích, školkách a v mladých lesních a parkových výsadbách. Optimální podmínky nachází v teplých nížinných polohách kolem větších vodních toků. Při masovém výskytu působí na dřevinách silné žíry až holožíry, a to zvláště v kombinaci s jinými fylofágními škůdci. Za nedostatku vhodné potravy imaga ožírají jemnou kůru a pupeny koncových částí výhonků. Imaga jsou vždy daleko (v průměru desetkrát) škodlivější než larvy. Před odchodem do zimovišť poškodí průměrně 5 cm^2 listové čepele *S. fragilis* a po přezimování dalších 23,3 cm^2, tj. celkem 28,3 cm^2. Dospělci poškozují vždy mladší listy než larvy. Tyto listy jsou na samotném počátku asimilační činnosti a jejich zničení znamená pro dřeviny vždy velkou újmu. Konce silně poškozených výhonků odumírají a výjimečně hynou i celé dřeviny. Přírůst dřevin se snižuje a pokud dřeviny poškození přežijí, pak se v následujícím roce větví.

14. Dospělce mandelinky lze efektivně hubit pomocí insekticidů, a to nejlépe začátkem období jejich náletu na hostitelské dřeviny. Chemické hubení larev je technicky obtížnější, protože larvy se po celou dobu vývoje vyskytují na abaxiální straně listů.

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