JOURNAL OF FOREST SCIENCE, *48*, 2002 (6): 248–270

Occurrence, development and natural enemies of *Pemphigus spyrothecae* (*Homoptera*, *Pemphigidae*)

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ABSTRACT: In 2001, galls were analysed of *Pemphigus spyrothecae* Pass. taken in one- to three-week intervals from *Populus nigra* and *P. nigra* var. *italica* at 4 localities in Brno. Fundatrices matured in the first half of June and during the first half of summer produced about 50 offsprings. Virgines produced about 10 offsprings which grew up in winged sexuparae. The winged individuals started to occur in galls from the beginning of August. In galls with intact development, on average 500 aphids developed. Galls with intact development on *P. nigra* var. *italica* reached larger average dimensions and contained at least by 4% more aphids than galls on *P. nigra*. About 5% of fundatrices died already in the 1st instar and other 3 to 6% in higher instars by the beginning of reproduction. At localities under investigation, 7.5 to 39.0% of galls on *P. nigra* and 3.9 to 13.7% of galls on *P. nigra* var. *italica* were occupied by the fly *Leucopis puncticornis* Meig. (*Chamaemyiidae*). About 24.3 to 32.2% of galls on *P. nigra* and 23.3 to 49.3% of galls on *P. nigra* var. *italica* were occupied by the bug *Anthocoris minki* Dohrn (*Anthocoridae*). Hover flies *Heringia heringi* (Zett.) and *Pipiza festiva* Meig. (*Syrphidae*) killing aphids in 3.8 to 30.4% of galls on *P. nigra* and 6.5 to 6.8% of galls on *P. nigra* var. *italica* were an important regulator. In August (i.e. at the beginning of the formation of winged sexuparae), the majority of galls opened through primary slit-shaped or oval emergence holes. A part (7.8 to 19.5%) of galls with so far intact development, however, remained closed and all aphids contained in them died. Diseases (particularly mycoses) often participated in the accelerated dying of aphids. The effect of mortality factors on the gall size differentiation was evaluated in details. The galls do not cause any leaf area reduction. In the case of mass outbreak, they decrease decorativeness of poplars in street alleys. In August and September, liquid excrements fall out from the galls (honeydew) polluting the environment in villages and housing estates.

Keywords: *Pemphigus spyrothecae*; *Leucopis puncticornis*; *Anthocoris minki*; *Heringia heringi*; *Pipiza festiva*; development; gall size; harmfulness

In the Czech Republic, aphids of the family *Pemphigidae* (= *Eriosomatidae*) are represented by at least 31 species comprising 5% of all aphid species (*Aphidinea*). The majority of the family representatives is diecious (or heteroecious). Such species migrate from primary hosts (tree species) where they form galls characteristic in their size and shape to roots of secondary hosts (herbs or tree species). Only few species are monecious, i.e. with life cycle occurring on one host species only. They develop intensively particularly in spring and in the first half of summer on rapidly growing plant organs (growing points and leaves including petioles). Hereditarily fixed migration of diecious species of aphids is undoubtedly related to fast changes occurring during the growing season in gall tissues (PAŠEK 1954). On the other hand, the development of galls and offsprings of monecious species of the family *Pemphigidae* proceeds much more slowly. And just the aphid *Pemphigus spyrothecae* Pass. = *P. spirothecae* Pass. belongs to such species.

P. spyrothecae is a holocyclic species (i.e. a species with a complete generation cycle including sexuales) that develops exclusively on a primary host. The generation cycle consists of the following forms: fundatrix, virgines, sexuparae and sexuales. It produces well-known spirally twisted true galls on petioles (exceptionally on young shoots) of poplars *Populus nigra* L. and particularly *P. nigra* L. var. *italica* (Figs. 1 to 3). The aphid is also reported in *P.* × *berolinensis* Dipp. (RUPAJS 1989) and rarely in *P. robusta* C.K. Schneid., *P. serotina* Htg., *P. simonii* Carr., *P. balsamifera* L. and related species (BUHR 1965). The occurrence of the aphid corresponds with the wide European distribution of its main host species. Only recently, the aphid was unintentionally introduced into North America (ALLEYNE, MORRISON 1977).

The author of the paper highly appreciates the support provided under MSM Research Project No. 434100005 solved at the Faculty of Forestry and Wood Technology, Mendel University of Agriculture and Forestry, Brno.

In the centre of its European range as well as in several regions of North America, *P. spyrothecae* is considered to be an abundant species that often shows mass outbreaks and sometimes is harmful. These facts (together with easy determination according to galls) have caused that there are relatively many data on the occurrence, bionomics, generation conditions and coenotic relations in the literature. A number of special papers deals with this species (e.g. GERHARDT 1922; TÓTH 1937, 1939; ROBERTI 1938; LAMPEL 1968/1969; GUSIC 1969; CHAN, FORBES 1975; MARCU et al. 1993; FURK, PRIOR 1975; PERKINS 1997; RIPKA et al. 1998, etc.). New findings on the bionomics of sexuparae and sexuales were presented particularly by FOSTER and BENTON (1992). Information on gall induction caused by the effect of toxic substances in aphid saliva was given e.g. by LECLANT (1998).

The control role of aphidophagous hover flies in galls of *P. spyrothecae* was studied by KURIR (1949/1950, 1963) and DUŠEK and KŘÍSTEK (1959). The defensive behaviour of the caste of robust-leg larvae of the 1st instar ('soldiers') to aphidophagous predators and the potential reproduction function of larvae with normal hind legs were described by AOKI and KUROSU (1986). The capability of 'soldiers' to protect effectively aphids in galls against larvae of the 1st instar of the ladybird *Adalia bipunctata* (L.), bugs *Anthocoris nemoralis* (F.) and *A. minki* Dohrn and young larvae of the 3rd instar of the hover fly *Metasyrphus corollae* (F.) was experimentally demonstrated by FOSTER (1990). The primary role of 'soldiers' in the protection of colonies of aphids against bugs *A. nemoralis*, *A. minki* and hover flies *Episyrphus auricollis* (Meig.) and *Syrphus ribesii* (L.) was described by FOSTER and RHODEN (1998). In Central Europe, *A. minki* is considered to be an important predator of aphids from the family *Pemphigidae*. In Great Britain, however, its occurrence was proved as late as in 1980–1982 just in the galls of *P. spyrothecae* on *P. nigra* var. *italica* in London (JESSOP 1983). JASNOŠ (1978) mentioned a species *Protaphelinus nikolskaja* Iasn. (*Aphelinidae*) which parasitized on the aphid.

The basic description of galls (sporadically also their originators) and the most important data on the occurrence and development or harmfulness of *P. spyrothecae* are also brought by many summary cecidiological, entomological and entomological/forest protection papers (e.g. SCHWERDTFEGER 1944, 1970; BÖRNER 1952; GUSEV, RIMSKIJ-KORSAKOV 1953; PFEFFER et al. 1954; BAUDYŠ 1954; GÄBLER 1955; BUHR 1965; SZELEGIEWICZ 1968; LAMPEL 1960; STEFFAN 1972; KOEHLER, SCHNAIDER 1972; VASILJEV et al. 1975; RUPAJS 1989; BLACKMAN, EASTOP 1994; UHLÍŘOVÁ et al. 1996, etc.).

Despite the existence of numerous papers, existing findings on *P. spyrothecae* show considerable gaps in many aspects. For example, the process of the formation of galls by the sucking of fundatrices and their offsprings is relatively little known and complicated. The reproduction potential of the aphid and its population dynamics including some control factors have not been satisfactorily revealed. Findings on the effect of galls on the size of the leaf assimilatory area and drying up and leaf fall and thus also on the growth and total health conditions of host trees are also incomplete.

The paper brings some new findings on the development and size of galls of *P. spyrothecae* on *P. nigra* and *P. nigra* var. *italica* in Brno. Special attention has been paid to factors participating in a decrease in the population density of the aphid. The effect of galls on the dimension of leaf blade and petiole length was studied in general.

MATERIAL AND METHODS

The paper is based on the results of laboratory analyses of *P. spyrothecae* galls that were taken in 1- to 3-week intervals from *Populus nigra* and *P. nigra* var. *italica* in Brno during the growing season 2001. In the period from 10 June to 25 August (including), galls were obtained from three older *P. nigra* and three older *P. nigra* var. *italica* trees growing in a riparian and accompanying stand differentiated from the aspect of species, age and space (altitude 205 to 210 m) along the Svratka river in the cadastre of the Brno-Komín and Brno-Jundrov urban district. In the rich mixture of trees, *Populus alba* L., *Salix fragilis* L., *S. alba* L., *S.* × *rubens* Schr., *Alnus glutinosa* (L.) Gaertn. and *Ulmus laevis* Pall. were also represented. Galls occurred mainly in the lower (ground) parts of crowns. Galls of different size and form were sampled including leaf blades regardless of their position with respect to cardinal points. Sets of galls from *P. nigra* and *P. nigra* var. *italica* were taken usually on the same days, however, their examination was always carried out separately. On particular inspection dates, at least 130 and maximally 327 galls were analysed at the locality.

On 25 August 2001, all available galls of *P. spyrothecae* in Brno-Komín and Brno-Jundrov were used for laboratory analyses. From 7 September to 12 November, the galls from three medium-aged poplars *P. nigra* growing along a busy road in a nearby housing estate in Brno-Žabovřesky were examined. From the poplars, at least 53 and maximally 218 galls were taken and examined in the laboratory on particular dates. A relatively small number of galls (53) analysed on 12 November was caused by leaf fall and their removal within the standard maintenance of areas of public greenery.

On 7 November 2001, an inspection was carried out of *P. spyrothecae* galls occurring less abundantly on overmature poplars *P. nigra* var. *italica* in a street alley in Brno-Černá Pole. In 2001, sporadic galls of the aphid were also observed on two medium-aged *P. nigra* var. *italica* at Bílovice nad Svitavou (District Brno-venkov). Leaves of both poplars were attacked on a mass scale by *P. bursarius* (L.) and *P. populinigrae* (Schrank) (= *P. filaginis* (B. de Fonsc.) and rarely by *P. lichtensteini* Tullgr. and *P. populi* Courch. The results of the study of these aphidocecidiae and their originators are not, however, included in the paper.

In the laboratory, the position of galls on a petiole was recorded at first. The galls were clipped off from leaf

blades and analysed individually under a microscope. Their length and width (and/or gall wall thickness) in mm were measured. The presence and size of fundatrices, virgines and sexuparae were examined. The number of living apterous and macropterous individuals was recorded both in galls with intact development and in galls occupied with insect predators, in galls with dying and dead aphids owing to the late opening of galls, entomophagous fungi, etc.

Galls occupied with the predatory fly *Leucopis punctipennis* Meig., the predatory bug *Anthocoris minki* Dohrn (det. by Dr. J. Stehlík, Brno) and aphidophagous hover flies *Heringia heringi* (Zett.) and *Pipiza festiva* Meig. were examined carefully in particular. The number of predators, their length (in mm) and the number of exuviae were also recorded. The number of hover fly eggs laid on the surface of galls was determined in a sample of 237 galls taken on 1 October 2001 on *P. nigra* in Brno-Žabovřesky. The appearance and position of emergence holes were also examined in the set of galls. The effect of galls on the leaf blade size and petiole length was examined on 1 October 2001 on 350 leaves with galls and 350 leaves without galls. The compared sets came from the same parts of the crown and the same sections of branches of the poplar *P. nigra* in Brno-Žabovřesky.

On 15 November 2001, puparia of *L. puncticornis* and grown-up larvae of hover flies including galls of *P. spyrothecae* were placed into 4 glass dishes 12 cm in diameter and 5 cm in height and covered with monofilament fabric above. Predators wintered under outdoor conditions (in a paper box protected outside by a plastic wrap).

From 10 June to 12 November 2001, some 2,587 galls were analysed in detail in the laboratory and partial laboratory examinations were carried out on other 178 galls (Table 1).

RESULTS AND DISCUSSION

LIFE CYCLE

Pemphigus spyrothecae is a holocyclic monoecious species. Its development occurs on a primary host, i.e. usually *Populus nigra* var. *italica* and *P. nigra*. Eggs laid in autumn by fertilized females of the generation sexuales are a wintering developmental stage. These apterous females lay one large thick-walled egg only especially into slits of the stem and branch bark of host trees. According to CHAN and FORBES (1975), they can lay eggs even under the thallus of the lichen *Cetraria* sp. growing on the bark of host trees.

At the beginning of flushing of poplar leaf buds (usually in mid-April), fundatrices representing individuals of the 1st generation emerge from the eggs. The 1st instar of fundatrix is about 0.5 mm long, glaucous with well developed hind legs and 4-segment (almost 0.1 mm long) antennas.

Fig. 1. The gall of *P. spyrothecae* on the petiole of a leaf of *P. nigra*. In a slit there is a chorion of the egg of an emerged hover fly. Brno-Žabovřesky, 1 October 2001

Fig. 2. Two galls of *P. spyrothecae* on the petiole of a leaf of *P. nigra.* Brno-Žabovřesky, 1 October 2001

Table 1. The number (percentage in parenthesis) of galls of *Pemphigus spyrothecae* with intact and disturbed development. Dates of gall sampling in *Populus nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Mean (from 24/10 inc.)
With intact development	217 (95.6)	110 (84.6)	195 (59.7)	171 (73.4)	92 (68.7)	72 (58.1)	74 (35.6)	66 (36.7)	26 (19.3)	14 (8.2)	7 (3.5)	11 (6.5)	18 (8.3)	4 (5 .2)	6 (11.3)	39 (7.5)
Uninhabited	–	–	–	–	–	–	2 (1.0)	2 (1.1)	1 (0.7)	7 (4.1)	12 (6.0)	13 (7.7)	16 (7.3)	4 (5.2)	4 (7.6)	37 (7.2)
With *Anthocoris*	1 (0.4)	–	39 (11.9)	20 (8.6)	9 (6.7)	13 (10.5)	58 (27.9)	38 (21.1)	13 (9.6)	17 (9.9)	27 (13.5)	38 (22.5)	49 (22.5)	38 (49.3)	12 (22.6)	137 (26.5)
With *Leucopis*	9 (4.0)	20 (15.4)	40 (12.2)	10 (4.3)	10 (7.5)	17 (13.7)	27 (13.0)	17 (9.4)	34 (25.2)	52 (30.2)	78 (39.0)	59 (34.9)	66 (30.3)	3 (3.9)	16 (30.2)	144 (27.9)
With *Anthocoris* + *Leucopis*	–	–	–	–	–	8 (6.5)	9 (4.3)	4 (2.2)	2 (1.5)	–	2 (1.0)	3 (1.8)	4 (1.8)	–	–	7 (1.3)
With *Syrphidae*	–	–	?	?	5 (3.7)	4 (3 .2)	8 (3.8)	12 (6.7)	39 (28.9)	41 (23.8)	44 (22.0)	23 (13.6)	29 (13.3)	5 (6.5)	7 (13.2)	64 (12.4)
With *Anthocoris* + *Syrphidae*	–	–	–	–	–	–	–	–	2 (1.5)	–	–	–	–	–	–	–
With *Lepidoptera*	–	–	–	2 (0.9)	–	–	7 (3.4)	3 (1.7)	–	5 (2.9)	6 (3.0)	2 (1.2)	8 (3.7)	2 (2.6)	2 (3.8)	14 (2.7)
With *Araneida*	–	–	–	–	–	–	2 (0.9)	4 (2.2)	–	–	–	–	–	–	–	–
With dying and dead aphids	–	–	–	–	–	–	–	–	1 (0.7)	9 (5.2)	7 (3.5)	7 (4.1)	17 (7.8)	15 (19.5)	4 (7.5)	43 (8.3)
Eaten up and pecked up	–	–	38 (11.6)	–	–	4 (3.2)	6 (2.9)	11 (6.1)	–	–	–	–	–	–	–	–
With dead fundatrix	–	–	–	14 (6.0)	16 (11.9)	4 (3.2)	6 (2.9)	14 (7.8)	7 (5.2)	15 (8.7)	5 (2.5)	1 (0.6)	2 (0.9)	1 (1.3)	–	4 (0.8)
Undeveloped (distorted) petiole	–	–	15 (4.6)	16 (6.8)	2 (1.5)	2 (1.6)	9 (4.3)	9 (5.0)	10 (7.4)	12 (7.0)	12 (6.0)	12 (7.1)	9 (4.1)	5 (6.5)	2 (3.8)	28 (5.4)
Total	227 (100.0)	130 (100.0)	327 (100.0)	233 (100.0)	134 (100.0)	124 (100.0)	208 (100.0)	180 (100.0)	135 (100.0)	172 (100.0)	200 (100.0)	169 (100.0)	218 (100.0)	77 (100.0)	53 (100.0)	517 (100.0)

Table 2. Mean length (width in parentheses) of *Pemphigus spyrothecae* galls (in mm). Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Mean (from 25/8 inc.)
With intact development	7.3 (5.3)	8.0 (6.2)	10.8 (7.5)	13.1 (8.5)	13.0 (8.9)	15.6 (10.4)	13.4 (9.8)	15.4 (9.6)	15.1 (10.0)	14.2 (9.1)	14.1 (8.6)	13.0 (7.9)	13.4 (8.6)	15.3 (9.8)	12.7 (8.7)	14.2 (9.2)
Uninhabited	–	–	–	–	–	–	12.0 (9.0)	15.0 (10.0)	15.0 (12.0)	14.7 (9.1)	16.2 (9.7)	12.4 (8.5)	13.6 (8.9)	12.0 (8.3)	13.5 (8.3)	13.9 (9.0)
With *Anthocoris*	6.0 (5.2)	–	8.9 (6.5)	9.1 (6.7)	10.2 (7.2)	10.3 (7.5)	12.0 (8.6)	14.1 (9.2)	12.4 (9.1)	10.9 (7.8)	12.4 (8.2)	11.2 (7.5)	11.0 (7.5)	11.1 (7.8)	12.5 (8.1)	11.9 (8.2)
With *Leucopis*	7.3 (5.3)	7.7 (6.0)	9.1 (6.9)	12.2 (8.4)	10.9 (8.3)	12.8 (9.3)	12.8 (9.2)	15.5 (9.3)	12.3 (8.7)	11.6 (7.9)	11.6 (8.0)	11.0 (7.7)	11.5 (7.7)	11.0 (8.3)	10.6 (7.2)	11.8 (8.1)
With *Anthocoris* + *Leucopis*	–	–	–	–	–	13.5 (10.0)	13.4 (9.2)	20.0 (13.5)	11.5 (8.5)	–	10.5 (7.5)	10.0 (8.0)	10.5 (6.8)	–	–	13.2 (9.2)
With *Syrphidae*	–	–	?	?	10.9 (8.4)	13.0 (9.4)	13.0 (9.5)	15.7 (9.5)	14.7 (10.0)	14.1 (9.0)	13.6 (8.7)	13.2 (8.3)	12.5 (8.4)	14.8 (10.2)	12.3 (8.0)	13.8 (9.0)
With *Anthocoris* + *Syrphidae*	–	–	–	–	–	–	–	–	15.5 (10.5)	–	–	–	–	–	–	15.5 (10.5)
With *Lepidoptera*	–	–	–	12.0 (8.8)	–	–	12.0 (8.3)	14.0 (8.0)	–	11.8 (8.2)	12.3 (8.0)	10.5 (7.0)	10.8 (7.1)	13.0 (10.0)	10.0 (9.0)	11.8 (8.0)
With *Araneida*	–	–	–	–	–	–	14.0 (11.0)	13.5 (8.0)	–	–	–	–	–	–	–	13.7 (9.0)
With dying and dead aphids	–	–	–	–	–	–	–	–	15.0 (10.0)	13.7 (9.1)	12.9 (7.7)	12.8 (8.3)	13.0 (8.3)	11.7 (9.7)	12.5 (8.0)	12.7 (8.7)
Eaten up and pecked up	–	–	8.1 (5.9)	–	–	14.5 (9.5)	12.7 (9.3)	15.8 (10.6)	–	–	–	–	–	–	–	14.7 (10.1)
With dead fundatrix	–	–	–	6.4 (4.6)	6.9 (5.9)	7.0 (5.5)	7.3 (6.0)	6.1 (4.7)	6.0 (4.9)	5.6 (4.6)	5.7 (4.5)	6.0 (5.0)	7.0 (5.0)	5.0 (4.0)	–	6.0 (4.8)
Undeveloped (distorted) petiole	–	–	3.3 (3.1)	4.1 (3.3)	3.0 (3.0)	3.0 (3.0)	3.6 (3.0)	5.2 (3.6)	4.7 (3.5)	3.7 (3.0)	3.9 (3.0)	3.9 (3.2)	4.0 (3.1)	5.2 (2.6)	3.5 (3.0)	4.2 (3.1)
Total	7.3 (5.3)	8.0 (6.2)	9.7 (6.9)	11.7 (7.8)	11.7 (8.3)	13.9 (9.6)	12.2 (8.9)	14.0 (8.9)	12.7 (8.8)	11.5 (7.7)	12.0 (7.9)	11.1 (7.5)	11.5 (7.7)	11.3 (8.1)	11.6 (7.7)	12.0 (8.2)

Table 3. The number of galls with the intact development (mean number of aphids in parentheses) of *P. spyrothecae* in relation to their length (in mm). Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Gall length	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Total	(%)
5	20 (0.2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20 (0.2)	1.8 –
6	50 (0.9)	8 (1.0)	–	–	–	–	–	–	–	–	–	–	–	–	–	58 (0.9)	5.3 –
7	91 (1.5)	23 (1.5)	5 (12.6)	1 (10.0)	–	–	–	–	–	–	–	–	–	–	–	120 (2.0)	11.1 –
8	45 (3.5)	60 (3.9)	19 (12.7)	4 (33.5)	–	–	–	–	–	–	–	1 (32.0)	–	–	1 (18.0)	130 (6.0)	12.0 (0.1)
9	8 (5.1)	15 (7.0)	31 (17.5)	6 (40.3)	2 (134.0)	–	2 (116.7)	–	–	–	–	–	2 (11.0)	–	–	66 (22.0)	6.1 (0.3)
10	3 (6.3)	4 (9.0)	34 (23.6)	10 (43.0)	4 (144.3)	2 (206.0)	2 (205.0)	1 (36.0)	–	1 (10.0)	1 (16.0)	1 (9.0)	2 (24.5)	–	1 (10.0)	66 (42.7)	6.1 (0.5)
11	–	–	42 (26.9)	15 (50.7)	12 (252.0)	2 (291.0)	5 (250.5)	–	–	2 (155.0)	–	1 (14.0)	1 (34.0)	–	–	80 (88.8)	7.4 (1.0)
12	–	–	30 (28.9)	25 (53.7)	15 (285.2)	4 (292.0)	13 (275.7)	5 (153.5)	2 (270.0)	1 (80.0)	1 (13.0)	1 (22.0)	2 (5.5)	–	–	99 (97.7)	9.1 (1.1)
13	–	–	18 (30.9)	28 (74.4)	18 (339.8)	6 (344.2)	20 (414.3)	15 (315.8)	5 (232.2)	2 (141.0)	1 (32.0)	1 (2.0)	2 (60.0)	1 (46.0)	1 (14.0)	118 (216.1)	10.9 (2.6)
14	–	–	9 (34.4)	30 (75.8)	26 (353.1)	7 (419.0)	10 (560.3)	10 (378.8)	2 (514.5)	2 (147.0)	1 (2.0)	3 (8.7)	1 (100.0)	1 (40.0)	–	102 (250.8)	9.4 (3.0)
15	–	–	5 (32.8)	29 (88.8)	13 (427.9)	8 (532.2)	9 (568.4)	10 (521.6)	7 (501.6)	4 (80.2)	1 (35.0)	2 (22.0)	4 (11.5)	–	3 (6.0)	95 (282.8)	8.8 (3.4)
16	–	–	–	13 (90.1)	2 (620.0)	11 (500.7)	7 (582.0)	8 (618.5)	4 (609.2)	–	–	–	1 (38.0)	–	–	46 (422.1)	4.2 (5.0)
17	–	–	1 (42.0)	4 (98.0)	–	10 (511.3)	4 (860.0)	3 (520.5)	4 (719.3)	1 (455.0)	1 (18.0)	1 (35.0)	1 (5.0)	2 (35.0)	–	32 (437.8)	3.0 (5.2)
18	–	–	1 (28.0)	3 (102.3)	–	7 (592.4)	2 (954.0)	3 (675.0)	–	–	1 (146.0)	–	2 (17.5)	–	–	19 (452.4)	1.8 (5.4)
19	–	–	–	2 (107.5)	–	7 (640.0)	–	2 (786.5)	2 **(1,031)**	–	–	–	–	–	–	13 (640.8)	1.2 (7.6)
20	–	–	–	1 (160.0)	–	4 (621.3)	–	2 (812.0)	–	–	–	–	–	–	–	7 (609.9)	0.6 (7.2)
21	–	–	–	–	–	2 (635.5)	–	2 (850.5)	–	1 (286.0)	–	–	–	–	–	5 (651.6)	0.5 (7.7)
22	–	–	–	–	–	1 (642.0)	–	2 (899.0)	–	–	–	–	–	–	–	3 (813.3)	0.3 (9.6)
23	–	–	–	–	–	1 (490.0)	–	–	–	–	–	–	–	–	–	1 (490.0)	0.1 (5.8)
24	–	–	–	–	–	–	–	2 **(1,227)**	–	–	–	–	–	–	–	2 **(1,227)**	0.2 (14.6)
25	–	–	–	–	–	–	–	1 **(1,682)**	–	–	–	–	–	–	–	1 **(1,682)**	0.1 (19.9)
Total	217 (1.8)	110 (3.7)	195 (24.3)	171 (70.7)	92 (328.8)	72 (493.8)	74 (458.2)	66 (513.8)	26 (523.7)	14 (145.6)	7 (37.4)	11 (16.7)	18 (25.5)	4 (39.0)	6 (10.0)	1,083 (151.0)	100.0 (100.0)
%	0.1	0.1	0.9	2.6	12.2	18.4	17.0	19.1	19.5	5.4	1.4	0.6	0.9	1.4	0.4	–	100.0

Table 4. The number of analysed galls (mean number of aphids in parentheses) *P. spyrothecae* with intact development in relation to their width. The percentage of the number of galls given in the last column (aphid number in parentheses) from the total number of galls (from the total number of aphids in parentheses). Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Gall width	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	Total	(%)
4	5 (0.2)	–	–	–	–	–	–	–	–	5 (0.2)	0.5 –
5	156 (1.5)	6 (1.1)	2 (10.5)	1 (20.0)	–	–	–	–	–	165 (1.7)	16.1 –
6	56 (3.0)	69 (3.2)	24 (14.2)	5 (25.4)	2 (40.0)	–	2 (30.0)	1 (36.0)	–	159 (6.2)	15.5 (0.1)
7	–	35 (5.5)	75 (23.1)	30 (41.4)	4 (99.0)	3 (167.0)	4 (147.5)	5 (186.4)	–	156 (35.8)	15.2 (0.6)
8	–	–	71 (26.7)	54 (58.7)	25 (316.3)	5 (313.5)	7 (217.0)	15 (238.0)	4 (241.2)	181 (113.8)	17.7 (2.1)
9	–	–	17 (31.2)	44 (87.5)	42 (349.1)	9 (350.6)	15 (79.3)	19 (412.0)	5 (254.6)	151 (245.0)	14.8 (4.5)
10	–	–	6 (36.0)	27 (91.9)	14 (328.1)	18 (464.1)	26 (482.3)	10 (606.6)	8 (593.0)	109 (357.7)	10.7 (6.5)
11	–	–	–	6 (116.7)	3 (530.0)	18 (546.7)	9 (644.8)	4 (715.0)	5 (840.6)	45 (555.5)	4.4 (10.1)
12	–	–	–	4 (125.0)	2 (510.0)	14 (656.7)	7 (714.5)	4 (933.5)	4 (608.0)	35 (625.2)	3.4 (11.4)
13	–	–	–	–	–	5 (588.0)	3 (614.3)	4 (812.0)	–	12 (669.2)	1.2 (12.2)
14	–	–	–	–	–	–	1 (860.0)	3 (1,318.3)	–	4 (1,203.7)	0.4 (21.9)
15	–	–	–	–	–	–	–	1 (1,682.0)	–	1 (1,682.0)	0.1 (30.6)
Total	217 (1.8)	110 (3.7)	195 (24.3)	171 (70.7)	92 (328.8)	72 (493.8)	74 (458.2)	66 (513.8)	26 (523.7)	1,023 (156.7)	100.0 (100.0)
%	0.1	0.2	1.0	2.9	13.6	20.4	19.0	21.2	21.6	–	100.0

Larvae of the instar move to the most burst buds where they begin sucking. Preferentially they colonise petioles of the 3rd and 4th leaves (RUPAJS 1989). Through salivary secretions discharged into incisions during sucking, the petioles bend first and soon twist right (seldom left). The first instar of fundatrix moults for the first time when the twisting of the petiole ends (i.e. about 2 weeks after eclosion). Generally, the petiole is twisted by 1 to 2 turns, i.e. by 360 to 720 degrees. Due to the petiole swelling and lengthening gradual prolongation and extension of the turns and sealing of the forming gall occurs. In the cavity of a spiral gall, the fundatrix moults still three times and matures. In about 0.8% of galls analysed in our laboratory, 2 fundatrices occurred together.

The mature fundatrix is 1.5 to 2.2 mm long, dully yellowish with 4-segment antennas about 0.22 mm in length. It has a well developed labium and stylets. At the studied localities in 2001, fundatrices matured in the first half (or the first two decades) of June, i.e. after about a 4-week sucking. On *P. nigra* (with larger leaves on average), they matured about one week earlier than on *P. nigra* var. *italica* (with smaller leaves on average). According to CHAN and FORBES (1975), fundatrices in British Columbia mature from the second half of June to the beginning of July. Mature females are viviparous and reproduce parthenogenetically.

Fundatrices live relatively for a long time (about 2.5 months). According to TÓTH (1937), they produce about 75 (according to CHAN, FORBES 1975 about 100) offsprings of the 2nd generation (virgines). Under natural conditions of the Brno region in 2001, the first individuals of the 2nd generation occurred as early as at the beginning of June and by mid-July the predominant part of the generation was produced. In British Columbia, fundatrices reproduce as late as during July to September (CHAN, FORBES 1975). Larvae of the 1st instar are of two types: with robust hind legs and with normal hind legs (LAMPEL 1968/1969). According to the author, the robust-leg larvae grow up to apterous imagoes (virginoparae) and larvae with normal legs to winged imagoes (sexuparae).

AOKI and KUROSU (1986) found that robust-leg larvae showed a protective role and, therefore they can be called

Fig. 3. Galls of *P. spyrothecae* on the petiole of a leaf of *P. nigra.* A fundatrix died in the early stage of development. Brno-Žabovřesky, 1 October 2001

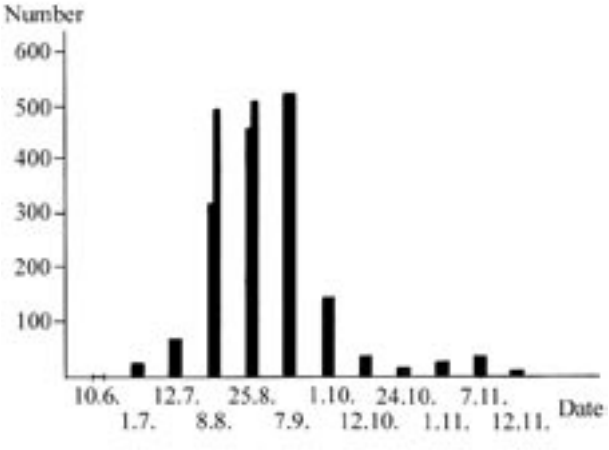

Fig. 4. The mean number of aphids of *P. spyrothecae* in galls with intact development. Brno, 2001

'soldiers'. In contrast to other known aphid species with 'soldiers', however, at least a part of the 'soldiers' of *P. spyrothecae* is not sterile because it matures into apterous adults producing the 1st instar of larvae of both types (AOKI, KUROSU 1986).

The offsprings of fundatrices (i.e. the 2nd generation of aphids) moult four times and mature to apterous females in the second half of July and in August (i.e. when the growth of galls ends – Table 2). These are up to 1.5 mm long, of light colour and distinguishable from a little larger fundatrices according to somewhat longer 6-segment antennas. According to TÓTH (1939), these females produce parthenogenetically about 30 offsprings of the 3rd generation of aphids changing into macropterous sexuparae after the last ecdysis. Mature sexuparae show 6-segment antennas with transverse sensoria on the 3rd and 4th segments. Their body is relatively heavily sclerotized, the head and thorax are black and abdomen yellow-green. Winged aphids are about 2 mm long (with backward oriented wings about 3 mm). All aphids (except the 1st instar) abundantly excrete wax fibres.

There were some 26 to 1,862 (on average 500) aphids in the examined galls with intact development of *P. spyrothecae* in the 2nd half of August and in the 1st half of September (Tables 3 and 4). According to TÓTH (1939), there are on average even 1,380 aphids in galls at the end of August. From the 2nd half of September, the average number of aphids in galls with intact development due to the exit of sexuparae gradually decreases up to mid-November when 10 aphids only were in galls (Fig. 4). According to our findings, fundatrices produce about 50 offsprings and virgines about 10 offsprings, i.e. substantially less than given in literature. Galls with more than 1,000 aphids were sporadic and it was probable that such numerous colonies were established by 2 fundatrices.

Winged sexuparae occurred at studied localities in galls from the beginning of August, at the end of August and in September being most numerous. The percentage of winged individuals (from the total number of aphids in galls with intact development) gradually increased up to a value of about 25% from August to October (November) (Table 5). The table shows that the average number of winged aphids in galls with intact development increases with gall size (from 1.5 aphids in galls 8 mm long up to 65.0 aphids in galls 25 mm long). The percentage of winged aphids, however, decreases with increasing length of galls, viz. from 9.4 (in galls 8 to 11 mm long) to 5.1% (in galls 20 to 25 mm long) (Table 5).

According to STEFFAN (1972) and others, not only the whole progeny produced by virgines but also larvae produced by fundatrices at the end of the period of reproduction develop to winged sexuparae. Mature sexuparae leave galls through slit-shaped holes and on the bark of the primary host tree they produce (always onto one place) a small number of males and females of the sexuales progeny (i.e. the 4th generation of aphids). According to CHAN and FORBES (1975), sexuparae produce maximally 6 females and 2 males and then die. The female produces on average 7 offsprings in 114 minutes (FOSTER, BENTON 1992). According to the authors, males moult four times during 42 hours (females during 51 hours). During the period, individuals of both genders are immovable.

The imagoes of sexuales are very small (over 1 mm in length), light-green, apterous, with 4-segment antennas. Males appear several hours earlier than females. Soon

Table 5. The mean number (percentage in parentheses) of winged aphids in galls of *P. spyrothecae* with intact development in relation to gall length. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Gall length	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Mean	(%)	(%)
8	–	–	–	–	–	–	–	3.0 (9.3)	–	–	0.0 (0.0)	1.5	0.4 (4.6)	(9.4)
9	0.0 (0.0)	–	14.3 (12.3)	–	–	–	–	–	1.0 (9.1)	–	–	5.1	1.2 (7.1)	
10	0.0 (0.0)	3.0 (1.4)	20.0 (9.8)	0.0 (0.0)	–	6.0 (60.0)	6.0 (37.5)	2.0 (22.2)	9.0 (36.7)	–	4.0 (40.0)	4.9	1.1 (17.0)	
11	2.3 (0.9)	4.0 (1.4)	25.5 (9.6)	–	–	6.0 (3.9)	–	6.0 (42.9)	4.0 (11.8)	–	–	8.0	1.9 (5.4)	
12	4.5 (1.6)	1.5 (0.5)	30.4 (10.9)	12.5 (8.1)	16.0 (5.9)	7.0 (8.8)	3.0 (23.1)	7.0 (31.8)	3.0 (54.5)	–	–	13.2	3.1 (8.9)	(7.8)
13	16.6 (4.9)	10.7 (3.1)	36.6 (8.6)	15.5 (4.9)	3.4 (1.5)	22.0 (15.6)	6.0 (18.8)	0.0 (0.0)	0.0 (0.0)	4.0 (8.7)	0.0 (0.0)	19.4	4.5 (5.8)	
14	5.5 (1.5)	5.7 (1.4)	50.6 (8.2)	15.7 (4.1)	27.5 (5.3)	10.0 (6.8)	2.0 (100.0)	1.0 (11.5)	9.0 (9.0)	8.0 (20.0)	–	15.0	3.5 (5.7)	
15	5.8 (1.4)	14.5 (2.4)	55.7 (12.1)	22.4 (4.3)	24.9 (5.0)	5.5 (6.8)	16.0 (45.7)	8.0 (36.4)	5.0 (43.5)	–	30.0 (50.0)	20.6	4.8 (11.4)	
16	30.0 (4.8)	5.4 (1.1)	63.9 (8.4)	22.3 (3.6)	10.0 (1.6)	–	–	–	12.0 (31.6)	–	–	24.1	5.6 (4.5)	(5.8)
17	–	9.4 (1.7)	80.0 (14.7)	30.0 (5.8)	28.5 (4.0)	60.0 (13.2)	10.0 (55.6)	4.0 (11.4)	0.0 (0.0)	9.7 (27.8)	–	26.3	6.1 (9.1)	
18	–	5.9 (0.9)	75.0 (6.8)	48.3 (7.2)	–	–	27.0 (18.5)	–	1.5 (8.6)	–	–	24.4	5.7 (5.1)	
19	–	5.9 (0.9)	–	50.0 (6.4)	50.0 (4.9)	–	–	–	–	–	–	21.9	5.1 (2.6)	
20	–	14.0 (2.2)	–	60.0 (7.4)	–	–	–	–	–	–	–	29.3	6.8 (3.9)	(5.1)
21	–	23.0 (3.6)	–	58.0 (6.8)	–	58.0 (20.3)	–	–	–	–	–	44.0	10.2 (8.2)	
22	–	0.0 (0.0)	–	61.5 (6.8)	–	–	–	–	–	–	–	41.0	9.5 (4.5)	
23	–	0.0 (0.0)	–	–	–	–	–	–	–	–	–	0.0	0.0 (0.0)	
24	–	–	–	66.0 (5.4)	–	–	–	–	–	–	–	66.0	15.4 (5.4)	
25	–	–	–	65.0 (3.9)	–	–	–	–	–	–	–	65.0	15.1 (3.9)	
Total	7.3 (2.1)	8.0 (1.6)	43.9 (9.8)	28.1 (5.1)	20.5 (3.7)	16.4 (13.0)	10.0 (42.7)	3.7 (20.4)	4.1 (24.6)	7.9 (21.1)	2.2 (31.7)	18.8	100.0 (7.4)	(7.4)

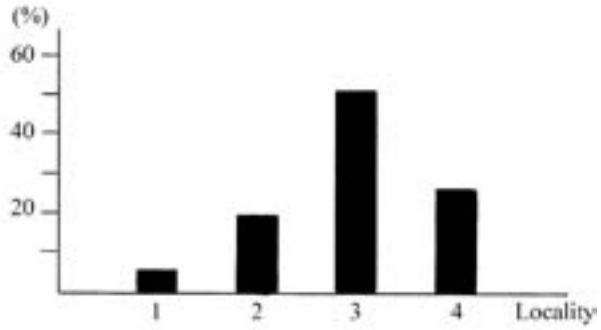

Fig. 5. The percentage of galls of *P. spyrothecae* in the basal quarter of a petiole (1) and in the last quarter of a petiole close to the leaf blade (4). Brno, 2001

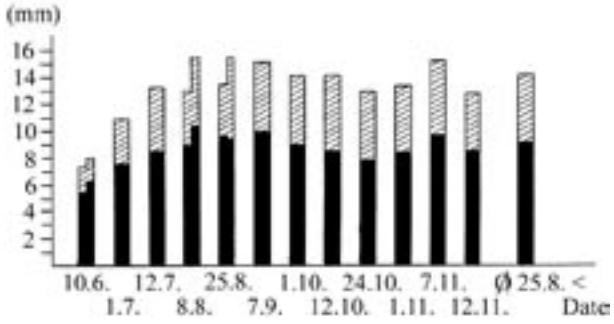

Fig. 6. The mean length of galls (solid and dashed columns) and width of galls (solid columns) of *P. spyrothecae* with intact development (with the exception of abandoned galls). Brno, 2001

after eclosion, adults mate. Fertilized females begin to excrete wax fibres and search for suitable slits in bark. The females lay into them always one egg densely covered with wax fibres. The eggs are initially whitish, later on dark-brown. Males live usually less than 3 days, females 5 days (FOSTER, BENTON 1992). Sexuales do not take any food and, therefore, their mouth parts are stunted.

LOCALIZATION OF GALLS

The majority of galls of *P. spyrothecae* on *P. nigra* var. *italica* (and often also on *P. nigra*) at localities under investigation occurred in basal parts of crowns. Usually 1 gall occurred per petiole, exceptionally up to 3 galls. In a riparian and accompanying stand along the Svratka river, 1 gall occurred in 95.7% (and 2 galls in 4.3%) of infested leaves. On *P. nigra* var. *italica,* 1 gall occurred in 96.5% (and 2 galls in 3.5%) of infested leaves at the locality. On *P. nigra* in Brno-Žabovřesky, 1 gall occurred in 81.7, 2 galls in 15.9 and 3 galls in 2.4% of infested leaves. On *P. nigra* in Brno-Komín, galls of *P. spyrothecae* occurred often together with galls of *P. populinigrae* (Schrank) in the same leaves. On the petioles of several leaves of *P. nigra* var. *italica* in Bílovice nad Svitavou, galls of *P. spyrothecae* occurred together with 1 to 2 galls of *P. bursarius* (L.). If compared with galls of *P. bursarius*, galls of *P. spyrothecae* were located on petioles always more closely to the leaf blade (see also PERKINS 1997).

Galls of *P. spyrothecae* were localized in various parts of petioles. The majority (50.3%) of galls occurred in the 3rd quarter of the petiole and much fewer (25.3%) galls in the 4th quarter of the petiole (i.e. close to the leaf blade). In the 2nd quarter and in the basal quarter of the petiole, 18.9 and only 5.5% of galls, respectively were located. No differences were found in the localization of galls on *P. nigra* and *P. nigra* var. *italica* (Table 6, Fig. 5).

SIZE OF GALLS WITH THE INTACT DEVELOPMENT OF APHIDS

The beginning of the formation of *P. spyrothecae* galls occurs within the period of poplar budbreak being considerably dependent on weather. At localities under investigation in 2001, galls closed in mid-May and as early as in mid-June reached a half of their final size (Fig. 6). Growth of galls continued in July and ended in August. Galls with intact development on *P. nigra* var. *italica* reached a greater average size (i.e. in August) after finishing their growth than galls on *P. nigra*. Galls on *P. nigra* var. *italica* in Brno-Komín and Brno-Jundrov were on average

Table 6. The number (percentage in parentheses) of galls of *P. spyrothecae* according to their position in various parts of petioles. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	Total
In the basal quarter	40 (15.4)	4 (3.1)	19 (8.5)	6 (2.2)	2 (1.4)	1 (0.9)	6 (2.8)	17 (11.0)	1 (0.8)	4 (2.3)	100 (5.5)
In the second quarter	75 (28.7)	15 (11.5)	61 (27.5)	46 (17.1)	25 (17.9)	7 (6.1)	20 (9.5)	40 (26.0)	21 (16.7)	31 (17.4)	341 (18.9)
In the third quarter	100 (38.3)	60 (46.2)	91 (41.0)	147 (54.7)	84 (60.0)	74 (64.9)	99 (46.7)	70 (45.5)	80 (63.5)	104 (58.4)	909 (50.3)
In the fourth quarter	46 (17.6)	51 (39.2)	51 (23.0)	70 (26.0)	29 (20.7)	32 (28.1)	87 (41.0)	27 (17.5)	24 (19.0)	39 (21.9)	456 (25.3)
Total	261 (100.0)	130 (100.0)	222 (100.0)	269 (100.0)	140 (100.0)	114 (100.0)	212 (100.0)	154 (100.0)	126 (100.0)	178 (100.0)	1,806 (100.0)

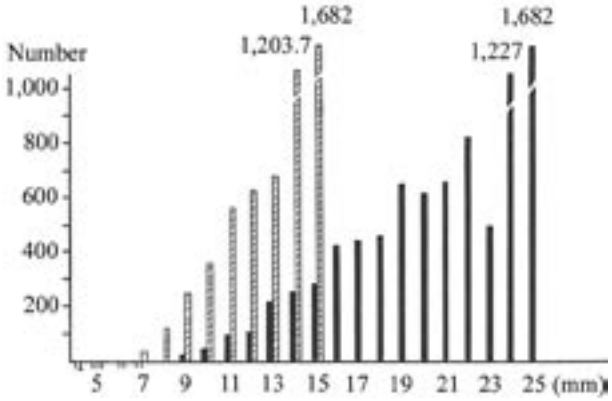

Fig. 7. The mean number of aphids of *P. spyrothecae* in galls with intact development as related to their length (solid columns) and width (dashed columns). Brno, 2001

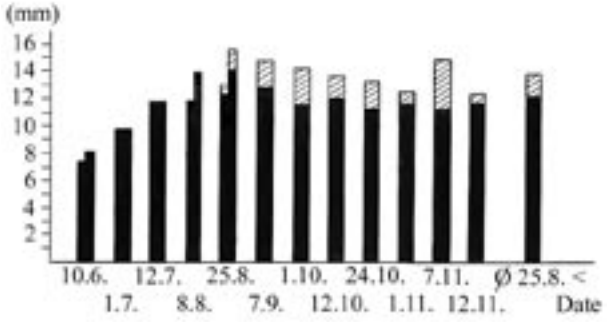

Fig. 8. The mean length of all galls of *P. spyrothecae* (solid columns) and galls with hover fly larvae (solid and dashed columns). On 8 August, the length of galls with hover flies was smaller (10.9 and 13.0 mm) than the length of all galls

15.5 mm long and 10.0 mm wide and in Brno-Černá Pole 15.3 mm long and 9.8 mm wide. On the other hand, galls on *P. nigra* in Brno-Komín and Brno-Jundrov were only 13.2 mm long and 9.3 mm wide and in Brno-Žabovřesky only 13.7 mm long and 9.0 mm wide. It means that galls with intact development on *P. nigra* var. *italica* were on average by 14.9% longer and by 8.8% wider than on *P. nigra*. Galls quite abandoned by aphids rank also in the category of galls with intact development. These galls were evaluated in the paper separately. With respect to an average size (13.9 × 9.0 mm), abandoned galls do not differ from other galls with intact development (Table 2).

The size of galls (i.e. length and width) with intact development is related to the abundance of aphid colonies (Tables 3 and 4, Fig. 7). With increasing size of galls the number of aphids in galls on *P. nigra* and *P. nigra* var. *italica* significantly increases. The abundance of aphid colonies in galls with intact development on both host species was compared in August 2001 (i.e. in the period of culmination of aphid quantity). While in galls on *P. nigra* there were on average 328.8 and 458.2 aphids on 8/8 and 25/8, respectively, on *P. nigra* var. *italica* there were on average 493.8 and 513.8 aphids on 8/8 and 25/8, respectively (Table 3). It follows that in galls on *P. nigra* var. *italica*, at least by 4% more aphids develop than in somewhat smaller galls on *P. nigra*.

The conclusion, however, does not correspond with the results of analyses of galls taken on *P. nigra* in Brno-Žabovřesky on 7 September. On that date, an extraordinarily high average number of aphids (523.7) was derived from mere 26 galls with intact development (Tables 1 and 3).

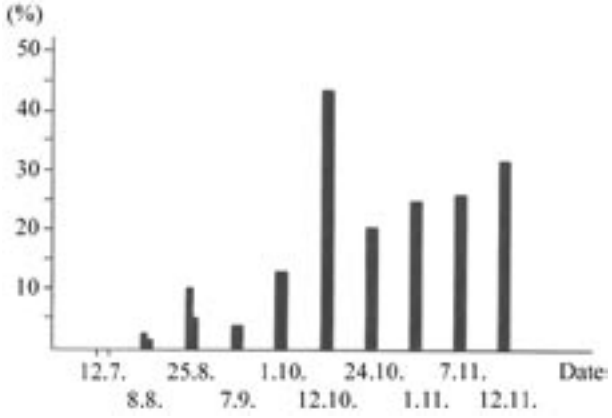

Fig. 9. The percentage of winged aphids of *P. spyrothecae* in galls with intact development. Brno, 2001

SIZE OF GALLS WITH THE DISTURBED DEVELOPMENT OF APHIDS

In the place of sucking of fundatrices, the petioles of young freshly flushed leaves bend, twist and swell (GERHARDT 1922). Through the hypertrophy and hyperplasia of petiole tissues the formation of a closed spirally twisted gall occurs. The galls grow intensively by the continuing sucking of fundatrices. In the period of maturation of fundatrices and production of the first offsprings the galls reach roughly their half size. From the beginning of June, aphids of the 2nd (and later to a smaller extent also of the 3rd) generation take part in the next growth of galls. The growth of galls with intact development ceases during August.

It happens rather frequently that a part (in Brno about 5%) of fundatrices dies for various reasons (e.g. due to predatory aphids) already in the 1st instar, i.e. in the period of the bending and twisting of petioles. Another part of fundatrices (in Brno-Komín and Brno-Jundrov about 6%, in Brno-Žabovřesky about 3%) dies in the next instar even before the beginning of reproduction (Table 1). After their death, petiole deformities and already closed small galls stop to change their size and form. At the studied localities, the mean length of undeveloped galls (bent and twisted petioles) was 4.2 mm and width 3.1 mm. The mean length of closed galls with died immature fundatrices amounted to 6.0 mm and width 4.8 mm (Table 2).

Table 7. Results of the analysis of galls of *P. spyrothecae* occupied with larvae of *Leucopis puncticornis* and galls with intact development. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Total (from 24/10 inc.)
Percentage of galls with larvae of *Leucopis*	4.0	15.4	12.2	4.3	7.5	13.7	13.0	9.4	25.2	30.2	39.0	34.9	30.3	3.9	30.2	27.9
Mean number of live aphids with larvae of *Leucopis*	1.5	3.4	11.4	47.0	6.0	4.5	1.5	1.0	0.2	0.4	0.3	0.0	0.0	4.0	0.0	0.1
Mean number of live aphids in galls with intact development	1.8	3.7	24.3	70.7	328.8	493.8	458.2	513.8	523.7	145.6	37.4	16.7	25.5	39.0	10.0	22.1
Mean length of *Leucopis* larvae (mm)	1.0	1.0	1.9	4.0	5.0	5.0	5.5	5.5	–	–	–	–	–	–	–	–
Length of *Leucopis* larvae (from–to) (mm)	0.8–1.2	0.8–1.2	1–3	2–5	4–6	4–6	5–6	5–6	–	–	–	–	–	–	–	–

Table 8. Mean number of live aphids (and % of live winged aphids) of *P. spyrothecae* in galls with intact development and in galls with bugs *Anthocoris minki*. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Gall content	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Total (from 24/10 inc.)
Mean number of aphids with intact development	1.8	3.7	24.3	70.7	328.8	493.8	458.2	513.8	523.7	145.6	37.4	16.7	25.5	39.0	10.0	22.0
Mean number of live aphids in galls with *Anthocoris*	1.1	–	8.7	0.5	0.0	37.7	20.2	66.8	0.1	0.1	0.3	0.2	0.0	0.0	0.2	0.1
Percentage of live aphids in galls with *Anthocoris*	61.1	–	35.8	0.7	0.0	7.6	4.4	13.0	0.0	0.1	0.8	1.2	0.0	0.0	2.0	0.5
Percentage of live winged aphids in intact galls	–	–	–	–	2.1	1.6	9.8	5.1	3.7	13.0	42.7	20.4	24.6	21.1	31.7	24.1
Percentage of live winged aphids in galls with *Anthocoris*	–	–	–	–	0.0	0.0	13.6	5.7	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0

Table 9. Results of the analysis of *P. spyrothecae* galls occupied with bugs *Anthocoris minki*. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls with *Anthocoris*	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Total (from 24/10 inc.)
Percentage of galls with *Anthocoris*	0.4	–	11.9	8.6	6.7	17.0	32.2	23.3	12.6	9.9	14.5	24.3	24.3	49.3	22.6	27.8
Mean number of *Anthocoris* in galls	1.0	–	1.0	1.3	1.3	1.1	2.0	1.3	1.4	0.9	0.4	0.2	0.1	0.1	0.2	0.2
Number of *Anthocoris* in galls (from–to)	1	–	1	1–2	1–2	1–3	1–10	1–7	1–6	1–2	1	1	1	1	1	0–1
Mean length of *Anthocoris* (mm)	0.9	–	1.5	1.7	1.8	1.8	1.9	1.8	2.7	2.4	2.9	3.1	3.8	3.8	3.7	3.6
Length of *Anthocoris* from–to (mm)	0.9	–	0.5–3	0.5–3	1–4	1–4	1–3.5	1–4	1.5–4	1–4	2–4	3–4	3.5–4	3.5–4	3.5–4	3–4
Mean number of *Anthocoris* exuviae in galls	–	–	–	–	–	1.0	2.0	1.3	2.0	2.2	2.5	2.0	2.3	2.6	2.2	2.3
Number of *Anthocoris* exuviae (from–to)	–	–	–	–	–	1	1–4	1–2	1–4	1–5	1–15	1–7	1–8	1–12	1–4	1–12
Percentage of galls with *Anthocoris* exuviae	–	–	–	–	–	8	15	25	30	55	68	80	95	95	83	90
Percentage of galls with adults of *Anthocoris*	–	–	–	–	–	–	–	10	15	25	50	66	100	50	50	71

The size differentiation of galls is also affected by the later death of fundatrices and their offsprings if, of course, the death occurs still in the period of intensive assimilatory activity of trees (in June to July or at the beginning of August). While the galls with intact development of aphids grow in this period rapidly, galls occupied with insect predators stop their growth. In the studied semi-grown galls (i.e. already in the 1st half of June), larvae of the predatory fly *Leucopis puncticornis* Meig. occurred very often (Table 7). These larvae killed the majority of aphids in occupied galls by the beginning of August. With respect to the relatively early disposal of aphid colonies the galls stopped to grow already during July. The grown-up galls with a fly were on average only 11.8 mm long and 8.1 mm wide. Against the galls with intact development, they were 16.9% shorter and 12.0% narrower (Table 2).

Bugs *Anthocoris minki* Dohrn belong to ordinary predators of *P. spyrothecae* in Brno region. The bug gets through primary fissures into galls from June to November (Tables 8 and 9). It begins to appear in galls at the same time as *L. puncticornis* and causes similar reduction of gall size. Grown-up galls with a bug were on average 11.9 mm long and 8.2 mm wide (Table 2).

The best-known natural regulators of *P. spyrothecae* are predatory hover flies *Heringia heringi* (Zett.) and *Pipiza festiva* Meig. Both predators occupy galls and kill aphid colonies much more later than *L. puncticornis*. Therefore, their final size does not differ significantly from galls with intact development. The analysed grown-up galls with hover fly larvae were on average 13.8 mm long and 9.0 mm wide (Fig. 8). Against the grown-up galls with intact development, they were on average only by 2.8% shorter and 2.2% narrower (Table 2). KURIR (1963) mentioned the more abundant occurrence of *H. heringi* and *P. festiva* larvae in large galls of *P. spyrothecae*, however, his assumption was not supported by measurements of galls.

Dynamics of the growth of galls at the localities under study was also rather frequently affected by common action of *L. puncticornis* and *A. minki* or by a not specified caterpillar from the family *Pyralidae.* Spiders (*Araneida*), another predatory insects and birds showed negligible effects on the gall size differentiation. Insects ate mainly tiny galls of average size of 8.1 × 5.9 mm whereas birds pecked out the largest galls only of average size of 14.7 × 10.1 mm.

Galls with dying and dead aphids owing to the late opening of galls appear to be a special category. In the 2nd half of July, in August and in the 1st half of September, aphids produce considerable amounts of whitish-grey droplet-like excrements. In August, the edges of 0.5 to 3 mm thick gall walls somewhat open by a slit-shaped or oval hole 1 to 5 mm in length and 0.3 to 0.5 mm in width. The beginning of opening the galls corresponds with the beginning of the formation of winged sexuparae (Fig. 9). Through the exit holes, excrements are partly removed from galls and the inner space of galls is ventilated. However, if the early or adequately large opening of the galls does not occur, small droplets of a diameter of 0.1 to 1 mm accumulate in the gall gradually merging into larger droplets (as large as 10 mm in diameter). The environment of aphids impairs gradually to such an extent in these galls that their colonies die during September and October. Physiologically weakened aphids are often subject to diseases (mainly viroses and mycoses). As the restriction of living functions of aphids in unopened galls occurs after the gall growth culmination only, the galls reach rather considerable dimensions (about 12.7 × 8.7 mm) (Table 2).

OPENING OF GALLS

In the 2nd half of August (i.e. after growth termination) galls usually open. The shape and position of emergence holes are given in Table 10. The majority (36.3%) of galls open through a slit-shape hole and a large part (24.9%) through a slit-shape and oval hole (Fig. 10.). 16.9% of galls are opened through one oval hole (less frequently through three holes) on the distal end, 3.0% of galls are opened through a hole on the base of the gall and 4.6% of galls through a hole in the central part. Some 14.3% of galls remain without any hole until winter. It is of interest that the majority of oval holes occurs in the lower part of galls. So the aphids can remove excrements more easily (Table 10).

Galls with intact development always usually open through one oval or oval/slit-shaped hole. Galls with larvae of hover flies and with bugs also always open, viz. by a slit-shaped or oval hole and/or by both holes. Only

Fig. 10. The open gall of *P. spyrothecae* on the petiole of a leaf of *P. nigra.* Brno-Žabovřesky, 1 October 2001

Table 10. The appearance and position of holes in galls of *P. spyrothecae*. Brno, 1 Oct. 2001

Galls	Number of galls	(%)
With slit-shaped hole	86	36.3
With slit-shaped and oval hole	59	24.9
With distal oval hole	40	16.9
With basal oval hole	7	3.0
With central oval hole	11	4.6
Closed	34	14.3
Total	237	100.0

a smaller part of galls with puparia of *L. puncticornis* opens at the end of summer and in autumn by a slit-shaped or oval hole or by both holes and a greater part remains closed. Closed galls open usually as late as in spring prior to the eclosion of the fly.

Galls with a dead sexually immature fundatrix and the majority of galls with aphids drowned in their own excrements do not open in the current year. The markedly oval form of many emergence holes and their predominant localization in the bottom (distal) part of galls signal that aphids probably participate in their formation (perhaps by the mechanical irritation of tissues around the mouth).

CONTROL FACTORS

Through various regulation factors (particularly insect predators, late or insufficient opening of galls and disease originators) the proportion of galls with the intact development of *P. spyrothecae* gradually decreases from 100% to about 8% during June to October (Fig. 11).

Leucopis puncticornis Meig.

The fly *Leucopis puncticornis* Meig. (*Chamaemyiidae*) ranks among the most abundant and most important predators of apterous forms of the studied aphid in galls on

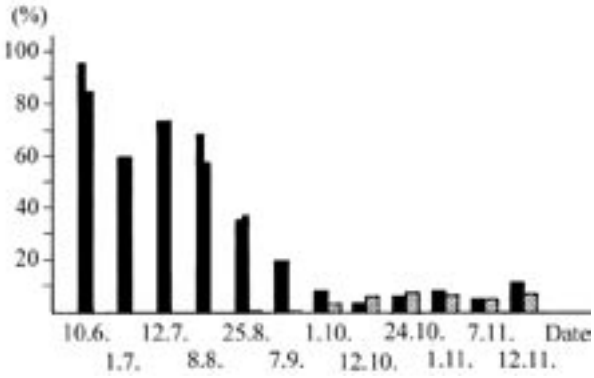

Fig. 11. The percentage of galls of *P. spyrothecae* with intact development (solid columns) and abandoned galls (dashed columns). Brno, 2001

Fig. 12. The puparium of *Leucopis puncticornis* in a gall of *P. spyrothecae* after the removal of its part. Brno-Žabovřesky, 1 October 2001

P. nigra and *P. nigra* var. *italica* in Brno. The larvae of the fly attacked 7.5 to 15.4% of galls on *P. nigra* and 4.0 to 13.7% of galls on *P. nigra* var. *italica* in Brno-Komín and Brno-Jundrov in 2001. Most galls (25.2 to 39.0%) were attacked by the fly on *P. nigra* in Brno-Žabovřesky, least (3.9%) on *P. nigra* var. *italica* in Brno-Černá Pole (Tables 1 and 7). In the small part of galls, together with *L. puncticornis* bugs *A. minki* were found. Some 0 to 6.5% (on average about 2.0%) of all galls were occupied by both predators in particular controls. In contrast to the larvae of hover flies *Heringia heringi* and *Pipiza festiva*, one *L. puncticornis* larva only can be developed in one gall.

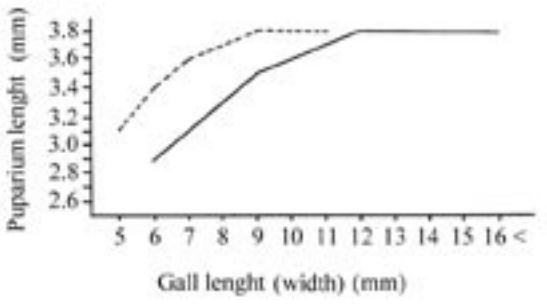

Fig. 13. Relation between the mean length (solid line) and width (dashed line) of galls of *P. spyrothecae* and the mean length of puparia of *Leucopis puncticornis*

The first larvae of *L. puncticornis* occur in *P. spyrothecae* galls as early as at the beginning of June, i.e. at the beginning of the period of reproduction of fundatrices. During June and July, the larvae of the fly rapidly develop so that at the end of July and at the beginning of August, the first puparia occur in galls (Fig. 12). The first grown-up larvae 5 to 5.5 mm in length occur sporadically even in the 2nd half of August. The larvae finally kill the fundatrix during their development and usually all its offsprings. In 20% of attacked galls only about 0.2% aphids survive.

At the end of summer and in autumn, winged individuals (sexuparae) can therefore occur sporadically with the fly puparia in galls. The galls are mostly closed in autumn. The fly winters in galls as a puparium and later develops in spring of the next year.

Puparia of *L. puncticornis* are 2.9 to 3.8 mm (on average 3.7 mm) long, brown, white-mealy. Their size increases with gall dimensions (Fig. 13). Puparia of the fly were found in galls of *P. spyrothecae* rather infrequently by DUŠEK and KŘÍSTEK (1959) at 5 localities in southern Moravia. According to the authors, the regulatory importance of the predator is small.

Anthocoris minki Dohrn

A tiny (max. 4 mm long) predatory bug *Anthocoris minki* Dohrn (*Anthocoridae*) is a common predator of *P. spyrothecae* (Fig. 14). Its abundant occurrence and decimating effects on the colonies of the aphid were mentioned e.g. by TÓTH (1939) and DUŠEK and KŘÍSTEK (1959). FOSTER (1990) and FOSTER and RHODEN (1998) reported on the effective defensive role of robust-leg larvae of the 1st instar of the aphid to insect predators (including *A. minki*).

The bug occurs abundantly from spring to autumn. It attacks all developmental stages of the aphid both in galls and outside them. The bug penetrates into galls even through minute slits killing always the whole aphid colony in the gall (Table 8). On *P. nigra* and *P. nigra* var. *italica* in Brno-Komín and Brno-Jundrov, the bug occupied 32.2 and 23.3% of galls, respectively, until 25 August 2001. On *P. nigra* in Brno-Žabovřesky, it occupied 24.3% of galls until November and on *P. nigra* var. *italica* in Brno-Černá Pole even 49.3% of galls (Table 9). The bugs occurred less abundantly also in galls occupied with the fly *L. puncticornis* and as a rarity also in galls with larvae of hover flies. In galls with bugs, on average 0.1 to 2.0 living bugs

Fig. 14. Four nymphs and two imagoes of *Anthocoris minki* obtained from galls of *P. spyrothecae* on *P. nigra* var. *italica*. Brno-Komín, 25 August 2001

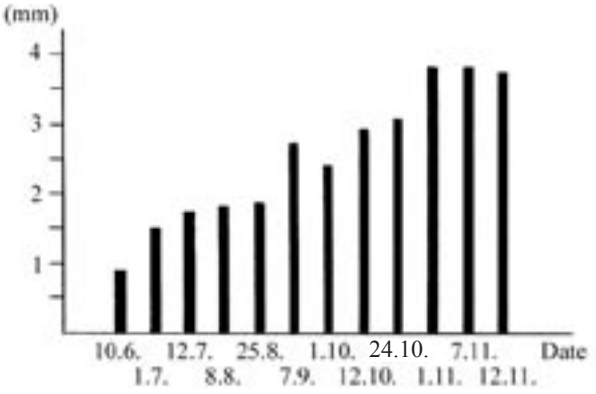

Fig. 15. The mean length of *Anthocoris minki* in galls of *P. spyrothecae.* Brno, 2001

were present. The highest mean number of living bugs (2.0) was found in galls on *P. nigra* in Brno-Komín on 25 August 2001. Even 10 bug nymphs were found per gall there. In the case of food shortage, the bugs leave galls completing their development in other suitable galls. Galls with bugs are always partly open by a slit-shaped or oval hole or by both holes.

The length of *A. minki* bugs gradually increases from 0.9 to 3.5–4 mm (on average 3.7 mm) during June to November (Fig. 15). The bugs moult in galls and the exuviae remain in the galls. The first exuviae were found in the studied galls in August. For example in galls on *P. nigra* in Brno-Žabovřesky, about 2.5 (max. 15) exuviae were found on 12 October 2001. In galls on *P. nigra* var. *italica* in Brno-Černá Pole, about 2.6 (max. 12) exuviae were observed on 7 November 2001 (Table 9). The adults of the bug occurred in galls as late as in the 2nd half of August and their number increased until November. Imagoes winter at dry hidden places outside galls. Their development is univoltine.

Heringia heringi (Zett.) and *Pipiza festiva* Meig.

According to DUŠEK and KŘÍSTEK (1959), hover flies *Heringia heringi* (Zett.) and *Pipiza festiva* Meig. (*Syrphidae*) are common predators of aphids of the genus *Pemphigus*. They are fully adapted to the life in cecidia so that it is not possible to keep them successfully on free-living aphids (DUŠEK, LÁSKA 1966). KURIR (1949/1950) deals with the occurrence and bionomics of *Heringia virens* (F.) and *P. festiva* in galls of *P. spyrothecae* on *P. nigra* var. *italica* in the environs of Vienna. According to KURIR (1949/1950), 15 to 48% of galls were attacked by the hover fly larvae and in one gall, 1 (max. 3) hover fly usually developed. Through the inspection of the material obtained from KURIR, DUŠEK and KŘÍSTEK (1959) found that, as a matter of fact, it was not *H. virens* (F.) but *H. heringi* (Zett.). In 1957 and 1958, these authors studied the occurrence of larvae of *H. heringi* and *P. festiva* in a total of 10 localities in Bohemia, Moravia and Silesia. The lowest attack of galls (2.7%) was found in Brno-

Table 11. The occurrence of eggshells after eclosion of hover fly larvae in galls of *P. spyrothecae*. Brno, 1 Oct. 2001

Number of eggshells	Number of galls	(%)
0	55	23.2
1	54	22.8
2	35	14.8
3	29	12.2
4	26	11.0
5	14	5.9
6	9	3.8
7	6	2.5
8	4	1.7
9	2	0.9
10	2	0.8
11	1	0.4
Total	237	100.0
Mean	2.4	–

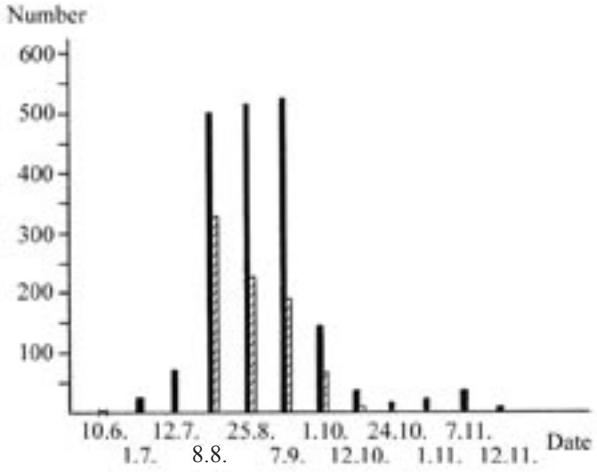

Fig. 17. Average number of live individuals of *P. spyrothecae* in galls with intact development (solid columns) and in galls with hover flies (dashed columns – see Table 9). Brno, 2001

Černá Pole and the highest (36.2%) at Vojkovice in southern Moravia. At all localities (with the exception of one), the species *P. festiva* dominated as for its number. Its proportion in the total population of hover fly larvae amounted to 81% on average. Many new findings on the occurrence and biology of *H. heringi* and *P. festiva* were reported by KURIR (1963) in his further paper.

The bionomics of both hover fly species is very similar. Grown-up larvae winter on fallen poplar leaves and other components of the litter surface layer including broken twigs and stones, less frequently also in galls. Through the flattened ventral body side they are attached to smooth objects on their bottom (shaded) side by means of salivary gland secretions. They survive snow, ice and low temperatures (even –24ºC) very well (KURIR 1949/1950).

With the advent of higher spring temperatures, the larvae pupate, viz. most frequently in the place of wintering. Only larvae wintering inside galls creep out from galls and

Fig. 16. Grown-up larvae of *Pipiza festiva* from galls of *P. spyrothecae* on *P. nigra*. Brno-Žabovřesky, 1 Ocober 2001

settle down on galls, stones, fallen leaves, surface roots, etc. The eclosion of imagoes is preceded by the formation of droplet-shaped or pear-shaped puparia stuck on the base. The pupa period in *H. heringi* takes on average 10.5 days, in *P. festiva* 13.5 days (KURIR 1963). In the environs of Vienna, *H. heringi* emerges from 5 May to 3 August and *P. festiva* from 5 May to 20 August and adults of both species live 6 days on average (KURIR 1949/1950, 1963).

Imagoes visit flowers of various plants and feed on their pollen or nectar. During the obligatory maturation feeding, they sexually mature and after copulation taking place in the air (like in other hover flies) females lay chalky and conspicuous eggs. They are placed most frequently into helical notches or various depressions on the gall surface (Fig. 1). Eggs adhere to galls with their chorions for a long time even after their eclosion, namely until the autumn leaf fall. On 1 October 2001, 1 to 11 (on average 3.1) emerged eggs occurred on galls on *P. nigra* in Brno-Žabovřesky. From the total number of 237 galls under investigation 182 (76.8%) galls were laid by hover flies (Table 11) while growing and grown-up hover fly larvae occupied 56 (23.8%) galls only. From 562 eggs laid on 182 galls almost 100% larvae of the 1st instar emerged, however, 56 (10.0%) larvae only successfully developed in galls. The majority (90%) of larvae died, namely particularly when looking for holes to penetrate into galls. High (73%) mortality of hover flies (mainly in the stage of the 1st instar) was also found by DUŠEK and KŘÍSTEK (1959).

The hover fly larvae undergo 3 growth stages during their development and grow up in October (Fig. 16). Usually 1 larva develops in one gall. For example on 7 September 2001 in Brno-Žabovřesky, 74.3% galls were occupied with 1 larva, 23.1% galls with 2 larvae and 2.6% galls with 3 larvae. The larvae totally suck aphids (fundatrices, virgines and sexuparae) except the integuments. The highest consumption was observed in larvae of the

Table 12. Results of the analysis of *P. spyrothecae* galls occupied with larvae of hover flies *Heringia heringi* and *Pipiza festiva* and galls with intact development. Dates of gall sampling in *P. nigra* are given in normal letters, in *P. nigra* var. *italica* bold letters. Brno, 2001

Galls	**10/6**	10/6	1/7	**12/7**	8/8	**8/8**	25/8	**25/8**	7/9	1/10	12/10	24/10	1/11	**7/11**	12/11	Total (from 24/10 inc.)
Percentage of galls with larvae of *Syrphidae*	–	–	?	?	3.7	3.2	3.8	6.7	28.9	23.8	22.0	13.6	13.3	6.5	13.2	12.4
Mean number of live aphids in galls with *Syrphidae*	–	–	?	?	260.5	330.7	89.4	224.7	191.7	67.4	10.3	1.4	1.0	0.0	0.7	1.0
Mean number of live aphids in galls with intact development	1.8	3.7	24.3	70.7	328.8	493.8	458.2	513.8	523.7	145.6	37.4	16.7	25.5	39.0	10.0	22.1
Percentage of winged aphids in galls with *Syrphidae*	–	–	–	–	3.2	1.9	14.8	4.7	1.2	2.7	17.0	14.3	14.3	0.0	5.0	12.2
Percentage of winged aphids in galls with intact development	–	–	–	–	2.2	1.6	9.8	5.5	3.9	11.2	26.7	22.2	16.1	20.2	21.7	19.1
Mean length of hover fly larvae (mm)	–	–	?	?	4.0	4.2	5.3	5.4	6.5	7.8	9.3	9.0	9.0	8.9	9.0	9.0
Length of hover fly larvae (from–to) (mm)	–	–	?	?	2–6	2–6	3–9	3–10	4–10	5–11	6–11	7–11	7–11	8–10	8–10	7–11

Table 13. The length of *Heringia heringi* and *Pipiza festiva* hover fly larvae and mean number of live individuals of *P. spyrothecae* in galls with one hover fly larva. Brno, 7 Sep. 2001

Length of hover flies (mm)	Number of galls	Mean number of live aphids
< 5.0	4	341.0
5.1–7.0	4	354.2
7.1–9.0	7	155.7
> 9.1	14	108.0
Total	29	185.6

3rd instar that occurred at the studied localities from mid-August to mid-October or even later. They gradually killed all (or almost all) aphids so that at the end of October and at the beginning of November, no living aphids usually occurred in galls with hover flies (in contrast to galls with intact development) (Table 12, Fig. 17). The table shows that the percentage of living winged aphids in galls with intact development is usually much higher than that in galls with larvae of hover flies. The hover flies preferentially suck larger apterous aphids including winged sexuparae. Therefore, in galls occupied with larvae of hover flies the fractional part of aphids only can successfully complete its development.

Galls with larvae of hover flies are the second largest category (from the size aspect) of galls after galls with intact development (Table 2). Galls of *P. spyrothecae* are occupied with hover flies usually as late as at the end of spring and in the 1st half of summer, i.e. in the period of intensive growth of galls. In high summer when the growth of galls gradually ceases, the abundance of colonies of aphids in galls with larvae of hover flies is roughly 50% lower than in galls with the intact development of aphids. With increasing dimensions of hover fly larvae the abundance of living aphids in galls decreases (Tables 12 and 13). With the size of galls the abundance of aphid colonies in galls with intact development significantly increases (Tables 3 and 4). Therefore numerous colonies of aphids in large galls satisfy better high food requirements of hover fly larvae. Moreover, large galls offer more favourable spatial and microclimatic conditions for their development (particularly optimum air humidity and darkness). In small galls, larvae of hover flies often suffer from the shortage of food and too low moisture of the environment. Such larvae lag behind in growth and sometimes also die. Under laboratory conditions, semi-grown starving larvae often left galls and through primary emergence holes they penetrated into other galls where they completed their development.

Grown-up larvae of hover flies leave galls in October and in the 1st half of November, i.e. in the period of leaf fall. A part of larvae leaves the galls already on a tree and another part on the soil surface after leaf fall. However, the small part of larvae does not leave galls at all in autumn and winters in the galls. The larvae further develop after a long diapause that takes 7 to 8 months (according to KURIR 1963). Both species of hover flies always show univoltine development.

In a riparian and accompanying stand in Brno-Komín and Brno-Jundrov, the larvae of hover flies occupied 3.8% of galls on *P. nigra* and 6.8% of galls on *P. nigra* var. *italica*. On *P. nigra* in Brno-Žabovřesky, the larvae occupied 13.2 to 30.4% (on average 24.5%) of galls and on *P. nigra* var. *italica* in Brno-Černá Pole 6.5% of galls (Table 1). The analyses show that the larvae of hover flies belonged to the most usual and most important predators of *P. spyrothecae* in Brno.

LATE OR INSUFFICIENT OPENING OF GALLS

All galls of *P. spyrothecae* with intact development, all galls with hover flies *H. heringi* and *P. festiva*, all galls with bugs *A. minki* and a smaller part of galls with puparia of *L. puncticornis* open through distinct holes from mid-August (see Chapter Opening of Galls and Table 10). By means of these slit-shaped or oval holes, galls are partly ventilated and through the holes, liquid excrements are partly removed from the galls by living aphids. Winged aphids (sexuparae) use the holes as emergence holes. It happens rather often that the holes in the galls are not formed in time or the holes are not sufficiently large. In these more or less closed galls, aphids produce excrements during August and September filling up the large part of the inner space of galls. The insufficient environment and excessive moisture negatively affect the vitality of aphids. They gradually die, often under interaction of polyhedral viruses and entomophagous fungi. DUŠEK and KŘÍSTEK (1959) mentioned a considerable importance of mycoses (caused mainly by *Cephalosporium* sp.). The authors found them on average in 13.4% (and in Brno-Černá Pole in 13.6%) of galls.

The primary cause of disintegration of so far normally thriving colonies of aphids is incongruity between the development of aphids and the course of opening the galls. It appears that originators of diseases are markedly of secondary character because they usually attack weakened or dying (in bacteria and fungi even dead) aphids. On *P. nigra* in Brno-Žabovřesky, in 7.8% of galls as a result of the above-mentioned disorders and on *P. nigra* var. *italica* in Brno-Černá Pole, aphids died even in 19.5% of galls (Table 1). Late or insufficient opening of galls can therefore be ranked among important regulatory (control) factors of *P. spyrothecae*.

HARMFULNESS

The aphid *P. spyrothecae* is of a small economic importance (STEFFAN 1972). It can cause greater damage mainly in parks (VASILJEV et al. 1975). Host trees are considerably physiologically weakened by the mass occurrence of galls. The increment of trees is undoubtedly negatively affected by the formation of galls. Leaves with galls take up considerable amounts of assimilatory substances from host trees and prematurely wilt. In the case

Table 14. Mean size of leaves without galls and leaves with galls of *P. spyrothecae*. Some 350 leaves without galls and 350 leaves with galls were measured. Brno, 1 Oct. 2001

Leaf size (mm)	Leaves		(%)
	without galls	with galls	
Mean length of leaf blade	67	68	+1.5
Mean width of leaf blade	53	58	+9.4
Mean length of petiole	42	53	+26.2

of the aphid outbreak, receptivity of affected trees to other pests, diseases and abiotic injurious agents increases.

Studies carried out in Brno have shown that leaves with galls turn yellow and brown roughly 2 weeks earlier than leaves without galls. In spite of this, leaves with galls remain on trees usually for a longer time than leaves without galls. Petioles and galls (mainly galls with intact development) remain at least two weeks alive after the death of leaf blades, viz. mostly also a certain time after the leaf fall. Thus green petioles and predominantly green gall tissues partly compensate for the cut-off of assimilation caused by the premature death of leaf blades. CHAN and FORBES (1975) stated that leaves with galls fell sooner than leaves without galls.

The slower dying and decaying of galls with intact development allows the aphids to take food as long as 3 weeks after the death of leaf blades. For example on *P. nigra* in Brno-Žabovřesky, on average 20 aphids with delayed development occurred in 6.5 to 11.3% (on average in 8.2%) of galls with intact development even in the 2nd half of October and the 1st half of November 2001 (Tables 1 and 3). In autumn, the trophic potential of galls rapidly decreases with their gradual dying and aphids usually die in them.

Measurements of leaf blade dimensions (length and width) showed that the average area of leaves with galls was somewhat larger than the average area of leaves without galls (Table 14). Thus the assumption of CHAN and FORBES (1975) was confirmed that the galls do not cause any reduction of leaf area. However, the length of petioles is markedly greater (on average by 26.2%) in leaves with galls. It is also interesting that with the length of a leaf blade the average length of galls decreases (Table 15).

From mid-August, the galls gradually open and minute droplets of excrements (honeydew) come out from them as late as mid-October. In street alleys, the excrements often pollute the environment (for example cars parking under the attacked poplars, etc.). Sugar-containing substances included in honeydew are a welcome food for ants, bees, wasps and numerous other insects (e.g. also for the fly *Themira putris* [L.] from the family *Sepsidae* – DRAEGER, SCHEURER 1999). In the mass occurrence of galls, decorativeness of poplars grown for ornamental purposes is decreased (RUPAJS 1989; RIPKA et al. 1998; RIPKA 1999, etc.).

Table 15. Relationship between the leaf blade length and mean length of *P. spyrothecae* galls. Brno, 1 Oct. 2001

Leaf blade length (mm)	Number of leaves	(%)	Mean length of galls (mm)	(%)
45–65	76	21.7	12.6	114.5
66–75	107	30.6	12.5	113.6
76–85	101	28.8	11.5	104.5
86–105	66	18.9	11.0	100.0
Total	350	100.0	12.0	–

References

ALLEYNE E.H., MORRISON F.O., 1977. Some Canadian poplar aphid galls. Canad. Ent., *109*: 321–328.

AOKI S., KUROSU U., 1986. Soldiers of a European gall aphid, *Pemphigus spyrothecae* (*Homoptera*: *Aphidoidea*): why do they molt? J. Ethol., *4*: 97–104.

BAUDYŠ E., 1954. Zoocecidie z oblasti Slezska a přilehlých částí Moravy. Praha, SPN: 288.

BLACKMAN R.L., EASTOP V.F., 1994. Aphids on the World's Trees. London, CAB Intern., Nat. Hist. Museum: 986.

BÖRNER C., 1952. Europae centralis Aphides. Beih. 3. Weimar, Mitt. Thür. Bot. Ges.: 488.

BUHR H., 1965. Bestimmungstabellen der Gallen (Zoo- und Phytocecidien) an Pflanzen Mittel- und Nordeuropas. Bd. II. Jena, VEB G. Fischer: 1572.

DRAEGER U., SCHEURER S., 1999. The carbohydrate diet of *Themira putris* adults (*Diptera*: *Sepsidae*) living in a sewage treatment plant in Central Europe. Studia Dipterol., *6*: 67–72.

CHAN C.-K., FORBES A.R., 1975. Life-cycle of a spiral gall aphid, *Pemphigus spirothecae* (*Homoptera*: *Aphididae*), on Poplar in British Columbia. J. Ent. Soc. Brit. Columbia, *72*: 26–30.

DUŠEK J., KŘÍSTEK J., 1959. Poznámky k výskytu a bionomii larev pestřenek (*Diptera*, *Syrphidae*) v hálkách topolových dutilek. Zool. listy, *8*: 299–308.

DUŠEK J., LÁSKA P., 1966. Occurrence of syrphid larvae on some aphids. Proc. Symposium held in Liblice near Prague, Sept. 27– Oct. 1, 1965. Akad. Prague: 37–38.

FOSTER W.A., 1990. Experimental evidence for effective and altruistic colony defence against natural predators by soldiers of the gall-forming aphid *Pemphigus spyrothecae* (*Hemiptera*: *Pemphigidae*). Behav. Ecol. Sociobiol., *27*: 421–430.

FOSTER W.A., BENTON T.G., 1992. Sex ratio, local mate competition and mating behaviour in the aphid *Pemphigus spyrothecae*. Behav. Ecol. Sociobiol., *30*: 297–307.

FOSTER W.A., RHODEN P.K., 1998. Soldiers effectively defend aphid colonies against predators in the field. Anim. Behav., *55*: 761–765.

FURK C., PRIOR R.N.B., 1975. On the life cycle of *Pemphigus* (*Pemphiginus*) *populi* Courchet with a key to British species of *Pemphigus* Hartig (*Homoptera*: *Aphidoidea*). J. Ent. (B), *44*: 265–280.

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

GERHARDT K., 1922. Über die Entwicklung der Spiralbockengalle von *Pemphigus spirothecae* an der Pyramidenpappel. Z. Pflkrankh., *32*: 177–189.

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

GUSIC W.J., 1969. Contribution à la connaissance de la pemphigose du peuplier et de son agent pathogène, *Pemphigus spirothecae* (*Homoptera*, *Aphidoidea*). Biológia (Bratislava), *24*: 166–172.

JASNOŠ B.A., 1978. Sem. *Aphelinidae* – afelinidy. In: MEDVEDEVA G.S. et al., Opredelitel nasekomych evropejskoj časti SSSR. Tom III. Leningrad, Izd. Nauka: 469–501.

JESSOP L., 1983. The British species of *Anthocoris* (*Hem*., *Anthocoridae*). Ent. Month. Mag., *119*: 221–223.

KOEHLER W., SCHNAIDER, Z., 1972. Owady naszych lasów. Warszawa, PWRL: 99.

KURIR A., 1949/1950. *Pipiza festiva* Meig. und *Heringia virens* Fabr., räuberische Syrphiden auf *Pemphigus spirothecae* Pass. Wien. Ent. Rundsch., *1*: 1–4, *2*: 550.

KURIR A, 1963. Zur Biologie zweier aphidophager Schwebfliegen (*Dipt*., *Syrphidae*): *Heringia heringi* Zetterstedt und *Pipiza festiva* Meigen in den Gallen der späten Blattstieldrehgallen-Pappelblattlaus (*Pemphigus spirothecae* Passerini) auf der Pyramidenpappel (*Populus nigra* var. *pyramidalis* Spach). Z. Angew. Ent., *52*: 61–83.

LAMPEL G., 1960. Die morphologischen und ökologischen Grundlagen des Generationswechsels monözischer und heterözischer Pemphiginen der Schwarz- und Pyramidenpappel. Z. angew. Ent., *47*: 334–375.

LAMPEL G., 1968/1969. Untersuchungen zur Morphenfolge von *Pemphigus spirothecae* Pass. 1860 (*Homoptera*, *Aphidoidea*). Bull. naturforsch. Ges. Freiburg, *58*: 56–72.

LECLANT F., 1998. Les pemphigiens du peuplier et la gallogenese. A la decouverte des pucerons provoquant des galles sur les peupliers. Phytoma, *507*: 15–19.

MARCU O., SIMON D., MARCU V., 1993. Untersuchungen betreffend gallenerzeugender *Pemphigus* Arten (*Homoptera*: *Pemphigidae*). Bull. Transylvania Univ. Brasov. Ser. B *I* (Silvicult.), *35*: 1–6.

PAŠEK V., 1954. Vošky našich lesných drevín (*Homoptera-Aphidoidea*). Bratislava, SAV: 323.

PERKINS C.J., 1997. Observations concerning aphid galls on Lombardy poplar. Cecidology, *12*: 64–66.

PFEFFER A. et al., 1954. Lesnická zoologie II. Praha, SZN: 622.

RIPKA G., 1999. Arthropod pests of ornamental trees and shrubs: scale insects, aphids, mites. (Orig. in Hungarian). Növényvédelem, *35*: 623–626.

RIPKA G., REIDER K., SZALAY-MARZSÓ L., 1998. New data to the knowledge of the aphid fauna (*Homoptera*: *Aphidoidea*) on ornamental trees and shrubs in Hungary. Acta Phytopath. et Ent. Hung., *33*: 153–171.

ROBERTI D., 1938. Contributi alla conoscenza degli afidi d´Italia. Part. I. I Pemphigini del Pioppo. Boll. Lab. Zool. Gen. Agr. Portici, *30*: 169–239.

RUPAJS A.A., 1989. Tli (*Aphidoidea*) Latvii. Riga, Zinatne: 328.

SCHWERDTFEGER F., 1944, 1970. Die Waldkrankheiten. Hamburg, Berlin, Verlag P. Parey: 479, 509.

STEFFAN A.W., 1972. Unterordnung *Aphidina*, Blattläuse. In: SCHWENKE W. et al., Die Forstschädlinge Europas. Bd. I. Hamburg, Berlin, Verlag P. Parey: 162–386.

SZELEGIEWICZ H., 1968. Mszyce, *Aphidoidea*. Warszawa, PWN: 316.

TÓTH L., 1937. Entwicklungszyklus und Symbiose *Pemphigus spirothecae* Pass. (*Aphidina*). Z. Morphol. u. Ökol. T., *33*: 412–437.

TÓTH L., 1939. Über die Biologie der Blattlaus *Pemphigus spirothecae* Pass. Z. angew. Ent., *26*: 297–311.

UHLÍŘOVÁ H. et al., 1996. Symptomy poškození lesních dřevin. Praha, MZe ČR: 244.

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

Received 5 March 2002

Výskyt, vývoj a přirození nepřátelé dutilky šroubovité (*Pemphigus spyrothecae*) (*Homoptera*, *Pemphigidae*)

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ABSTRAKT: V roce 2001 byly analyzovány hálky *Pemphigus spyrothecae* Pass., které byly v týdenních až třítýdenních intervalech odebírány z *Populus nigra* a *P. nigra* var. *italica* na čtyřech lokalitách v Brně. Fundatrices tam pohlavně dospívaly v první

polovině června a během první poloviny léta rodily kolem 50 potomků. Virgines zplodily kolem 10 potomků, kteří dorůstali v okřídlené sexuparae. Okřídlení jedinci se v hálkách začínali objevovat od začátku srpna. V hálkách s neporušeným vývojem se vyvinulo průměrně 500 mšic. Hálky s neporušeným vývojem na *P. nigra* var. *italica* dorůstaly větší průměrné velikosti a obsahovaly nejméně o 4 % více mšic než hálky na *P. nigra*. Kolem 5 % fundatrices uhynulo již v 1. instaru a dalších 3–6 % ve vyšších instarech do začátku rozmnožování. Na vyšetřovaných lokalitách bylo 7,5–39,0 % hálek na *P. nigra* a 3,9–13,7 % hálek na *P. nigra* var. *italica* obsazeno mouchou *Leucopis puncticornis* Meig. (*Chamaemyiidae*). Kolem 24,3–32,2 % hálek na *P. nigra* a 23,3–49,3 % hálek na *P. nigra* var. *italica* obsadila ploštice *Anthocoris minki* Dohrn (*Anthocoridae*). Důležitým regulátorem *P. spyrothecae* byly pestřenky *Heringia heringi* (Zett.) a *Pipiza festiva* Meig. (*Syrphidae*), které zahubily mšice v 3,8–30,4 % hálek na *P. nigra* a v 6,5–6,8 % hálek na *P. nigra* var. *italica*. V srpnu (tj. na začátku tvorby okřídlených sexuparae) se většina hálek otevírala primárními štěrbinovitými nebo oválnými výletovými otvory. Část (7,8–19,5 %) hálek s dosud neporušeným vývojem však zůstala uzavřena a všechny mšice v nich zahynuly. Na urychleném hynutí mšic se často podílely choroby (hlavně mykózy). Podrobně je vyhodnocen vliv mortalitních faktorů na velikostní diferenciaci hálek. Hálky nepůsobí redukci plochy listů. Při přemnožení snižují dekorativnost topolů v uličních stromořadích. V srpnu a září z nich vypadávají tekuté exkrementy (tzv. medovice), které v obcích znečišťují životní prostředí.

Klíčová slova: *Pemphigus spyrothecae*; *Leucopis puncticornis*; *Anthocoris minki*; *Heringia heringi*; *Pipiza festiva*; vývoj; velikost hálek; škodlivost

P. spyrothecae Pass. je holocyklický monoekní zástupce čeledi *Pemphigidae*. Žije výlučně na primárním hostiteli, jímž je především *Populus nigra* L. a *P. nigra* L. var. *italica*. Na řapících listů vytváří charakteristické spirálně stočené pravé hálky, uvnitř nichž probíhá převážná část jeho vývoje. Je široce rozšířený v Evropě a začátkem sedmdesátých let minulého století byl zavlečen do Severní Ameriky. V centru evropského areálu i v některých oblastech Severní Ameriky se občas přemnožuje a někdy i škodí.

Práce přináší poznatky o výskytu, vývoji, regulačních faktorech a škodlivosti *P. spyrothecae* na *P. nigra* a *P. nigra* var. *italica* na čtyřech lokalitách v Brně. Je založena na laboratorních analýzách hálek, odebíraných v týdenních až třítýdenních intervalech v roce 2001. Od 10. 6. do 25. 8. byly hálky získávány ze starších *P. nigra* a *P. nigra* var. *italica* v břehovém a doprovodném porostu kolem řeky Svratky v Brně-Komíně a Brně-Jundrově. Soubory hálek byly z obou dřevin odebírány v tytéž dny a vyšetřovány odděleně. Po zpracování všech dostupných hálek byly od 7. 9. do 12. 11. analyzovány hálky ze středně starých *P. nigra* rostoucích v sídlišti v Brně-Žabovřeskách. Jednorázově (7. 11.) byly vyšetřeny hálky, které se nehojně vyskytovaly na starých *P. nigra* var. *italica* v Brně-Černých Polích. Byly získány tyto hlavní výsledky:

1. Fundatrices (tj. první generace mšice) se líhly v první polovině dubna v období rašení listových pupenů topolů. Sáním 1. instaru na řapících čerstvě vyrašených listů se řapíky nejdříve ohýbají a zkrucují až o 720 stupňů. Pak se fundatrices poprvé svlékají. Zduřováním a prodlužováním řapíku se vytváří spirální hálka. V dutině hálky se fundatrix třikrát svléká a v první polovině června pohlavně dospívá. V 0,8 % analyzovaných hálek se vyskytovaly dvě fundatrices. Dorostlé fundatrices jsou 1,5–2,2 mm dlouhé. Mají čtyřčlánková tykadla a dobře vyvinuté labium a stylety. Rozmnožují se od začátku června a většinu potomků (virgines), představujících druhou generaci mšic, zplodí do poloviny července. Celkem zplodí kolem 50 potomků a koncem léta hynou.
2. Potomci fundatrices se čtyřikrát svlékají a ve druhé polovině července a v srpnu pohlavně dospívají v apterní živorodé samičky. Ty jsou až 1,5 mm dlouhé s šestičlánkovými tykadly. Rodí kolem 10 potomků, kteří se vyvíjejí v okřídlené sexuparae (tj. ve třetí generaci mšice). Sexuparae jsou dlouhé kolem 2 mm. Mají šestičlánková tykadla a hlavu s hrudí černou, poměrně silně sklerotizovanou. Okřídlené sexuparae se v analyzovaných hálkách vyskytovaly od začátku srpna a hlavně koncem srpna a v září.
3. Nejvyšší počet mšic (26–1 862, průměrně 500) se v hálkách s neporušeným vývojem vyskytoval ve druhé polovině srpna a v první polovině září. Sporadické hálky s více než 1 000 mšicemi byly zřejmě vždy založeny dvěma zakladatelkami. Počet mšic v hálkách s neporušeným vývojem v důsledku výletu sexuparae od poloviny září až do listopadu klesal. Sexuparae rodí na kůře primárních hostitelských dřevin několik jedinců pokolení sexuales (tj. čtvrtou generaci mšice). Sexuales se během dvou dnů čtyřikrát svlékají. Dospělci sexuales jsou asi 1 mm dlouzí se čtyřčlennými tykadly. Oplodněné samičky kladou do štěrbin kůry jedno veliké silnostěnné vajíčko, které přezimuje.
4. Na řapíku bývá obvykle jedna (maximálně tři) hálky *P. spyrothecae*, a to nejčastěji (v 50,3 %) ve třetí čtvrtině řapíků (blíže k čepeli). Hálky s neporušeným vývojem na *P. nigra* var. *italica* dosahovaly po skončení růstu (tj. v srpnu) větší průměrné délky a šířky (15,4 × 9,9 mm) než hálky na *P. nigra* (13,4 × 9,1 mm). V hálkách s neporušeným vývojem na *P. nigra* var. *italica* se vyvinulo minimálně o 4 % více mšic než v hálkách na *P. nigra*.
5. Hálky s porušeným vývojem jsou v průměru vždy menší. Na zkoumaných lokalitách kolem 5 % fundatrices uhynulo v 1. instaru za vzniku znetvořenin

řapíku o rozměrech kolem 4,3 × 3,1 mm. Dalších 3–6 % fundatrices uhynulo v některém z dalších instarů do začátku rozmnožování. Tyto hálky dosahovaly průměrné velikosti 6,0 × 4,8 mm.

6. Během června a července (příp. začátkem srpna) se v hálkách *P. spyrothecae* často vyvíjely larvy mouchy *Leucopis puncticornis* Meig. (*Chamaemyiidae*). Na vyšetřovaných lokalitách moucha napadla 7,5–39,0 % hálek na *P. nigra* a 3,9–13,7 % hálek na *P. nigra* var. *italica*. V jedné hálce se může vyvíjet vždy jen jedna larva, která během tří instarů zahubí celou kolonii mšic. Její hnědá, bíle zaprášená puparia o délce kolem 3,7 mm se objevovala již koncem července a začátkem srpna a v hálkách zimovala. Vzhledem k časné likvidaci kolonií mšic hálky dosahovaly podprůměrné velikosti (11,8 × 8,1 mm). Vývoj je univoltinní.
7. K nejhojnějším a nejvýznamnějším predátorům mšice *P. spyrothecae* v analyzovaných hálkách i mimo ně patřila ploštice *Anthocoris minki* Dohrn (*Anthocoridae*). Ve vyšetřovaných hálkách byla nalézána od jara až do podzimu, nejhojněji pak během léta. Na *P. nigra* obsadila až 32,2 % hálek a na *P. nigra* var. *italica* až 49,3 % hálek. V hálkách bylo přítomno průměrně 0,1–2 (maximálně 10) živých ploštic. Dospělci se v hálkách objevovali od druhé poloviny srpna a jejich procentuální zastoupení (z celkového počtu ploštic) až do listopadu vzrůstalo. Ploštice *A. minki* měla na velikostní diferenciaci hálek stejný vliv jako *L. puncticornis*. Vývoj je univoltinní.
8. Důležitým regulátorem v hálkách *P. spyrothecae* byly larvy pestřenek *Heringia heringi* (Zett.) a *Pipiza festiva* Meig. (*Syrphidae*). Hálky byly obsazovány obvykle až koncem jara a v první polovině léta, tj. v době, kdy dosahovaly značné velikosti. Larvy se vyvíjely v 3,8–30,4 % hálek na *P. nigra* a v 6,5–6,8 % hálek na *P. nigra* var. *italica*. V jedné hálce byla obvykle jen jedna larva (nejvíce tři). Do konce října larvy zahubily v obsazených hálkách všechny (nebo téměř všechny) mšice. Velké hálky s početnými koloniemi mšic lépe uspokojují vysoké potravní nároky pestřenek a vytvářejí optimální prostorové a mikroklimatické podmínky pro jejich vývoj. V říjnu a v první polovině listopadu většina dorostlých larev hálky opouštěla a jen menší část v nich zimovala. Dorostlé hálky s pestřenkami patřily k nadprůměrně velkým hálkám a svou velikostí (kolem 13,8 × 9,0 mm) se příliš nelišily od hálek s neporušeným vývojem. Vývoj obou species pestřenek je univoltinní.
9. V srpnu (tj. na začátku tvorby okřídlených sexuparae) se hálky obvykle otevírají primárními štěrbinovitými nebo oválnými výletovými otvory. Jimi je vnitřní prostor částečně odvětráván a jimi jsou z hálek částečně odstraňovány tekuté výkaly (tzv. medovice). Většina oválných otvorů je na spodní straně hálek, a to na jejich distálním konci, což umožňuje snazší odstraňování exkrementů. Nedojde-li k včasnému a dostatečně velkému otevření hálek, mšice během září a října hynou. Hynutí fyziologicky oslabených mšic je často urychlováno virózami a mykózami. Na sledovaných lokalitách v důsledku inkoincidence vývoje mšic a období otevírání hálek zahynuly mšice v 7,8–19,5 % hálek. K úhynu mšic docházelo až koncem období růstu hálek, a proto hálky dorůstaly nadprůměrné velikosti (kolem 12,7 × 8,7 mm).
10. Listy s hálkami *P. spyrothecae* odumíraly asi o dva týdny dříve, avšak na dřevinách setrvávaly většinou déle než listy bez hálek. Hálky včetně řapíků zůstávaly po úhynu listových čepelí minimálně dva týdny živé; tím byl částečně kompenzován výpadek v asimilaci vzniklý předčasným úhynem čepelí. Bylo prokázáno, že hálky nepůsobí redukci plochy listů. Řapíky napadených listů jsou nápadně (průměrně o 26,2 %) delší. Při přemnožení v uličních stromořadích mohou hálky snižovat dekorativnost topolů a výkaly mšic mohou od poloviny srpna do poloviny září znečišťovat prostředí (např. parkující automobily).

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