Bionomics and harmfulness of *Tetraneura ulmi* (L.) (Aphidinea, Pemphigidae) in elms

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ABSTRACT: The paper deals with the bionomics and harmfulness of a common cecidogenous aphid *Tetraneura ulmi* L. (Pemphigidae) which showed outbreak in elms in Moravia in 2002. The majority of examinations was conducted in *Ulmus minor* in a riparian and accompanying stand of the Svitava river, Bílovice nad Svitavou near Brno. The aphid was most abundant in *U. minor*, much less in *U. glabra* and never occurred in *U. laevis*. In one leaf, about 2.5 (max. 16) galls were found there (at Čejkovice near Znojmo, as much as 21 galls). Fundatrices hatched from 15 April to 7 May. Through the areal sucking on the abaxial face of leaves, they damaged on average 1.4 cm^2 (about 6%) of the leaf blade, in leaves with 10 and more galls often the whole blade. Within 3–4 weeks from hatching (from mid-May), fundatrices matured and during 1–3 weeks they produced on average 35.2 fundatrigeniae. At the beginning of June, galls reached 10.8 mm in length and 6.2 mm in width. Fundatrigeniae developed about 18 days and from 10 to 30 June they formed migrantes alatae. Aphids left 73.3% galls. In 10.4% galls, fundatrices were killed by insect and other predators in the 1st instar (in the initial stage of the gall formation). In 7.0% galls, immature fundatrices died in later stages of development due to the effect of a protective activity of plant tissues. The mortality of fundatrigeniae including migrantes alatae was caused to a very small extent only by e.g. *Anthocoris confusus* Reut., larvae of Syrphidae, caterpillars of Pyralidae and birds. Effects of mortality factors on the shape and size differentiation of galls are documented in the paper.

Keywords: elm; *Tetraneura* (= *Byrsocrypta*) *ulmi*; occurrence; development; mortality factors; gall differentiation

In some localities of Moravia, increased numbers of galls of the aphid *Tetraneura ulmi* (Linnaeus, 1758) in elms was recorded in 2001. Some species of elm (particularly *Ulmus minor* Mill.) were massively attacked in 2002 when often more than 10 galls occurred in leaves (at Čejkovice near Znojmo as much as 21). The gradation of the cecidogenous aphid was a suitable occasion for the study of its development, size differentiation of galls and harmfulness in elms.

T. ulmi ranks among a phylogeneticaly advanced and economically important family of Pemphigidae which is represented by about 30 species (HOLMAN, PINTERA 1977) in the region of the Czech Republic (CR). Amphigonic males and females of the family are apterous and show a stunted mouth system (without rostrum). Wax glands occur in the family very often. The glands produce wax sprinkling or fibres particularly in apterous forms. Antennae are relatively short consisting of 6 segments. Primary rhinaria are with an annulus of five apical sense lashes, secondary rhinaria are mostly narrowly transversely annular in winged forms. Siphunculi are porous or are missing. A cauda is small, hemispherical or is missing. Tarsi of virginogen generations are 2-segment, in the genus *Tetraneura* 1-segment. They usually migrate from primary host plants (wood species) where they mostly form species-characteristic galls to roots of secondary host plants (grasses, herbs, woody species). Numerous species show capability to preserve and reproduce by thelytokous parthenogenesis only.

In the literature, *T. ulmi* has been often referred to as *Byrsocrypta ulmi* L. or *T. ulmi* Deg. In the past, it was also mentioned as *Aphis ulmi* L., *A. ulmi* Geoffr., *A. gallarum ulmi* Deg., *T. gallarum* Gmel., *T. ulmi* Htg., *T. coerulescens* Del. Guerc., *T. ulmifoliae* Baker, *Pemphigus coerulescens* Pass., *P. coerulescens* Mordv., *B. ulmi* Hal. etc. Numerous scientific names of the species give evidence of certain difficulties connected with its proper and correct inclusion into the system of aphids which has not been completed so far.

To a certain extent, taxonomic problems are related to the complex annual generation cycle. In the course of the cycle, aphids regularly migrate from primary host plants (some species of the genus *Ulmus*) to secondary host plants (numerous species of the *Poaceae* family).

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Thus, it concerns a heteroecious species. It reproduces by heterogony when one amphigonic generation (sexuales) usually alternates with four parthenogenetic generations. This complete generation cycle (holocycle) is related to the season-conditioned polymorphism which is shown in the formation of several hereditary morphological types of apterous and pterygote females, so called morphs. The amphigonic generation, however, can be suppressed so that aphids reproduce parthenogenetically only in secondary hosts by 'virginoparous anholocycling' (RUPAJS 1989).

The developmental cycle of *T. ulmi* takes place according to the following pattern. Larvae of future adults of fundatrices (1st generation of the aphid) hatch from fertilized wintering eggs laid in the previous year into fissures (or under lichens) on the bark of stems and large-diameter branches of elms in spring. Parthenogenetic females can, however, winter also on roots of grasses. Young larvae of fundatrices move towards freshly unfolded buds where they soon settle between veins on the abaxial face of young leaves. Closed follicle-like galls form due to sucking on the opposite (adaxial) face of leaves. In these usually shortly pedunculate and surface-smooth galls fundatrices mature. Within the period of 3 to 4 weeks, they produce larvae (fundatrigeniae) maturing during 2 to 3 weeks in winged migrantes alatae (2nd generation of the aphid).

Toward the end of spring and at the beginning of summer, galls open at their base (apertures in the form of a slit) and migrants leave the galls through the apertures. They fly on secondary host plants where produce several larvae of the 3rd virginogen generation (exules). These larvae freely suck on roots and soon mature. During summer, 2 virginogen generations usually develop whereas the second (generally the fourth) generation matures in winged sexuparae (remigrants). Usually in September, sexuparae return to primary hosts and on their bark, they produce 2 or 3 larvae of the last (usually the 5th) generation. After several ecdyses, the larvae mature in apterous males and females of the amphigonic generation of sexuales. Fertilized females lay always one egg only.

T. ulmi is a widely distributed Euro-Asian species which was secondarily introduced into North America. It attacks numerous species of elm (in Europe particularly *Ulmus minor* Mill. and *U. glabra* Huds.) and often heavily infests them. In case of a mass outbreak, it weakens the species from the viewpoint of physiology and in elms grown as orchard species the aphid lowers their aesthetic value. Considerable damages are caused by radicicolous virginogen generations to cultivated crops (e.g. to *Zea mays* L., *Triticum aestivum* L., *Avena sativa* L., *Oryza sativa* L., *Hordeum* spp., *Panicum* spp. etc.).

In spite of an indisputable economic importance and easy species determination according to galls, the aphid *T. ulmi* is known very little only. Particularly various entomological, aphidological and cecidological publications mention the species nearly regularly. As for special papers aimed at e.g. its biology, natural enemies and gall formation, the number of the papers is, however, very limited. In the 2nd half of the last century, the development of *T. ulmi* was dealt with e.g. by PANIZZA (1969), and WHEELER and JUBB (1979) and RASPI (1983, 1988) studied its predators. New findings from the ultramicroscopic study of galls bring DEXHEIMER et al. (1973, 1975). LJUBESIĆ and WRISCHER (1992) reported on chloroplasts and their behaviour in parenchymatous cells of galls. The movement of phosphates in leaves without and with galls (and in particular galls) was studied by KUNKEL (1968). Effects of gamma radiation on *T. ulmi* were described by KAN (1972). New findings on the possibility of using insecticides in the control of aphids in elm were obtained e.g. by JANCKE (1951), KRAMM (1953), ZLATANOV (1964) etc.

The aphid is commonly distributed in the region of the CR wherever its primary host plants grow (mainly *U. minor* and *U. glabra*). *U. minor* is a south European and Central European species which, due to its distribution, reaches to Near East, Central Asia and northern Africa. In the CR, it occurs particularly in floodplain forests and on soils rich in nutrients in warm uplands. In the 2nd half of the last century, its forest-steppe ecotype was heavily affected by Dutch elm disease caused by *Ophiostoma ulmi* (Buism.) Nannf. Also *U. glabra* which shows autochthonous occurrence in uplands and piedmont regions of Europe (with the exception of the predominant part of the Pyrenean peninsula and northern half of Scandinavia) was considerably affected by this mycosis of vascular bundles. In the CR, both the wildly growing species (particularly in uplands) and its cultivars planted for ornamental purposes in gardens and parks in warm regions of the country in the past were heavily affected by the disease. It appears that the process of decline and dieback of elms sensitive to Dutch elm disease has stopped in many places recently. Similar situation occurred at localities under study in Moravia where *T. ulmi* attacked on a mass scale relatively well-growing species.

MATERIAL AND METHODS

Field and laboratory studies were systematically carried out on *U. minor* in 2002, viz. in a riparian and accompanying stand of the Svitava river in Bílovice nad Svitavou near Brno (altitude about 230 m). From May to October, leaves with galls were taken from the species in 14-day intervals for laboratory investigations and/or predator keeping. In 9 main inspection dates, in total 650 leaves with 1,540 galls were analysed in detail, i.e. in each of samplings on average 72 leaves and 171 galls. In a spring period, partial observations were carried out according to requirements also in other dates. Occasionally, galls were investigated from *U. minor* growing in Brno-Obřany and at Bystřička (the district of Vsetín) and in windbreaks in the region of Znojmo.

At first, length and width of a leaf blade were measured in each of the attacked leaves in our laboratory. Using planimetry, the total leaf blade area and the blade area sucked by larvae of the 1st instar of fundatrices were then measured. In each of the galls, the blade length and mean width (in two ⊥ directions) were determined under a microscope. On a careful longitudinal cut (carried out under a microscope) through a gall, mean wall thickness at base, in mid-length and at the gall top were determined using micrometry. The content of each of the galls was then analysed in detail, particularly health conditions and the growth stage of fundatrices, and health conditions, number and the growth stage of fundatrigeniae (including the health condition and number of migrantes alatae). Using micrometry, the length and width of the body of fundatrices, fundatrigeniae and migrantes alatae were measured. The fertility of fundatrices was derived from the number of produced fundatrigeniae and according to the number of unproduced embryos in naturally died fundatrices on the basis of microscopic dissection. Through microscopic dissection, the fertility was also determined of migrantes alatae in the period before their emergence from galls. Considerable attention was paid to mortality factors and their effects on the shape and size differentiation of galls.

The general appearance and size of galls were evaluated not only in the time of the occurrence of aphids in galls but also after their leaving by aphids. The frequency of the occurrence of galls and their size on leaves of various dimensions were evaluated in detail. Interesting findings were obtained by the study of the process of opening the galls through fissures and by the study of the effects of damage to leaves.

RESULTS AND DISCUSSION

Primary host plants

In the literature, *T. ulmi* is mentioned at least in 10 species of elm, in Europe most frequently in *Ulmus glabra* Huds. and *U. minor* Mill. (e.g. GÄBLER 1955; PINTERA 1959; BUHR 1965; STEFFAN 1972; RUPAJS 1989 etc.) or only in *U. glabra* (BAUDYŠ 1954; PFEFFER et al. 1954; KUNKEL 1968 etc.) or *U. minor* (KRAMM 1953; DEXHEIMER et al. 1973, 1975 etc.). RUPAJS (1989) mentions the infrequent occurrence of *T. ulmi* in *U. minor* var. *suberosa* (Moench) Sóo and *U. procera* Salisb. *U. pumilla* L. (PANIZZA 1969), *U. pumilla* L., *Pinnato-ramosa*, *U. japonica* (Rehd.) Sarg., *U. densa* Litw. (BLACKMAN, EASTOP 1994) rank also among host species. The last mentioned authors and also e.g. GUSEV, RIMSKIJ-KORSAKOV (1953), BUHR (1965) and ŽIVANOVIČ (1978) refer to the aphid also in *U. laevis* Pall. and LJUBESIĆ, WRISCHER (1992) even in *Zelkova serrata* (Thunb.).

Our observations show that *T. ulmi* occurred most abundantly in Moravia in *U. minor* and much less in *U. glabra*. In a very abundant, thermophilic and rather resistant to Dutch elm disease *U. laevis* galls were never found at all. However, tiny erinea of the mite *Aceria ulmicola brevipunctata* Nal. from the phytoparasitic family Eriophyidae occurred frequently on a mass scale on the adaxial face of leaves of the elm.

The development of fundatrices

T. ulmi winters in the stage of fertilized eggs laid by females of the sexuales generation at the end of summer and at the beginning of autumn. As mentioned above, apterous virginogen generations can also winter on roots of secondary hosts. Larvae of the 1st instar of fundatrices hatch from eggs placed in fissures and other hidden places on the bark of stems and large-diameter branches of elms in spring of the next year. Mass hatching occurs in the period of elm budbreak. Young larvae are markedly negatively geotactic. They move towards the most broken buds and suck on them at first. After unfolding the first leaves the larvae settle on their abaxial face between veins. In the coincidence of the period of hatching with the period

Table 1. Number and mean size of the examined leaves of *Ulmus minor* including the average sucked up area of leaves, number and mean size of galls of *Tetraneura ulmi*. Bílovice nad Svitavou, 2002

Date	Number of leaves	Mean length/width of the blade (cm)	Mean area of the blade (cm^2)	Mean sucked area: per one leaf (cm^2)	Mean sucked area: per one leaf (%)	Mean sucked area: around one gall (cm^2)	Total/mean number of galls	Mean length/width of galls (mm)
8. 5.	38	8.7/5.6	31.0	2.2	7.1	1.6	52/1.4	5.7/2.7
22. 5.	84	7.8/4.5	25.1	3.8	15.1	1.4	231/2.7	8.1/4.3
5. 6.	56	7.6/4.5	23.9	3.7	15.5	1.6	127/2.3	9.7/6.1
19. 6.	55	7.8/4.9	27.9	3.1	11.1	1.4	119/2.2	11.2/6.2
3. 7.	83	6.7/4.1	19.5	(3.2)	(16.4)	(0.9)	288/3.5	8.6/4.7
17. 7.	84	7.4/4.3	22.2	(3.0)	(13.5)	(1.1)	231/2.7	7.5/4.5
14. 8.	84	6.4/4.0	17.6	(2.3)	(13.1)	(1.3)	155/1.8	7.0/4.1
11. 9.	83	7.1/4.3	21.1	(1.8)	(8.5)	(0.8)	181/2.2	5.5/3.3
9. 10.	83	6.8/4.2	21.0	?	?	?	156/1.9	5.7/3.4
Total (mean)	650	7.2/4.4	22.5	(2.9)	(12.9)	(1.2)	1,540/2.5	7.7/4.4

Fig. 1. Part of the leaf of *U. minor* damaged by sucking and creating the gall of *T. ulmi*. Bílovice nad Svitavou, 8 May 2002

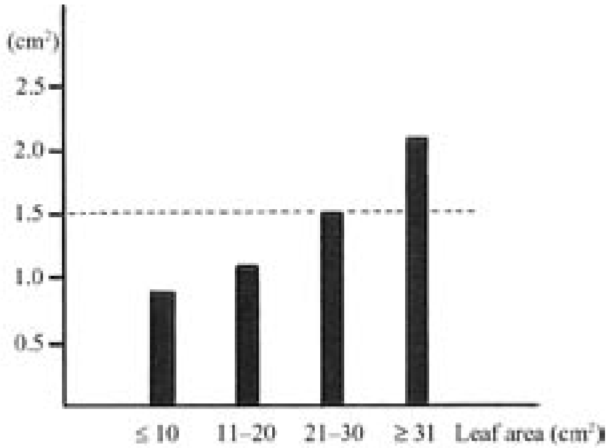

Fig. 2. Average area sucked by 1 fundatrix of *T. ulmi* in leaves of *U. minor* of 4 areal categories. An average area sucked by 1 fundatrix is depicted by dashed lines. Bílovice nad Svitavou, 8 May, 22 May, 5 June and 19 June 2002

of budbreak the larvae starve and die. Owing to various macroclimatic and microclimatic conditions, the start and course of the larva hatching differs considerably. There are very few detailed data on the period of hatching. For example RUPAJS (1989) mentions that in Latvia larvae hatch usually in the second decade of April and at the latest at the beginning of May. At the main locality under study in Bílovice nad Svitavou, larvae hatched for a considerably long time, viz. from mid-April to 7 May.

Young larvae suck intensively on the abaxial face of the leaf blade. Roughly by 20 to 60 punctures (0.3 to 2 mm apart) they inject salivary secretions into young leaf tissues. Due to growth substances included in saliva the leaf blade between veins in the place of sucking is slightly deformed and the leaf thickness is somewhat increased. Fresh green colouring in the place of sucking and its immediate vicinity grows pale and changes in yellow-green, green-yellow or reddish. If particular punctures are placed within a short distance of each other the blade is irregularly corrugated (Fig. 1). If particular punctures are placed within a long distance of each other separate slightly gib-

Table 2. Mean area of leaves sucked by one fundatrix of *T. ulmi* in leaves of *U. minor* in relation to their area. Bílovice nad Svitavou, 2002

Leaf area (cm²)	8. 5.	22. 5.	5. 6.	19. 6.	Mean	
					8. 5.–19. 6.	3. 7.–11. 9.
≤ 10	0.8	0.8	1.1	1.0	0.9	1.0
11–20	1.1	0.8	1.4	1.1	1.1	1.0
21–30	1.3	1.4	1.7	1.2	1.5	1.1
≥ 31	1.9	2.2	2.4	2.0	2.1	1.0
Mean	1.6	1.4	1.6	1.4	1.5	1.0

Table 3. Mean area of leaves sucked by one fundatrix of *T. ulmi* (cm²) in leaves of *U. minor* with the various number of galls. Bílovice nad Svitavou, 2002

Number of galls per 1 leaf	8. 5.	22. 5.	5. 6.	19. 6.	Mean	
					8. 5.–19. 6.	3. 7.–11. 9.
1	2.2	1.4	2.5	1.5	1.9	1.4
2	0.9	1.4	1.4	1.8	1.4	1.1
3–4	1.1	1.6	1.4	1.3	1.4	0.9
≥ 5	0.4	1.4	1.2	0.8	1.3	0.8
Mean	1.6	1.4	1.6	1.4	1.5	1.0

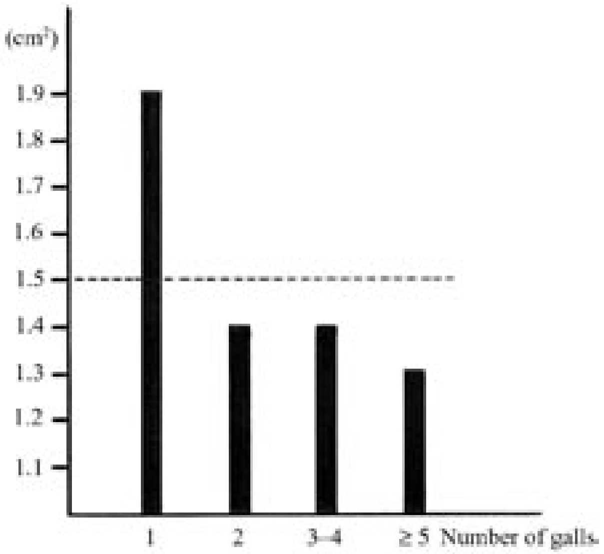

Fig. 3. Average area sucked by 1 fundatrix of *T. ulmi* in leaves of *U. minor* with the various number of galls. Dashed lines depict an average area sucked by 1 fundatrix. Bílovice nad Svitavou, 8 May, 22 May, 5 June and 19 June 2002

bous spots of a diameter of 1 to 2 mm are formed around them. The spots are dull on the abaxial face and bright on the adaxial face.

Symptoms of damage to leaves due to sucking are very conspicuous already in May and June. Sucking of one larva affects the leaf blade of an average area of 1.5 cm^2, i.e. about 6% of the leaf area (area of about 22 cm^2). From July, however, symptoms of damage (particularly colour changes) are more evident on an average area of only 1.0 cm^2 (Table 1). Greater number of larvae sucks on one leaf often (in Bílovice nad Svitavou as many as 16 and near Čejkovice, District of Znojmo, as many as 21 larvae). A total sucked area increases and in case of the mass occurrence of larvae even whole leaf blades can be damaged by sucking. With the mean number of 2.5 larvae per 1 leaf of an average area of 22.5 cm^2 the sucking affected about 2.9 cm^2, i.e. about 12.9% of the leaf blade in Bílovice nad Svitavou (Table 1). On leaves of an average size attacked by about 10 larvae a sucked area amounted to about 50% (on smaller leaves even as much as 100%) of the total leaf area.

It has been found that in young leaves (from May and June), the area sucked by 1 fundatrix significantly (as much as 2.3 ×) increases with the size of leaves (Table 2, Fig. 2). In older (from July and later months) leaves, the sucked area does not substantially change with the size of leaves (Table 2). This, at the first glance paradoxical finding, is undoubtedly related to a certain revitalization of sucked leaves which takes place particularly in July. With the increasing number of sucking larvae an average area sucked in young leaves by 1 larva significantly (1.5 to 1.8 times) decreases. For example, in the occurrence of 1 larva on a leaf 1 fundatrix sucked on average 1.9 cm^2, in the occurrence of 5 and more larvae 1.3 cm^2 only (Table 3, Fig. 3). Detailed examinations showed that an average area sucked by 1 fundatrix increased to a certain extent also with the size (length and width) of subsequently created galls (Tables 4 and 5).

After several days of areal sucking on the blade of leaves, larvae of the 1st instar of fundatrices settle and then suck virtually on one place. Through sucking they induce pathological proliferation of tissues manifested by the rapid formation of a gall on the opposite (i.e. adaxial) face of a leaf. At first, galls are bulge-like or dully conical, later on follicle-like, lengthwise oval and sometimes slightly pointed at their top (Figs. 4 and 5), sporadically even cleft (with 2 peaks). At their base, they are mostly tapered and often pedunculate (Fig. 6). On the surface, they are always smooth, semi-glossy to dull, at first green

Table 4. Mean area of leaves sucked by one fundatrix of *T. ulmi* around galls in leaves of *U. minor* (within three length categories of galls). Bílovice nad Svitavou, 2002

Gall length (mm)	5. 6.	19. 6.	3. 7.	17. 7.	Mean	
					5. 6.–19. 6.	3.7.–17. 7.
≤ 9	1.3	1.3	0.9	1.0	1.3	1.0
10–11	1.5	1.2	0.9	1.2	1.4	1.1
≥ 12	2.2	1.4	0.9	1.1	1.6	1.1
Mean	1.6	1.4	0.9	1.1	1.5	1.0

Table 5. Mean area of leaves sucked by one fundatrix of *T. ulmi* around galls in leaves of *U. minor* (within three width categories of galls). Bílovice nad Svitavou, 2002

Gall width (mm)	5. 6.	19. 6.	3. 7.	17. 7.	Mean	
					5. 6.–19. 6.	3. 7.–17. 7.
≤ 4	1.4	1.3	0.8	0.9	1.4	0.9
5–6	1.3	1.4	1.0	1.1	1.4	1.0
≥ 7	1.8	1.4	1.0	1.3	1.6	1.2
Mean	1.6	1.4	0.9	1.1	1.5	1.0

Fig. 4. Young galls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 8 May 2002

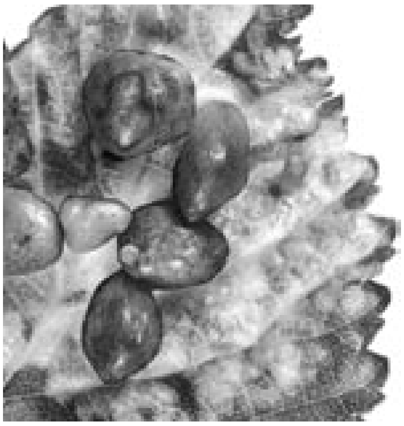

Fig. 5. Young galls of *T. ulmi* in leaves of *U. minor* (detail). Bílovice nad Svitavou, 8 May 2002

Fig. 6. A young gall of *T. ulmi* in a leaf of *U. minor*. Bílovice nad Svitavou, 20 May 2002

Table 6. Length and width of particular instars of larvae and imagoes of fundatrices of *T. ulmi* in galls in leaves of *U. minor* (1 division = 0.0357 mm). Bílovice nad Svitavou, 8 May, 22 May 2002, Bystřička, 26 May 2002

Body length (divisions)	1st instar		2nd instar		3rd instar		4th instar		Imago	
	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width
16–17	10	7.0	–	–	–	–	–	–	–	–
18–19	2	7.0	–	–	–	–	–	–	–	–
20–21	–	–	2	11.0	–	–	–	–	–	–
22–23	–	–	10	11.7	–	–	–	–	–	–
24–25	–	–	9	12.5	2	13.0	–	–	–	–
26–27	–	–	5	13.0	3	14.6	–	–	–	–
28–29	–	–	–	–	10	15.2	–	–	–	–
30–31	–	–	–	–	15	16.9	–	–	–	–
32–33	–	–	–	–	16	17.5	–	–	–	–
34–35	–	–	–	–	15	18.5	5	19.5	–	–
36–37	–	–	–	–	8	19.3	13	19.9	–	–
38–39	–	–	–	–	5	20.0	14	20.1	–	–
40–41	–	–	–	–	4	23.3	20	23.6	–	–
42–43	–	–	–	–	–	–	23	26.2	4	24.3
44–45	–	–	–	–	–	–	18	26.1	6	27.7
46–47	–	–	–	–	–	–	7	26.7	5	28.0
48–49	–	–	–	–	–	–	5	28.5	5	30.5
50–51	–	–	–	–	–	–	3	30.5	5	30.6
52–53	–	–	–	–	–	–	1	32.0	4	31.3
54–55	–	–	–	–	–	–	–	–	4	32.0
56–57	–	–	–	–	–	–	–	–	3	38.0
58–59	–	–	–	–	–	–	–	–	3	38.5
60–61	–	–	–	–	–	–	–	–	1	33.0
Total	12	–	26	–	78	–	109	–	40	–
Length (from–to)	–	16–18	–	21–27	–	25–40	–	34–52	–	42–60
Width (from–to)	–	6–8	–	11–14	–	13–24	–	18–32	–	23–40
Mean length	–	16.8	–	23.8	–	32.7	–	41.7	–	50.7
Mean width	–	7.0	–	12.2	–	17.7	–	24.2	–	30.6

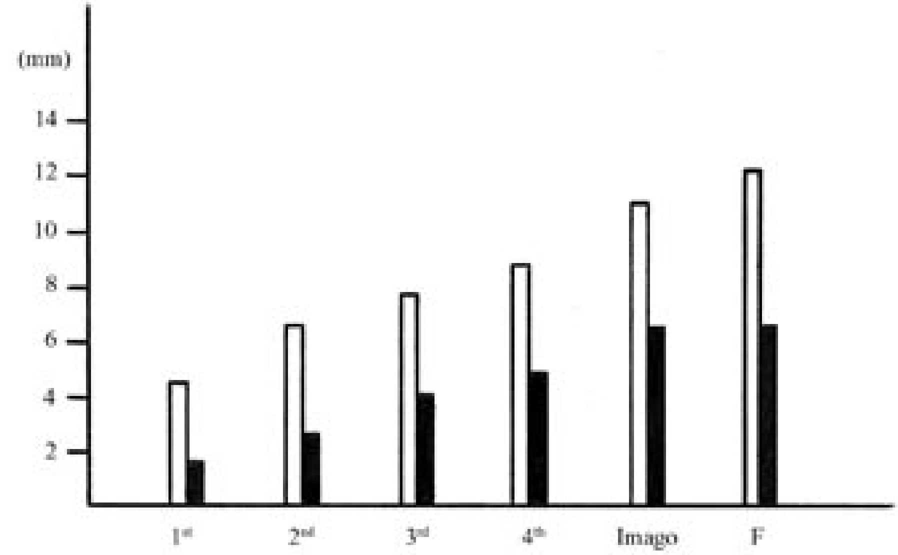

Fig. 7. Average length (light) and width (dark) of galls induced by fundatrices and fundatrigeniae (F) of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 8 May, 22 May and 5 June 2002

or yellow-green. The mouth (throat) of growing galls is gradually closed and fulfilled with dense (about 0.5 mm long) light trichomes which are partly evident from the abaxial face of leaves. Inside the galls, a spacious cavity is formed where the whole further development of fundatrices and the 2nd generation established by them takes place. In one gall always one fundatrix develops.

The first moulting takes place in a period when galls reach about 1/3 of their final length and width (Fig. 7). At the main locality under investigation in Bílovice nad Svitavou, larvae moulted for the first time at the beginning of May. After next three ecdyses, mature fundatrices began to occur in galls from mid-May. The whole development from hatching up to maturity took 3 to 4 weeks. The growth stage of fundatrices can be safely determined on the basis of exuviae (the first of them is black and other are light) which accumulate in galls (Fig. 8). With the development of fundatrices the gall wall thickness also gradually increases (Fig. 9). Walls at the base of galls are always on average thinnest. In the half of the gall length, walls are of medium thickness and at the top are thickest. Galls with the undisturbed development of aphids grow up usually at the beginning of June. Figs. 7 and 9 show that fundatrices and to a small extent only fundatrigeniae participate mostly in the formation of galls.

Fig. 8. A longitudinal cut through the gall of *T. ulmi* in a leaf of *U. minor* with fundatrix in the 4th instar including exuvia. Bílovice nad Svitavou, 20 May 2002

The size (length and width) of particular instars and mature fundatrices is given in Table 6 and Figs. 10 and 11. They show that larvae of the 1st instar are 0.57 to 0.64 (on average 0.60) mm long and 0.21 to 0.28 (on average 0.25) mm wide. The size of larvae of the 2nd instar is 0.75 to 0.96 (on average 0.85) mm × 0.39 to 0.50 (on average 0.44) mm. The size of larvae of the 3rd instar is 0.89 to 1.43 (on average 1.17) mm × 0.46 to 0.86 (on average 0.63) mm and that of larvae of the 4th instar 1.21 to 1.86 (on average 1.49) mm × 0.64 to 1.14 (on average 0.86) mm. Mature fundatrices are 1.50 to 2.14 (on average 1.81) mm long and 0.82 to 1.43 (on average 1.09) mm wide.

Ovaries of mature fundatrices contain various numbers of embryos of various size before reproduction. In principle, the mean number of embryos corresponds to the mean fertility of females (35.2 pc). The length of embryos is 0.18 to 0.68 (on average 0.47) mm and width 0.14 to 0.29 (on average 0.21) mm. Not very distinct embryos of a number of 0 to 44 (on average 20.3) pc are usually already formed in ovaries of the 4th instar of fundatrices. Their length is 0.11 to 0.39 (on average 0.25) mm and width 0.11 to 0.18 (on average 0.15) mm.

Mature fundatrices produce larvae – fundatrigeniae (Fig. 12) for the period of 1 to 3 weeks. In the Netherlands, mature fundatrices and young larvae occur in the 2nd

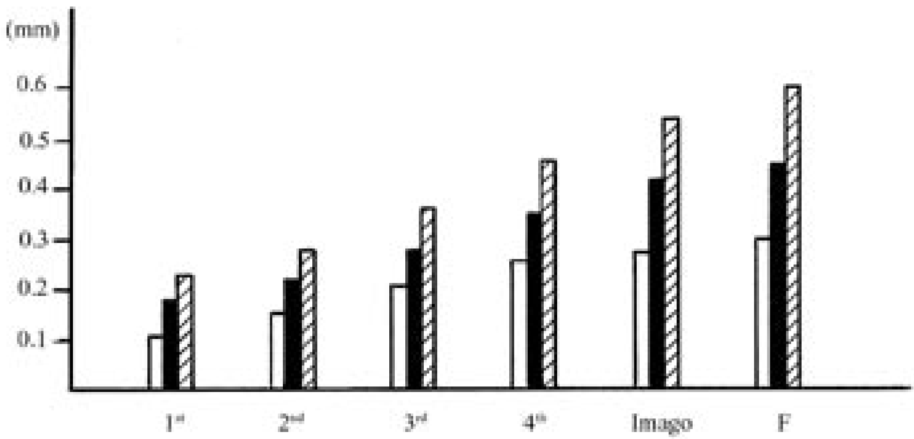

Fig. 9. Average thickness of the gall wall with particular instars of larvae and imagoes of fundatrices and fundatrigeniae (F) of *T. ulmi* in leaves of *U. minor*. The wall thickness at the base of galls is depicted as light, in the mid-length of galls as dark and in the apical part of galls as dashed lines. Bílovice nad Svitavou, 8 May, 22 May, 5 June and 19 June 2002. Bystřička, 26 May 2002

Table 7. Mean potential fertility of *T. ulmi* fundatrices in galls in leaves of *U. minor*. The galls were divided into three length and three width categories. Bílovice nad Svitavou, 2 May, 5 June 2002, Bystřička, 26 May 2002

Gall length (mm)	Number		Mean fertility	Gall width (mm)	Number		Mean fertility
	fundatrices	embryoes			fundatrices	embryoes	
≤ 9	51	1,306	25.6	≤ 4	18	301	16.7
10–11	71	2,456	34.6	5–6	85	2,640	31.1
≥ 12	60	2,654	44.2	≥ 7	79	3,475	44.0
Total	182	6,416	35.2	Total	182	6,416	35.2

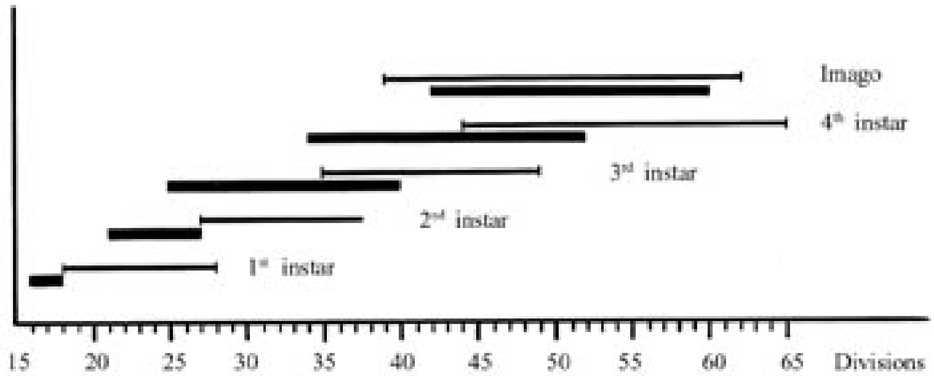

Fig. 10. The length of particular instars of larvae and adults of fundatrices (bold) and fundatrigeniae including migrantes alatae of *T. ulmi* (thin) in galls in leaves of *U. minor* (1 division = 0.0357 mm). Bílovice nad Svitavou, Bystřička, May and June 2002

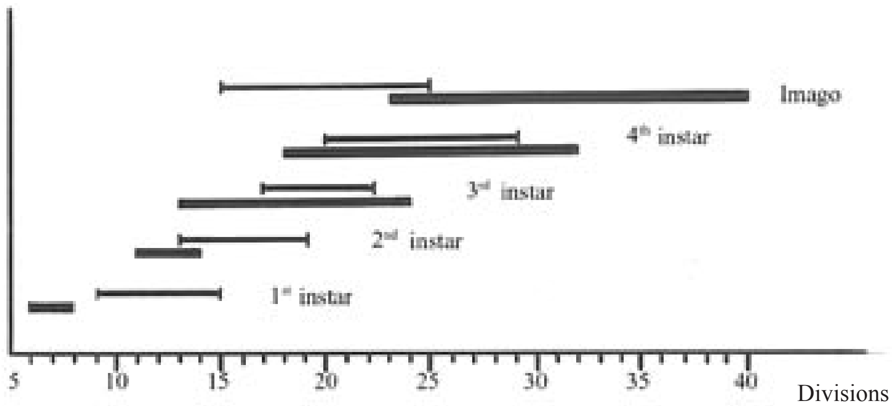

Fig. 11. The width of particular instars of larvae and adults of fundatrices (bold) and fundatrigeniae including migrantes alatae of *T. ulmi* (thin) in galls in leaves of *U. minor* (1 division = 0.0357 mm). Bílovice nad Svitavou, Bystřička, May and June 2002

Table 8. Mean length and width of mature fundatrices of *T. ulmi* in the period of sexual maturity until their death. Bílovice nad Svitavou, 22 May–19 June 2002, Bystřička, 26 May 2002

Size of fundatrices	Body length (mm)		Body width (mm)	
	from–to	mean	from–to	mean
Immediately before reproduction	1.43–2.14	1.81	0.96–1.25	1.11
In the half of the reproduction period	1.00–2.07	1.59	0.75–1.36	1.09
At the end of the reproduction period	1.00–1.94	1.39	0.89–1.50	1.19
Soon after completing the reproduction	0.89–1.50	1.11	0.82–1.43	1.04
About 2 weeks after reproduction	0.78–1.60	1.01	0.71–1.25	0.98
Immediately after death	0.82–1.40	1.00	0.64–1.36	0.97

half of May (GOOT, v.d. 1915). In Bílovice nad Svitavou, fundatrices began to reproduce already in mid-May and in the course of the whole period of reproduction they produced 3 to 78 (on average 35.2) of offsprings. According to RUPAJS (1989), in Latvia fundatrices reproduce 3.5 to 4 weeks producing in total 20 to 60 (on average 30) offsprings. After completing the reproduction, females stop sucking and after several days to 2 weeks they die.

It has been demonstrated that fundatrices in larger galls show significantly higher fertility than in smaller galls. For example, in galls 12 (and more) mm long, the fertility of fundatrices was 1.7 times higher than in galls 9 (and less) mm long (Table 7, Fig. 13). In galls 7 (and more) mm wide, the fertility of fundatrices was 2.6 times higher than in galls 4 (and less) mm wide (Table 7). It has been found through a microscopic dissection that fundatrices produce the overwhelming majority (98.8%) of offsprings created as embryos in ovaries. It means that the potential (physiological) fertility of fundatrices is virtually equal to real (ecological) fertility. During the reproduction, the fundatrices body length is substantially (1.6 times) shortened while the body width is nearly unchanged (Table 8).

Fig. 12. A longitudinal cut through the gall of *T. ulmi* in a leaf of *U. minor* with a mature fundatrix and fundatrigeniae in the 1st instar. Bílovice nad Svitavou, 20 May 2002

The development of fundatrigeniae including migrantes alatae

Fundatrigeniae of *T. ulmi* change after 3 ecdyses in nymphs (larvae of the 4th instar) and after the 4th hatching in winged migrantes alatae. At the main investigated locality in Bílovice nad Svitavou, the first fundatrigeniae were found as early as 15 May and the first migrants on 5 June. The development of fundatrigeniae from their conception to the hatching of migrantes alatae took 14 to 21 (on average 18) days. From 10 to 25 June, galls with the undisturbed development of aphids opened through secondary emergence fissures (Fig. 14). The winged aphid emergence began about 10 June and on 30 June finished. The timely emergence of aphids from galls (even before the end of June) refers to already RATZEBURG (1844). The development of offsprings of fundatrices towards winged individuals takes 14 to 17 days only in Latvia (RUPAJS 1989). A rather rapid development of fundatrigeniae and the most abundant occurrence of migrantes alatae in the

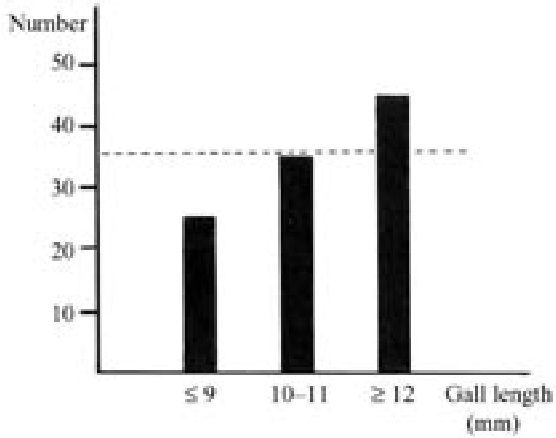

Fig. 13. The average fertility of fundatrices of *T. ulmi* in galls of three length categories in leaves of *U. minor*. Dash lines depict average fertility. Bílovice nad Svitavou, 22 May and 5 June 2002. Bystřička, 26 May 2002

Table 9. Length and width of particular instars of fundatrigeniae including migrantes alatae of *T. ulmi* in galls in leaves of *U. minor* (1 division = 0.0357 mm). Bílovice nad Svitavou, 5 June, 19 June 2002

Body length (divisions)	1st instar		2nd instar		3rd instar		4th instar		Imago	
	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width	Number of aphids	Mean width
18–19	12	9.4	–	–	–	–	–	–	–	–
20–21	40	10.1	–	–	–	–	–	–	–	–
22–23	45	10.9	–	–	–	–	–	–	–	–
24–25	48	12.0	–	–	–	–	–	–	–	–
26–27	30	13.9	5	13.8	–	–	–	–	–	–
28–29	10	14.1	42	14.5	–	–	–	–	–	–
30–31	–	–	91	15.4	–	–	–	–	–	–
32–33	–	–	100	16.7	–	–	–	–	–	–
34–35	–	–	97	17.6	5	17.5	–	–	–	–
36–37	–	–	47	18.0	30	18.7	–	–	–	–
38–39	–	–	8	18.4	92	19.0	–	–	1	17.0
40–41	–	–	–	–	145	19.5	–	–	7	17.6
42–43	–	–	–	–	109	20.6	–	–	22	16.8
44–45	–	–	–	–	100	20.7	6	20.7	26	17.7
46–47	–	–	–	–	35	20.7	30	20.7	16	18.1
48–49	–	–	–	–	7	21.5	33	22.3	16	19.1
50–51	–	–	–	–	–	–	49	22.7	28	19.4
52–53	–	–	–	–	–	–	49	23.8	13	20.8
54–55	–	–	–	–	–	–	50	24.8	15	20.5
56–57	–	–	–	–	–	–	38	25.3	10	21.5
58–59	–	–	–	–	–	–	25	25.8	7	21.6
60–61	–	–	–	–	–	–	24	26.1	6	23.7
62–63	–	–	–	–	–	–	1	26.0	1	25.0
64–65	–	–	–	–	–	–	2	28.5	–	–
Total	185	–	390	–	523	–	307	–	168	–
Length (from–to)	–	18–28	–	27–39	–	35–49	–	44–65	–	39–62
Width (from–to)	–	9–15	–	13–19	–	17–22	–	20–29	–	15–25
Mean length	–	23.3	–	32.6	–	41.6	–	53.0	–	49.1
Mean width	–	11.6	–	16.5	–	19.9	–	23.8	–	19.2
Length: width	–	2.0: 1	–	2.0: 1	–	2.1: 1	–	2.2: 1	–	2.6: 1

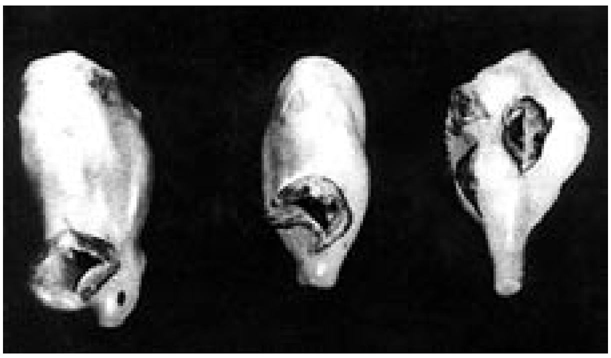

Fig. 14. Emergence holes in galls of *T. ulmi*. Bílovice nad Svitavou, 15 June 2002

Netherlands in the second half of June mentions GOOT, v. d. (1915).

The length and width of particular instars of fundatrigeniae (including migrantes alatae) is given in Table 9 and in Figs. 10 and 11. They show that larvae of the 1st instar are 0.64 to 1.00 (on average 0.83) mm long and 0.32 to 0.53 (on average 0.41) mm wide. The size of larvae of the 2nd instar is 0.96 to 1.39 (on average 1.16) mm × 0.46 to 0.68 (on average 0.59) mm. The size of larvae of the 3rd instar is 1.25 to 1.75 (on average 1.48) mm × 0.61 to 0.79 (on average 0.71) mm and of larvae of the 4th instar 1.57 to 2.32 (on average 1.89) mm × 0.71 to 1.04 (on average 0.85) mm. Migrantes alatae are 1.39 to

Table 10. Number and size of embryoes in the body of migrantes alatae of *T. ulmi* before their emergence from galls in leaves of *U. minor* (all within 3 length and width categories) (1 division = 0.0357 mm). Bílovice nad Svitavou, 19 June 2002

Aphid length (divisions)	Number of embryoes		Length/width of embryoes (mm)	Aphid width (divisions)	Number of embryoes	
	from–to	mean			from–to	mean
≤ 45	2–6	4.1	0.71/0.29	≤ 18	2–8	4.7
46–50	2–9	5.5	0.73/0.30	19–21	2–9	5.6
≥ 51	3–10	7.4	0.75/0.34	≥ 22	4–10	7.5
Total	2–10	5.8	0.74/0.32	Total	2–10	5.8

Table 11. Numerical and percentage representation of galls of *T. ulmi* with intact and disturbed walls in leaves of *U. minor*. Bílovice nad Svitavou, 17 July 2002

Galls	Number	(%)
Unclosed – conical (length ≤ 2.5 mm)	58	25.3
Unopened (with developed 2nd generation)	18	7.9
Open – 1 fissure	70	30.6
– 2 fissures	33	14.4
– 3 fissures	9	3.9
– 4 fissures	1	0.4
– 1 fissure and pecking up	12	5.3
– 2 fissures and pecking up	3	1.3
– 3 fissures and pecking up	3	1.3
– 1 fissure and eating up	1	0.4
– pecking up	16	7.0
– eating up	5	2.2
Total	229	100.0

2.21 (on average 1.75) mm long and 0.54 to 0.89 (on average 0.69) mm wide.

Under optimum conditions, all fundatrigeniae of *T. ulmi* develop to migrantes alatae. In a period of the development of the 2nd generation, anatomical structure of galls changes and the trophic value of galls for aphids rapidly impairs. In the period of hatching of migrantes alatae sucking intensity gradually decreases. Ageing and drying of galls induces their spontaneous opening.

Ovaria of newly hatched migrantes alatae (in a period before their emergence from galls) contain 2 to 10 (on average 5.8) embryos. The length of embryos is 0.71 to

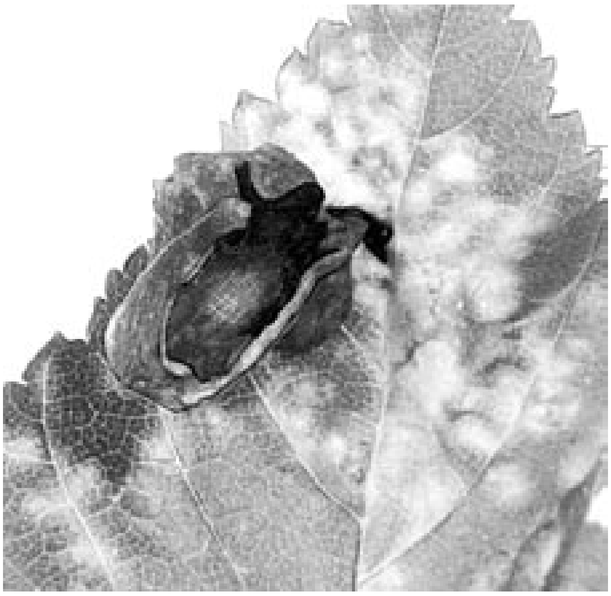

Fig. 15. A pecked up gall of *T. ulmi* in a leaf of *U. minor*. Bílovice nad Svitavou, 17 July 2002

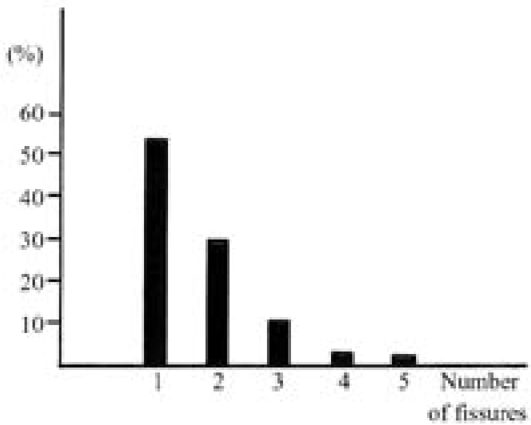

Fig. 16. Frequency of the occurrence of fissures in gall walls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 19 June–9 October 2002

Table 12. Causes of the origin of holes and their localization in galls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 17 July 2002

Hole origin	Hole localization mainly in the third	Number	(%)	
Rupture of the gall wall	basal	112	78.9	83.1
	middle	5	3.5	
	apical	1	0.7	
Pecking up by birds	basal	1	0.7	12.7
	middle	1	0.7	
	apical	4	2.8	
	basal and middle	3	2.1	
	middle and apical	6	4.3	
	basal, middle and apical	3	2.1	
Eating up by insect	basal	2	1.4	4.2
	middle	1	0.7	
	apical	3	2.1	
Total		142	100.0	100.0

0.75 (on average 0.74) mm and width 0.29 to 0.34 (on average 0.32) mm. The average number and size of embryos significantly increase (about 1.7 times) with the size of females (Table 10).

Opening the galls

Emergence holes are formed due to fissuring the gall wall and gradual increasing the bursts in the course of a relatively short time of several hours to several few days. The whole process of opening the galls in a host species or locality extends, however, for a period of about 2 weeks (in Bílovice nad Svitavou for 15 days). Within the period, fundatrices gradually die and the proportion of winged aphids increases in galls. In the period of fissuring the walls, 0 to 90% migrantes alatae occur in galls, the rest is formed by nymphs and larvae. Similarly as fundatrices, fundatrigeniae (including migrantes alatae) show also well developed rostrum. Winged females suck still for a period of several days after hatching and then gradually leave the galls through fissures and fly over to secondary host plants. Usually the predominant part of individuals of the 2nd generation completes its development in already open galls and on average the small proportion of migrants only leaves the galls immediately after the formation of emergence holes. In Bílovice nad Svitavou even on 19 June in the same open galls, larvae of all instars of fundatrigeniae including migrantes alatae occurred ordinarily. The process of gall leaving culminated there at the end of the 2nd decade of June when on average 14.4 aphids occurred in galls, i.e. by 59.1% less than at the beginning of the period of emergence.

Through fissures in gall walls part of galls opens only (in Bílovice nad Svitavou about 57.6%). It refers particularly to full-grown galls with intact development of aphids of the 1st and 2nd generations. Table 11 shows that the smaller part (7.9%) of galls with the completed development of aphids does not open at all or opens through only insufficiently large fissure. The fissures originate never in small (max. 2.5 mm long) bulge-like up to dully conical galls where fundatrices died in the earliest stages of their development. These incomplete and often open (at their mouth/throat) or imperfectly closed galls were very abundant in Bílovice nad Svitavou amounting to 25.3% of all galls. Concurrently with opening the galls through fissures, in the 2nd half of June pecking up the galls by

Table 13. Frequency of the occurrence of fissures in galls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 19 June –9 October 2002

Number of fissures in one gall	Number of galls	(%)	Number of fissures	(%)
0	476	42.5	–	–
1	473	42.3	473	54.0
2	129	11.5	258	29.5
3	32	2.9	96	11.0
4	7	0.6	28	3.2
5	2	0.2	20	2.3
Total	1,119	100.0	875	100.0
Mean	–	–	1.4	–

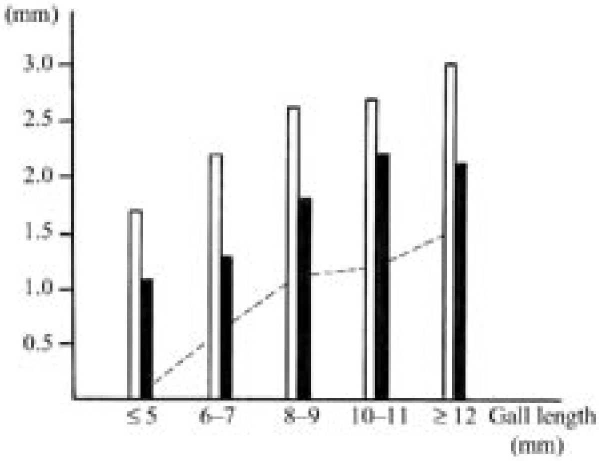

Fig. 17. Mean length and width of fissures (light and dark columns, respectively) in gall walls of *T. ulmi* distributed into 5 length categories. The average number of fissures in 1 gall is depicted by dashed lines. Bílovice nad Svitavou, 19 June, 3 July and 17 July 2002

birds (Fig. 15) and eating up the galls by polyphagous insect occur. The two factors disturb roughly to the same extent both galls with fissures and galls which are closed so far. In Bílovice nad Svitavou, birds ate up on average 14.9% galls (from this 7.9 with fissures and 7.0% without fissures). Insect ate up about 2.6% galls (from this 0.4 with fissures and 2.2% without fissures) (Table 11).

As for disturbed galls, the majority (83.1%) of galls is cracked and 12.7% galls only are pecked up by birds and 4.2% are eaten up by insect. Galls usually (94.9%) crack in the basal third, in 4.2% in the middle third and in 0.9% in the apical third. The most frequent opening the galls in the basal third is undoubtedly related to the different thickness of gall walls. It is usually smallest at the gall base (about 0.30 mm), in the half of the gall height is medium (about 0.45 mm) and at the top of galls is greatest (about 0.60 mm) (Fig. 9). Birds disturb the galls in various parts, however, far most frequently (78.8%) in the apical and middle thirds. The origin of holes in galls including their localization is given in Table 12.

In Bílovice nad Svitavou, the majority (54.0%) of burst galls was opened by one fissure, 29.5% galls by two fissures, 11.0% galls by three fissures, 3.2% galls by four fissures and 2.3% by five fissures. On average 1.4 fissures occurred in cracked galls (Table 13, Fig. 16). However, 42.5% were without fissures and, therefore, generally on average 0.9 fissures only occurred in galls. The number of fissures in galls significantly increased with gall dimensions (length and width) (Tables 14 and 15). The majority (60.0%) of fissures were more or less parallel with the longitudinal axis of galls, 11.6% fissures were transverse and 28.4% fissures were oval. The mean length of fissures (measured always along the gall length) was 2.7 mm and width 2.0 mm. The mean length and width of fissures significantly increased with increasing length and width of galls. For example, in galls 12 (and more) mm long fissures were 1.8 times longer and 1.9 times wider than in galls 5 (and less) mm long. In galls 7 (and more) mm in width, fissures were 1.6 times longer and 2.6 times wider

Table 14. Number and mean length/width of fissures in galls of *T. ulmi* including the number and % of galls pecked up by birds and eaten up by insect (all within five length categories of galls). Bílovice nad Svitavou, 19 June–17 July 2002

Body length (mm)	Number of galls	Number of fissures	Mean number of fissures in one gall	Mean length/ width of fissures (mm)	Number of pecked up galls	(%)	Number of eaten up galls	(%)
≤ 5	148	8	0.05	1.7/1.1	–	–	2	1.3
6–7	39	22	0.6	2.2/1.3	–	–	3	7.7
8–9	126	133	1.1	2.6/1.8	17	13.5	1	0.8
10–11	180	224	1.2	2.7/2.2	20	11.1	2	1.1
≥ 12	142	206	1.5	3.0/2.1	23	16.2	3	2.1
Total (mean)	635	593	0.9	2.7/2.0	60	9.4	11	1.7

Table 15. Number and mean length/width of fissures in galls of *T. ulmi* including the number and % of galls pecked up by birds and eaten up by insect (all within four width categories of galls). Bílovice nad Svitavou, 19 June–17 July 2002

Gall width (mm)	Number of galls	Number of fissures	Mean number of fissures in one gall	Mean length/ width of fissures (mm)	Number of pecked up galls	(%)	Number of eaten up galls	(%)
≤ 2	145	6	0.04	1.8/0.9	–	–	2	1.4
3–4	67	60	0.9	2.5/1.6	–	–	3	4.5
5–6	246	273	1.1	2.7/2.0	19	7.7	3	1.2
≥ 7	177	254	1.4	2.9/2.3	41	16.1	3	1.7
Total (mean)	635	593	0.9	2.7/2.0	60	9.4	11	1.7

Table 16. Frequency of the occurrence of galls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 2002

Number of galls per one leaf	Number of leaves										Number of galls	
	8. 5.	22. 5.	5. 6.	19. 6.	3. 7.	17. 7.	14. 8.	11. 9.	9. 10.	total	total	(%)
1	31	39	25	25	24	33	48	32	38	295	295	19.2
2	5	15	13	11	15	16	18	20	27	140	280	18.2
3	1	11	5	8	10	13	10	20	11	89	267	17.3
4	–	3	6	8	14	11	2	9	4	57	228	14.8
5	–	5	5	2	5	3	4	–	3	27	135	8.8
6	–	4	2	1	6	2	1	1	–	17	102	6.6
7	–	2	–	–	1	3	1	1	–	8	56	3.6
8	1	1	–	–	3	1	–	–	–	6	48	3.1
9	–	2	–	–	1	–	–	–	–	3	27	1.8
10	–	–	–	–	2	–	–	–	–	2	20	1.3
11	–	–	–	–	–	–	–	–	–	–	–	–
12	–	1	–	–	1	–	–	–	–	2	24	1.6
13	–	–	–	–	–	1	–	–	–	1	13	0.8
14	–	–	–	–	–	1	–	–	–	1	14	0.9
15	–	–	–	–	1	–	–	–	–	1	15	1.0
16	–	1	–	–	–	–	–	–	–	1	16	1.0
Number of leaves	38	84	56	55	83	84	84	83	83	650	–	–
Number of galls	52	231	127	119	288	231	155	181	156	–	1,540	100.0
Mean number of galls	1.4	2.7	2.3	2.2	3.5	2.7	1.8	2.2	1.9	–	2.4	–

than in galls 2 (and less) mm in width (Tables 14 and 15, Fig. 17). Tables 14 and 15 show that the largest galls are positively most affected by pecking up and galls of below-average dimensions are rather affected by insect eating.

In order aphids to be able to leave the galls, fissures have to reach at least 1.5 mm in length and 0.9 mm in width. Fissures of smaller dimensions do not enable the emergence of aphids from galls and the aphids die on a mass scale in galls. In Bílovice nad Svitavou, such fissures occurred in less than 4% galls.

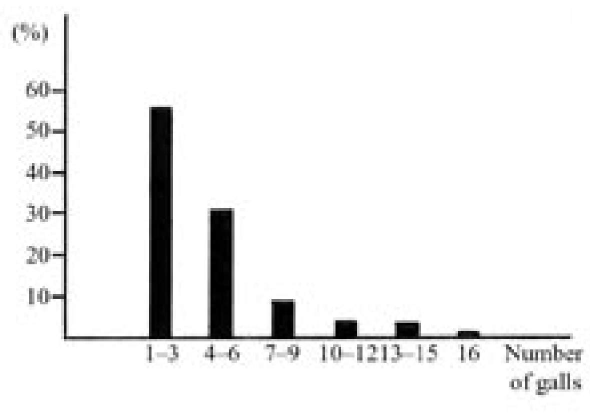

Fig. 18. Frequency of the occurrence of galls of *T. ulmi* in leaves of *U. minor*. Bílovice nad Svitavou, 8 May to 9 October 2002

Gall localization on leaves

Galls of *T. ulmi* are always localized between lateral veins on the adaxial face of leaves. In case of mass outbreak, as much as 30 galls can occur on one leaf (RUPAJS 1989 etc.). In 2002, nearly all leaves were affected by galls

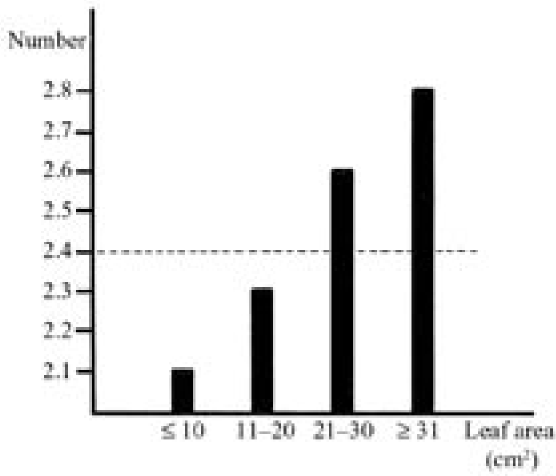

Fig. 19. Average number of galls of *T. ulmi* in leaves of *U. minor* of 4 areal categories. The average number of galls per 1 leaf is depicted by dashed lines. Bílovice nad Svitavou, 8 May to 11 September 2002

Table 17. Mean number of galls of *T. ulmi* in leaves of *U. minor* in relation to their area. Bílovice nad Svitavou, 2002

Leaf area (cm^2)	8.5.	22.5.	5.6.	19.6.	3.7.	17.7.	14.8.	11.9.	Mean
≤ 10	1.5	2.5	2.5	1.6	2.3	2.0	1.7	1.8	2.1
11–20	1.2	2.4	2.8	2.6	2.8	1.9	2.1	2.0	2.3
21–30	2.2	3.2	2.3	1.4	4.0	3.0	1.8	2.3	2.6
≥ 31	1.2	3.0	1.4	2.1	6.3	4.4	1.0	2.9	2.8
Mean	1.4	2.7	2.3	2.2	3.5	2.7	1.8	2.2	2.4

Table 18. Localization of galls of *T. ulmi* with respect to the longitudinal axis of leaves of *U. minor*. Bílovice nad Svitavou, 2002

Localization of galls	8. 5.	22. 5.	3. 7.	14. 8.	Total	(%)
In the upper third of the blade	30	139	214	126	509	70.1
In the middle third of the blade	14	67	63	27	171	23.6
In the lower third of the blade	8	25	11	2	46	6.3
Total	52	231	288	155	726	100.0

in heavily attacked *U. minor* in Bílovice nad Svitavou and in Brno-Obřany. In Bílovice nad Svitavou, on average 2.4 galls and max. 16 galls on 1 leaf occurred (Table 16, Fig. 18). Near Čejkovice (Znojmo District), leaves of *U. minor* were attacked on average by 4.1 galls while max. 21 galls were found on 1 leaf.

Examinations of the mean number of galls on 567 leaves of four size categories showed that the mean number of galls on one leaf increases with the size of a leaf blade (Table 17, Fig. 19). The fact is obviously related to the marked negative geotaxis of newly hatched young larvae of fundatrices and their tendency to occupy the most unfolded buds. Leaves developed from early flushed buds are on average always larger than leaves from buds flushing later.

According to RATZEBURG (1844), galls occur in the central and apical part of the leaf blade, according to GOOT, v. d. (1915), in any place of the blade. In Bílovice nad Svitavou, the predominant majority of galls (70.1%) occurred in the upper (apical) third of the leaf blade, much less (23.6%) in the middle third of the blade and least (6.3%) in the basal third of the blade (Table 18). If assessed in perpendicular direction to the main leaf vein 42.4% galls were localized in the inner third of the blade (i.e. bilaterally along the main longitudinal vein), 35.0% in both middle thirds of the blade and 22.6% in both peripheral (marginal) thirds of the blade. It is of interest that the majority (66.1%) of galls was localized in the smaller 'half' of eccentric leaf blades. Causes of the most abundant occurrence of galls in the apical third of the leaf blade and in the inner part of leaves (near the main vein) or in the smaller 'half' of leaves consist in the character of budbreak and growth of leaves, i.e. in the different disposition of various parts of leaves to the attack by young larvae of fundatrices.

Mortality factors

Larvae of *Leucopis palumbii* Rond. (Chamaemyiidae) (RASPI 1983, 1988) in Italy and *Scymnus brullei* Muls. (Coccinellidae) (WHEELER and JUBB 1979) in USA were observed as predators of *T. ulmi* in primary hosts. Root morphs of *T. ulmi* show other natural enemies [in the CR, e.g. the parasitoid *Paralipsis enervis* (Nees) (Aphididae)] (STARÝ 1966).

A study of the health condition of *T. ulmi* populations in galls on *U. minor* in Bílovice nad Svitavou did not find any important abiotic and biotic factors which could significantly affect the population density of the aphid (Table 19). Development was successfully completed by aphids in 73.3% of galls. Most frequently (in 10.4% galls), insect and other predators (e.g. from the families Coccinellidae, Chrysopidae and Thrombidiidae) killed fundatrices already in the early stage of the 1st instar development, i.e. in the period of 'areal' sucking on leaves and at the beginning of gall formation. In 7.0% galls fundatrices died at the end of the period of the 1st instar development or during the development of the 2–4 instars. These fundatrices died already in galls due to the protective activity of plant tissues. Their dead bodies were found in galls.

On the other hand, insect enemies showed quite negligible control role in the population dynamics of *T. ulmi.* Galls were occupied only rarely by the predatory bug *Anthocoris confusus* Reut. (Anthocoridae) (determined by Dr. J. Stehlík, Brno). The bug can penetrate into galls which are not perfectly closed or (much more frequently) to galls open through fissures only which originated by the burst of gall walls. Bugs at the locality under study occupied about 8% of all galls after the emergence of aphids. The bugs find in galls not only a suitable shelter but probably also food (sweet excrements of aphids, i.e. honeydew or dead aphids). Nymphs and adults of *A. confusus* were ordinarily and often found in great numbers (as many as 20) in false leaf galls of the aphid *Eriosoma* (= *Schizoneura*) *ulmi* (L.) (Pemphigidae) in *Ulmus glabra* in Bílovice nad Svitavou, Brno-Obřany, Brno-Jundrov etc. Biology of the bug was studied in detail in the galls and results would be dealt with in a separate paper.

Table 19. Numerical/percentage representation of galls of *T. ulmi* with intact and disturbed development in leaves of *U. minor*. From the category of galls with the intact development (second line) galls were detached with insect predators which occurred in them after the emergence of aphids only. Therefore, data on these galls during inspections from 17 July to 9 October are given in parentheses. Bílovice nad Svitavou, 2002

Galls	8.5.	22. 5.	5. 6.	19. 6.	3. 7.	17. 7.	14. 8.	11. 9.	9. 10.	Mean (5. 6.–3. 7. inclusive)	Total
With the intact development of aphids	39	174	101	91	184	(85	(75	(40	(29	125.3	(818
	75.0	75.3	79.5	76.5	63.9	36.8)	48.4)	22.1)	18.6)	73.3	53.1)
Without fundatrix	9	33	12	6	48	61	33	67	38	22.0	307
	17.3	14.3	9.4	5.0	16.7	26.4	21.3	37.0	24.4	10.4	19.9
With dead fundatrix	4	21	10	7	21	21	10	20	23	12.7	137
	7.7	9.1	7.9	5.9	7.3	9.1	6.5	11.1	14.7	7.0	8.9
With *Anthocoris*	–	1	2	3	2	17	10	9	15	2.4	59
		0.5	1.6	2.5	0.7	7.4	6.5	5.0	9.6	1.6	3.8
With Syrphidae	–	–	2	2	1	–	1	–	–	1.7	6
			1.6	1.7	0.3		0.6			1.2	0.4
With Chrysopidae	–	–	–	–	–	1	–	–	–	–	1
						0.4					0.1
With Lepidoptera	–	–	–	4	–	1	1	–	1	1.3	7
				3.4		0.4	0.6		0.6	1.1	0.5
With Araneida	–	–	–	–	–	1	2	13	7	–	23
						0.4	1.3	7.2	4.5		1.5
Eaten up by Insecta	–	1	–	2	2	4	2	1	7	1.3	19
		0.4		1.7	0.7	1.8	1.3	0.5	4.5	0.8	1.2
Pecked up by Aves	–	1	–	4	24	34	13	29	21	9.3	126
		0.4		3.3	8.3	14.7	8.4	16.0	13.5	3.9	8.2
Unopened	–	–	–	–	6	6	8	2	4	2.0	26
					2.1	2.6	5.1	1.1	2.5	0.7	1.7
Fallen, pulled up	–	–	–	–	–	–	–	–	11	–	11
									7.1		0.7
Total	52	231	127	119	288	231	155	181	156	179	1,540
	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

In Bílovice nad Svitavou, larvae of the family Syrphidae participated only minimally (1.2% only) in the mortality of *T. ulmi* in galls. Bright white eggs of Syrphidae (1 to 3 eggs) were found on the surface of 16.2% galls or on leaves in the immediate vicinity of galls. On 17 July, all eggs were hatched. Some 67.9% egg shells were localized at the base of galls, 17.8% in the middle third of galls, 3.6% in the apical third of galls and 10.7% on leaves near galls. It follows that the majority of newly hatched larvae of Syrphidae did not find sufficiently large holes to penetrate into the interior of galls and died of.

Sporadically (1.1%), small caterpillars of an undetermined moth from the family of Pyralidae occurred in galls of *T. ulmi*. The caterpillars ate up the interior of galls (up to the half of the gall wall thickness) and in the period of aphid emergence they left galls through a small bitten out hole of a diameter of about 1 mm. In 1 gall, 1 caterpillar occurred always only which damaged through its feeding max. 70% of the inner surface of a gall and sometimes completed its feeding (in the form of skeletonization) on the adaxial face of leaves being protected by thin web. Caterpillar feeding in galls was easily identifiable according to light (later black) frass, thin light web, light (later black) surface feeding marks and oval emergence holes in gall walls. In the majority of galls occupied by a caterpillar no aphids occurred and thus, it is sure that aphids were nearly always killed by the inquiline.

A negligible proportion (0.8%) of galls was eaten up by undetermined polyphagous insect and the small part (about 3.9%) of galls was pecked up by birds. Early after the emergence of migrantes alatae from galls, the proportion of pecked up galls roughly tripled which showed a certain food attractiveness of aphids for birds. Galls with the partly or completely developed 2nd generation of the aphid were rather rare (0 to 5.1%). In the period of gall opening, they did not open either at all or they opened only

Table 20. Mean length/width of galls of *T. ulmi* with intact and disturbed development (mm) in leaves of *U. minor*. Bílovice nad Svitavou, 2002

Galls	8. 5.	22. 5.	5. 6.	19. 6.	3. 7.	17. 7.	14. 8.	11. 9.	9. 10.	Mean (5. 6–3. 7. inclusive)	Mean Total
With the intact development of aphids	7.0	9.4	10.8	12.1	10.2	10.0	8.8	8.4	8.1	10.8	9.9
	3.3	5.0	6.8	6.6	5.7	6.1	5.1	4.8	4.7	6.2	5.6
Without fundatrix	1.5	3.0	2.6	3.2	2.8	2.2	1.6	1.7	1.6	2.8	2.1
	0.7	1.6	1.6	1.3	1.3	1.3	1.1	1.0	0.9	1.4	1.2
With dead fundatrix	3.0	5.0	6.3	6.4	5.4	5.3	3.8	2.6	3.4	5.8	4.5
	1.3	2.4	4.2	3.1	2.6	3.2	2.0	1.5	1.7	3.1	2.4
With *Anthocoris*	–	12.0	12.0	10.7	9.0	10.2	9.4	7.9	8.3	10.6	9.3
		7.0	7.0	6.7	5.0	5.5	5.5	5.1	4.7	6.3	5.4
With Syrphidae	–	–	10.0	11.0	5.0	–	10.0	–	–	9.4	9.5
			6.0	6.5	6.0		3.0			6.2	5.7
With Chrysopidae	–	–	–	–	–	11.0	–	–	–	–	11.0
						5.0					5.0
With Lepidoptera	–	–	–	11.5	–	10.0	9.0	–	9.0	11.5	10.6
				7.7		6.0	5.0		6.0	7.7	6.8
With Araneida	–	–	–	–	–	11.0	8.0	9.4	7.8	–	8.9
						6.0	5.5	5.2	5.4		5.3
Eaten up by Insecta	–	8.0	–	11.0	5.0	9.8	6.0	2.0	4.2	8.0	7.4
		4.0		7.0	3.5	3.3	3.2	2.0	3.1	5.2	3.6
Pecked up by Aves	–	7.0	–	11.8	11.7	10.2	8.7	10.0	9.6	11.7	10.2
		4.0		7.5	6.7	6.6	6.0	6.0	6.0	6.8	6.3
Unopened	–	–	–	–	6.3	9.7	8.3	7.5	6.5	6.3	7.8
					3.7	5.3	4.5	5.0	4.0	3.7	4.5
Naturally fallen and pulled up	–	–	–	–	–	–	–	–	?	–	?
Mean	5.7	8.1	9.7	11.2	8.6	7.5	7.0	5.5	5.7	9.4	7.8
	2.7	4.3	6.1	6.2	4.7	4.5	4.1	3.3	3.4	5.4	4.4

through an insufficient fissure. In these galls, all aphids naturally always died usually as nymphs and migrantes alatae adults.

Some arthropods (particularly Araneida) use galls of *T. ulmi* after their abandonment by aphids only, viz. particularly as a dwelling. In September 2002, spiders occupied as much as 7.2% galls in Bílovice nad Svitavou (Table 19).

Size differentiation of galls

The gall is established always by 1 fundatrix only in the 1st larval instar. In the period when a gall reaches about one fourth of its final size larvae of the 2nd instar and later larvae of the 3rd and 4th instars begin to participate in its formation. A considerable effect on the gall size shows also a mature fundatrix and to a smaller extent also fundatrigeniae produced by the fundatrix (Fig. 7). With the increase of length and width the thickness of gall walls also gradually increases (Fig. 9). Originally green colouring of galls changes to yellow-green to green-yellow or reddish. In mid-June, galls with intact development are completely grown up and according to the author's examinations they reach an average length of 10.8 mm (according to DARBOUX and HOUARD 1901 12 mm) and width 6.2 mm (Table 20). Above all, galls of the category show a characteristic vesicular form which is described in more details in the chapter Development of fundatrices.

After the emergence of migrantes alatae, galls (and sometimes also parts of leaves around the galls) die of and brown or turn black. In July and later, also leaves on a sucked surface die frequently (Fig. 20) and with the great number of galls per one leaf even the whole leaves prematurely die. Dead galls gradually become dry and get hard whereas they decrease considerably and somewhat change

Fig. 20. Three galls of *T. ulmi* with flown out aphids in leaves of *U. minor*. Dead galls and their vicinity are nearly black. Bílovice nad Svitavou, 17 July 2002

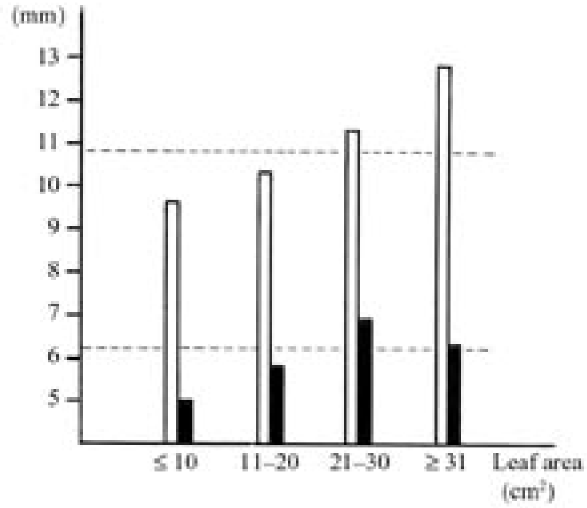

Fig. 21. Average length of grown up and so far unopened galls of *T. ulmi* with the intact development of aphids (light) and disturbed development of aphids (dark) in leaves of *U. minor* of 4 areal categories. The average length of galls with intact and disturbed development of aphids is depicted by dashed lines. Bílovice nad Svitavou, 5 June, 19 June and 3 July 2002

their surface and shape. Table 20 shows that the size of galls with the intact development of aphids decreases by 33% in length and by 31% in width during July to October. At the end of September and at the beginning of October, leaf tissues sucked under moist weather gradually disintegrate around galls and at the beginning of October the galls rather often (ca. 8%) fall even before the natural fall of leaves. The majority of galls (over 90%) persists on leaves and occurs on the ground surface together with fallen leaves as late as in October.

In the main locality under study in Bílovice nad Svitavou with notified dimensions of galls about 10.8 × 6.2 mm, particularly galls with the undisturbed development of fundatrices grew up. Provided fundatrices die the formation of galls soon completely stops. If fundatrices are killed already in the first instar galls are either not created at all or bulge-like or dully conical galls originate on the adaxial face of leaves reaching an average dimension of 2.8 ×1.4 mm only in Bílovice nad Svitavou. These subtle (often imperfectly closed at their base) galls remained usually green until autumn. At the death of higher instars of larvae (or adults) of fundatrices, galls reached greater (however, highly below-average) size of about 5.8 × 3.1 mm.

On the other hand, grown up galls with the bug *A. confusus* did not differ from galls with the intact development of aphids as for their colouring, shape and size (10.6 × 6.3 mm). Galls with larvae of Syrphidae reached also considerable average dimensions (9.4 × 6.2 mm). Galls with caterpillars of a pyralid reached the greatest dimensions (about 11.5 × 7.7 mm). It follows that insect

Table 21. Mean length/width of galls with the intact development of *T. ulmi* (mm) in leaves of *U. minor* of four areal categories (cm²). Bílovice nad Svitavou, 2002

Date	≤ 10	11–20	21–30	≥ 31	Mean
8. 5.	4.2/2.0	6.6/3.1	8.3/2.7	6.9/3.6	7.0/3.3
22. 5.	8.6/4.7	8.2/4.6	9.4/4.9	11.2/5.6	9.4/5.0
5. 6.	10.0/6.1	10.1/6.5	11.5/7.2	13.1/8.2	10.8/6.8
19. 6.	11.3/6.3	11.4/6.5	12.4/7.9	13.7/6.8	12.1/6.6
3. 7.	9.1/5.1	9.4/5.5	11.0/5.8	11.4/6.3	10.2/5.7
17. 7.	9.2/5.0	9.8/5.6	10.1/6.4	10.4/6.6	10.0/6.1
14. 8.	9.1/4.8	9.1/5.2	8.8/5.0	8.0/5.6	8.8/5.1
11. 9.	8.3/4.0	8.4/4.8	8.4/4.6	9.0/5.5	8.4/4.8
9. 10.	7.5/4.0	8.2/4.7	8.5/5.5	9.0/6.0	8.1/4.7
Mean (5. 6.–3. 7. inclusive)	9.6/5.5	10.3/6.1	11.3/6.4	12.4/6.8	10.8/6.2
Mean (all inspections)	9.0/5.0	9.4/5.5	10.2/5.7	10.9/6.0	9.8/5.6

Table 22. Mean length/width of galls with the disturbed development of galls of *T. ulmi* (mm) in leaves of *U. minor* of four areal categories (cm^2). In the last column, mean length/width is given of all galls under investigation. Bílovice nad Svitavou, 2002

Date	≤ 10	11–20	21–30	≥ 31	Mean	Mean (all galls)
8. 5.	1.5/1.0	1.6/0.9	1.5/0.7	3.0/1.1	2.0/0.9	5.7/2.7
22. 5.	2.2/1.5	4.1/2.2	3.3/1.6	4.6/2.3	4.1/2.1	8.1/4.3
5. 6.	3.2/2.0	5.0/3.2	6.9/4.8	5.3/2.8	5.3/3.3	9.7/6.1
19. 6.	9.5/6.5	9.4/5.8	10.0/6.0	7.3/4.0	8.3/4.9	11.2/6.2
3. 7.	4.8/2.4	4.6/2.8	6.8/3.6	6.1/3.2	5.8/3.1	8.6/4.7
17. 7.	6.1/3.2	6.1/3.8	6.1/3.4	6.0/3.7	6.1/3.6	7.5/4.5
14. 8.	4.6/2.5	4.5/2.8	6.4/3.9	10.0/6.0	5.1/3.1	7.0/4.1
11. 9.	3.7/1.9	4.3/2.5	4.9/3.0	5.8/3.4	4.7/2.8	5.5/3.3
9. 10.	3.7/1.9	4.3/2.5	6.2/3.6	8.3/5.7	5.1/3.1	5.7/3.4
Mean (5. 6.–3. 7. inclusive)	5.0/2.9	5.8/3.5	6.9/3.9	6.3/3.3	6.2/3.4	9.4/5.4
Mean (all inspections)	4.5/2.4	4.8/2.9	5.7/3.3	6.0/3.5	5.3/3.0	7.7/4.4

predators and caterpillars of the pyralid occupy usually galls of an above-average size and aphids in the galls are killed only at the end of their development when the growth of galls ceases.

Galls eaten up by insect or pecked up by birds can be easily identified according to the appearance of damage. The eaten up holes are as compared with pecked up holes usually smaller and their edges are jagged. They occur both in the basal and in the middle and apical thirds of galls. Pecked up holes are usually much larger and their edges are smoother. They occur also in various parts of galls, however, particularly in their apical (or middle) third (Table 12). They often (17%) affect simultaneously the base, middle and top of a gall. Newly eaten up galls are of slightly below-average size (about 8.0 × 5.2 mm) while pecked up galls are of above-average size (about 11.7 × 6.8 mm). In searching galls birds follow obviously exclusively their eyes and preferentially peck up the largest galls with the highest number of aphids.

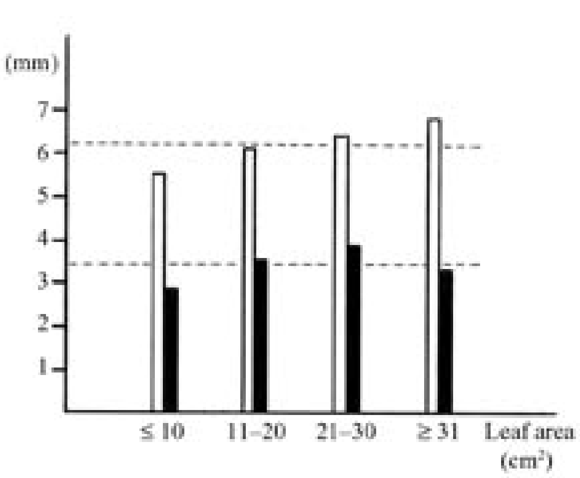

Fig. 22. Average width of grown up and so far unopened galls of *T. ulmi* with the intact development of aphids (light) and disturbed development of aphids (dark) in leaves of *U. minor* of 4 areal categories. The average width of galls with intact and disturbed development of aphids is depicted by dashed lines. Bílovice nad Svitavou, 5 June, 19 June and 3 July 2002

The last category are galls with partly or entirely completed development of aphids which opened by insufficiently large fissures or did not open at all. These galls reached only below-average dimensions of about 6.3 × 3.7 mm (Table 20). The table shows that far the greatest effect on the shape and size differentiation of galls of *T. ulmi* shows the early death of larvae of fundatrices in the 1st instar.

The mean length and width of *T. ulmi* galls with intact and disturbed development (in leaves of 4 areal categories) is given in Tables 21 and 22 and Figs. 21 and 22. Newly grown up galls with the undisturbed development of aphids were on average 10.8 mm long and 6.2 mm wide. Galls with the disturbed development of aphids were on average 6.2 mm long and 3.4 mm wide only. During July to October, their dimensions decreased due to drying approximately by one third. Galls with intact development were 9.4 mm long and 5.4 mm wide after finishing the growth and in October 5.7 mm long and 3.4 mm wide. In the course of July to October, their length and width thus decreased by 39 and 37%, respectively (Table 22). It is evident from Tables 21 and 22 and Figs. 21 and 22 that the mean size of galls with the intact development of aphids significantly increases with the size of a leaf blade. The fact was already noticed e.g. by RUPAJS (1989). According to the author, galls in small leaves are 8 mm long only whereas in large leaves as much as 16 mm.

Harmfulness in elms

Opinions of harmfulness of *T. ulmi* in elms differ often diametrically. In some publications (e.g. STEFFAN 1972), the aphid is considered to be nearly harmless whereas in other (e.g. VASILJEV et al. 1975; RUPAJS 1989) very harmful. Its economic importance in secondary hosts (particularly in various kinds of cereals) is evaluated similarly.

In assessing effects of *T. ulmi* on host species of elms it is necessary to take into consideration both damage to newly unfolded leaves both by 'areal' sucking and by the creation of galls. As given above, in case of individual occurrence, the sucking damages about 1.5 cm^2 (about 6%) of the leaf blade. In the course of mass outbreaks, as many as 30 (according to the author's studies 21) galls can occur on 1 leaf. Elms are considerably physiologically weakened by extensive sucking of aphids (affecting the predominant part of the leaf blade or even the whole blade) on leaves and by numerous galls. Mass-attacked leaves are deformed and show the substantially decreased content of chlorophyll. Amounts of nutrients are also taken to plants during the creation of galls and nutrition of aphids. Heavily damaged leaves grow old more rapidly and often fall off prematurely. Assimilation and the total increment of trees decrease substantially. Branches of elms sometimes bend due to the weight of innumerable galls. Aesthetic values of elms grown in parks and gardens decrease.

According to the author's findings, the aphid *T. ulmi* should be considered to be an important occasional pest of elms. In case of a mass outbreak, it would be useful, therefore, to control it. In the past, a timely collection and burning the attacked leaves were recommended as preventive and control measures (Lederer 1928–1932). Later, various insecticides were tested successfully to control the pest (Jancke 1951; Kramm 1953; Zlatanov 1964 etc.). At present, a number of environmentally-friendly insecticides can be recommended to control *T. ulmi*. It is suitable to carry out the measure shortly before or in the period of budbreak.

SUMMARY

In 2001 and 2002, an outbreak of the cecidogenous aphid *Tetraneura* (= *Byrsocrypta*) *ulmi* (L.) was recorded in elms in several localities of Moravia. It refers to a heteroecious member of the family Pemphigidae with a complete (holocyclic) annual development. During the development, the aphid migrates from galls on primary hosts [(some species of elm (*Ulmus* spp.)] to roots of secondary host plants (numerous species of Poaceae). It reproduces by heterogony when 1 amphigonic generation (sexuales) alternates usually with 4 parthenogenetic generations (fundatrices, fundatrigeniae including migrantes alatae, virginogeniae and sexuparae). With the exception of virginogeniae and sexuparae other generations develop in elms.

The outbreak of *T. ulmi* was used for the study of its occurrence, development and harmfulness in elms. The majority of investigations was conducted in *Ulmus minor* Mill. in a riparian and accompanying stand of the Svitava river, Bílovice nad Svitavou near Brno in 2002. From May to October, leaves with galls were sampled from the species for laboratory investigations in 14-day intervals. Partial observations were carried out according to requirements also in other dates and in other localities (e.g. in Brno-Obřany, Bystřička – District of Vsetín etc.). The following results have been obtained:

1. In localities under investigation, galls occurred most frequently in *U. minor* Mill. and much less in *U. glabra* Huds. In a very abundant *U. laevis* Pall., they were never found.
2. In Bílovice nad Svitavou, fundatrices hatched from mid-April to 7 May. Young larvae settle on the abaxial face of newly unfolded leaves and damage them by areal sucking at first. During the sucking, they inject salivary secretions into tissues by means of 20 to 60 punctures (0.3 to 2 mm apart). The secretions contain growth substances inducing deformities and colour changes of leaves. One larva can suck on average 1.5 cm^2 (about 6% of the leaf blade). In Bílovice nad Svitavou, as many as 16 (in a shelterbelt near Čejkovice, Znojmo District as many as 21) galls were found on 1 leaf. In leaves with more than 10 galls, the sucking often damages the whole leaf blade. With the average number of 2.5 galls per 1 leaf (average area 22.5 cm^2) the sucking damaged 2.9 cm^2, i.e. about 13% of the leaf blade. An average area sucked by 1 fundatrix significantly increased with the leaf size (as many as 2.3 times) and significantly decreased (as many as 1.8 times) with the increasing number of galls on leaves.
3. By later more or less sedentary sucking, larvae of the 1st instar induce the creation of true galls on the adaxial face of leaves. In Bílovice nad Svitavou, larvae moulted for the first time when galls reached the third of their final size. After next 3 ecdyses, mature fundatrices appeared. The development from hatching to maturity took 3 to 4 weeks. The galls grew up as early as at the beginning of June, and larvae and adults of fundatrices participated quite substantially in their creation. In 1 gall, 1 fundatrix develops always only.
4. Mature fundatrices produce for a period of 1 to 3 weeks larvae – fundatrigeniae. In total, they produce 3 to 78 (on average 35.2) offsprings. Average fertility of females significantly increases (ca. 2 times) with the size of galls. During the reproduction, fundatrices gradually (as many as 1.6 times) get shorter. Potential fertility corresponds to real fertility.
5. Fundatrigeniae change in nymphs after 3 ecdyses and after the 4th ecdysis in pterygote migrantes alatae. The development of fundatrigeniae took on average 18 days. Migrants left the galls from 10 to 30 June. In the period shortly before emergence from galls, their ovaries contained 2 to 10 (on average 5.8) embryos. The number of embryos significantly increased with the size of females.
6. For the emergence from galls, aphids use holes originating by the spontaneous fissuring the gall walls. In Bílovice nad Svitavou, 57.6% galls opened through fissures, 25.3% opened imperfectly (holes smaller than 1.5 × 0.9 mm) or not at all. The overwhelming majority of galls (94.9%) opened in the basal third, 4.2% in the middle third and 0.9% in the apical third. Localization of emergence holes is related to the mean thickness of gall walls which is 0.30 mm at the base, 0.45 mm at

the half of gall height and 0.60 mm at the top of galls. In galls, 1 to 5 (on average 1.4) fissures occurred of a mean length of 2.7 mm and width 2.0 mm. Both the number and size of fissures increased with the size of galls. Some 60.0% fissures were longitudinal, 11.6% transverse and 28.4% oval.

7. The mean number of galls per 1 leaf increased with the blade size. Some 70.1% galls occurred in the apical third of the blade, 23.6% in the middle and 6.3% in the basal third of the leaf blade. The majority (66.1%) of galls occurred on the 'smaller' half of the blade.
8. Aphids left 73.3% of all galls. In 10.4% galls, fundatrices were killed by insect and other predators in the 1st instar in the initial stage of the gall development. In 7.0% galls, fundatrices died as late as at the end of the 1st instar development or during the development of the 2–4 instars, viz. due to the protective activity of plant tissues. In 1.6% galls, aphids were killed by the bug *Anthocoris confusus*, in 1.2% by larvae of Syrphidae, in 1.1% by caterpillars of Pyralidae. Some 0.8% galls were eaten up by insect and 3.9% were pecked up by birds. Owing to disorders in gall opening aphids died in 0.7 to 1.7% galls.
9. Grown up galls with the intact development of aphids reached on average 10.8 mm in length and 6.2 mm in width. In case of the death of fundatrices as early as in the 1st instar, galls either did not form at all or small galls originated only of a mean length of 2.8 mm and width 1.4 mm. At the later death of fundatrices, galls were on average 5.8 mm long and 3.1 mm wide. Galls with *A. confusus* reached a size of about 10.6 × 6.3 mm, with larvae of Syrphidae 9.4 × 6.2 mm and with caterpillars of Pyralidae 11.5 × 7.7 mm. Above-average sizes (about 11.7 × 6.8 mm) were pecked up galls and below-average sizes (about 8.0 × 5.2 mm) galls eaten up by insect. Below-average sizes (about 6.3 × 3.7 mm) were also galls with the intact development of aphids so far, however, with disorders in opening. The average size of galls increased with the size of a leaf blade both in aphids with intact and disturbed development.
10. The aphid *T. ulmi* is an important occasional physiological pest of elms. In case of mass outbreaks, it damages leaves by extensive sucking and creation of innumerable galls. In elms grown for ornamental purposes, it decreases their aesthetic values. In case of the enormous occurrence of the pest it is necessary to control it, viz. preferably using insecticides. The measure should be carried out shortly before or during budbreak.

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Bionomie a škodlivost *Tetraneura ulmi* (L.) (Aphidinea, Pemphigidae) na jilmech

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ABSTRAKT: Práce pojednává o bionomii a škodlivosti běžné cecidogenní mšice *Tetraneura* (= *Byrsocrypta*) *ulmi* (L.) (Pemphigidae), která se v roce 2002 přemnožila na jilmech na Moravě. Většina šetření byla vykonána na *Ulmus minor* v břehovém a doprovodném porostu řeky Svitavy v Bílovicích nad Svitavou na Brněnsku. Mšice se nejhojněji vyskytovala na *U. minor*, mnohem méně na *U. glabra,* nikdy ne na *U. laevis*. Na jednom listu tam bylo nalezeno kolem 2,5 (nejvíce 16) hálek (u Čejkovic na Znojemsku až 21 hálek). Fundatrices se líhly od 15. dubna do 7. května. Plošným sáním na abaxiální straně listů poškodily průměrně 1,4 cm^2 (kolem 6 %) čepele, na listech s 10 a více hálkami často celou čepel. Za 3 až 4 týdny od vylíhnutí (od poloviny května) fundatrices dospívaly a během 1 až 3 týdnů zplodily průměrně 35,2 fundatrigenií. Začátkem června hálky dorůstaly průměrné délky 10,8 mm a šířky 6,2 mm. Fundatrigenie se vyvíjely kolem 18 dnů a od 10. do 30. června vytvářely migrantes alatae. Mšice opustily 73,3 % hálek. V 10,4 % hálek byly fundatrices zahubeny hmyzími a jinými predátory v 1. instaru (v počátečním období tvorby hálek). V 7,0 % hálek uhynuly nedospělé fundatrices v pozdějších fázích vývoje, a to vlivem obranné činnosti rostlinných pletiv. Na mortalitě fundatrigenií včetně migrantes alatae se ve velmi malé míře podíleli např. *Anthocoris confusus* Reut., larvy Syrphidae, housenky Pyralidae a ptáci. V práci je dokumentován vliv mortalitních faktorů na tvarovou a velikostní diferenciaci hálek.

Klíčová slova: jilm; *Tetraneura* (= *Byrsocrypta*) *ulmi*; výskyt; vývoj; mortalitní faktory; diferenciace hálek

V roce 2001 a 2002 bylo na několika lokalitách na Moravě zaznamenáno na jilmech přemnožení cecidogenní mšice – vlnatky hladké [*Tetraneura* (= *Byrsocrypta*) *ulmi* (L.)]. Jedná se o heteroekního zástupce čeledi Pemphigidae s úplným (holocyklickým) anuárním vývojem, během něhož migruje z hálek na primárních hostitelích (některých druzích jilmů – *Ulmus* spp.) na kořeny sekundárních hostitelských rostlin (četných druhů lipnicovitých – *Poaceae*). Rozmnožuje se heterogonií, v rámci které se střídá jedna generace amfigonická (sexuales) obvykle se čtyřmi generacemi partenogenetickými (fundatrices, fundatrigeniae včetně migrantes alatae, virginogeniae a sexuparae). S výjimkou virginogenních generací se ostatní generace vyvíjejí na jilmech.

Přemnožení *T. ulmi* bylo využito ke studiu jejího výskytu, vývoje a škodlivosti na jilmech. Většina šetření byla prováděna v roce 2002 na jilmu habrolistém (*Ulmus minor* Mill.) v břehovém a doprovodném porostu řeky Svitavy v Bílovicích nad Svitavou na Brněnsku. Od května do října (včetně) byly z této dřeviny ve 14denních intervalech odebírány listy s hálkami k laboratornímu vyšetření. Dílčí pozorování byla podle potřeby konána i v dalších termínech a na dalších lokalitách (např. v Brně-Obřanech, Bystřičce – okres Vsetín aj.). Byly získány tyto hlavní výsledky:

1. Na sledovaných lokalitách se hálky nejčastěji vyskytovaly na *U. minor* Mill. a mnohem méně na jilmu horském (*U. glabra* Huds.). Na velmi hojném jilmu vazu (*U. laevis* Pall.) nebyly nikdy nalezeny.
2. V Bílovicích nad Svitavou se fundatrices líhly od poloviny dubna do 7. května. Mladé larvy se usazují na abaxiální straně čerstvě vyrašených listů, které

zpočátku poškozují plošným sáním. Při něm 20 až 60 vpichy (vzdálenými od sebe 0,3 až 2 mm) injektují do pletiv slinné sekrety, obsahující růstové látky, které indukují deformace a barevné změny listů. Jedna larva posaje průměrně 1,5 cm^2 (kolem 6 %) čepele. V Bílovicích nad Svitavou bylo na jednom listu nalezeno až 16 (a ve větrolamu poblíž Čejkovic na Znojemsku až 21) hálek. U listů s více než 10 hálkami je sáním často poškozena celá čepel. Při průměrném počtu 2,5 hálky na jednom listu (o průměrné ploše 22,5 cm^2) bylo sáním poškozeno 2,9 cm^2, tj. kolem 13 % čepele (tab. 1). Průměrná plocha posátá 1 fundatrix s velikostí listů průkazně (až 2,3krát) stoupala (tab. 2) a se vzrůstajícím počtem hálek na listech průkazně (až 1,8krát) klesala (tab. 3).

3. Pozdějším víceméně sedentárním sáním larvy 1. instaru indukují na adaxiální straně listů tvorbu pravých hálek. V Bílovicích nad Svitavou se larvy poprvé svlékaly v době, kdy hálky dosahovaly třetiny své konečné velikosti. Po dalších třech svlékáních se objevovaly dospělé fundatrices. Vývoj od vylíhnutí z vajíček až do dospělosti trval 3 až 4 týdny. Hálky dorůstaly již začátkem června a na jejich tvorbě se daleko nejvíce podílely larvy a dospělci fundatrices (obr. 7). V 1 hálce se vždy vyvíjí jen 1 fundatrix.
4. Dospělé fundatrices rodí po dobu 1 až 3 týdnů larvy – fundatrigenie. Celkem zplodí 3 až 78 (průměrně 35,2) potomků. S velikostí hálek průměrná plodnost samiček průkazně (asi dvakrát) vzrůstá (tab. 7). Během reprodukce se fundatrices postupně (až 1,6krát) zkracují (tab. 8). Potenciální plodnost se rovná plodnosti reálné.
5. Fundatrigenie se po třech svlékáních mění v nymfy a po čtvrtém v okřídlené migrantes alatae. Vývoj fundatrigenií trval průměrně 18 dnů. Migranti hálky opouštěli od 10. do 30. června. V době těsně před výletem z hálek jejich ovaria obsahovala 2 až 10 (průměrně 5,8) embryí. Počet embryí s velikostí samiček průkazně vzrůstal (tab. 10).
6. K výletu z hálek mšice využívají otvorů, které vznikají spontánním pukáním hálkových stěn. V Bílovicích nad Svitavou se prasklinami otevřelo 57,6 % hálek, dalších 25,3 % hálek se otevřelo nedokonale (otvorem menším než 1,5 × 0,9 mm) anebo vůbec ne (tab. 11). Drtivá většina hálek (94,9 %) se otevřela v bazální třetině, 4,2 % ve střední třetině a 0,9 % ve vrcholové třetině (tab. 12). Lokalizace výletových otvorů souvisí s průměrnou tloušťkou stěn hálek, která je při bázi 0,30 mm, v polovině výšky hálek 0,45 mm a při vrcholu 0,60 mm (obr. 9). V hálkách se vyskytovalo 1 až 5 (průměrně 1,4) prasklin o průměrné délce 2,7 mm a šířce 2,0 mm. S velikostí hálek stoupal jak počet, tak i velikost prasklin (tab. 14 a 15). 60,0 % prasklin bylo podélných, 11,6 % příčných a 28,4 % oválných.
7. Průměrný počet hálek na jednom listu s velikostí čepele vzrůstal (tab. 17). 70,1 % hálek se vyskytovalo v apikální třetině čepele, 23,6 % ve střední a 6,3 % v bazální třetině čepele (tab. 18). Většina (66,1 %) hálek byla na menší „polovině“ čepele.
8. Mšice opustily 73,3 % všech hálek. V 10,4 % hálek byly fundatrices zahubeny hmyzími a jinými predátory v 1. instaru v počátečním období tvorby hálek. V 7,0 % hálek fundatrices uhynuly až koncem období vývoje 1. instaru nebo během vývoje 2. až 4. instaru, a to vlivem obranné činnosti rostlinných pletiv. V 1,6 % hálek byly mšice zahubeny plošticí *Anthocoris confusus*, v 1,2 % larvami Syrphidae, v 1,1 % housenkami Pyralidae. 0,8 % hálek bylo vyžráno hmyzem a 3,9 % vyzobáno ptáky. Vlivem poruch v otevírání hálek mšice uhynuly v 0,7 až 1,7 % hálek (tab. 19).
9. Dorostlé hálky s neporušeným vývojem mšice dosahovaly průměrné délky 10,8 mm a šířky 6,2 mm. Při úhynu fundatrices již v 1. instaru se hálky buďto vůbec nevytvářely, nebo vznikaly drobné hálky o průměrné délce 2,8 mm a šířce 1,4 mm. Při pozdějším úhynu fundatrices byly hálky průměrně 5,8 mm dlouhé a 3,1 mm široké. Hálky s *A. confusus* dosahovaly velikosti kolem 10,6 × 6,3 mm, s larvami Syrphidae 9,4 × 6,2 mm a s housenkami Pyralidae 11,5 × 7,7 mm. Nadprůměrné velikosti (kolem 11,7 × 6,8 mm) byly hálky vyzobané a podprůměrné velikosti (kolem 8,0 × 5,2 mm) hálky vyžrané hmyzem. Podprůměrné velikosti (kolem 6,3 × 3,7 mm) byly také hálky s dosud neporušeným vývojem mšic, avšak s poruchami v otevírání (tab. 20). Průměrná velikost hálek s neporušeným i porušeným vývojem mšic s velikostí listové čepele vzrůstala (tab. 21, 22).
10. Mšice *T. ulmi* je významný občasný fyziologický škůdce jilmů. Při přemnožení poškozuje listy rozsáhlým posátím a tvorbou nesčetných hálek. U jilmů pěstovaných pro ozdobné účely snižuje estetickou hodnotu. V případě enormního výskytu je třeba proti ní bojovat, a to nejlépe pomocí insekticidů. Zásah je nutné provést krátce před rašením nebo v době rašení pupenů.

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