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Occurrence, bionomics and harmfulness of *Chrysomela populi* L. (Coleoptera, Chrysomelidae)

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ABSTRACT: In 2003 to 2005, *Chrysomela populi* L. gradated on yearly cut *Populus nigra* var. *italica* in street alleys in Brno and elsewhere. Imagoes occurred on trees from the end of April or from the beginning of May. In rearing, the chrysomelid consumed unwillingly leaves of 2-year shoots and laid on average 142 eggs. On leaves of shoots, imagoes damaged 100 to 200 cm^2 during 5 to 7 weeks, produced 480 to 900 frass pellets and laid on average 506 eggs. Oviposition was continual with breaks amounting to on average 2.6 days. Embryonal development took 6 to 8 (in the laboratory 5) days. Larvae of the 1st generation occurred from mid-May to mid-July. In the course of 2 weeks (in the laboratory during 10 days) of life, they damaged about 20 cm^2 leaves and produced about 300 frass pallets. In the laboratory, prepupae took 2 days and pupae 4 days. Imagoes of the 1st generation occurred from June to September. They damaged on average 113 cm^2 and produced on average 553 frass pellets and 653 eggs. At a temperature of 24 to 28°C, imagoes damaged on average 84 cm^2 during 2 to 3 weeks and diapaused until the next year. On growing up leaves, imagoes lived longer showing higher consumption of food and higher fecundity as against new fully-grown leaves. Larvae of the 2nd generation destroyed on average 2 cm^2 smaller area than larvae of the 1st generation. Part or all imagoes of the 2nd generation diapaused. Imagoes of the 3rd generation damaged 40 to 70 cm^2 leaves before departure to wintering grounds. In our natural conditions, the prospective 3rd generation is always incomplete. *Cleonice callida* Meig. and *Schizonotus sieboldi* (Ratz.) rank among important enemies.

Keywords: Chrysomelidae; *Chrysomela populi*; occurrence; host tree species; bionomics; generation conditions; natural enemies; harmfulness

There are over 25 thousand species of the family Chrysomelidae in the world (in the CR about 300). Many of them rank among serious agricultural and forest pests. *Chrysomela* (= *Melasoma*, *Lina*) *populi* L. belongs to the most abundant and evidently most important species from the viewpoint of forestry. This chrysomelid as well as the majority of about 50 Central-European dendrophagous species lives on species of the family Salicaceae and also often graduates on some of them. Similarly as in many other insect pests its activity is mainly affected by moderate winters and dry and warm springs. Frequent climatic anomalies at the end of the last and at the beginning of this century markedly affected the water balance of trees and their resistance to insect defoliators. Increased food quality (particularly the higher proportion of sugars) and favourable living conditions manifested themselves in the general increase of the population density of Chrysomelidae (including *C. populi*) in the CR. Gradation of some phyllophagous species of chrysomelids related to heavy feeding to defoliation of trees was used for the study of their occurrence, bionomics and harmfulness (Urban 1997, 1998a,b, 1999, 2000, 2005, etc.). In recent years, attention was also paid to *C. populi*.

With respect to generally abundant to harmful occurrence on extensive areas and considering striking size and colouring, *C populi* is rather well known. It is dealt with by numerous special entomological and entomological/forest protection papers as well

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as numerous summary publications. In the CR, however, its biology and harmfulness have not been yet studied in detail.

C. populi occurs in the best part of the Palaearctic Zoogeographic Region and in the part of the Oriental Region. Most reports on its occurrence comes from the Mediterranean and Euro-Siberian Subregion. It ranks among common species, e.g. in Turkey (Schimitschek 1944; Kasap 1988; Zeki, Toros 1990, 1996; Aslan, Ozbek 1999), in Greece (Kailidis in Maisner 1974), in former Yugoslavia (Živojinovič 1948; Kovačevič 1957; Plavšić 1958; Georgijević, Vaclav 1958; Jodal 1985; Glavas et al. 1997), in Bulgaria (Penev, Ovčarov 1992; Georgiev 2000), in Italy (Loi 1970; Cavalcaselle 1972; Goidanich 1983; Allegro 1989; Sabatti et al. 2000), in Spain (Vicente et al. 1998), in Portugal (Nogueira 1968; Nogueira, Ferreira 1968) and France (Attard 1979; Augustin et al. 1992, 1993, etc.). It belongs to quite common species with marked gradation trends also in Great Britain and Northern Ireland and in the majority of countries of Western, Central and Northern Europe including the European part of the former USSR. For example in Germany, Ratzeburg (1839) and Kaltenbach (1874) and later a number of other authors rank the chrysomelid among harmful species. It is frequent also in Denmark and (with the exception of the utmost north) in Scandinavia (Hellén et al. 1939) where it does considerable damages, e.g. in central Sweden (Uteberg, Olsson 1978). In the Ukraine, the species is ecologically related to flooded or artificially irrigated areas along large rivers (Lopatin 1960). It is most harmful in the eastern part of the Ukraine and in the Crimea (Timčenko, Treml 1963).

C. populi is mentioned also from the eastern part of the Euro-Siberian Zoogeographical Subregion (e.g. an area around Baikal), the Central-Asian Subregion (e.g. Azerbaijan and Iran – Damanabi et al. 1977) and East-Palaearctic Subregion (e.g. Japan – Matsuda, Sugawara 1980), China (Ge et al. 2004) and Korea (Hwang et al. 1992; Lee 1996). In the Oriental Region, the range of distribution of *C. populi* reaches India (Chandel, Verma 1998; Thakur 1999, etc.). Unlike *Chrysomela tremulae* F., the beetle *C. populi* has not been spread to the American continent yet.

Some species of the genus *Populus* and *Salix* are host plants of *C. populi.* According to Ratzeburg (1839), the chrysomelid injures most quickly growing shoots of *P. tremula* L. Kaltenbach (1874) mentions the general occurrence of the beetle on young fine leaves of shoots of *P. tremula* L., *P.* × *canescens* (Ait.) Sm. (= *P. alba* L. × *P. tremula* L.) and *P. nigra* L. The author notes that the beetles also occur on *S. triandra* L., *S. fragilis* L. (= *S. russiliana* Sm.) and *S. viminalis* L. The more specified spectrum of hosts is mentioned by Escherich (1923). According to the author, the chrysomelid attacks certain species of *Populus* (mainly *P. tremula*) and also *S. purpurea* L., *S. pentandra* L., *S. fragilis* L., *S.* × *rubra* Huds. and *S. viminalis* L. In Austria, Pernersdorfer (1941) found the species on *P. tremula*, *P. alba*, *P. nigra*, *S. fragilis* and *S. purpurea*. In India, it was noted on *P. ciliata* Wall. and *S. alba* L. However, numerous authors (e.g. Calwer 1876; Reitter 1912; Kuhnt 1913; Scheidter 1926; Roubal 1937–1941; Gusev, Rimskij-Korsakov 1953; Kovačevič 1957; Georgijević, Vaclav 1958; Lopatin 1960; Medvedev, Šapiro 1965; Schwerdtfeger 1970; Warchałowski 1973; Vasiljev et al. 1974, 1975; Aslan, Ozbek 1999) do not mention the trophic preference of *C. populi* to actual species of *Populus* spp. and *Salix* spp. or state higher trophic affinity of the chrysomelid to poplars.

The priority attack of poplars is stressed, e.g. by Ratzeburg (1839), Henschel (1895), Březina (1927), Schimitschek (1944), Stark et al. (1951), Györfi (1952), Charvát and Čapek (1954), Schnaiderowa (1954), Plavšić (1958), Nogueira (1968), Nogueira and Ferreira (1968), Loi (1970), Cavalcaselle (1972), Vasiljev et al. (1974), Goidanich (1983), Jodal (1985), Penev and Ovčarov (1992), Thakur (1999) and Georgiev (2000). Sporadically, only *Salix* spp. (Fleischer 1927–1930; Javorek 1947, etc.) are regarded as host plants. However, according to the minority opinion, *C. populi* is often ranked among pests of osier plantations, i.e. specifically managed willow stands designed for the production of wicker for wickerwork purposes (e.g. Escherich 1923; Rubner et al. 1942; Nejedlý 1946, 1950; Gäbler 1955; Wagner, Ortmann 1959; Kadłubowski, Czalej 1962; Schnaider 1972). Problems of trophic relationships between *C. populi* and host tree species have not been yet satisfactorily done. In recent decades, it was proved many times that unlike *C. tremulae* its imagoes reproduced (and larvae developed optimally) only on *P. tremula* and some other species of *Populus* spp. but not on *Salix* spp.

C. populi is characterized by high requirements for food quality. Leaves of poplars show the higher content of water and total nitrogen as compared with willows. Generally, their nutrition value is substantially higher than in willows. Larvae develop normally and imagoes reproduce on poplars. Larvae feeding on leaves of willows develop very slowly reaching 6 times smaller weight. They die nearly

always (Edelman 1953). According to the author, imagoes on willows live for a longer time than on poplars, however, they are not able to reproduce. In addition to the content of water, sugars and proteins trophic specialization is given by the content silica dioxide, phenolic glucosides (e.g. salicin and populin), tannins, etc. In reservoirs of defence glands, salicin is hydrolyzed to salicyl alcohol saligenin. Salicylaldehyde which is the main defence compound against predators and parasitoids originates through its oxidation (Brückmann et al. 2002). The production of salicylaldehyde by larvae of *C. populi* on poplars is also mentioned by Matsuda and Sugawara (1980), Pasteels et al. (1988), etc.

The content and proportion of basic nutrients including secondary metabolites is the basic factor deciding on the selection of hosts and feeding behaviour and development of *C. populi.* For example, on *S. nigra* Marsh. and *S. babylonica* L., larvae totally die probably due to food inhibitors or the shortage of basic nutrients (Zareh et al. 1984). According to the authors, larvae are well adapted for the development on *P. alba* and *P. nigra* and worse for the development on *S. alba*. There are considerable differences in the development, mortality and fecundity of *C. populi* on various clones of *Populus* spp. For example, in rearings of Augustin et al. (1992, 1993), larvae and pupae developed most quickly (showing almost the smallest mortality) on hybrids of *P. tremula* L. × *P. tremuloides* Michx. (= *P.* × *wettsteini* L. Häm. Ahti). Preimaginal development on *P. alba* L. was somewhat worse and even more worse on *P. alba* × *P. tremula*. The lowest mortality and the highest fecundity showed imagoes on *P. tremula* × *P. tremuloides*, medium mortality and fecundity occurred on *P. alba* × *P. tremula* and the highest mortality and the lowest fecundity was on *P. alba*. Similar studies were carried out by Jodal et al. (1991) on 5 clones of *P. deltoides* Marsh. and 1 clone of *P.* × *canadensis* Moench (= *P.* × *euroamericana* /Dode/ Guin.).

Bionomics of *C. populi* is briefly discussed, e.g. by Henschel (1895), Schaufuss (1916), Escherich (1923), Živojinovič (1948), Stark et al. (1951), Gäbler (1955) and Maisner (1974). Copulation, ovogenesis and egg laying were noted by Scheidter (1926) in Germany. The development of eggs in ovaries was studied by Hwang et al. (1992) in Korea. The development of the chrysomelid on *P. nigra*, *P.* × *canadensis*, *P. alba* and *S. babylonica* was studied by Zeki and Toros (1992, 1996) in Turkey and on poplars in former Yugoslavia, e.g. by Plavšić (1958) and Jodal et al. (1991). Interesting bionomic findings were obtained by Chandel and Verma (1998) in the NW Himalayas (India). Effects of temperature on the preimaginal development of *C. populi* on poplars were studied by Loi and Belcari (1983) and Belcari et al. (1983) Tuscana (Italy). The development of *C. populi* in Iran was described by Damanabi et al. (1977) and in Italy by Loi (1970), etc. Effects of sex and life pattern on the accumulation of Cd, Cu, Fe and Zn in the body of *C. populi* and *Pterostichus niger* (Sch.) were studied by Lindqvist and Block (1997) in Sweden.

Natural enemies of *C. populi* are discussed recently, e.g. by Teodorescu (1980) in Romania and Zeki and Toros (1990) in Turkey. Findings on Central-European parasitoids of Chrysomelidae (including *C. populi*) from the family Tachinidae were summarized by Tschorsnig and Herting (1994). For example, *Hexamermis albicans* (v. Sieb.) (Mermithidae) (Poinar 1988) and *Linobia coccinellae* (Sc.) (Hemisarcoptidae) (Haitlinger 1999; Tarasi et al. 2001) rank among parasitoids of *C. populi*. *Schizonotus sieboldi* (Ratz.) (Pteromalidae) as a widely distributed and important parasitoid of pupae is recently mentioned, e.g. by Pettersen (1976) from Norway, Džanokmen (1978) from the European part of the former USSR and Lotfalizadeh and Ahmadi (1998) from Iran. In Kazakhstan, the spectrum of predators completed Marikovskaja and Šterbakova (1989) by *Symmorphus murarius* (L.) and *Ancistrocerus nigricornis* (Curt.) (Eumenidae). In the former Yugoslavia, Sidor (1979) and Sidor and Jodal (1986) found intense (54 to 82%) intracellular infection of larvae of *Nosema melasomae* (Microsporida, Nosematidae). According to Toguebay et al. (1988), in total 17 species of microsporidia were described from Chrysomelidae. Reputedly, none of them attacks *C. populi* in nature. It is of interest that the chrysomelid participates in the reduction of abundance of *Gypsonoma aceriana* (Dup.) (Tortricidae) on poplar (Kusevska 1972) in Macedonia (former Yugoslavia).

Considerable number of authors mentions the harmfulness of *C. populi* particularly on poplars (recently, e.g. Loi 1970; Damanabi et al. 1977; Uteberg, Olsson 1978; Attard 1979; Glavas et al. 1997; Goidanich 1983; Kasap 1988; Thakur 1999; Georgiev 2000, etc.). The use of insecticides to control the chrysomelid was studied in Italy, e.g. by Cavalcaselle (1972) and Arzone et al. (1981), in former Yugoslavia by Jodal (1985), in Portugal by Figo and Cabral (1964), in Poland by Schnaiderowa (1954) and in India by Khan and Ahmad (1991). Allegro (1989) deals with traditional and alternative environmentally friendly methods of control with main insect pests including *C. populi.* Orechov et al. (1978) found in the Ukraine that

predatory ants *Formica polyctena* Först. were able to carry bacteria *Bacillus thuringiensis* (Berl.) to larvae of *C. populi* bitten by the ants. Breeding and growing poplars and their hybrids resistant to pathogens and insect pests appear to be progressive (Sabatti et al. 2000). Delledonne et al. (2001) found that transgenic *P. alba* was resistant to larvae of *C. populi*. They explain the resistance by the enzymatic activity of papain in tissues of this genetically modified poplar inhibiting the digestive proteinases of larvae. The inhibitor could be used in clone programmes for the selection of new poplar genotypes resistant to main insect pests.

MATERIAL AND METHODS

Field and laboratory studies of the occurrence, development and harmfulness of *C. populi* were carried out mainly in 2003 to 2005. The majority of field investigations was realized in avenues created by *P. nigra* var. *italica* in Brno urban districts Královo Pole and Černá Pole. Mean altitude of the districts is about 180 m, mean annual temperature 8.4°C, mean annual precipitation 547 mm and mean growing season 168 days. In both localities, tree crowns were yearly either partly or totally removed. Inspections were carried out throughout the growing season in week (maximally two-week) intervals. Bionomics of the chrysomelid was also occasionally studied on *P. tremula* and *P. nigra*, Forest District Křtiny and Forest District Bílovice nad Svitavou (Training Forest Enterprise Křtiny) and on *P. tremula*, Forest District Valtice (Forest Enterprise Břeclav).

Findings obtained from field studies were faced with results of laboratory studies. Imagoes or other developmental stages of the chrysomelid were placed in wire breeding cages of a base of 17 × 17 cm and height 33 cm or in glass vessels of a diameter of 10 (or 20) cm and height 5 (or 10) cm. In the cages, the chrysomelids were fed on new foliaged (about 25 cm long) terminal sections of shoots of *P. nigra* var. *italica*. Lower ends of the sections were put in small vessels with water the necks of the vessels being sealed by cotton wool. In glass breeding vessels, only leaves of *P. nigra* var. *italica* were usually placed. Petioles of the leaves were put in a test tube with water or wrapped by a moistened piece of cotton wool. In regular two-day (in larvae daily) intervals, damaged are slightly wilting shoots and leaves were changed for new ones.

Laboratory studies were carried out from the beginning of May (i.e. from the period of intense leaf unfolding) to the beginning of stronger frosts and mass leaf-fall. In individual and collective rearings (up to 30-member) of imagoes, the damaged area of growing-up leaves (the 3rd and the 4th leaf from the shoot top) as well as that of newly grown-up leaves (the 5th to the 7th leaf from the shoot top) was measured using planimetric methods. As necessary, the average area of leaves, their weight and dry matter percentage were determined. The number of frass pellets was recorded and their dimensions were measured by micrometry (in fresh condition). Through continual weekly monitoring, the frequency of copulation was determined during 24-hour cycles including the period of copulation, period of egg laying and the number of eggs. In dead females, the number of unlaid eggs was determined by means of ovary dissection. The number and localization of laid eggs or their dimensions during embryogenesis were recorded.

Larvae were kept in 3 to 50-member groups. The period of the development of larvae of particular instars and leaf area damaged by them were determined. Effects of the abundance of larva groups and food quality on the mortality of larvae and food consumption were also studied. On the basis of the number and size of frass pellets defecated by larvae of particular instars the mean volume of frass pellets was determined from 1 cm^2 damaged leaf area.

Fig. 1. A male (a smaller individual) and a female of the 1st generation of *Chrysomela populi* on the adaxial face of a leaf of *Populus nigra* var. *italica*. Brno-Královo Pole, 2 May 2003

According to the indicator the effectiveness was compared of using the food by larvae of the 1st to the 3rd instar. Diurnal activity of larvae was studied particularly the number and the period of stages of feeding and rest, etc.

RESULTS AND DISCUSSION

Host tree species

P. tremula L. and *P. nigra* L. including its cultivar *P. nigra* var. *italica* are the primary host species of *C. populi* (Fig. 1). On these hosts, the chrysomelid was studied by the author both in nature and in the laboratory. From poplars of a section *Leuce*, *C. populi* is optimally trophically adapted (in addition to European aspen) also to *P.* × *wettsteini* L. Häm. Ahti (= *P. tremula* L. × *P. tremuloides* Michx.). *P.* × *canescens* (Ait.) Sm. is damaged less by the chrysomelid and *P. alba* L. even lesser (Augustin et al. 1992, 1993). Imagoes feed first always on preferred clones and only under conditions of food shortage they feed on normally undamaged clones. In actual rearings, *C. populi* damaged *P. alba* only minimally.

From poplars of a section *Aigeiros*, *C. populi* attacks, in addition to *P. nigra* and *P. nigra* var. *italica*, also some clones of the North-American *P. deltoides* Marsh. and its hybrid with *P. nigra*, i.e. *P.* × *canadensis* Moench (= *P.* × *euroamericana* /Dode/ Guin.) (Jodal et al. 1991). According to Zeki and Toros (1996), *P.* × *canadensis* is a more suitable host for *C. populi* than *P. alba*. From a section *Leucoides*, *C. populi* damages *P. ciliata* Wall. (Chandel, Verma 1998). Among poplars of a section *Tacamahaca*, no species or hybrid have been found yet which would be intensively damaged by *C. populi*. Even hybrids of *P.* × *berolinensis* Dipp. and *P.* × *generosa* Henry do not rank among host species of the chrysomelid.

According to the author's findings, *C. populi* occurs frequently on willows, however, it does not gradate on them. In the arboretum of Mendel University of Agriculture and Forestry Brno, imagoes and larvae were found, e.g. on *S. fragilis* L. and *S. purpurea* L. In Brno-Obřany and Bílovice nad Svitavou, grown-up larvae and pupae were found on shoots of *S. fragilis* on 25. 8. 2003. From the larvae and pupae, imagoes of normal size hatched in the laboratory from 29. 8. 2003. The fact differs from the statement of a number of authors that larvae can complete their development only on poplars. Huge and fine leaves of freely growing coppice shoots of *S. fragilis* on the bank of the Svitava river were far more suitable for the development of larvae than small and tough leaves of a nearby 50-year-old *P. nigra* var. *italica* where the chrysomelid was not found. Laboratory rearings of *C. populi* on leaves of *S. fragilis* L., *S.* × *rubens* Schr., *S. purpurea* L. and *S. viminalis* L. in 1996 were, however, always totally unsuccessful. The development of *C. populi* on *S. fragilis* was rather best. About 5% larvae reached the 3rd instar on the species. The development of larvae lasted unnaturally long (about 19 days) always resulting in death. In rearings carried out in 2001 to 2004, larvae on willows died already during the 1st or the 2nd instar.

Imagoes of *C. populi* consumed leaves of *S. viminalis*, *S.* × *rubra*, *S.* × *smithiana* Willd. and *S. americana* hort. only minimally. They damaged somewhat more leaves of *S. purpurea* and *S.* × *rubens* and mostly leaves of *S. fragilis.* Imagoes reared in the laboratory (from larvae fed on leaves of *P. nigra* var. *italica*) lived on *S. fragilis* on average 14 days (males about 13 days and females about 15 days), i.e. about 9 times shorter time than on *P. nigra* var. *italica* and did not lay the only egg (Table 1, Fig. 2). Thus, the chrysomelid was not able to reproduce even on the relatively most damaged *S. fragilis*. With respect to the potential species confusions with *C. saliceti* (Ws.) and *C. tremulae* F. it is necessary to assess information on the harmfulness of *C. populi* on *Salix* spp. with considerable restraint. The study of insect pests in 6 osier plantations in Moravia in 1969 to 1976 (with 12 cultivated species or hybrids of willows) showed that *C. populi* (unlike *C. saliceti*) occurred in surveyed plantations mostly rarely and never as a harmful species. However, in contrast to the experimentally demonstrated total mortality of larvae on *Salix* spp., larvae living in nature can successfully develop on large leaves of actively growing shoots of some *Salix* spp. (e.g. *S. fragilis*). Such leaves resemble, as for nutrition aspects (particularly the content of proteins and easily degestible sugars), far more nutritive leaves of *Populus* spp. It is necessary

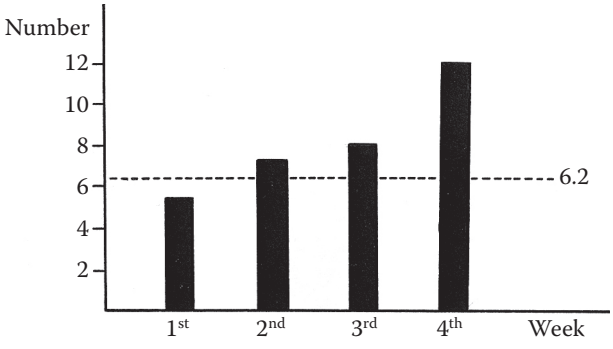

Fig. 2. Average number of frass pellets defecated by imagoes of *C. populi* (sex ratio 1:1) from 1 cm^2 of the damaged leaf area of *Salix fragilis*. Dash line illustrates the total average number of frass pellets from 1 cm^2 leaf. Laboratory examination, 16 July–9 August 2003

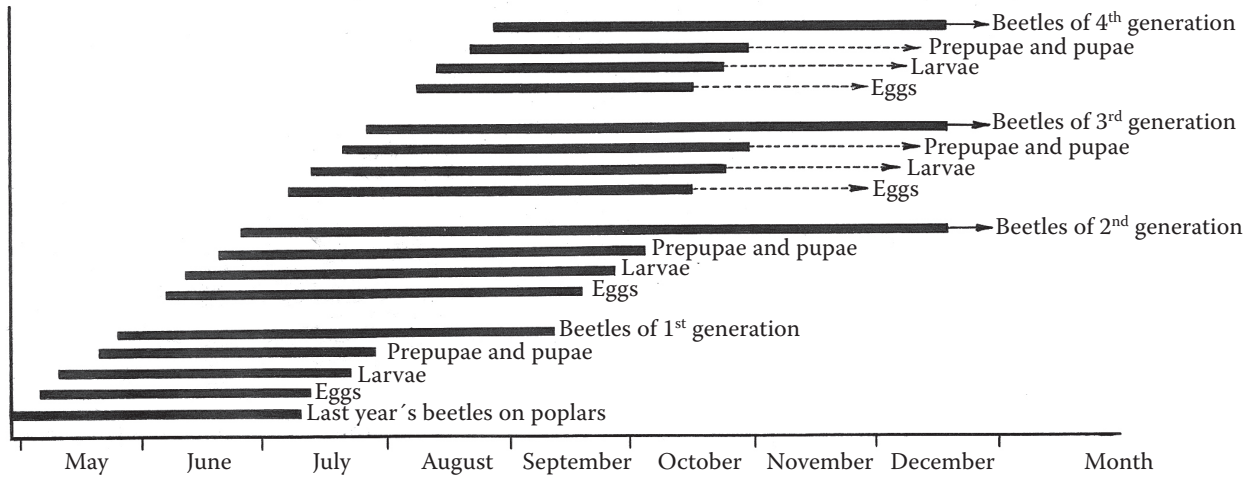

Fig. 3. A diagram of the development of *C. populi* on leaves of *P. nigra* var. *italica*. Laboratory rearing, 2004

to find if females mature on shoots of some species of willows and lay viable eggs or if they are totally sterile also in nature. Present findings obtained from rearings do not make possible we to express final conclusions.

Hibernation and leaving wintering places

Beetles of *C. populi* survive winter in various shelters (Scheidter 1926), however, particularly on land under leaves (Henschel 1895; Escherich 1923; Wagner, Ortmann 1959; Zareh et al. 1984, etc.). They winter also in tufts of grass (Loi 1970) or allegedly in soil at a depth of 3 to 5 cm (Damanabi et al. 1977). At a temperature of 12 to 13°C, they come out from hibernation shelters and soon appear on host species. The onset and course of leaving wintering places depend on climate and the factual course of weather. The occurrence of beetles on trees coincides usually with the period of leaf unfolding.

In warm regions of Italy, the beetles are already active at the end of March and at the beginning of April (Loi 1970). In Iran, wintering beetles can be found from the beginning of April (Zareh et al. 1984), in India, in the course of April and May (Chandel, Verma 1998) and in the floodplain zone of the Ukraine at the beginning of May (Lopatin 1960). In regions of Europe with predominating temperate climate, beetles attack trees usually at the end of April and at the beginning of May (Schnaiderowa 1954; Vasiljev et al. 1974; Maisner 1974, etc.), according to Pernersdorfer (1941) already from mid-April. Also in the region of southern and central Moravia, the beetles occur on trees usually from the end of April or at the beginning of May (Fig. 3).

Table 1. The average weekly area of leaves of *Salix fragilis* damaged by imagoes of *Chrysomela populi* (sex ratio 1:1) including the weekly number of frass pellets and the average weekly number of frass pellets from 1 cm^2 damaged leaf. Laboratory examination, 2003

Week (from– to)	Average damaged area (cm^2)	Average number of frass pellets	Average number of frass pellets per 1 cm^2
17.–22. 7.	15.9	86	5
23.–29. 7.	8.6	62	7
30. 7.–5. 8.	1.8	14	8
6.–9. 8.	0.1	1	12
Total	26.4	163	(6)

Beetle feeding after wintering and egg laying

Individuals of both sexes occur on trees at the same time, viz at 1:1 ratio. Beetles are very weakened and,

Fig. 4. A leaf of *P. nigra* var. *italica* damaged by imagoes of *C. populi* after wintering. Brno-Černá Pole, 3 June 2003

Table 2. The average weekly area of leaves of *Populus nigra* var. *italica* damaged by male and female imagoes of *C. populi* after wintering in nature (including the average weekly number of frass pellets and laid eggs). Imagoes (10 males and 10 females) were caught on 4. 5. 2004 (i.e. soon after leaving winter places) on *Populus tremula* in Křtiny (TFE – Training Forest Enterprise Křtiny). Until 31 May, the imagoes were separately reared on leaves of 2-year-old shoots (of an average area of 23.8 cm^2 and 30.5% dry matter) and then on leaves of coppice shoots (of an average area of 52.6 cm^2 and 27.1% dry matter). Laboratory examination, 2004

Week (from–to)	Males		Females		
	average damaged area (cm^2)	average number of frass pellets	average damaged area (cm^2)	average number of frass pellets	average number of eggs
4.–10. 5.	4.4	51	7.8	71	46.5
11.–17. 5.	5.6	65	8.5	65	–
18.–24. 5.	2.0	20	2.8	46	–
25.–31. 5.	–	–	5.3	59	–
1.–7. 6.	–	–	32.5	121	136.3
8.–14. 6.	–	–	27.5	109	125.0
15.–21. 6.	–	–	39.0	109	87.2
22.–28. 6.	–	–	24.3	81	84.5
29. 6.–5. 7.	–	–	8.9	33	26.5
6.–12. 7.	–	–	0.4	2	–
Total	12.0	136	157.0	696	506.0

therefore, after reaching host species they begin to feed immediately. Into newly unfolded leaves, they begin to bite out irregular incisions from the adaxial face of leaves (Fig. 4), more sparsely holes. Leaves are often browsed up to the central vein, many times including lateral veins and terminal parts of the central vein. They leave often only small irregular remains of blades along veins or leaf edges. In laboratory rearings, small part of a leaf blade in the form of small cuttings falls to the earth ("waste feeding"). After several days of feeding (in the laboratory already after 4 to 8 days), imagoes begin to copulate and soon lay the first eggs. Females often ingest during copulation. Males strike sometimes duels for the females. By means of mandibles they attack copulating males trying to drive away them from females.

The lifespan of imagoes, food consumption and fecundity are markedly related to trophic properties of host species. For example, imagoes caught on 4. 5. 2004 on *P. tremula* in Křtiny consumed in captivity leaves of 2-year-old shoots of *P. nigra* var. *italica* only very unwillingly and did not lay any eggs. Males refused the food even more than females and died during 3 weeks. From 31 May, leaves of *P. nigra* var. *italica* shoots were served to survived starving females. Females began to consume the leaves intensively and soon laid eggs. They lived on average 61 days and damaged on average 157 cm^2 leaves. They produced on average 696 frass pellets and laid 153 to 799 (on average 506) eggs (Table 2).

Leaves on 2-year-old shoots of *P. nigra* var. *italica* are on average 2 times smaller as against leaves

Table 3. Results of individual rearings of imagoes of the wintering generation of *C. populi* on *P. nigra* var. *italica*. Imagoes were caught on *P. tremula* in Valtice (Forest Enterprise Břeclav) at the beginning of maturation feeding (5. 5. 2003). They were fed on newly unfolded leaves of 2-year-old shoots of an average area of 20 cm^2 and 28.0% dry matter. Laboratory examination, 2003

Evaluated character	Males (12 individuals)	Females (8 individuals)
Average damaged area (cm^2)	12.8	23.5
Average number of laid eggs	–	141.8
Average life (days)	21.9	26.5
Average number of frass pellets	124.7	198.0
Number of frass pellets from 1 cm^2 damaged area	9.7	8.4
Average length/width of frass pellets (mm)	1.64/0.66	1.61/0.74
Average volume of a frass pellet (mm^3)	0.56	0.69
Volume of frass pellets (mm^3)	69.8	136.6
Volume of frass pellets from 1 cm^2 (mm^3)	5.4	5.8

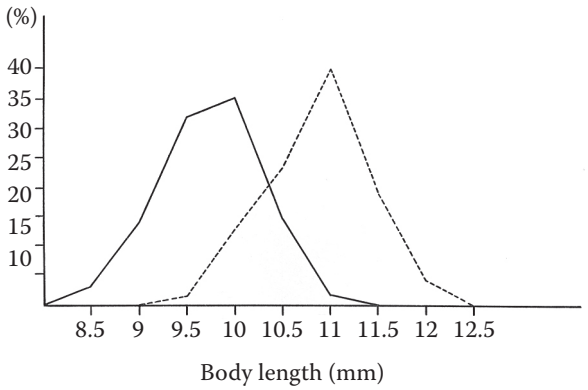

Fig. 5. Length of the body of male imagoes (solid line) and female imagoes of *C. populi* (dash line). Some 272 males and 296 females were measured. Laboratory examination, 2003 to 2005

on coppice shoots containing higher DM% being also much more tough. In nature, such leaves are consumed only under conditions of the shortage of more suitable food. It was demonstrated by findings obtained from rearings of males and females in 2003 (Table 3). Imagoes lived in the captivity only 2 to 3 weeks and damaged up to 7 times smaller area than on leaves of coppice shoots. It comes to this that imagoes on unsuitable leaves of *P. nigra* var. *italica* were hungry in principle. Nevertheless, males are more sensitive to low-quality food than females. It became evident both in the shorter period of life and in the two-time smaller consumption of food in males. The mean number of eggs laid by undernourished females was markedly subnormal (on average 142 eggs). With respect to the generally larger average size of females (Fig. 5) and high expenditures of nutrients for the creation of eggs the consumption of food in females is always higher (about by one third) than in males even under normal conditions.

Frass pellets of imagoes are at first dark green, later black. They show funicular, fusiform or rounded cylindrical form and rough surface. Average dimensions of female frass pellets are always larger as compared with male pellets. Substantially larger are also frass pellets of imagoes consuming trophically optimal fine leaves of coppice shoots (Table 4). Frass pellets of imagoes consuming rather unsuitable leaves of *P. nigra* var. *italica* were on average 1.67 mm long and 0.72 mm wide. Frass pellets of imagoes consuming trophically valuable leaves of coppice shoots were on average 2.24 mm long and 0.77 mm wide. The average volume of frass pellets defecated by imagoes fed by quality food was 1.7 times greater than the average volume of frass pellets defecated by imagoes fed by less-quality food.

Eggs are produced in ovaries of females always only during feeding. Mature fertilized eggs are laid in oval single-layer groups ("egg plates") on the abaxial face of leaves (Fig. 6). Through a short false ovipositor the female first examines a suitable place for oviposition and then places a sticky egg on it by a rear end. To a laid egg the female gradually places other eggs in an interval of 30 to 80 seconds orienting them nearly perpendicularly or crossways to the leaf surface. The female deposits 20 to 65 (on average 55) eggs into one group (clutch) of eggs in the course of 30 to 45 minutes. In the laboratory, females sometimes divide the clutch into 2 (or more partial groups) and so the average number of eggs in clutches is lower than in

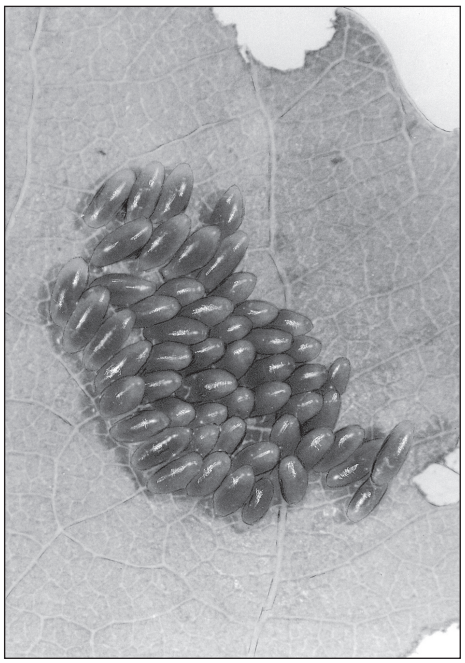

Fig. 6. The group (clutch) of 54 eggs of *C. populi* on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 18 May 2003

Table 4. Average size of frass pellets of males and females of *C. populi*. In 2003, beetles fed on leaves of 2-year-old shoots of *P. nigra* var. *italica*, in 2004 on leaves of coppice shoots. Laboratory examination

Sex of imagoes	May 2003		June 2003		June 2004	
	average length/ width (mm)	average volume (mm^3)	average length/ width (mm)	average volume (mm^3)	average length/ width (mm)	average volume (mm^3)
Males	1.64/0.66	0.56	1.64/0.69	0.61	2.18/0.67	0.77
Females	1.61/0.74	0.69	1.81/0.82	0.95	2.30/0.87	1.36
Average	1.62/0.70	0.62	1.72/0.75	0.78	2.24/0.77	1.07

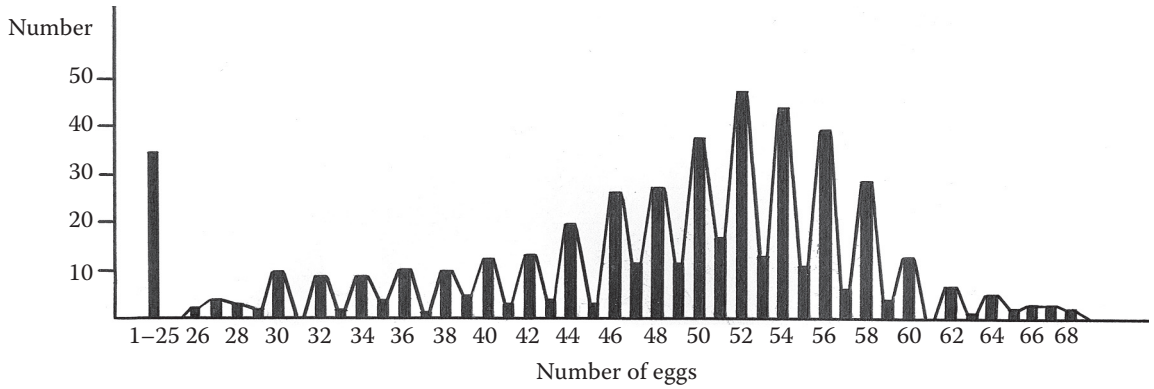

Fig. 7. Frequency of the occurrence of egg groups of *C. populi* according to the number of eggs in groups on leaves of *P. nigra* var. *italica*. Laboratory examination, 2003 to 2005

nature (on average 47). Thus, the number of eggs in clutches varies from 1 to 68 (Fig. 7).

According to Escherich (1923), Živojinovič (1948), Stark et al. (1951), Gäbler (1955), etc. there are 20 to 30 eggs in one clutch. Scheidter (1926) does not agree with the opinion of Escherich (1923) and mentions that females deposit about 50 to 60 eggs into one clutch. According to Blunck et al. (1954), there are 10 to 60 eggs in a clutch, according to Vasiljev et al. (1974) 20 to 60 eggs and according to Loi (1970) 20 to 65 eggs. In Iran, females lay 42 to 58 eggs, viz both on the abaxial face of leaves and (surprisingly) also on the adaxial face of leaves and sometimes also on the bark of trees (Damanabi et al. 1977). Plavšić (1958) found that the average number of eggs in a group was higher (about 48) at a mean temperature of 19°C than at a temperature of 24°C (about 40). The number of eggs in groups is also related to the quality of food (Jodal et al. 1991). In there laboratory rearings of imagoes on *P. deltoides* Marsh. and *P.* × *canadensis* Moench, the smallest average number of eggs in a group (56) was on *P. deltoides* (clone 725) and the greatest number (63) on *P. deltoides* (clone 618). In principle, the number of eggs in a group corresponds to the number of functional ovarioles (Scheidter 1926). In each of the ovarioles, usually one egg (rarely two eggs) matures (being also laid). In the same females, the number of eggs in clutches is, therefore, rather constant whereas the number of ovarioles in ovaries is allegedly usually different (Scheidter 1926). According to our findings this statement is not accurate because the even number of eggs markedly predominates in particular clutches corresponding to the pair structure of ovaries (Fig. 7). From the examined number of 528 clutches some 408 (77%) clutches contained even number of eggs and only 120 (23%) clutches contained odd number of eggs. From the total number of 24,851 eggs laid in the laboratory 19,200 eggs occurred in groups of the even number of eggs and only 5,651 eggs were in groups with the odd number of eggs.

Eggs of *C. populi* are lengthwise oval, rounded, cylindrical to fusiform. Immediately after oviposition, they are on average 1.8 mm long and 0.75 mm wide. In the course of embryonal development, their mean length and width increase up to 2.0 and 0.83 mm, respectively. According to Maisner (1974), eggs are

Table 5. Partial results of rearings of *C. populi* imagoes on growing up leaves of *P. nigra* var. *italica*. In a rearing marked*, imagoes were caught in Křtiny (TFE Křtiny), in other cases imagoes were reared from eggs in the laboratory. Laboratory examination, 2004

Average	Date of hatching (*caught) and the number of ♂♂/♀♀								
	18. 5.* 1/4	9. 6. 2/4	13. 6. 2/5	25. 6. 15/15	13. 7. 4/2	19. 7. –/3	29. 9. 1/1	3. 10. 6/2	8. 10. 1/1
Period of the life of males (days)	(37)	59	46	26	30	–	200	33	231
Period of the life of females (days)	(56)	58	42	26	13	71	82	19	212
Number of laid eggs	(409)	477	189	92	–	202	–	–	–
Damaged area (cm^2)	(153.4)	163.3	95.1	52.0	44.6	144.0	77.3	27.3	23.0

Table 6. A period between laying of eggs of *C. populi* on *P. nigra* var. *italica* (including the period of feeding till the beginning of oviposition and the total period of egg laying). Studied imagoes were reared in the laboratory. Imagoes caught in Křtiny (TFE Křtiny) on 4 May appear to be an exception (see a column marked *). These imagoes were fed on leaves of 2-year-old shoots till 2 June, later on leaves of coppice shoots. After laying an average clutch (about on 7 May) females laid eggs from 4 June to 6 July. Laboratory examination

Evaluated character (days)	Period of oviposition 2003			Period of oviposition 2004			
	4.7.–4. 8.	29.7.–26.8.	31.7.–13.9.	4.6. (7.5.) –6.7.*	28.6.–1.8.	1.7.–1.8.	4.9.–5.11.
Intervals between egg laying (from–to)	1–3	1–5	3–12	1–9	1–6	1–8	3–30
Average interval	1.4	2.9	7.5	2.6	3.7	4.5	12.9
Period of life till the beginning of egg laying	15	15	15	(240)	18	15	15
Period of egg laying	31	29	45	(32)	35	32	62

only 1.0 mm long and 0.56 mm wide. The colouring of eggs is usually light, ochre or brown (with yellow poles). Clutches with predominating brown-red to violet colouring are also rather frequent. Within the same clutch the colouring is always uniform. However, the colour of eggs in clutches of various females is often different. Causes of this colour polymorphism are not known. The chorion of eggs is shiny, smooth and rather soft. There is a sticky air-toughening substance on its surface. By means of the secretion eggs are stuck not only to a bed (i.e. as a rule to the abaxial face of a leaf) but also each other.

Beetles of a wintering generation occur after hibernation on trees from the end of April or the beginning of May till mid-July, i.e. for a period of 2.5 months (Fig. 3, Tables 2 and 5). They live on average 2 months. In our rearings on *P. nigra* var. *italica*, beetles laid eggs (and copulated repeatedly) for a period of 5 to 7 weeks. After hibernation, they damaged 100 to 200 cm^2 leaves and produced 480 to 900 (on average 700) frass pellets. After the cessation of reproduction, feeding intensity of beetles quickly decreased and during 3 to 9 days after laying the last clutch of eggs females died. In ovaries of dead females, usually no unlaid eggs occurred. The process of oviposition was always continual without any long regeneration breaks. There was an interval of 1 to 9 (on average 2.6) days (Tables 6 and 7) between two consecutive clutches. Table 7 shows that intervals between particular clutches significantly increase with the age of females (from 1.4 to 7.0 days).

For example, data of Maisner (1974) who mentions that females of *C. populi* deposit eggs in three periods with a 5 to 35-day regeneration interval are inconsistent with our findings. Also Plavšić (1958) writes that there are 3 breaks taking about 10 days

Table 7. Average intervals between subsequent egg laying of *C. populi* on *P. nigra* var. *italica* during the period of oviposition (days). Imagoes were reared in the laboratory or caught in Křtiny (TFE Křtiny) (see a column marked *). Until 2 June, these imagoes were fed on leaves of shoots, later on leaves of coppice shoots. After laying an average clutch (about on 7 May), females laid eggs from 4 June to 6 July. Laboratory examination

Week No.	Period of egg laying		
	4. 7.–4. 8. 2003	4. 6. (7. 5.)–6. 7. 2004*	28. 6.–1. 8. 2004
1	1.2	–	2.8
2	1.2	–	3.5
3	1.2	–	3.5
4	3.5	–	3.5
5	2.3	1.8	7.0
6	–	1.4	–
7	–	3.5	–
8	–	3.5	–
9	–	7.0	–
Mean (days)	1.4	2.6	3.7

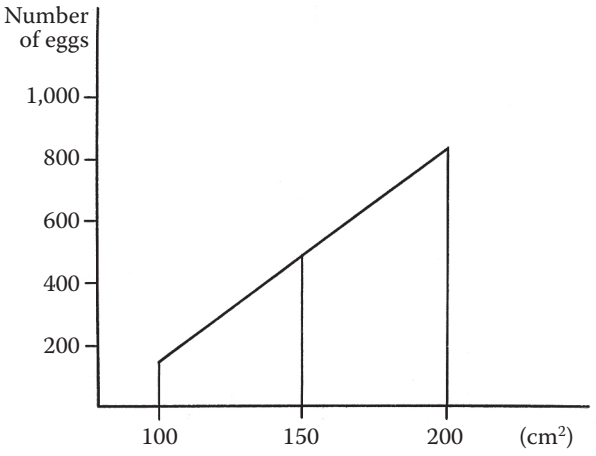

Fig. 8. The diagram of a relationship between the average area of leaves of *P. nigra* var. *italica* damaged by female imagoes of *C. populi* (after wintering) and the average number of laid eggs. Laboratory examination, 2003 to 2005

Table 8. The average period of development of particular developmental stages and growth degrees of *C. populi* on growing up leaves of *P. nigra* var. *italica* (in days). Laboratory (in parenthesis outside) examination, 2004

Developmental stage (growth degree)	Period of rearing						
	15 May–June	July	August	September	June–September	(October)	(November)
Egg	5	5	5	6	5.3	(11)	?
1st instar	2.5	2.4	2.3	2.7	2.5	(16)	?
2nd instar	3	2.8	2.6	3.8	3	(9)	?
3rd instar	4.5	4	3.6	5.5	4.4	(15)	?
Prepupa	2	2	2	2.5	2.1	(3)	(4)
Pupa	4	4	4	4.5	4.1	(5)	(7)
Total	21	20.2	19.5	25	21.4	(59)	?

in the period of egg-laying at 19°C. Average intervals between consecutive clutches are 2.2 days. At 25°C, breaks take only 5 days and average intervals between clutches take 1.1 days. In rearings of Jodal et al. (1991), about 20% of females laid eggs continually and 80% with 1 to 3 breaks taking 4 to 9 days. Intervals between particular clutches took usually 1 to 3 days.

Fecundity of females of the wintering generation of *C. populi* was high. In orientation laboratory rearings of Scheidter (1926) carried out from 17 May to 23 June, a female laid in 19 clutches (intervals between particular egg-laying 1 to 4 days) 1,042 eggs. Also Escherich (1923) mentions that females deposit more than 1,000 eggs. Jodal et al. (1991) found that the highest fecundity (1,369 eggs) occurred in females consuming leaves of *P. deltoides* (clone 618) and the lowest fecundity was in females consuming leaves of *P. deltoides* (clone 725). A rather low fecundity of females of a wintering generation (220 to 500 eggs) is mentioned, e.g. by Vasiljev et al. (1974). According to Plavšić (1958), females live about 65 days at an average temperature of 19°C and lay on average 811 eggs in 17 clutches. In rearings carried out by Zeki and Toros (1996) in Turkey, fecundity of females varied from 33 to 989 eggs. Loi (1970) mentions high fecundity (486 to 1,641 eggs) and Damanabi et al. (1977) medium fecundity (maximally 680 eggs). In our rearings on *P. nigra* var. *italica*, females laid 153 to 850 (on average 558) eggs. The average number of laid eggs increased significantly with the area of damaged leaves (Fig. 8).

Development of the 1st generation

The embryonal development of *C. populi* takes in nature 6 to 8 days and under ordinary laboratory conditions about 5 days (Table 8, Fig. 9). According to Henschel (1895) and Nüsslin and Rhumbler (1922) egg larvae hatch after 8 to 10 days, according to Escherich (1923) and Živojinovič (1948) after 8 to 12 days and according to Maisner (1974) after 5 to 12 days. Rather unusual range of the period of embryonal development (5 to 15 days) is given by Chandel and Verma (1998). On the other hand, Loi (1970) mentions that the eclosion of larvae from eggs occurs as early as after 4 to 5 days. Similar conclusions were also mentioned by Damanabi et al. (1977). According to the authors larvae hatch already after 4 days at 24°C and 60% relative humidity. Effects of temperature on the period of embryonal development were demonstrated by Plavšić (1958). According to the author egg larvae hatch after 8 days at a temperature of 19°C and at a constant temperature of 25°C already after 4.5 days.

According to our studies, larvae from eggs of the same clutch hatch within 60 to 80 minutes, namely most frequently between 6 and 9 o'clock. Egg larvae are brightly yellow-orange to yellow-brown. For a period of about 4 hours, they stay in cracked egg chorions by their rear part and gradually become darker.

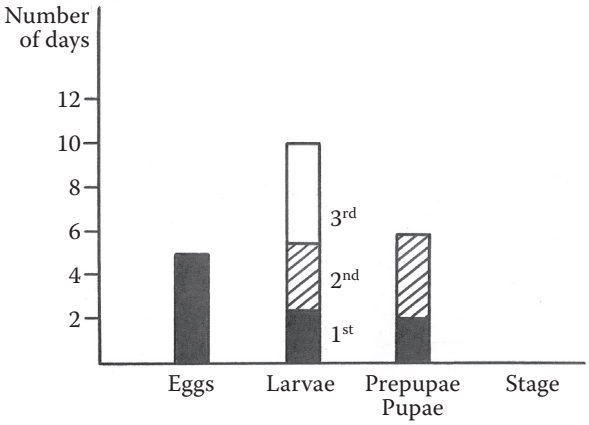

Fig. 9. The average period of development of preimaginal stages and growth degrees of *C. populi* on growing up leaves of *P. nigra* var. *italica*. Laboratory examination, June and July, 2003, 2004

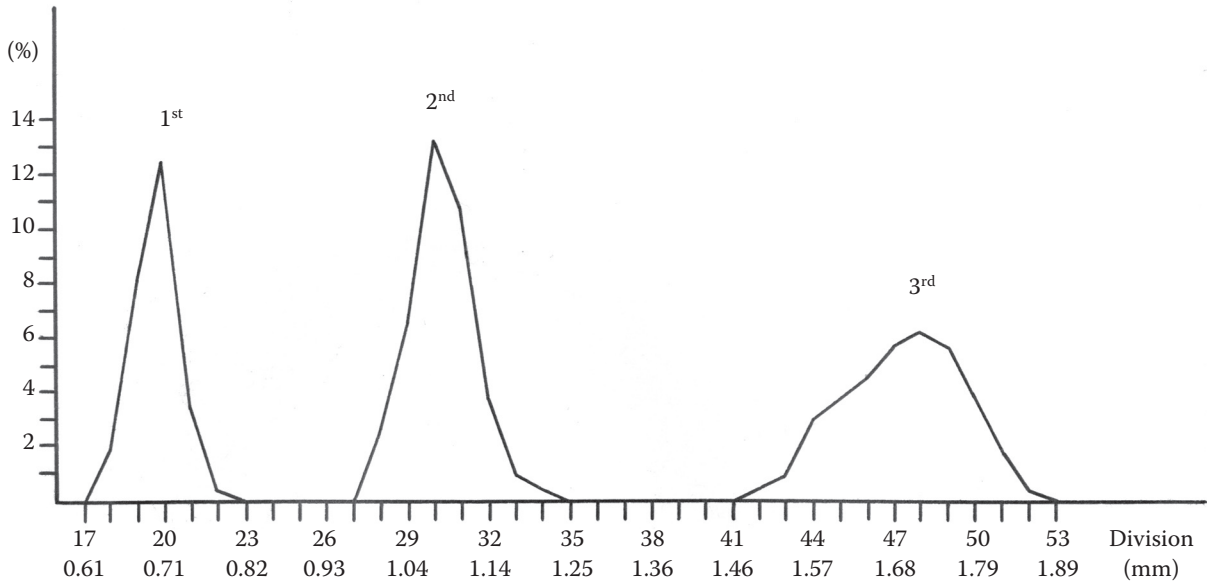

Fig. 10. The width of a cranium of particular instars of *C. populi* (1 division = 0.0357 mm). In total 1,092 larvae were measured. The average width of the cranium of larvae of the 1st instar is 0.7 mm, of the 2nd instar 1.08 mm and of the 3rd instar 1.69 mm. Laboratory examination, 2003, 2004

After about 6 hours from the beginning of hatching, all larvae are concentrated on abandoned chorions. Their first food consists usually of chorions of eggs which are partly or totally consumed by the larvae. After 6 to 12 (20) hours from hatching, larvae line up nearby the place of hatching (head ends in the same direction) and begin jointly to skeletonize leaves.

Larvae of the 1st instar are at first only 2 mm long. Their cranium is 0.64 to 0.78 mm wide (Fig. 10). They eat out minute holes in the leaf blade without damaging the upper epidermis and venation of leaves. In the laboratory, the larvae reach a length of even 4 mm during about 2 days of feeding damaging on average 0.6 cm^2 leaf blade of *P. nigra* var. *italica* (Table 9, Figs. 11 and 12). Between particular feeding marks and close to leaf veins and anastomoses they leave small irregular residues of leaf blades. However, under conditions of standard observation the feeding of larvae appears to be total defoliation. Leaves in the place of damage become brown and die. I case of damage of the best part of a leaf blade the whole leaf dies. Indigested residues of food are defecated by larvae in the form of dark green (growing black in the open air) fusiform to cylindrical (usually tapered on both ends) frass pellets. Frass pellets of larvae of the 1st instar are very minute (almost invisible by naked eye), on average 0.4 mm long and 0.2 mm wide (Table 10). Frass pellets of growing up larvae of this instar are somewhat larger. Larvae of the 1st instar produce on average 77 frass pellets of a total volume of 1.1 mm^3 (Table 11, Fig. 13). When the larvae grow up they cease to ingest and after 30 to 60 minutes they stick by their caudal part to a leaf by means of thin yellowish secretion. After about 3 hours from the termination of feeding the larvae moult for the first time.

Newly moulted larvae of the 2nd instar are largely of yellow colour. During 2 to 3 hours, they become dark and soon begin to skeletonize leaves. Larvae of this instar are 3.5 to 8 (on average 6) mm long. They can

Table 9. Average leaf area damaged by larvae of the 1st to the 3rd instar of *C. populi* (in cm^2 and %). Laboratory rearings on leaves of coppice shoots of *P. nigra* var. *italica*, 2003

Instar	Period of rearing				Average area (cm^2)	(%)
	14. 6.–24. 6.	29. 6.–9. 7.	30. 6.–13. 7.	1. 7.–13. 7.		
1st	0.6	0.5	0.6	0.6	0.6	2.8
2nd	3.0	3.9	2.9	3.1	3.2	16.1
3rd	17.3	16.6	17.0	13.8	16.2	81.1
Total	20.9	21.0	20.5	17.5	20.0	100.0

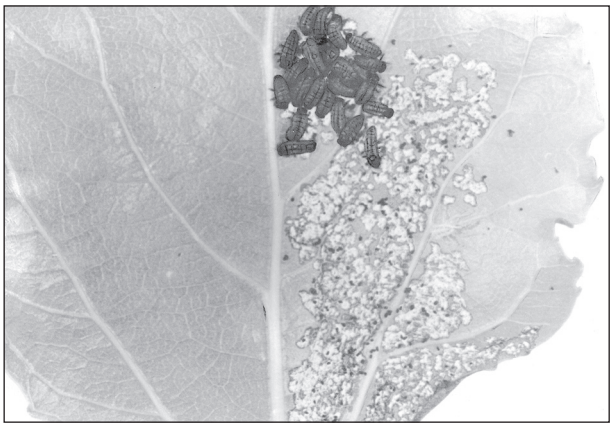

Fig. 11. Larvae of the 1st instar of *C. populi* during feeding on the abaxial face of a leaf of *P. nigra* var. *italica*. Laboratory rearing, 17 May 2003

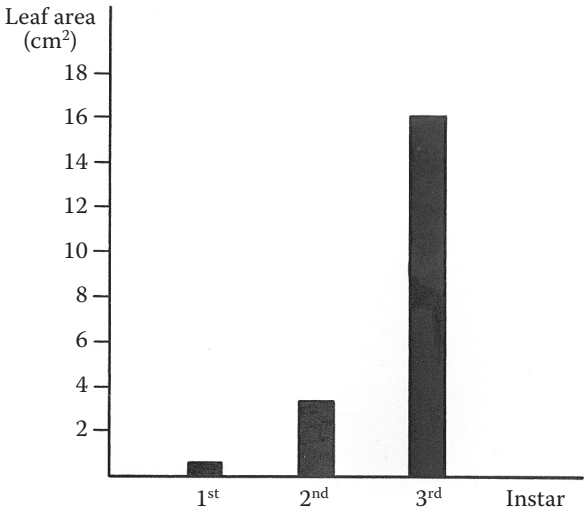

Fig. 12. Average area of leaves of *P. nigra* var. *italica* damaged by larvae of particular instars of *C. populi*. Laboratory examination, 14 June–13 July 2003

be easily distinguished from other instars by means of the width of cranium ranging from 1.00 to 1.21 mm (Fig. 10). In the laboratory, larvae grow up during about 3 days damaging on average 3 cm^2 leaf area of *P. nigra* var. *italica* (Tables 8 and 9, Fig. 12). Frass pellets defecated by larvae of the 2nd instar are well visible by naked eye. Their average dimensions are 1.1 × 0.4 mm (in growing up larvae 1.2 × 0.45 mm) (Table 10). Larvae produce on average 84 frass pellets of a total volume of 14.3 mm^3 (Table 11, Fig. 13). During the best part of their life they live gregariously, later in smaller groups, rarely also separately (Fig. 14). Older leaves are skeletonized by larvae from the abaxial face, younger leaves are sometimes also perforated. Lateral veins are mostly undamaged (Fig. 15). Grown up larvae of the 2nd instar (Fig. 16) moult on the abaxial face of leaves. In the laboratory, larvae attach to a bed by sticky secretion after the termination of ingest already after 2 to 3 hours and after next 20 minutes they moult. The actual ecdysis takes on average 10 minutes.

Newly moulted larvae of the 3rd (i.e. last) instar persist 1 to 3 hours in exuviae of larvae of the 2nd instar by the body end. Only then, larvae quite leave exuviae and prepare for feeding. Based on laboratory studies, larvae of the 3rd instar begin to ingest only 8 to 12 hours after the cessation of feeding of grown up larvae of the 2nd instar. Larvae of the last instar are 7 to 16 mm long (Figs. 16 and 17). Their cranium is 1.50 to 1.86 mm wide (Fig. 10). They live on average 4.5 days, i.e. 2.2 times longer than larvae of the 1st instar and 1.5 times longer than larvae of the 2nd instar. During the time, they damage on average 17.3 cm^2 leaves of *P. nigra* var. *italica* (Tables 8 and 9, Fig. 12). Larvae of the 3rd instar damage on average 28.8 times larger leaf area than larvae of the 1st instar and 5.8 times larger leaf area than larvae of the

Table 10. Average length, width and volume of frass pellets of larvae of the 1st to the 3rd instar of *C. populi* during feeding on leaves of 2-year-old shoots and leaves of coppice shoots of *P. nigra* var. *italica*. Dimensions and volume of frass pellets of growing up larvae of respective instars (in parenthesis). Laboratory examination, 2003 to 2005

Instar	Leaves of 2-year shoots		Leaves of coppice shoots	
	average length/width (mm)	average volume (mm^3)	average length/width (mm)	average volume (mm^3)
1st	0.36/0.18	0.01	0.38/0.19 (0.51/0.21)	0.01 (0.02)
2nd	1.07/0.36	0.11	1.11/0.41 (1.21/0.45)	0.15 (0.19)
3rd	1.50/0.64	0.48	2.32/0.75 (2.14/0.68)	1.02 (0.78)

Table 11. Average number and average volume of frass pellets of larvae of the 1st to the 3rd instar of *C. populi* on leaves of coppice shoots of *P. nigra* var. *italica*. Average volume of one frass pellet of the 1st instar is 0.015 mm^3, of the 2nd instar 0.17 mm^3 and of the the 3rd instar 0.9 mm^3. Laboratory examination, 2003

Instar	Period of rearing		Average				Average number of frass pellets/ 1 cm^2	Average volume of frass pellets/ 1 cm^2
	30. 6.–13. 7.	1. 7.–13. 7.	number of frass pellets	(%)	volume (mm^3)	(%)		
1st	75	80	77	26.2	1.1	0.8	138	2.0
2nd	84	84	84	28.6	14.3	10.5	26	4.4
3rd	128	139	134	45.2	120.3	88.7	8	7.4
Total	287	303	295	100.0	135.7	100.0	(14.8)	(6.8)

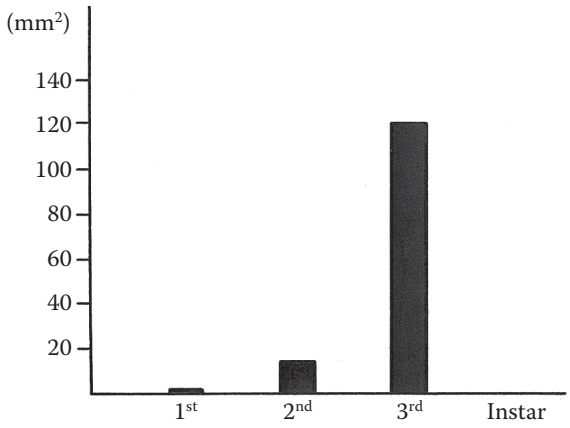

Fig. 13. Average volume of frass pellets produced by larvae of particular instars of *C. populi* during feeding on leaves of *P. nigra* var. *italica*. Laboratory examination, 30 June–13 July 2003

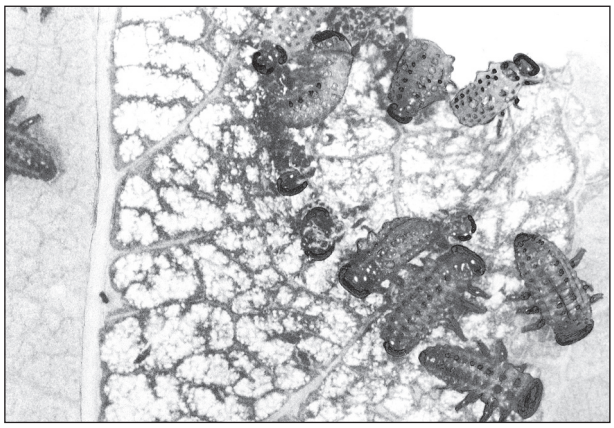

Fig. 14. Larvae of the 2nd instar of *C. populi* (including several exuviae of larvae of the 1st instar) during feeding on the abaxial face of leaves of *P. nigra* var. *italica*. Laboratory rearing, 18 May 2003

2nd instar. On nutritionally suitable coppice shoot leaves of *P. nigra* var. *italica*, they defecate frass pellets of an average size of 2.3 × 0.75 mm. On nutritionally suboptimal leaves of 2-year- old shoots of the poplar, they defecate frass pellets of a size of mere 1.5 × 0.64 mm. Unlike both previous instars, frass pellets of growing up larvae of the 3rd instar are on average always smaller (Table 10). Larvae of the 3rd instar defecate on average 134 frass pellets of a total volume of 120.3 mm^3 (Table 11, Fig. 13). Leaves are as a rule perforated or laterally browsed (Fig. 18).

Larvae of the 1st generation of *C. populi* occur in nature roughly from mid-May to mid-July. They develop quickly and already during 2 weeks (in the laboratory during about 10 days) they grow up. Within the period, they damage on average 20 cm^2 leaves of *P. nigra* var. *italica* and produce about 300 frass pellets of a total volume of 136 mm^3. During their development, the size of a damaged leaf area increases every day (Fig. 19). It is of interest that the average consumption of food and mortality of larvae are also dependent on the number of larvae

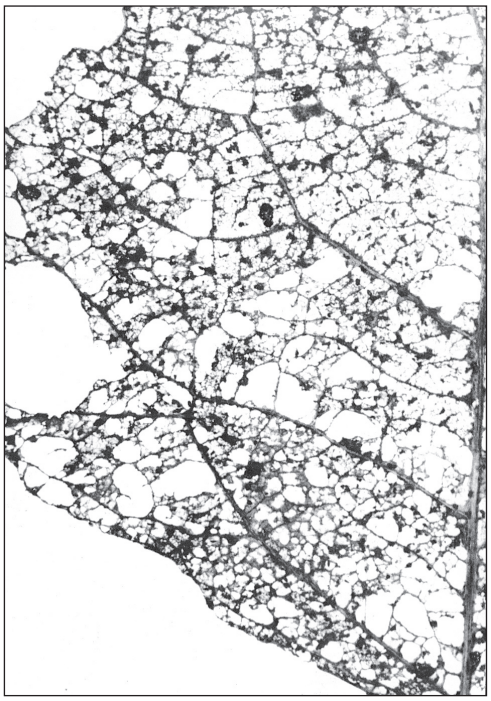

Fig. 15. Defoliation of *P. nigra* var. *italica* caused by larvae of the 2nd instar of *C. populi*. Laboratory rearing, 3 June 2003

Fig. 16. A grown up larva of the 2nd instar and a young larva of the 3rd instar of *C. populi* (before the beginning of feeding) on the abaxial face of a leaf of *P. nigra* var. *italica*. Laboratory rearing, 28 May 2003

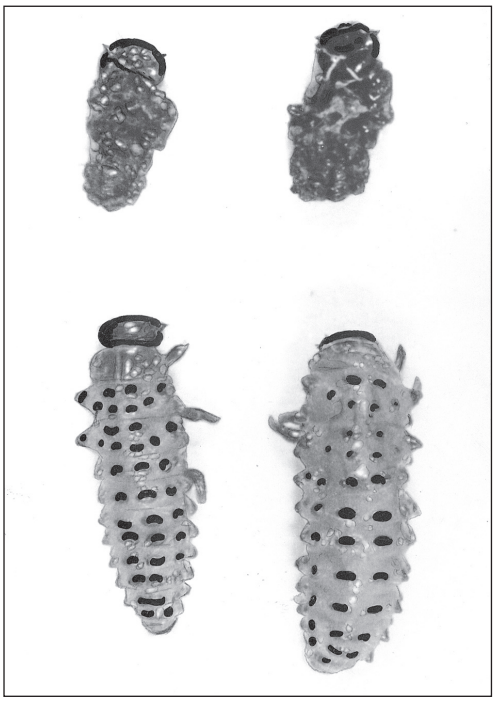

Fig. 17. A growing up and a grown up larva the 3rd instar of *C. populi* (including an exuvia)

Fig. 18. A growing up larva of the 3rd instar of *C. populi* during feeding on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 28 May 2003

in a group. Through laboratory studies it has been demonstrated that the highest average consumption of food occurs in larvae developing in 21 to 30-member groups. The smallest average consumption show larvae in the least numerous groups (up to 10 larvae) (Fig. 20). Nevertheless, this fact is not surprising at all. The gregariousness of larvae significantly increases the defence of individuals by the cumulative effect of toxins in secretions of dorsal glands. Mutual contacts inhibit the movement of larvae significantly supporting their feeding. It is similar as in other socially living larvae of Chrysomelidae (e.g. in *Plagiodera versicolora* /Laich./, *Phratora vitellinae* /L./, etc.). The time behaviour of feeding and defecation are described in more detail in larvae of the 2nd generation.

Grown up larvae of *C. populi* empty the content of their digestive system within 10 hours after the cessation of food intake. After next ca. 6 hours, they attach by the end of their abdomen to the abaxial face of leaves by means of yellowish secretion (Fig. 21). According to Schaufuss (1916), larvae settle nearby a central leaf vein. The period of prepupa takes in the laboratory about 2 days and then pupae hatch

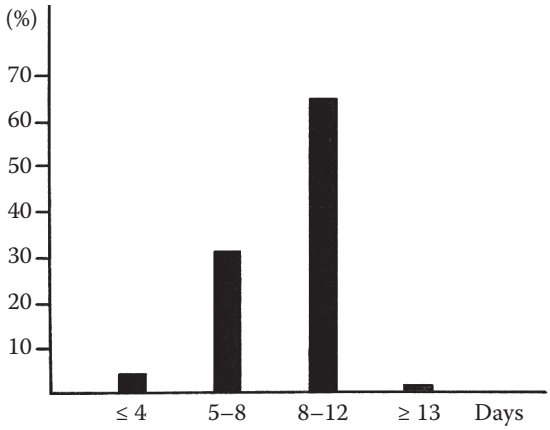

Fig. 19. Increase in the damage to leaves of *P. nigra* var. *italica* by *C. populi* during their development (% of the total damage to a leaf area). Laboratory examination, June, 2004

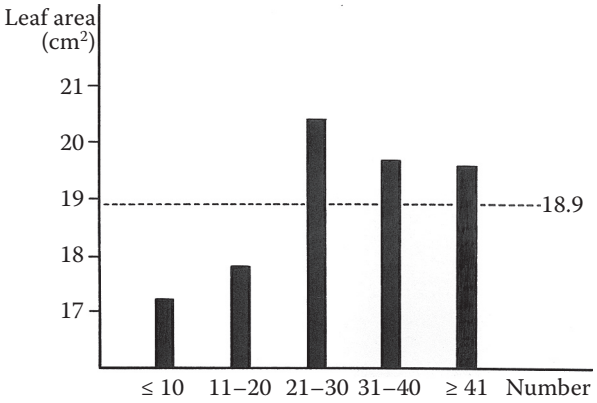

Fig. 20. Average area of leaves of *P. nigra* var. *italica* damaged by larvae of *C. populi* in relation to the number of larvae in a group. Dash line depicts the total average area of leaves damaged by one larva. Laboratory examination, 2004

Fig. 21. A prepupa of *C. populi* on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 28 May 2003

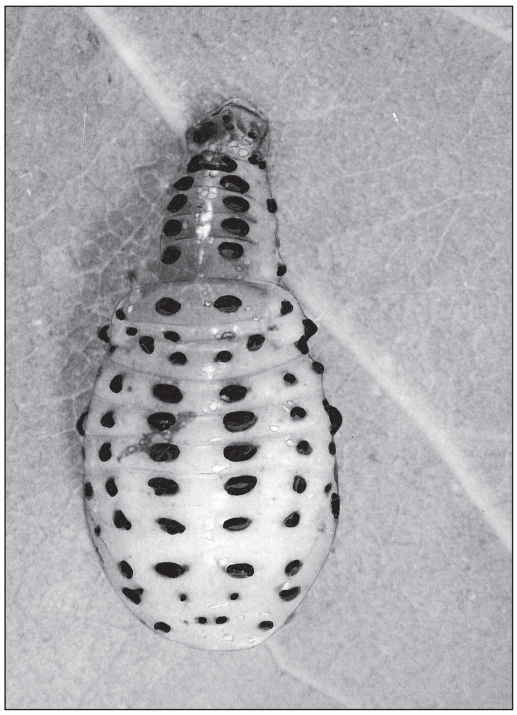

Fig. 22. A pupa of *C. populi* on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 28 May 2003

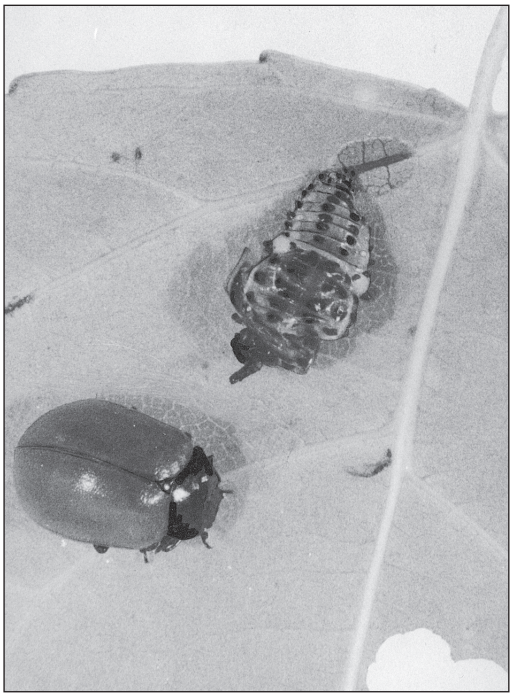

Fig. 23. A newly coloured imago of *C. populi* soon after leaving a pupal exuvia on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 3 June 2003

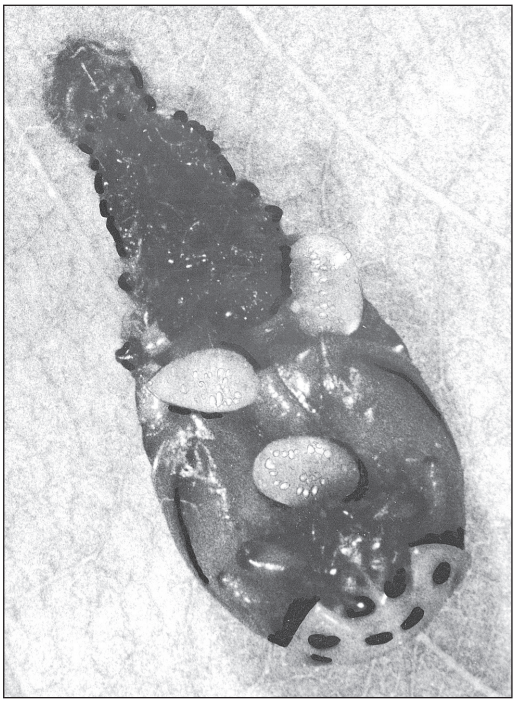

Fig. 24. The ventral side of a dead pupa of *C. populi* with growing up larvae of *Schizonotus sieboldi* on the abaxial face of a leaf of *P. nigra* var. *italica*. Brno-Královo Pole, 3 June 2003

(Fig. 22). Pupae are firmly fixed to the larval exuvia by lateral projections of the 7th abdomen segment. The pupal stage takes in the laboratory only 4 days. The first beetles occur in nature at the beginning of June (in the laboratory already at the end of May) (Fig. 23).

According to Henschel (1895), Nüsslin and Rhumbler (1922), Escherich (1923), Živojinovič (1948), Gäbler (1955), Maisner (1974), etc. larvae of *C. populi* develop about 3 weeks, according to Schaufuss (1916) only 2.5 weeks. Loi (1970) mentions that larvae develop 2 to 5 weeks depending on a

Table 12. Results of rearings of the 1st and the 2nd generation of imagoes of *C. populi* on growing up leaves of *P. nigra* var. *italica*. Imagoes were reared in the laboratory from the stage of eggs (or from growing up larvae of the 2nd instar – see a column marked *). Laboratory examination, 2003

Average	Date of hatching and number of ♂♂/♀♀					
	18. 6. 1/1	21. 6.* 4/2	25. 6. 2/8	15. 7. 7/3	17. 7. 5/–	17. 7. –/5
Period of life of females (days)	316	45	133	134	–	258
Number of eggs	52	845	–	461	–	206
Damaged area (cm^2)	94.9	109.0	72.6	116.7	87.6	122.8
Number of frass pellets	456	407	290	659	733	751
Number of frass pellets/cm^2	4.8	3.7	4.0	5.6	8.4	6.1

temperature and photoperiod, Vasiljev et al. (1974) 16 to 20 days, Damanabi et al. (1977) 15 to 20 days and Chandel and Verma (1998) 12 to 19 days. At an average temperature of 19°C, larvae grow up within 18.5 days and at a constant temperature of 25°C already after 7 days (Plavšić 1958). Loi and Belcari (1983) mention that larvae finish their development within the limits of 13 to 29°C and pupae 13 to 31°C. According to our findings, larvae of the 1st instar are most sensitive to low temperatures. At outside temperatures 5 to 10°C, they ingest only minimally and soon die. On the other hand, larvae of the 3rd instar tolerate temperatures 5 to 10°C quite well and successfuly survive even morning frosts up to –7°C.

Literature data on the period of the pupal stage differ, however, considerably. The majority of older authors (e.g. Escherich 1923) mentions 10 days, Maisner (1974) 6 to 10 days, Živojinovič (1948) 15 days and Chandel and Verma (1998) 7 to 16 days. According to Plavšić (1958) the pupal stage takes on average 10.5 days at 19°C, at 25°C only 5.5 days.

In the region of central and southern Moravia, *C. populi* develops (from egg laying to hatching imagoes) about 1 month (in the laboratory about 21 days). On the other hand, Escherich (1923) mentions that the total period of development amounts to 39 to 43 days, Maisner (1974) 35 to 45 days, Damanabi et al. (1977) 27 to 32 days, Chandel and Verma (1998) 24 to 50 days and Loi (1970) 22 to 51 days. According to Plavšić (1958) the development takes about 40 days at a temperature of 19°C and at a constant temperature of 25°C about 19 days. The development of larvae from hatching from eggs to hatching imagoes takes 17 to 21 days at 24°C and 65% relative air humidity (Zeki, Toros 1992).

Development of other generations

In the region of southern and central Moravia, imagoes of the 1st generation occur on host species from June to September (in the laboratory from the end of May to mid-September) (Fig. 3). They feed intensively on young leaves and during the maturation feeding they mature. They mate first after 10 days of feeding, according to Scheidter (1926) only after 13 days of feeding. After next 1 to 3 days (according to Scheidter 1926 after other 3 days) they lay their first eggs. These non-diapausing imagoes laid intensively eggs in the laboratory and after finishing their reproduction they mostly (80%) died even in the same year (Table 12 columns 2 and 4, Table 13). Males lived 35 to 125 days, females 45 to 134 days. At the same time, they damaged on average 113 cm^2 leaves of *P. nigra* var. *italica* and produced on average 553 frass pellets. Females deposited on average 653 (maximally 893) eggs. According to literature

Table 13. Average weekly area of leaves of *P. nigra* var. *italica* damaged by the 1st generation of imagoes of *C. populi* (including the average number of frass pellets and laid eggs). Results of rearings of 4 males and 2 females hatched on 21. 6. 2003 are given in a numerator, results of rearings of 7 males and 3 females hatched on 15. 7. 2003 are given in a denominator. In the first case, imagoes were reared from growing up larvae of the 2nd instar, in the second case from eggs taken from nature. Laboratory examination, 2003

Week No.	Average damaged area (cm^2)	Average number of frass pellets	Average number of eggs
1	24.5/33.1	70/156	–/135
2	21.0/10.4	92/55	44/118
3	14.8/16.6	42/86	276/86
4	18.0/30.1	75/168	262/103
5	20.3/13.5	83/93	128/19
6	7.1/6.9	37/53	99/–
7	3.3/4.7	8/33	36/–
8	–/0.6	–/6	–
9	–/0.6	–/6	–
10	–/0.2	0/3	–
Total	109.0/116.7	407/659	845/461

Table 14. Average weekly area of leaves of *P. nigra* var. *italica* damaged by the 1st generation of imagoes of *C. populi* (including the average weekly number of frass pellets and laid eggs). Results of the rearing of 1 male and 1 female are given in a nominator, results of the rearing of 2 males and 8 females in a denominator. Imagoes were reared from eggs obtained from nature. Laboratory examination, 2003

Week (from–to)	Average damaged area (cm^2)	Average number of frass pellets	Average number of eggs
25. 6.–1. 7.	39.5/31.2	111/107	–
2.–8. 7.	10.0/18.2	74/33	–
9.–15. 7.	12.3/1.6	50/10	17/–
16.–22. 7.	4.0/2.3	23/17	23/–
23.–29. 7.	4.5/6.4	32/50	12/–
30. 7.–5. 8.	3.5/2.9	43/20	–
6.–12. 8.	7.9/6.2	44/32	–
13.–19. 8.	10.7/3.4	55/18	–
20.–26. 8.	2.5/0.4	24/3	–
27.8.–2. 9.	–	–	–
Total	94.9/72.6	456/290	52/–

data the fecundity of females of the 1st generation was higher than that of females of a wintering generation, viz on average by 147 eggs.

At a high temperature (24 to 28°C) occurring in the second half of June and in July 2003, considerable part of females took intensively food for the period of the first 2 to 3 weeks. However, the females laid eggs only minimally or not at all (Table 12 columns 1 and 3, Table 14). At the beginning of October 2003, these diapausing imagoes were displaced to outside conditions. About 50% imagoes experienced the end of April of the next year when imagoes were converted again to laboratory rearings. Males lived 55 to 255 days, females 133 to 316 days. In 2003, they damaged on average 84 cm^2 leaves of *P. nigra* var. *italica* and produced on average 358 frass pellets. A summer diapause (gradually changing to a winter diapause) was probably induced by above-mentioned high temperatures or increased relative air humidity inside breeding glass vessels and perhaps also by nutrition through physiologically older leaves.

Imagoes of *C. populi* are demanding for food quality at least in the same way as larvae. They quite refuse newly unfolding leaves of *P. nigra* var. *italica* and consume only growing up leaves or newly grown up leaves. By means of comparative rearings of the 1st generation of imagoes grown from eggs obtained in Brno-Královo Pole on 31 May 2004 it was demonstrated that growing up leaves (the 3rd to the 4th leaf from the top) were more suitable for the nutrition of imagoes than newly grown up leaves (the 5th to the 7th leaf from the top). When feeding by growing up leaves imagoes (sex ratio 1:1) damaged on average 118 cm^2 and laid 372.2 eggs. When feeding by newly grown up leaves imagoes (sex ratio 1:1) damaged on average only 88 cm^2 (i.e. 25.4% less) and laid 213.2 eggs (i.e. 42.6% less) (Table 15). Imagoes consuming growing up leaves lived on average 45.3 days (males on average 49 days, females on average 41.6 days). Imagoes consuming newly grown up leaves lived on average only 39.4 days (males on average 41.3 days, females on average 37.6 days), i.e. on average by 5.9 days (13%) less.

Imagoes of the 1st generation of *C. populi* (sex ratio 1:1) grown from eggs laid by females of the wintering generation consumed on average 2 times smaller amount of food than imagoes grown from

Table 15. Average weekly area of growing up (A) and newly unfolding leaves of *P. nigra* var. *italica* (B) damaged by the 1st generation of imagoes of *C. populi* (including the average weekly number of laid eggs). Imagoes were reared from eggs obtained in nature on 31 May 2004. In rearings A and B, the same number of imagoes (10 males and 10 females) was observed. Laboratory examination, 2004

Week (from–to)	A. Growing up leaves (the 3rd to the 4th leaf from the top)		B. Newly grown up leaves (the 5th to the 7th leaf from the top)	
	average damaged area (cm^2)	average number of eggs	average damaged area (cm^2)	average number of eggs
17.–23. 6.	23.5	–	22.4	–
24.–30. 6.	18.0	–	17.6	–
1.–7. 7.	19.5	120.0	16.4	96.8
8.–14. 7.	22.5	149.9	19.7	74.0
15.–21. 7.	15.5	73.6	8.8	42.4
22.–28. 7.	14.7	23.1	2.8	–
29.7.–4. 8.	4.0	4.6	0.3	–
5.–9. 8.	0.1	–	–	–
Total	118.0	371.2	88.0	213.2

Table 16. Average area of younger and older leaves of *P. nigra* var. *italica* damaged by the 1st generation of imagoes of *C. populi* (including the average number of laid eggs and the average period of life). Imagoes (sex ratio 1:1) were reared from eggs laid in the laboratory. Laboratory examination, 28 June–5 August 2004

Leaves	Rearing No.	Number of ♂♂/♀♀	Average damaged area (cm^2)	Average number of eggs	Average period of life of ♂♂/♀♀ (days)
Younger (the 3rd to the 4th leaf from the top)	1	4/5	41.2	60.0	26/24
	2	1/–	49.5	–	35/–
	3	8/2	57.8	105.0	28/34
	4	4/6	54.8	45.0	33/23
	5	–/2	105.0	27.5	–/46
	Mean	17/15	54.9	55.7	29/27
Older (the 5th to the 7th leaf from the top)	1	7/9	35.0	6.6	28/24
	2	2/–	48.0	–	23/–
	3	8/8	51.9	40.8	30/26
	4	4/3	40.9	15.7	27/19
	5	11/11	43.6	29.9	24/27
	Mean	32/31	43.4	24.6	27/25

eggs obtained in nature (Table 16). On growing up leaves of *P. nigra* var. *italica*, they damaged on average 54.9 cm^2 and laid on average 55.7 eggs. On newly grown up leaves, they damaged on average only 43.4 cm^2 (i.e. 20.9% less) and laid on average 24.6 eggs (i.e. 55.8% less). Imagoes feeding on growing up leaves lived about 28 days (males 29 days, females 27 days). Imagoes feeding on newly grown up leaves lived on average only 26 days (males 27 days, females 25 days), i.e. on average by 2 days (7.1%) less.

Larvae of the 2nd generation hatched from eggs laid by females of the 1st generation damaged 0.5 to 3.5 (on average 2) cm^2 smaller leaf area than larvae of the 1st generation (Table 9). Their development was shorter by 0.8 to 1.5 (on average 1.2) days (Table 8). It was found that larvae did not took food continually but in certain time intervals broken by rest. The number and period of stages of feeding and rest are dependent not only on the instar of larvae but also on their age within the same instar. For example, younger larvae of the 2nd instar of the 2nd generation ate on average 10 times and 10 times were at rest in the course of 12 hours of the daytime (from 6 am to 6 pm). The stage of feeding took on average 9 min (12.7% of the time) and the stage of rest 62 min (87.3% of the time). Older larvae of the 2nd instar ate only 7 times during 12 hours of the daytime, namely on average 21 min (21.6% of the time) and 76 min (78.4% of the time) were at rest. Young larvae of the 3rd instar ate from 6 am to 6 pm in total 17 times for a period of 11 min, moderately old larvae 12 times for a period of 17 min and growing up larvae only 5 times for a period of 31 min. Young larvae of the 3rd instar spent during feeding on average 26.2% of the time, moderately old larvae 28.8% of the time and growing up larvae 22.3% of the time. Larvae of the 2nd instar spent during feeding on average 17.1% of the time and larvae of the 3rd instar 25.8% of the time (Table 17). Larvae ingest also during the dark part of the day (from 6 p.m. to 6 a.m.). For example, larvae of the 3rd instar of the 2nd generation spent on average 22.3% of the time during feeding (younger larvae about 19%, moderately old larvae about 26% and growing up larvae about 22% of the time).

Indigested remains of food are always secreted only in the period of rest. For example, larvae of the

Table 17. Characteristics of feeding of larvae of the 2nd and the 3rd instar of the 2nd generation of *C. populi* on *P. nigra* var. *italica* during the light part of the day (from 6 a.m. to 6 p.m.). Laboratory examination, 27–31 August 2004

Average	2nd instar		3rd instar		
	younger	older	young	medium old	growing up
Number of stages of feeding and rest	10	7	17	12	5
Period of the stage of feeding (min/%)	9/12.7	21/21.6	11/26.2	17/28.8	31/22.3
Period of the stage of rest (min/%)	62/87.3	76/78.4	31/73.8	42/71.2	108/77.7
Number of frass pellets during the stage of rest	1.9	2.7	1.6	2.9	5.2
Number of frass pellets before metamorphoses	–	4.0	–	–	11.0

Table 18. Average weekly area of leaves of *P. nigra* var. *italica* damaged by male imagoes (numerator) and female imagoes of the 2nd generation of *C. populi* (denominator) (including the average weekly number and the volume of frass pellets and the weekly number of laid eggs). Examined imagoes (5 males and 5 females) were reared from eggs laid in the laboratory. The average volume of a male frass pellet amounted to 0.61 mm^3, that of a female frass pellet 0.95 mm^3. Laboratory examination, 2003

Week (from–to)	Average damaged area (cm^2)	Average number of frass pellets	Average volume of frass pellets (mm^3)	Average number of laid eggs
	♂♂/♀♀	♂♂/♀♀	♂♂/♀♀	
18.–24. 7.	20.0/27.2	131/124	80.0/117.8	–
25.–31. 7.	9.3/14.9	63/84	38.4/80.2	2.4
1.–7. 8.	10.4/19.8	115/117	69.9/111.5	45.2
8.–14. 8.	16.8/15.1	139/112	84.9/106.0	62.0
15.–21. 8.	18.8/19.4	141/117	86.4/111.0	53.4
22.–28. 8.	8.0/12.6	77/81	46.9/76.8	36.8
29.8.–4. 9.	1.9/8.0	41/65	25.0/61.9	4.2
5.–11. 9.	2.4/5.2	26/44	15.9/41.4	–
12.–18. 9.	–/0.6	–/7	–/6.7	1.6
19.–25. 9.	–	–	–	–
Total	87.6/122.8	733/751	447.4/713.3	205.6

Table 19. Average weekly area of leaves of *P. nigra* var. *italica* damaged by imagoes of the 2nd generation of *C. populi* (including the average weekly number of laid eggs). In rearing A, 15 males and 15 females reared in the laboratory from one group of eggs were used. In rearing B, the same number of imagoes reared from 4 groups of eggs of 4 different females was used. On 31. 12. 2004, some 10% imagoes lived which were put into outside conditions. Half of them experienced the end of April and was transferred to laboratory rearings. Laboratory examination, 2004

Week (from–to)	Rearing A		Rearing B	
	average area (cm^2)	average number of eggs	average area (cm^2)	average number of eggs
20.–26. 8.	34.5	–	27.1	–
27. 8.–2. 9.	8.4	6.6	19.0	–
3.–9. 9.	8.9	92.1	11.9	43.0
10.–16. 9.	11.1	51.1	12.1	36.3
17.–23. 9.	8.1	51.5	7.7	16.1
24.–30. 9.	3.7	19.7	4.3	15.3
1.–7. 10.	2.3	17.7	2.9	11.8
8.–14. 10.	1.6	10.0	1.9	2.2
15.–21. 10.	0.3	–	–	–
22.–28. 10.	–	–	–	–
29.10.–4. 11.	–	–	0.7	2.7
5.–11. 11.	–	–	–	–
12.–18. 11.	0.3	–	–	–
19.–25. 11.	1.6	–	–	–
26.11.–2. 12.	2.5	4.2	–	–
3.–9. 12.	2.3	–	0.5	–
10.–16. 12.	0.9	–	–	–
17.–23. 12.	0.2	–	–	–
24.–30. 12.	–	–	–	–
≥ 31. 12	–	–	–	–
Total	86.7	252.9	88.1	127.4
Days of life	15 ♂♂ 31–187(90) 15 ♀♀ 28–239(81)		15 ♂♂ 28–103(53) 15 ♀♀ 22–308(98)	

Table 20. Daily (24 hour) and average weekly number of copulations of imagoes of the 2nd generation of *C. populi*. The period of copulation including the hour of egg laying and the number of laid eggs were also monitored. Laboratory examination, 2004

Evaluated characteristic	Date of observation							Average
	16. 9.	17. 9.	18. 9.	19. 9.	20. 9.	21. 9.	22. 9.	
Number of copulations per day (24 hours)	8	9	10	9	6	9	9	8.7
Period of one copulation (from–to) (min)	4–43	10–450	3–40	15–75	30–420	5–21	4–40	3–450
Average period of copulation (min)	20	63	15	41	119	17	13	41
Total period of copulation (min) and %	160/11	570/40	146/10	367/25	714/50	150/10	120/8	318/22
Time of laying eggs	–	6.00–6.40	–	7.50–8.25	18.00–18.35	22.00–22.40	–	–
Number of laid eggs	–	54	–	54	56	55	–	

2nd instar of the 2nd generation secreted 1 to 6 (on average 2.3) frass pellets during particular stages of rest and larvae of the 3rd instar 0 to 9 (on average 3.2) frass pellets. In the course of growth of the actual instar, the number of defecated frass pellets increases. The highest number of frass pellets is defecated by larvae before moulting or pupation. For example, larvae of the 2nd instar excrete on average 4 frass pellets before ecdysis and larvae of the 3rd instar even 11 frass pellets. The feeding of larvae is more intensive throughout a day than during a night which is manifested both in the size of a damaged leaf area and in the number of defecated frass pellets. For example, younger larvae of the 3rd instar excreted during the daytime (from 6 a.m. to 6 p.m.) on average 78 frass pellets and during the dark part of the day (from 6 p.m. to 6 a.m.) on average 55 frass pellets (i.e. 29.5% less). Moderately old larvae excreted during the daytime on average 63 frass pellets and during the dark part of the day on average 52 frass pellets (i.e. 17.5% less).

Under conditions of southern and central Moravia, beetles of the 2nd generation occur on trees from July to the end of the growing season. While early-hatching beetles reproduce (after maturation feeding) even in the same year later-hatching beetles leave for wintering places and reproduce as late as the next year. Beetles of the 2nd generation (hatched on 18. 7. 2003) reproduced in the laboratory only rarely and after the cessation of feeding they left for wintering places during the 1st half of September (Table 18). After translocation to outdoor conditions, males lived on average 219 days and females 258 days. Part of beetles of the 2nd generation hatched on 20. 8. 2004 reproduced in captivity even in the same year. However, average leaf area damaged by the beetles and the number of laid eggs were substandard. Only the minority part of the beetles experienced the year 2005 (Table 19). Survived females laid unfertilized eggs at the end of April and in May. Obviously only females entering a diapause after maturation feeding in 2004 experienced 2005.

Through laboratory rearings of *C. populi* from eggs of the same clutch, it was found that there was a moderate protogyny in hatching imagoes. Imagoes hatched during a 2.5-day period. While in the 1st third of the period some 80% females hatched, in the 2nd third of the period the sex ratio was balanced (1:1) and in the 3rd third some 80% males hatched.

Interesting results were obtained by the continual 7-day monitoring of sexual activities and egg laying in imagoes of the 2nd generation of *C. populi* (Table 20). During the period, imagoes copulated every day (i.e. in the course of 24 hours) 6 to 10 times (on average 8.7 times). One copulation took 3 to 450 minutes (on average 41 minutes). Every day, beetles copulated on average 318 minutes (i.e. 22% of the day). Throughout the life (i.e. during about 41 days of reproduction) they copulated on average 357 times. Nevertheless, according to sporadic literature data, the only copulation is sufficient to fertilize the whole production of eggs. Recently, however, Jodal et al. (1991) substantiate biological foundation of repeated copulation. According to the authors, part of females deposits sterile eggs already 11.5 days after the death of males.

Generation conditions of *C. populi* are rather complicated. Under favourable climatic/meteorological conditions, there are 3 generations (in the laboratory even 4 generations) in the Czech Republic throughout the year. However, a great deal of imagoes of the 2nd generation (particularly those which hatched

Table 21. Average weekly area of leaves of *P. nigra* var. *italica* damaged by imagoes of the 3rd generation of *C. populi* (including the average weekly number of laid eggs). Imagoes reared in the laboratory from eggs (obtained from females in captivity) were fed on leaves of coppice shoots or leaves of 2-year-old shoots. Laboratory examination, 2004

Week (from–to)	Leaves of coppice shoots					Leaves of 2-year-old shoots	
	5 ♂♂ + 5 ♀♀		5 ♂♂	7 ♀♀		5 ♂♂ + 5 ♀♀	
	average damaged area (cm^2)	average number of eggs	average damaged area (cm^2)	average damaged area (cm^2)	average number of eggs	average damaged area (cm^2)	average number of eggs
5.–11. 9.	35.9	–	22.4	33.3	–	22.3	–
12.–18. 9.	10.6	–	12.1	15.7	–	7.8	–
19.–25. 9.	0.2	–	0.9	0.3	–	–	–
26.9.–2. 10.	0.8	43.6	1.1	2.9	7.0	–	–
3.–9. 10.	4.5	10.4	2.4	2.9	6.0	1.9	–
10.–16. 10.	5.3	–	0.1	2.7	–	0.2	–
17.–23. 10.	2.2	–	–	2.0	–	0.5	8.4
24.–30. 10.	0.2	0.4	–	–	–	0.4	–
31.10.–6. 11.	0.2	–	–	0.4	–	–	–
7.–13. 11.	–	–	–	1.0	–	–	–
14.–20. 11.	–	–	–	3.4	6.0	–	–
21.–27. 11.	–	–	–	2.9	–	0.8	–
28.11.–4. 12.	–	–	–	1.7	–	1.3	8.4
5.–11. 12.	0.6	–	–	0.1	–	0.8	–
12.–18. 12.	1.1	–	–	0.6	–	0.2	–
19.–25. 12.	1.1	–	–	0.4	–	–	–
26.–31. 12.	1.1	–	–	–	–	0.1	–
Total	63.8	54.4	39.0	70.3	19.0	36.3	16.8

later) enters diapause after regeneration feeding. Thus, the 3rd generation is always incomplete under natural conditions of our country. In nature, imagoes of the 3rd generation occur in September or at the beginning of October. In the laboratory, small part of imagoes of the 3rd generation established the 4th generation (Table 21). Imagoes of this generation did not copulate and reproduced only after wintering (Fig. 3). Table 21 shows that male imagoes of the 3rd generation damage about 40 (female about 70) cm^2 leaves of *P. nigra* var. *italica* before leaving for wintering places.

According to the majority of literature sources, 2 (under favourable conditions 3) overlapping generations develop throughout the year. The possibility of developing only one generation within a year was mentioned, e.g. by Stark et al. (1951) or Damanabi et al. (1977). Under exceedingly favourable conditions, even 4 generations can occur in Transcaucasia within a year (Vasiljev et al. 1974). The chrysomelid shows the shortest development and lowest mortality at a temperature of about 19°C (Plavšić 1958). According to the author, high summer temperatures affect unfavourably the development and harmfulness of *C. populi.* Thus, with the autumn decrease of average daily temperatures in Serbia the harmfulness of *C. populi* increases again. Loi (1970) mentions the 3rd generation of *C. populi* in Italy and notes that only the 2nd generation of imagoes shows the normal period of maturation feeding after hatching. The 3rd generation is always incomplete and allegedly also undernourished and unable to survive the critical period of winter.

Natural enemies

At examined localities in Moravia, larvae of an ovoviviparous tachina fly *Cleonice* (= *Steiniella*) *callida* Meig. (Tachinidae) often occurred in grown up larvae of the 3rd instar of *C. populi* prepared for pupation. It refers to a Eurosiberian species parasiting on *C. populi*, more rarely on *C. saliceti* (Ws.) and *C. vigintipunctata* (Scop.) (Tschorsnig, Herting 1994). The tachina fly deposits one or several eggs on its victim. Larvae hatch immediately from the eggs and bore into the victim body. In the host, always the only larva develops (cannibalism) during 2 or 3 weeks. Larvae left their hosts in the 1st half of

June and pupated in the attached moistened cotton wool. In Brno-Královo Pole, the tachina fly killed about 20% larvae of the 1st generation of *C. populi* in 2004.

The polyvoltine chalcid *Schizonotus sieboldi* (Ratz.) (Pteromalidae) ranks among the most important parasitoids of *C. populi*. It is a quite common pupal parasitoid of chrysomelids living on willows and poplars (Nikolskaja 1952). In the CR, it often attacks also *C. tremulae* F., *C. vigintipunctata* (Scop.) and *Plagiodera versicolora* (Laich.) (Urban 1998a,b, 2005). Females deposit their eggs on the ventral side of pupae which were previously paralyzed by a secretion injected into the body of their victim by means of an ovipositor. Larvae hatch from the eggs growing up during less than 2 weeks. They pupate in the place of their development, i.e. under the protection of bases of wings and other body appendages of parasitized pupae. In Brno-Královo Pole, the chalcid killed about 40% pupae of the 1st generation of *C. populi* in 2004. For example in Turkey, the chalcid attacked 14 to 93% pupae (Zeki, Toros 1990).

Harmfulness

C. populi is one of the most important pests of poplars and more rarely also willows. Its harmful occurrence is known nearly in all countries of Europe including the European part of the former USSR (Březina 1927; Stark et al. 1951; Györfi 1952; Charvát, Čapek 1954; Georgijević et al. 1961; Gusev, Rimskij-Korsakov 1961; Timčenko, Treml 1963; Nogueira, Ferreira 1968; Loi 1970; Uteberg, Olsson 1978; Attard 1979; Goidanich 1983; Sidor, Jodal 1986; Penev, Ovčarov 1992; Glavas et al. 1997; Georgiev 2000; Sabatti et al. 2000, etc.). It causes important economic damages also in Turkey (Kasap 1988; Zeki, Toros 1992, 1996; Aslan, Ozbek 1999), Iran (Damanabi et al. 1977), India (Khan, Ahmad 1991; Thakur 1999) and in some other Asian countries. In Europe, *C. populi* is considered (however, quite sporadically) to be an abundant but unimportant species from economic aspects (Eckstein 1897; Warchałowski 1973).

C. populi damages most in well insolated forest nurseries, young natural advance regeneration and plantations including forest shelterbelts. Food quality and quantity appear to a limiting factor of its occurrence and development which are highest in spring. Food quality and its availability worsen during the growing season because the number of undamaged leaves on actively growing shoots rapidly decreases already from June (Raupp, Sadof 1991). In addition to the content of water, nutrients and tannins the quality of food is also affected by phenolic glucosides which are used by larvae of *C. populi* as a precursor of a defensive secretion. The chrysomelid damages mainly nutritionally rich, young and juicy leaves of some species of the genus *Populus.* Under conditions of suitable nutrition, larvae consume first preferred food and only after its destruction they also feed on less suitable food on commonly damaged or normally undamaged species (Augustin et al. 1992, 1993). Leaves of *Salix* spp. are not mostly nutritionally suitable for the nutrition of larvae and beetles due to their biochemical composition (particularly the low content of total nitrogen). Therefore, they are damaged much less (Edelman 1953). However, in spite of this opinion, there are numerous literature data on the considerable harmfulness of *C. populi* on willows (mainly in osier plantations) (see the introductory chapter). Our findings from the 8-year study of insect pests of osier plantations in Moravia, however, do not confirm the harmfulness of *C. populi.* In southern and central Moravia, beetles occur on trees from the end of April and at the beginning of May. For the period of 2 to 3 months, they intensively feed on newly unfolded leaves. After wintering, the beetles destroy 100 to 200 (on average 150) cm^2 leaves of *P. nigra* var. *italica*, i.e. on average 6.5 times more than *Plagiodera versicolora* (Laich.) and 5.3 times more than *Phratora vitellinae* (L.) on *Salix fragilis* L.

Some 14 days after the spring invasion of beetles to host species, the first larvae occur. They skeletonize leaves jointly from their abaxial face. Heavily damaged leaves look like leaves attacked by *Melampsora* spp. The leaves gradually brown and die. During a 2-week feeding, larvae damage on average 20 cm^2 leaves of *P. nigra* var. *italica* and grow up. Thus, the total average consumption of larvae is, therefore, 7.5 times lower than that of beetles and 7.1 times higher than that of larvae of *P. versicolora* and *P. vitellinae* on *S. fragilis.* With the transition of larvae to higher instars the effectiveness of using the food rapidly decreases (Table 11). The proportion of the average volume of frass pellets produced by larvae of the 1st, 2nd and 3rd instars from the damaged area of 1 cm^2 is 1:2.2:3.7. Similarly as other species of chrysomelids important from the viewpoint of forestry larvae damage mostly somewhat older leaves than beetles. It is logical that older leaves fulfilled their assimilation function for the most part than just grown up leaves. Thus, damage caused by imagoes is always more dangerous for host species.

From the 1st half of June, feeding of beetles of a wintering generation and larvae of the 1st generation is associated with this year's feeding of beetles of the 1st generation and subsequently also feeding of larvae of the 2nd generation. Under favourable conditions, part of beetles of the 2nd generation establishes the 3rd generation. Late-hatched beetles of the 2nd generation and beetles of the 3rd generation leave for wintering places after previous maturation feeding and reproduce only in the next year. Before leaving for wintering places, the beetles damage on average 40 to 70 cm^2 leaves of *P. nigra* var. *italica*. Beetles of the wintering generation destroy (before and after hibernation) in total 140 to 270 cm^2 leaves, i.e. on average 7.2 times more than *P. versicolora* on *S. fragilis*. In consequence of the long period of reproduction and rather rapid development of larvae and pupae, all developmental stages of the chrysomelid occur at the same time for the best part of the growing season and thus, it is sometimes very difficult to be acquainted with generation conditions.

C. populi is a pest with high gradation potential which reproduces frequently and then causes heavy feeding or even complete defoliation. Warm and dry spring and moderately warm summer markedly contribute to its activation. At the late unfolding of leaves starveling beetles can heavily damage buds of trees. In the course of gradation, beetles can browse even fine bark at the end of totally eaten annual shoots. Under conditions of mass occurrence the chrysomelid can prevent the development of planted cuttings and stand regeneration. Heavy feeding and complete defoliation cause undesirable branching of shoots and technical impairment of trees. The damage is related to indispensable losses in total and quality increment, insufficient lignification of annual shoots and their low frost resistance. Therefore, it is necessary to take into account preventive measures and in case of the serious damage to trees we have to control the chrysomelid.

Possibilities of protection and control

Particularly in former times, the collection of remarkable beetles of *C. populi* by sweep nets was recommended as well as shaking off the beetles into vessels or collection by means of various portable or mobile catching devices. It was also recommended to look for and kill larvae, pupae and eggs. In forest nurseries, imagoes were killed by raking up and burning leaf litter in the extra-vegetative period. Where it was technically realizable controlled long-term flooding was also used. In the 1st half of the 20th century, insecticides were used to control the chrysomelid on large areas (mainly arsenates, rarely nicotine and other preparations). After World War 2, a boom occurred in the use of preparations based on chlorinated hydrocarbons (particularly DDT and HCH). After their prohibition, an era followed of using organophosphate and other preparations. Roughly since the mid-80s of the last century, synthetic pyrethroids have been intensively introduced into the practical plant protection. These pyrethroids together with insecticides on the basis of acylurea (e.g. diflubenzurone) are the basis of chemical control of the pest.

References

ALLEGRO G., 1989. La difesa contro cli insetti parassiti del pioppo: un aggiornamento tecnico. Informàción Agraria, *45*: 93–96.

ARZONE A. et al., 1981. Further killing of bees in spring by spray in poplar groves. Apicoltore Moderno, *72*: 171–176.

ASLAN I., OZBEK H., 1999. Faunistic and systematic studies on the subfamily Chrysomelinae (Coleoptera, Chrysomelidae) in Artvin, Erzincan and Erzurum provinces of Turkey. Turkish Journal of Zoology, *23*: 751–767.

ATTARD G., 1979. Principales insectos del chopo en el sureste de Francia. Boletin del Servicio de Defensa contra Plagas e Inspeccion Fitopatologica, *5*: 25–29.

AUGUSTIN S., COURTIN C., DELPLANQUE A., 1992. Preferences of *Chrysomela* (= *Melasoma*) *populi* L. and *Chrysomela tremulae* F. (Col., Chrysomelidae) for *Leuce* section poplar clones. Journal of Applied Entomology, *115*: 370–378.

AUGUSTIN S., COURTIN C., DELPLANQUE A., 1993. Poplar clones effect on development, mortality, and fecundity of *Chrysomela* (= *Melasoma*) *populi* L. and *Chrysomela tremulae* F. (Col., Chrysomelidae). Journal of Applied Entomology, *116*: 39–49.

BELCARI A., LOI G., DAVIDSON J., 1983. Influence of temperature on the development of the egg of *Chrysomela populi* L. (Coleoptera, Chrysomelidae). Atti XIII. Congresso Nazionale Italiano di Entomologia: 661–667.

BLUNCK H. et al., 1954. Handbuch der Pflanzenkrankheiten. 5. Bd., 2. Teil. Berlin, Hamburg, P. Parey: 600.

BRÜCKMANN M., TERMONIA A., PASTEELS J.M., HARTMANN T., 2002. Characterization of an extracellular salicyl alcohol oxidase from larval defensive secretions of *Chrysomela populi* and *Phratora vitellinae* (Chrysomelina). Insect Biochemistry and Molecular Biology, *32*: 1517–1523.

BŘEZINA A., 1927. Ochrana lesů. Praha, Zemědělské knihkupectví, A. Neubert: 217.

CALWER C.G., 1876. Käferbuch. 4. Auflage. Stuttgart, J. Hoffman Verlag: 668.

CAVALCASELLE B., 1972. Pilot experiments for the control of insect pests of poplar in the nursery by means of

systemic insecticides in granular form. Celulosa e Carta, *23*: 17–25.

CHANDEL R.S., VERMA T.D., 1998. Bionomics of *Chrysomela populi* Linn. (Coleoptera: Chrysomelidae) in northwestern Himalaya. Annals of Forestry, *6*: 191–195.

CHARVÁT K., ČAPEK M., 1954. Škody spôsobené chrobákmi na topoľoch Žitného ostrova. Les, *9*: 20–28.

DAMANABI K., KAZEMI M.H., AKRAMI F., 1977. *Melasoma populi* L. (Col., Chrysomelidae). Entomologie et Phytopathologie Appliquees, *45*: 32–40.

DELLEDONNE M. et al., 2001. Transformation of white poplar (*Populus alba* L.) with a novel *Arabidopsis thaliana* cysteine proteinase inhibitor and analysis of insect pest resistance. Molecular Breeding, *7*: 35–42.

DŽANOKMEN K.A., 1978. Sem. Pteromalidae- Pteromalidy. In: MEDVEDEV G. et al., Opredelitel nasekomych evropejskoj časti SSSR. Tom 3, 2. časť. Leningrad, Izdateľstvo Nauka: 57–228.

ECKSTEIN K., 1897. Forstliche Zoologie. Berlin, Verlagsbuchh. P. Parey: 664.

EDELMAN N.M., 1953. Vlijanie kormovogo režima na razvitie neparnogo šelkoprjada (*Lymantria dispar* L.) i topolevych listoedov (*Melasoma populi* L. i *M. tremulae* F.). Entomologičeskoe Obozrenie, *33*: 36–46.

ESCHERICH K., 1923. Die Forstinsekten Mitteleuropas. Zweiter Bd. Erste Abt. Berlin, Verlagsbuchh. P. Parey: 663.

FIGO M.L., CABRAL M.T., 1964. Trials with high dosage of dusts for the control of *Melasoma populi*. Estudos e Informação Serviços Florestais e Aquícolas, Portugal, *204*: 11.

FLEISCHER A., 1927–1930. Přehled brouků fauny Československé republiky. Brno, Nákladem Moravského musea zemského: 483.

GÄBLER H., 1955. Forstschutz gegen Tiere. Radebeul, Berlin, Neumann Verlag: 368.

GE S.Q., YANG X.K., CUI J.Z., 2004. Comparative morphology of the mouthparts of Chrysomelinae (Coleoptera, Chrysomelidae). Acta Zootaxonomica Sinica, *29*: 423–429.

GEORGIEV G., 2000. Species composition and impact of the phytophagous insects on the poplars (*Populus* spp.) in Bulgaria. Nauka za Gorata, *37*: 45–54.

GEORGIJEVIĆ E., VACLAV V., 1958. Prilog poznavanju štetnih insekata lišćara NR Bosne i Hercegovine. Topola, *6*: 521–525.

GEORGIJEVIĆ E., FICE K., VACLAV V., 1961. Insect pest on soft-wooden broadleaved trees in Bosnia and Hercegovina. Radovi Šumarskog Fakulteta i Inst. Drvnu Industr. (Sarajevo), *6*: 153–170.

GLAVAS M., DIMINIC D., HRASOVEC B., MARGALETIC J., JURC M., 1997. Pests and diseases in Croatian forest nurseries recorded in 1996. Zbornik ob 50. obletnici obstoja in delovanja Gozdarskega instituta Slovenije, *1*: 245–252.

GOIDANICH G., 1983. Adverse factors affecting ornamental trees. Informatore Fitopatologico, *33*: 18–23.

GUSEV V.I., RIMSKIJ-KORSAKOV M.N., 1953. Klíč k určování škůdců lesních a okrasných stromů a keřů evropské části SSSR. Praha, SZN: 532.

GUSEV V.I., RIMSKIJ-KORSAKOV M.N., 1961. Lesnaja entomologija. Moskva, Leningrad, Goslesbumizdat: 486.

GYÖRFI J., 1952. Krankheiten und Schädlinge der Pappeln in Ungarn. Acta Agronomica Academiae Scientiarum Hungaricae, *2*: 41–79.

HAITLINGER R., 1999. *Linobia coccinellae* (Scopoli, 1763) (Acari: Astigmata: Hemisarcoptidae) a species new to the fauna of Poland, associated with *Chrysomela populi* L. (Coleoptera: Chrysomelidae: Chrysomelinae). Przegląd Zoologiczny, *43*: 181–182.

HELLÉN W. et al., 1939. Catalogus Coleopterorum Daniae et Fennoscandiae. Helsingforsiae, Societas Fauna et Flora Fennica: 129.

HENSCHEL A., 1895. Die schädlichen Forst- und Obstbaum-Insekten. Berlin, Verlag P. Parey: 758.

HWANG M.S., HA M.J., CHOI W.C., LEE C.E., 1992. Egg formation in panoistic ovary of *Chrysomela populi* and *Chrysochus chinensis* of Coleoptera. Nature and Life, *22*: 9–14.

JAVOREK V., 1947. Klíč k určování brouků ČSR. Olomouc, R. Promberger: 955.

JODAL I., 1985. Suzbijanje stetnih insekata – defolijatora topola preparatima na bazi diflubenzurona i carbofurana. Radovi, Institut za Topolarstvo (Novi Sad), *16*: 295–324.

JODAL I., AVRAMOVIĆ G., MARKOVIĆ A., 1991. Ocena nekih klonova topola sa aspekta važnijih pokazatelja razmnožavanja *Melasoma populi* L. (Col., Chrysomelidae). Radovi, Institut za Topolarstvo (Novi Sad), *23*: 53–66.

KADŁUBOWSKI W., CZALEJ B., 1962. Sklad gatunkowy i dynamika populacji chrząszczy występujących na plantacjach wikliny w powiecie Nowy Tomysl. Prace Komisji Nauk Rolniczych i Komisji Nauk Leśnych, *13*: 53–69.

KALTENBACH J.H., 1874. Die Pflanzenfeinde aus der Klasse der Insekten. Stuttgart, J. Hoffmann: 541–704.

KASAP H., 1988. A list of some Chrysomelinae (Col., Chrysomelidae) from Turkey. II. Turkiye Entomoloji Dergisi, *12*: 85–95.

KHAN M.A., AHMAD D., 1991. Comparative toxicity of some chlorinated hydrocarbon insecticides to poplar leaf beetle – *Chrysomela populi* L. (Coleoptera: Chrysomelidae). Indian Journal of Forestry, *14*: 42–45.

KOVAČEVIČ Ž., 1957. Die Probleme des Forstschutzes in Jugoslawien. Übersicht der wichtigsten Forstschädlinge. Anzeiger für Schädlingskunde, *30*: 55–58.

KUHNT P., 1913. Illustrierte Bestimmungstabellen der Käfer Deutschlands. Stuttgart, E. Schweizerbartische Verlagsbuchh.: 1139.

KUSEVSKA M., 1972. Morphological and bioecological studies of the poplar Tortricid (*Gypsonoma aceriana* Dup.). Godišnik, Šumarski Institut, Skopje, *7*: 107–208.

LEE J.E., 1996. Systematic study of Korean Chrysomelinae (Coleoptera: Chrysomelidae) by larval characters. Korean Journal of Entomology, *26*: 125–134.

LINDQVIST L., BLOCK M., 1997. Influence of life history and sex on metal accumulation in two beetle species (Insecta: Coleoptera). Bulletin of Environmental Contamination and Toxicology, *58*: 518–522.

LOI G., 1970. Biological notes on *Melasoma populi* L. (Col., Chrys.) in Tuscany. Frustula Entomologica, *9*: 57.

LOI G., BELCARI A., 1983. Temperature effects on the development of the immature stages of poplar leaf beetle, *Chrysomela populi* L. (Coleoptera, Chrysomelidae). Frustula Entomologica, *6*: 89–101.

LOPATIN J.K., 1960. Materialy po faune i ekologii žukov-listoedov (Coleoptera, Chrysomelidae) južnogo Zadneprovja. Entomologičeskoje Obozrenije, *39*: 629–642.

LOTFALIZADEH H., AHMADI A.A., 1998. New record of *Schizonotus sieboldi* Ratzeburg (Hym.: Pteromalidae), pupal parasitoid of poplar leaf beetle, *Chrysomela populi* L. (Col.: Chrysomelidae) from Iran. Applied Entomology and Phytopathology, *66*: 45.

MAISNER N., 1974. Chrysomelidae, Blattkäfer. In: SCHWENKE W. (ed.), Die Forstschädlinge Europas. 2. Bd. Hamburg, Berlin, Verlag P. Parey: 202–236.

MARIKOVSKAJA T.P., ŠTERBAKOVA T.I., 1989. Wasps in artificial breeding sites. Zaštita Rastenij, *6*: 29–31.

MATSUDA K., SUGAWARA F., 1980. Defensive secretion of chrysomelid larvae *Chrysomela vigintipunctata costella* (Marseul), *C. populi* L. and *Gastrolina depressa* Baly (Coleoptera: Chrysomelidae). Applied Entomology and Zoology, *15*: 316–320.

MEDVEDEV L.N., ŠAPIRO D.S., 1965. Sem. Chrysomelidae – listoedy. In: BEJ-BIENKO G.J., Opredelitel nasekomych evropejskoj časti SSSR. II. Moskva, Leningrad, Izdateľstvo Nauka: 419–474.

NEJEDLÝ J., 1946. Vrbařství z praxe pro praxi. Praha, Nákladem Ministerstva zemědělství republiky Československé: 152.

NEJEDLÝ J., 1950. Praktické vrbařství. Praha, Vydavatelství Brázda: 189.

NIKOLSKAJA M.N., 1952. Chalcidy fauny SSSR (Chalcidoidea). Moskva, Leningrad, Izdateľstvo AN SSSR: 574.

NOGUEIRA C.D.S., 1968. Pests of Poplar in nurseries an young plantations. Folhetos de Divulgacao Serviços Florestais e Aquícolas, Portugal, *7*: 14.

NOGUEIRA C.D.S., FERREIRA L.J.C., 1968. Pests of Poplar. Folhetos de Divulgacao Serviços Florestais e Aquícolas, Portugal, *5*: 32.

NÜSSLIN O., RHUMBLER L., 1922. Forstinsektenkunde. Berlin, Verlagsbuchh. P. Parey: 568.

ORECHOV D.A., GRIMALSKIJ V.I., LOZINSKIJ V.A., 1978. Ants- vectors of infection. Zaštita Rastenij, *9*: 25.

PASTEELS J.M., BRAEKMAN J.-C., DALOZE D., 1988. Chemical defence in the Chrysomelidae. In: JOLIVET P., PETITPIERRE E., HSIAO T.H. (eds.), Biology of Chrysomelidae. Dordrecht, Boston, London, Kluwer Academic Publisher: 233–252.

PENEV D., OVČAROV D., 1992. Proučvane vrchu biologijata na dvadesettočkovija listojad *Melasoma vigintipunctata* (Chrysomelidae, Coleoptera). Nauka za Gorata, *29*: 70–76.

PERNERSDORFER M., 1941. Untersuchungen über die Futterpflanzen einheimischer Chrysomeliden unter Ausschluss der Halticinen. Heidelberg, Verhandlungen des Naturhist.-Medizin. Vereins zu Heidelberg, *18*: 332–361.

PETTERSEN H., 1976. *Schizonotus sieboldi* Ratzeburg, 1852 (Hym., Pteromalidae) reared from *Melasoma populi* (L.) (Col., Chrysomelidae). Norwegian Journal of Entomology, *23*: 206–207.

PLAVŠIĆ V., 1958. Prilog poznavanju života i razvića velike topoline buba-listare (*Melasoma populi* L.). Topola, *6*: 463–468.

POINAR, G.O. Jr., 1988. Nematode parasites of Chrysomelidae. In: JOLIVET P., PETITPIERRE E., HSIAO T.H. (eds.), Biology of Chrysomelidae. Dordrecht, Boston, London, Kluwer Academic Publisher: 433–448.

RATZEBURG J.T.C., 1839. Die Forst-Insecten. Erster Teil. Die Käfer. Berlin, Nicolai´sche Buchhandlung: 248.

RAUPP M.J., SADOF C.S., 1991. Responses of Leaf Beetles to Injury-related Changes in Their Salicaceous Host. Phytochemical Induction by Herbivores. New York, J. Wiley: 183–204.

REITTER E., 1912. Fauna Germanica. IV. Stuttgart, K. H. Lutz Verlag: 236.

ROUBAL J., 1937–1941. Katalog Coleopter (brouků) Slovenska a východních Karpat. III. Praha, Nakladatelství Orbis: 363.

RUBNER K. et al., 1942. Neudammer forstliches Lehrbuch. I. Bd. Neudamm, Verlag J. Neumann: 798.

SABATTI M. et al., 2000. Experienze di rinaturalizzazione di terreni agricoli in Pianura padana mediante piantagioni forestali. Italia Forestale e Montana, *55*: 241–252.

SCHAUFUSS C., 1916. Calwer's Käferbuch. II. Stuttgart, E. Schweizerbartische Verlagsbuchhandlung: 1390.

SCHEIDTER F., 1926. Forstentomologische Beiträge. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz, *36*: 193–226.

SCHIMITSCHEK E., 1944. Forstinsekten der Türkei und ihre Umwelt. Prag, Amsterdam, Berlin, Wien, Volk und Reich Verlag: 371.

SCHNAIDER Z., 1972. Szkodniki wikliny i ich zwalczanie. Warszawa, Akademia Rolnicza: 57.

SCHNAIDEROWA J., 1954. O zwalczaniu stonek wystepujacych na topolach. Sylwan, *98*: 316–321.

SCHWERDTFEGER F., 1970. Die Waldkrankheiten. Hamburg, Berlin, Verlag P. Parey: 509.

SIDOR C., 1979. The role of insect pathogenic microorganism in environmental protection. Mikrobiologija, *16*: 173–186.

SIDOR C., JODAL I., 1986. *Nosema melasomae* causing a

disease of the poplar leaf beetle (*Melasoma populi* L., Chrysomelidae, Coleoptera). Zaštita Bilja, *37*: 243–249.

STARK V.N. et al., 1951. Vrediteli i bolezni polezaščitnych lesnych nasaždenij i mery borby s nimi. Moskva, Leningrad, Gosudarstvennoje izdateľstvo selskochozjajstvennoj literatury: 326.

TARASI J., SABOORI A.R., SADEGHI S.E., 2001. Report of an ectoparasitic mite on adults of *Melasoma populi* L. from Iran. Journal of the Entomological Society of Iran, *21*: 107–108.

TEODORESCU I., 1980. Beneficial insect fauna (predators) in the woods of northern Oltenia. Studii si Cercetari de Biologie, Biologie Animala, *32*: 3–6.

THAKUR M.L., 1999. Insect pest status of poplars in India. Indian Forester, *125*: 866–872.

TIMČENKO G.A., TREML A.G., 1963. Vrediteli topolej v vostočnoj časti Ukrainy i Krymu. Entomologičeskoje Obozrenije, *42*: 793–816.

TOGUEBAYE B.S., MARCHAND B., BOUIX G., 1988. Microsporidia of the chrysomelidae. In: JOLIVET P., PETITPIERRE E., HSIAO T.H. (eds.), Biology of Chrysomelidae. Dordrecht, Boston, London, Kluwer Academic Publisher: 399–416.

TSCHORSNIG H.-P., HERTING B., 1994. Die Raupenfliegen (Diptera, Tachinidae) Mitteleuropas: Bestimmungstabellen und Angaben zur Verbreitung und Ökologie der einzelnen Arten. Stuttgart, Stuttgarter Beiträge zur Naturkunde, Ser. A, *506*: 1–170.

URBAN J., 1997. On the occurrence, bionomics and harmfulness of *Chrysomela vigintipunctata* Scop. in the territory of the Czech Republic. Lesnictví-Forestry, *43*: 11–27.

URBAN J., 1998a. Příspěvek k poznání mandelinky *Gonioctena* (= *Phytodecta*) *quinquepunctata* F. (Chrysomelidae, Coleoptera). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis (Brno), *46*: 7–23.

URBAN J., 1998b. Insect parasitoids of the chrysomelid *Chrysomela vigintipunctata*. Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis (Brno), *46*: 13–39.

URBAN J., 1999. Výsledky studia biologie a škodlivosti bázlivce olšového (*Agelastica alni* L.) (Chrysomelidae, Coleoptera). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis (Brno), *47*: 47–71.

URBAN J., 2000. Výskyt, bionomie a škodlivost mandelinky olšové (*Linaeidea aenea* L.). Journal of Forest Science, *46*: 468–484.

URBAN J., 2005. Contribution to the knowledge of development and harmfulness of imported willow leaf beetle (*Plagiodera versicolora*) (Coleoptera, Chrysomelidae). Journal of Forest Science, *51*: 481–507.

UTEBERG E., OLSSON H., 1978. Insect damage to fast-growing *Salix* and *Populus* species. Rapporter och Uppsatser, Institutionen for Skogsforyngring, *103*: 101.

VASILJEV V.P. et al., 1974. Vrediteli selskochozjajstvennych kultur i lesnych nasaždenij. II. Kiev, Izdateľstvo Urožaj: 500.

VASILJEV V.P. et al., 1975. Metody i sredstva borby s vreditel-jami, sistemy meroprijatij po zaščite rastenij. III. Kiev, Izdateľstvo Urožaj: 526.

VICENTE C.D.L. et al., 1998. Entomología agroforestal. Madrid, Ediciones Agrotécnicas, S.L.: 1309.

WAGNER H., ORTMANN C., 1959. Anbau und Nutzung der Flechtweiden. Berlin, Deutsche Bauernverlag: 206.

WARCHAŁOWSKI A., 1973. Klucze do oznaczania owadów Polski. Cześć XIX. Chrzaszcze – Coleoptera. Zeszyt 94a. Stonkowate – Chrysomelidae. Warszawa, Państwowe Wydawnictvo Naukowe: 98.

ZAREH N., AHMADI A.A., ALISHAH A., 1984. Evaluation of feeding response, age specific survival and longevity of poplar leaf beetle *Chrysomela populi* L. (Coleoptera, Chrysomelidae) on five host plants. Iran Agricultural Research, *3*: 129–138.

ZEKI H., TOROS S., 1990. Determination of natural enemies of *Chrysomela populi* L. and *Chrysomela tremulae* F. (Coleoptera, Chrysomelidae) harmful to poplars and the efficiency of their parasitoids in Central Anatolia Region. In: Proceedings of the Second Turkish National Congress of Biological Control: 251–260.

ZEKI H., TOROS S., 1992. The effect of host plant on development of *Chrysomela populi* L. and *Chrysomela tremulae* F. (Coleoptera: Chrysomelidae). In: Proceedings of the Second Turkish National Congress of Entomology: 43–52.

ZEKI H., TOROS S., 1996. The effect of host on the adults of *Chrysomela populi* L. and *Chrysomela tremulae* F. (Col.: Chrysomelidae). Bitki Koruma Bülteni, *36*: 25–38.

ŽIVOJINOVIČ S., 1948. Šumarska entomologia. Beograd, Izdavačko preduzece narodne republike Srbije: 430.

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Výskyt, bionomie a škodlivost *Chrysomela populi* L. (Coleoptera, Chrysomelidae)

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ABSTRAKT: V letech 2003 až 2005 se na každoročně seřezávaných *Populus nigra* var. *italica* v uličních stromořadích v Brně a jinde přemnožila *Chrysomela populi* L. Imaga se na dřevinách objevovala od konce dubna, příp.

od začátku května. V chovech neochotně konzumovala listy dvouletých výhonků a vykladla kolem 142 vajíček. Na listech výmladků imaga během pěti až sedmi týdnů poškodila 100 až 200 cm^2, vyprodukovala 480 až 900 trusinek a vykladla průměrně 506 vajíček. Kladení bylo kontinuální s přestávkami kolem 2,6 dne. Embryonální vývoj trval 6 až 8 (v laboratoři 5) dnů. Larvy 1. generace se vyskytovaly od poloviny května do poloviny července. Během dvou týdnů (v laboratoři během 10 dnů) života poškodily kolem 20 cm^2 listů a vyprodukovaly kolem 300 trusinek. V laboratoři trvaly předkukly dva dny a kukly čtyři dny. Imaga 1. generace se vyskytovala od června do září. Poškodila průměrně 113 cm^2 a vyprodukovala 553 trusinek a 653 vajíček. Při teplotě 24 až 28 °C poškodila během dvou až tří týdnů kolem 84 cm^2 a až do příštího roku diapauzovala. Na dorůstajících listech imaga žila déle a měla větší spotřebu potravy i fekunditu než na listech čerstvě dorostlých. Larvy 2. generace zničily průměrně o 2 cm^2 menší plochu než larvy 1. generace. Část imag 2. generace diapauzovala (příp. všechna). Imaga 3. generace před odchodem do zimovišť poškodila 40 až 70 cm^2 listů. V našich přírodních poměrech je případná 3. generace vždy neúplná. K významným nepřátelům patří *Cleonice callida* Meig. a *Schizonotus sieboldi* (Ratz.).

Klíčová slova: Chrysomelidae; *Chrysomela populi*; výskyt; hostitelské dřeviny; bionomie; generační poměry; přirození nepřátelé; škodlivost

Mandelinka topolová (*Chrysomela populi* L.) je významný fytofágní škůdce topolů, který se často vyskytuje i na vrbách. Je známa z palearktické zoogeografické oblasti a z části oblasti orientální. Její přemnožení bylo v letech 2003 až 2005 zaznamenáno na *Populus tremula* L. a *P. nigra* L. na polesí Křtiny a Bílovice nad Svitavou (ŠLP Křtiny) a na polesí Valtice (LZ Břeclav). Hojně se vyskytovala mj. i na každoročně seřezávaných *P. nigra* var. *italica* v uličních stromořadích v Brně-Králově Poli a Brně-Černých Polích. Systematickým terénním a laboratorním studiem jejího výskytu, bionomie a hospodářského významu byly získány tyto hlavní výsledky:

1. Topoly *P. tremula*, *P. nigra* a *P. nigra* var. *italica* patří k primárním hostitelským dřevinám *C. populi*. Imaga, larvy a kukly mandelinky byly v arboretu MZLU v Brně nalézány i na *Salix fragilis* L. a *S. purpurea* L. a v břehových porostech řeky Svitavy v Brně-Obřanech na *S. fragilis* L. Při studiu hmyzích škůdců, prováděném v letech 1969 až 1976 v šesti vrbovnách (se 12 druhy, resp. hybridy vrb) na jižní, střední a severní Moravě, byla *C. populi* nalézána zřídka nebo vůbec ne. Imaga v laboratoři minimálně konzumovala *S. viminalis* L., *S.* × *rubra* Huds., *S.* × *smithiana* Willd. a *S. americana* hort. Poněkud více poškozovala *S. purpurea* L. a *S.* × *rubens* Schr. a nejvíce *S. fragilis* L. Na *S. fragilis* žila průměrně 14 dnů a poškodila kolem 26,4 cm^2, ale vajíčka nekladla. Larvy na vrbách hynuly obvykle v 1. nebo 2. instaru. Pouze na *S. fragilis* kolem 5 % larev přežívalo do 3. instaru a v něm hynulo.
2. Na jižní a střední Moravě brouci opouštějí zimoviště koncem dubna a začátkem května. Na dřevinách se vyskytují až do poloviny července, tj. průměrně dva a půl měsíce. Již po jednom až dvou týdnech žíru (v laboratoři po čtyřech až osmi dnech) poprvé kopulují a brzy nato kladou první vajíčka. V chovech samičky kladly vajíčka po dobu pěti až sedmi týdnů. Brouci jsou velmi náročni na kvalitu potravy – např. na listech dvouletých výhonků *P. nigra* var. *italica* poškodili průměrně jen 18,5 cm^2 a vykladli kolem 142 vajíček. Intenzivně však ožírali listy výmladků, na nichž samičky zničily průměrně 157 cm^2 a vykladly 153 až 799 (průměrně 506) vajíček. Jedinci obou pohlaví poškodili 100 až 200 cm^2 a defekovali 480 až 900 (průměrně 700) trusinek o délce 2,24 mm a šířce 0,77 mm. Samičky poškodily průměrně o třetinu větší plochu než samečci.
3. Samičky kladou vajíčka na abaxiální stranu listů v jednovrstevných skupinách (snůškách) po 20 až 65 (průměrně 55) kusech. Ve snůškách vykladených v laboratoři bylo 1 až 68 (průměrně 47) vajíček. V 77 % snůšek byl sudý počet vajíček, odpovídající párové stavbě ovarií. Po vykladení jsou vajíčka dlouhá kolem 1,8 mm a široká 0,7 mm. Během embryonálního vývoje se jejich rozměry zvětšují až na 2,0 × 0,83 mm. Snůšky vajíček od různých samiček jsou často barevně polymorfní. Proces kladení byl kontinuální, a to v intervalech 1 až 9 (průměrně 2,6) dnů. S věkem samiček intervaly mezi snůškami průkazně vzrůstaly. Po vykladení poslední snůšky samičky během tří až devíti dnů hynuly. Samičky přezimující generace vykladly na výmladcích v chovech na *P. nigra* var. *italica* celkem 3,3 až 18,1 (průměrně 11,9) snůšek o celkovém počtu 153 až 850 (průměrně 558) vajíček. Zjištěná fekundita odpovídá průměrné trofické hodnotě listů výmladků tohoto topolu.

4. Embryonální vývoj *C. populi* trval šest až osm dnů, v laboratoři kolem pěti dnů. Larvy se z téže snůšky líhly během 60 až 80 minut. Asi po šesti hodinách od vylíhnutí obvykle zkonzumovaly choriony a po 6–12 hodinách začínaly společně skeletovat listy *P. nigra* var. *italica*. Larvy 1. instaru mají cranium široké 0,64 až 0,78 mm. V chovech během dvou dnů dorůstaly délky až 4 mm a poškodily kolem 0,6 cm^2. Defekovaly průměrně 77 trusinek o průměrné délce 0,4 mm a šířce 0,2 mm a celkovém objemu 1,1 mm^3. Larvy 2. instaru mají cranium široké 1,0 až 1,21 mm a délku 3,5 až 8 mm. Během tří dnů poškodily kolem 3 cm^2 listů a vyloučily průměrně 84 trusinek o průměrných rozměrech 1,1 × 0,4 mm a celkovém objemu 14,3 mm^3. Larvy 3. instaru mají cranium široké 1,50 až 1,86 mm a délku 7 až 16 mm. Během 4,5 dne poškodily průměrně 17,3 cm^2 a vyloučily průměrně 134 trusinek o průměrných rozměrech 1,5 × 0,64 mm a celkovém objemu 120,3 mm^3. Larvy 1. generace se na zkoumaných lokalitách vyskytovaly od poloviny května do poloviny července. Jejich vývoj trval průměrně dva týdny, v laboratoři pouze 10 dnů. Celkem poškodily kolem 20 cm^2 listů. Průměrná spotřeba potravy a mortalita závisí mj. i na počtu larev ve skupině, přičemž nejvyšší spotřebu a nejnižší mortalitu mají larvy ve 21–30členných skupinách. Po dvoudenním období předkukly se objevovalo stadium kukly, které trvalo v laboratoři čtyři dny. Celkový vývoj od vykladení vajíček až po vylíhnutí imag trval asi 30 dnů, v laboratoři kolem 21 dnů. V líhnutí imag vychovaných z vajíček téže skupiny se projevovala mírná protogynie.
5. Imaga 1. generace se na jižní a střední Moravě vyskytují na dřevinách od června do září, v laboratoři od konce května do poloviny září. Poprvé se pářila po 9–11 dnech zralostního žíru a za další jeden až dva dny kladla první vajíčka. Na listech *P. nigra* var. *italica* samečci žili v zajetí 35 až 125 dnů, samičky 45 až 134 dnů. Poškodili průměrně 113 cm^2 a vyprodukovali kolem 553 trusinek. Samičky vykladly 413 až 893 (průměrně 653) vajíček, tj. průměrně o 147 více než samičky přezimující generace. Při vysokých teplotách 24–28 °C imaga poškodila během tří týdnů kolem 84 cm^2 a defekovala kolem 358 trusinek. Pak vstupovala do letní diapauzy, která postupně přecházela v diapauzu zimní.
6. Bylo zjištěno, že brouci *C. populi* nekonzumují čerstvě rašící listy *P. nigra* var. *italica*. V chovech dávali přednost dorůstajícím listům (3. a 4. list od vrcholu), na nichž poškodili kolem 118 cm^2 a vykladli kolem 372 vajíček. Na listech čerstvě dorostlých (5. až 7. list od vrcholu) poškodili kolem 88 cm^2 a vykladli kolem 213 vajíček. Na dorůstajících listech imaga žila kolem 49 dnů, na čerstvě dorostlých listech kolem 39 dnů. Je zajímavé, že imaga 1. generace vychovaná z vajíček získaných z přírody poškodila asi dvakrát větší plochu listů než imaga 1. generace vychovaná z vajíček vykladených v laboratoři.
7. Larvy 2. generace poškodily o 0,5–3,5 (průměrně 2) cm^2 menší plochu listů *P. nigra* var. *italica* než larvy 1. generace. Také jejich doba vývoje byla o 0,8–1,5 (průměrně 1,2) dne kratší. Bylo prokázáno, že larvy nepřijímají potravu kontinuálně. Např. mladé larvy 3. instaru žraly během světlé části dne (od 6 do18 hodin) průměrně 17krát po dobu 11 minut, středně staré larvy žraly 12krát po dobu 17 minut a dorůstající larvy pětkrát po dobu 31 minut. To znamená, že mladé larvy tohoto instaru strávily při žíru průměrně 26 % doby, středně staré larvy 29 % doby a dorůstající larvy 22 % doby. Larvy přijímají potravu také během tmavé části dne (od 18 do 6 hodin) – např. larvy 3. instaru strávily během tmavé části dne při žíru průměrně 22 % doby. Žír přes den je však vždy intenzivnější než v noci, což se projevuje jak ve velikosti poškozené plochy, tak i v počtu defekovaných trusinek. Např. mladší larvy 3. instaru vyprodukovaly během světlé části dne kolem 78 trusinek, zatímco během tmavé části dne kolem 55 trusinek, tj. o 30 % méně.
8. Dospělci 2. generace se vyskytují na dřevinách od července do konce vegetační sezony. V témže roce se však rozmnožují pouze dříve vylíhlí dospělci. Ostatní brouci během úživného žíru nekopulují a rozmnožují se až po hibernaci. Nediapauzující dospělci kopulovali během 24 hodin šestkrát až desetkrát po dobu 3–450 (průměrně 41) minut. Při vlastní kopulaci strávili kolem 318 minut (22 % dne). Během 41 dnů života kopulovali asi 357krát. Před odchodem do zimovišť dospělci zničili 40 až 70 cm^2 listů *P. nigra* var. *italica*. Na jižní a střední Moravě je vývojový cyklus *C. populi* bivoltinní až trivoltinní. Pokud se tam třetí generace mandelinky vyskytuje, pak je vždy neúplná.
9. V larvách *C. populi* často parazituje ovoviviparní kuklice *Cleonice callida* Meig. (Tachinidae), která např. v Brně-Králově Poli zahubila kolem 20 % larev 1. generace. K nejvýznamnějším parazitoidům kukel patří kovověnka *Schizonotus sieboldi* (Ratz.) (Pteromalidae). V Brně-Králově Poli napadla kolem 40 % kukel 1. generace.
10. Dospělci přezimující generace ožírají čerstvě vyrašené listy od konce dubna, resp. od začátku května. Během zralostního a regeneračního žíru

poškodí průměrně 150 cm^2 listů *P. nigra* var. *italica*, tj. 6,5krát více než *Plagiodera versicolora* (Laich.) a 5,3krát více než *Phratora vitellinae* (L.) na *Salix fragilis*. Asi po dvou týdnech od náletu na dřeviny se objevují první larvy. Během dvoutýdenního žíru larvy zničí průměrně 20 cm^2 listů, tj. 7,5krát více než larvy *P. versicolora* a *P. vitellinae*. Larvy poškozují vždy poněkud starší listy než dospělci. Tyto listy splnily asimilační funkci z větší části než listy dorůstající. Také proto je žír dospělců vždy nebezpečnější. Od poloviny června se k žíru dospělců přezimující generace a larev 1. generace připojuje žír dospělců 1. generace a následně i žír larev 2. generace. Část dospělců 2. generace za příznivých podmínek zakládá 3. generaci. Později vylíhlí dospělci 2. generace a dospělci 3. generace před odchodem do zimovišť poškodí kolem 55 cm^2 listů.

11. *C. populi* nejvíce škodí v dobře prosluněných lesních školkách, mladých nárostech dřevin a v mladých kulturách; tím často brání obnově porostů. K její aktivizaci přispívá hlavně teplé a suché jaro a mírné léto. Poškozením až úplným zničením mladých listů, příp. kůry a pupenů na aktivně rostoucích výhoncích dochází ke ztrátám na přírůstu a k nežádoucímu větvení dřevin. Těžce poškozené výhonky nedostatečně dřevnatí a jsou následně poškozovány mrazem. V případě vážného ohrožení dřevin je proto nutné proti mandelince bojovat.

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