ACTA UNIVERSITATIS AGRICULTURAE ET SILVICULTURAE MENDELIANAE BRUNENSIS

Volume 63 177 Number 5, 2015

http://dx.doi.org/10.11118/actaun201563051601

OCCURRENCE, BIOLOGY AND HARMFULNESS OF *BYCTISCUS BETULAE* (L.) (COLEOPTERA, RHYNCHITIDAE)

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Abstract

URBAN JAROSLAV. 2015. Occurrence, Biology and Harmfulness of *Byctiscus betulae* (L.) (Coleoptera, Rhynchitidae). *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis,* 63(5): 1601–1624.

In 2012 and 2013, was studied the occurrence, biology and harmfulness of *Byctiscus betulae* (L.) (Rhynchitidae) on forest woody plants in the Brno region. Leaf rolls were found on 13 species (and 10 genera) of woody plants. Most frequently, they occurred on *Fagus sylvatica*, *Tilia* spp. (namely on *T. cordata*), *Salix caprea* and *Populus tremula*. The beetles hibernate in ground pupal chambers and appear on woody plants in the last decade of April. After hibernation, females live on average seven (males five) weeks, and damage on average 40 (males 25) cm^2 of leaves. The females create leaf rolls on annual shoots they have gnawed, exceptionally (in 2%) on leaves with damaged petioles. In the rolls on *F. sylvatica*, they roll on average 5.6 leaves whose total average area is 49.5 cm^2 and lay on average 5.1 eggs. In the rolls on *Tilia* spp., they roll on average 3.3 leaves whose total area is 63.2 cm^2 and lay on average 4.9 eggs. In the rolls on *S. caprea*, they roll on average 3.3 leaves whose total area is 38.3 cm^2 and lay on average 3.5 eggs. The maximum number of laid eggs (on average 8.0) was observed in the leaf rolls on *Vitis vinifera*. The average number of eggs in the leaf rolls was decreasing from May to July. The number of eggs was increasing with the increasing total leaf area rolled. The females lay on average 50 eggs. On *P. tremula*, *S. caprea* and *Pyrus pyraster* they create about 15 leaf rolls, on *F. sylvatica* and *Tilia* spp. about 10 leaf rolls and on *V. vinifera* ca. 8 leaf rolls. Embryogenesis lasts from 8 to 9 days. Larvae develop over 3 instars and damage ca. 300 mm^2 of leaves. Coming of age within 4–7 weeks, they leave the leaf rolls from mid-June to the beginning of September.[1]

Keywords: *Byctiscus betulae*, Rhynchitidae, host woody plants, occurrence, leaf roll characteristics, development, mortality, harmfulness

INTRODUCTION

Vine (pear, hazel, grape) leaf roller- *Byctiscus betulae* (Linnaeus, 1758) is a representative from the family of leaf-rolling weevils (Rhynchitidae) from the superfamily of Curculionoidea. Beetles of this family are morphologically and biologically close to leaf rolling weevils from the family of Attelabidae. From the other Curculionoidea they differ particularly by non-angular antennae and by the noticeable instinct of mothering the progeny. All leaf-rolling weevils are phytophagous obligates. Females of most species (apart from several inquilins) typically damage vegetative and reproductive organs of plants (leaves, shoots, buds and fruits), causing their wilting and decay. Eggs are then deposited into thus prepared tissues or between the folds of the leaves in species-specific leaf rolls. Larvae live endophytically in the damaged organs or inside the leaf rolls, which either persist on the plants or eventually fall onto the ground.

In the past, the leaf-rolling weevils (i.e. representatives of Rhynchitidae and Attelabidae families) used to be classified with the very rich-in-species

1 The study was elaborated at the Faculty of Forestry and Wood Technology, Mendel University in Brno.

family of Curculionidae, namely in its subfamily of Rhynchitinae (and/or in the subfamilies of Rhynchitinae, Attelabinae and Apoderinae). Opinions about the position of leaf-rolling weevils in the zoological system have not been stabilized yet. Even at present, some authors classify the leaf-rolling weevils in the single autonomous family of Rhynchitidae or Attelabidae, which they further divide into two up to three above-mentioned subfamilies.

The leaf-rolling weevils occur mainly in subtropical and tropical zones. According to Oberprieler *et al.* (2007), there are about 2 500 species and 150 genera of leaf-rolling weevils that have been described over the world. In the territory of the Czech Republic, 32 species occur (Strejček, 1993). Biology of most species is little known or unknown. Their economic importance in forestry is generally low. However, some species may occasionally cause harm to young woody plants. Damages in agriculture, fruit and vine growing can be significant.

A relatively well-known harmful species is vine leaf roller (*B. betulae*). This polyphagous species belongs in the biological group of so-called lengthwise "leaf rollers". It is known particularly as a vine (*Vitis vinifera* L.) pest, less frequently as a pest on fruit trees (especially *Pyrus* spp.). This is why its harmful occurrence was studied mostly in vineyards. With the contemporary establishment and cultivation of vineyards, the species' harmfulness is much lesser than in the past. The vine leaf roller occurs in abundance on various forest woody plants where it is usually considered an economically insignificant species. Detailed studies focused on its occurrence and development on forest trees are apparently missing.

The submitted monograph is a product of systematic study of the occurrence, biology and harmfulness of *B. betulae* in forest ecosystems occurring in the Brno region (South Moravia). Most field surveys were done in 2012 and 2013 at the Training Forest Enterprise Masaryk Forest Křtiny, Lesy města Brna (Forests of the City of Brno), a. s., and at Forest Administration Bučovice (Lesy ČR, s. p. – Forests of the Czech Republic, State Enterprise).

Geographic Distribution

Vine leaf roller (*B. betulae*) is a West Palaearctic to Middle Palaearctic species, widely spread especially in Europe (Legalov, 2007, 2011). According to Legalov (2002, 2006, 2010, 2011), it occurs also in the Asian part of Russia, namely from the north to the northern Caucasus. Its eastern distribution limits reach in Siberia up to the town of Cita, situated some 200 km north of the border with eastern Mongolia. It does not occur in the Russian Far East (Legalov and Shevnin, 2007) and is missing in Japan too (Kôno, 1930). The species occurrence is reported from Transcaucasia, Asia Minor, Kazakhstan and Turkmenistan (Legalov, 2006) and even from China (Hua, 2002). Therefore, the statement of Podlussány (1984) about the occurrence of *B. betulae* in Europe, Southwest Asia, Central Asia and Siberia is inaccurate. Southern distribution limits are in Sicily (Abbazzi *et al.*, 1995), in Turkey (Aslan and Calmasur, 2002) and in Israel (Legalov and Friedman, 2007). The species was not found in the Province of Palermo, Sicily (Stejskal, 2004). In the north, it reaches up to Scandinavia (Gønget, 2003) and to the Russian Republic of Komi (Mingaleva, Pestov and Zagirova, 2011), in the west to the Pyrenean peninsula and to Great Britain (Ruiz Castro, 1946; Domingues Garcia-Tejero, 1955–1956; Morris, 1990; Fowles, 2009 and others). According to Dosse (1954), it occurs in Central America, too.

In general, the occurrence of *B. betulae* is bound to biotopes with broadleaved woody plants (Nazarenko and Petrenko, 2008). The species preferably colonizes medium moist and medium warm sites with broadleaved and mixed woods, orchards, parks, and woody plants on road and field margins (Mazur, 2002, 2011). Some authors (e.g. Papi, 2009) take it for a mesophilous Palaearctic species. According to Miller (1956), it avoids areas with both cold and too warm soils as well as areas with heavy and sandy soils. The species is rather abundant on aeolian sands of the forest steppe zone in southern Slovakia (near the Danube River) (Majzlan, Rychlík and Deván, 1999).

Host Woody Plants

B. betulae is a polyphagous species. Its host plants are numerous forest and fruit trees and shrubs. According to Ratzeburg (1839), it lives most often on *Vitis*, less frequently on *Alnus*, *Betula*, *Corylus*, and/or on *Tilia* and *Populus tremula* L. Jäger (1876) considers *Fagus* and *Populus* to be hosts too, and Kleine (1910) adds *Prunus*, *Crataegus*, *Salix* and *Acer*. According to Formánek (1911), the main hosts include *Vitis*, *Malus*, *Pyrus* and *P. tremula*, according to Roubal (1937–1941), the main hosts are *Vitis*, *Pyrus*, *Alnus*, *Betula*, *Corylus*, *Populus*, *Tilia* and other woody plant species. Reitter (1916) and Schaufuss (1916) for example classify fruit trees and shrubs as the main host plants. Miller (1956) mentions extensive polyphagia and claims that the species does harm to *Vitis*, *Pyrus*, *Prunus*, *Malus*, *Acer*, *Alnus*, *Populus* (incl. *P. tremula*), *Corylus*, *Ulmus*, *Tilia*, *Quercus*, *Fagus*, *Betula*, *Rosa* and *Rubus idaeus* L. According to Vicente *et al.* (1998), hosts include in addition to fruit trees also *Acer*, *Alnus*, *Corylus*, *Betula*, *Fagus*, *Rubus idaeus*, *Castanea sativa* Müll., *Carpinus*, *Fraxinus* and *Sorbus*. Apart from *Vitis* and fruit trees, Gønget (2003) considers the species' hosts to be also *Salix*, *Populus*, *Betula*, *Acer*, *Fagus*, *Alnus*, *Corylus*, *Tilia*, *Carpinus* and *C. sativa*. According to Scherf (1964), the species develops on *Betula pendula* Roth., *Alnus glutinosa* Gaertn., *Pyrus communis* L., *Cydonia oblonga* Mill., *Corylus avellana* L., *Salix caprea* L., *Vitis vinifera* L., rarely on *Fagus sylvatica* L., *Tilia cordata* Mill. and *P. tremula* L. Vasiljev *et al.* (1974, 1975) mention a wide range of *B. betulae* hosts. The authors claim the tooth-nosed snout beetle causes damage most frequently to *Pyrus*, *Cydonia*, *Prunus*, *Malus* and *S. caprea* L., to a lesser extent also to *Populus* (namely *P. tremula*), *Betula*, *Acer*, *Fagus*, *Alnus*, *Corylus*, *Tilia*, *Ulmus*, *R. idaeus*, *Rosa* and *Sorbus*.

The brief overview of literature indicates that the studied species occurs on a large number of woody plants from about nine different families. The most preferred ones are doubtlessly those from the families of Rosaceae (Malaceae), Salicaceae and Vitaceae. Nevertheless, trophic affinity for some above-mentioned plants (e.g. *Rosa*, *Quercus*, *Fraxinus* and *Crataegus*) is disputable and should be thouroughly verified.

Biology and Economic Importance

Basic data about the *B. betulae* morphology, determination, occurrence, development and damages can be found in numerous comprehensive entomological and entomology-focused nature conservation works (Ratzeburg, 1839; Jäger, 1876; Henschel, 1895; Klapálek, 1903; Kleine, 1910; Formánek, 1911; Kuhnt, 1913; Reitter, 1916; Schaufuss, 1916; Escherich, 1923; Lederer, 1928–1932; Smolák, 1941; Javorek, 1947; Baudyš, 1952; Dosse, 1954; Miller, 1956; Brauns, 1964; Foltýn *et al.*, 1965; Ter-Minasjan, 1965; Koehler and Schnaider, 1972; Francke-Grosmann, 1974; Vasiljev *et al.*, 1974; Mamajev *et al.*, 1976; Freude, Harde and Lohse, 1981; Vicente *et al.*, 1998; Křístek and Urban, 2004; Lelei *et al.*, 2007).

Relatively many authors studied in detail the biology of *B. betulae* and damages (Marre, 1916; Stellwaag, 1918, 1919; Krieg, 1924; Perepechai, 1930; Ruiz Castro, 1946; Dobrovoľskij, 1950; Becker, 1954; Bournier, 1976; Konopleva, 1974; Andreetti and Osella, 1994; Ocete, Del Tio and Lopez, 1996; Peršurić, 1995; Aslan and Calmasur, 2002; Trdan and Valič, 2004; Antonie, Todorescu and Oprean, 2006). Numerous ecologico-faunistic and zoogeographic works contributed to the knowledge of *B. betulae*, too (Turček, 1956; Podlussány, 1984; Majzlan, Rychlík and Deván, 1999; Mazur, 2002, 2011; Pešić, Mladićević and Živković, 2005; Kodrík, Kodrík and Hlaváč, 2006; Germann, 2010; Mingaleva, Pestov and Zagirova, 2011).

There are many insect parasitoid species developing in *B. betulae* (Scherf, 1964). Silvestri (1916) described an important parasitoid of eggs – *Poropoea defilippii* (family of Trichogrammatidae) and studied its biology. Papp (2000) succeeded in breeding a new parasitoid from the larvae of *B. betulae* – *Bracon* (*Glabrobracon*) *admotus* (family of Braconidae). Parasitoids of the species are mentioned in papers published for example by Taschenberg (1874), Nikolskaja (1952), Subba Rao (1969), Trjapicyn (1978), Nikolskaja and Trjapicyn (1978), Vicente *et al.* (1998), Polaszek (2010) and others.

Many authors deal with the possibilities of protection and counter measures against losses caused by *B. betulae* namely on *Vitis vinifera* in vineyards (Ratzeburg, 1839; Krieg, 1924; Perepechai, 1930; Smolák, 1941; Baudyš, 1952; Dosse, 1954; Miller, 1956; Foltýn *et al.*, 1965; Konopleva, 1974; Antonie and Todorescu, 2008). Nonetheless, the number of works based on the systematic study of *B. betulae* occurrence, biology and harmfulness is still low so far.

MATERIAL AND METHODS

Inquiries took place in a number of localities, mainly in the Brno region, in 2012 and 2013. Most of the controlled stands occur north and northwest of Brno (localities in the forest districts of Bílovice n. Sv. and Vranov – operated by the Training Forest Enterprise Masaryk Forest Křtiny). Another locality of interest (Horákov) is situated northeast of Brno and is under management of the Pozořice forest district (Forest Administration Bučovice, Lesy ČR, State Enterprise). The localities of Žabovřesky, Komín and Podkomorské lesy Forests, which fall under management of the Forest Administration Brno (Forests of the City of Brno/Lesy města Brna, a. s./ with headquarters in Kuřim) are situated for the most part west of the Moravian metropolis. Partial surveys were conducted also in the Tišnov region, Vsetín region and elsewhere.

The research was made in broadleaved and/or mixed forest stands of the first age class. The woods consisted of planted tree species (beech and lime in particular) and of admixed self-seeded woody plants (mainly goat willow, European aspen, hornbeam, hazel and birch). Attention was also paid to young woody plants growing on stand margins, along forest rides, roads, watercourses, and occasionally in urban parks. In 2012, field surveys were irregular and focused on the main period of pest development (i.e. May and June). In 2013, the species was studied almost during the entire growing period (from the beginning of May to mid-September) at regular ± week intervals. The incidence of adults and leaf rolls was monitored on various woody plants from 09.00 to 16.00 o'clock. Beetles were captured by simple collection or by using a sweep net.

Adults of *B. betulae* harvested in the open and adults emerged in the laboratory from the collected leaf rolls were placed into glass dishes with the diameter of 15–20 cm and height of 6–8 cm. For breeding, we used terminal leafy sections of the shoots of host woody plants long about 15 cm. Bases of shoots were placed into small receptacles with water, the necks of which were sealed with paper wadding. The shoots were replaced with fresh ones at regular weekly inspections of longevity, size of damaged leaf area, defecation, oviposition etc.

Leaf rolls were taken from the trees together with complete annual shoots at ± week intervals. Records were taken of shoot length above the damage (bite, puncture) and beneath the damage. The area of individual leaves not included in the leaf rolls was measured planimetrically. In addition to their surface area, the rolled leaves were measured also for their length and width. Direction of the coiling (rolling) of individual leaves (or their parts) was recorded too. Ascertained was the number of laid vital and dead eggs, the number of larvae of individual instars etc. The growth stage (instar) of the larvae was determined from the micrometrically ascertained head case width.

RESULTS AND DISCUSSION

Host Woody Plants

Byctiscus betulae ranks with the most abundant species of leaf-rolling weevils in Europe. It harms numerous forest and fruit woody plants including *Vitis vinifera* L. by its maturation (i.e. maturity and regeneration) feeding and creation of leaf rolls. According to the available literature, *B. betulae* occurs on woody plants of 22 diverse genera. The species is most frequently (in nearly 96% of publications) reported from fruit trees (occurring namely on *Pyrus* and often also on *Malus*, *Prunus*, and *Cydonia oblonga* Mill., rarely on *Castanea sativa* Müll.). Some 79% of authors consider its hosts to be *V. vinifera* L., 59% *Populus* (especially *P. tremula* L.), 47% *Betula*, 34% *Corylus*, 31% *Alnus*, 27% *Tilia*, 26% *Salix* (especially *S. caprea* L.) and 23% *Fagus*. In about 10% of publications, the authors mention a host of *B. betulae* to be *Acer* and *Ulmus*, *Rubus idaeus* L. (7%), *Carpinus* (6%), *Rosa* (5%), *Quercus* (4%), *Sorbus* (3%), and *Fraxinus* and *Crataegus* (1%).

In this study, the occurrence of *B. betulae* was monitored particularly on forest trees including wild, out-of-cultivation or planted species from the families of Malaceae (namely *Pyrus*, *Malus* and *Prunus*) and Vitaceae. Leaf rolls produced by *B. betulae* were found on 13 species of woody plants from 10 genera. They occurred most frequently on *Fagus sylvatica* L., *Tilia cordata* Mill., *T. platyphyllos* Scop., *Salix caprea* L. and rather often also on *Populus tremula* L. The rolls were observed non-profuse also in the lower crown parts of the full-grown solitary trees of *T. cordata* in the densely built-up area of the Brno City district Žabovřesky. Rarely were they recorded on *P. alba* L., *P.* × *canescens* (Aiton) J. E. Smith, *Pyrus pyraster* L., *Cerasus avium* (L.) Moench. and *Vitis vinifera* L., and only sporadically on *Rubus idaeus* L., *Malus sylvestris* Mill., *Sorbus torminalis* (L.) Crantz and *Corylus avellana* L. Curiosity was a damage by the maturation feeding of beetles on leaves and punctures (mines) in young shoots or petioles of *Carpinus betulus* L., *Quercus robur* L. and *Partenocissus quinquefolia* Planch.

In contrast to the scientific name of the species, host substrate suitability often reflects in the species name of *B. betulae* in national languages. Most frequently, the species is named according to *Vitis* spp., on which it often overpopulated and caused serious damage in the past. In Czech language, for example, it is denoted as "*zobonoska révová*", formerly also "*zobonoska viničná*" or "*zobonoska březová*". In Slovak language, it is named "*zobonoska viničová*" or "*nosánik viničový*", in German language "*Rebenstecher, Rebstecher, Rebenstichler*" a.o., in Russian "*vinogradnyj (gruševyj) trubkovërt*" a.o., in French "*cigarier de la vigna*" a.o., in Spanish "*cigarrero de la viol*" a.o., in Italian "*sigarairo della vite*" and the like. In accordance with the species scientific name, *B. betulae* is denoted for example in Polish language ("*zdobnik brzozowiec*"), in Dutch ("*berkenbladroller*" a.o.), in Turkish ("*hortumlu betula böceği*"), sometimes even in Russian ("*berëzovyj trubkovërt*") and in some other languages. By *Betula*, the species was given a local (alternative) name also in German ("*stahlblauer Birkenstecher*"). Much surprising is that in the Brno region the leaf rolls were not found on the commonly occurring *Betula pendula* Roth.

The detailed study into the occurrence of *B. betulae* in the Brno region showed that the most favoured species' hosts are *Fagus sylvatica* L., *Tilia* (namely *T. cordata* Mill.), *Salix caprea* L. and *Populus tremula* L. In contradiction with the literary data are the sporadical findings of leaf rolls on *Corylus avellana* L., and particularly the absence of leaf rolls on *Alnus glutinosa* Gaertn. and on the above-mentioned *B. pendula* Roth. New was the finding of feeding notches of the beetles on young sprouts and leaves of *Partenocissus quinquefolia* Planch. In the laboratory, the beetles consumed most the leaves of *Vitis vinifera* L. and *Rubus idaeus* L. Considerably less they consumed the leaves of *T. cordata* Mill., *S. caprea* L. and *F. sylvatica* L.

Wintering Stage

The grown-up larvae of *B. betulae* crawl into the ground where they create oval pupal chambers with smoothed walls reinforced with rubber-like secretion at a depth from 2 to 5 cm (according to Taschenberg, 1874 only from 3 to 4 cm, according to Vasiljev *et al.*, 1974 up to 10 cm). The larvae pupate in the chamber, and adults emerge in the Brno region from mid-August to mid-October. Many authors maintain that some beetles leave the ground pupal chambers already towards the end of summer and at the beginning of autumn, and appear on the host plants. These beetles, after a short maturation feeding on leaves, look for winter hiding places in the upper soil layers (according to Perepechai, 1930 under the bark as well). Vasiljev *et al.* (1974), for example, mention the hibernation of beetles in the ground at a depth of 1–1.5 cm. Some beetles would stay in the pupal chamber to appear in the open only in the spring of the following year (Ratzeburg, 1839; Escherich, 1923; Perepechai, 1930; Dosse, 1954; Brauns, 1964; Francke-Grosmann, 1974; Freude, Harde and Lohse, 1981; Aslan and Calmasur, 2002). Prior to hibernation, the beetles appear in the open nature only in very warm years (Ruiz Castro, 1946). These are apparently beetles originating from early-laid eggs or from individuals whose development was boosted by favourable weather (Taschenberg, 1874).

According to Henschel (1895), Schaufuss (1916) and others, the beetles emerge already from the end of August and in September but stay in the ground until the next spring. Hibernation in the ground pupal chambers and the scarce occurrence of beetles on trees are mentioned for example by Dobrovoľskij (1950), Baudyš (1952), Miller (1956), Vasiljev *et al.* (1974), Mellings (2002) and others. In years with unfavourable climatic conditions, a part of the population may overwinter even in the larval or pupal stage (Ratzeburg, 1839; Becker, 1954; Scherf, 1964; Konopleva, 1974).

In the Brno region, the beetles hibernated in the ground pupal chambers in 2012 and 2013 and this is why they were never found on the trees before wintering. In the laboratory, the beetles emerged in August and September, and most of them stayed in the pupal chambers until the next spring.

Occurrence of Beetles on Woody Plants After Hibernation

After a longer period of warm spring weather, the beetles of *B. betulae* leave their wintering places and start searching for suitably sprouted host woody plants in their surroundings. They invade particularly young, well-insolated trees and sprouts to a height of 2 metres, more scarcely lower branches of older, marginal or solitary trees. They do not occur inside forest stands with fully closed canopies. The beginning and the course of tree colonization depend on weather. In the studied localities of the Brno region, beetles started to appear in the open nature usually towards the end of April. In the extremely warm and dry spring of 2014, the first leaf rolls of *B. betulae* were found even on 13 April, on lower branches of medium-aged *Fagus sylvatica* trees.

The beetles are very weakened by the long starvation, lasting from 6 to 8 months and start eating immediately upon having reached the host tree. If there are no trees available with sufficiently developed sprouts, they browse on young buds at the beginning, and only later on young leaves (Baudyš, 1952; Dosse, 1954; Miller, 1956; Vasiljev *et al.*, 1974). They appear on the upper (adaxial) face of fine leaves and bite out inconspicuous narrow (bandshaped) notches in their blades. According to literature, the feeding notches reach to the lower leaf epidermis, which as a rule remains intact. A detailed examination of the feeding notches of *B. betulae* beetles on the leaves of different tree species revealed numerous exceptions from the typical skeleting of leaves on the adaxial face. The skeleting of leaves from the adaxial face was demonstrated for example on *Vitis vinifera*, where the pest was most studied in the past. The leaves of *Tilia* are usually skeleted (rarely windowed) mostly (80%) from below (i.e. from the abaxial face). The leaves of *Fagus sylvatica* are usually windowed from above (adaxially). The leaves of *Salix caprea* are heavily pilous on the abaxial face; this is why the beetles cause damage to them only from the adaxial face, as a rule by making windows. At that, they leave the entire leaf nervation (including vein anastomoses) intact. In the laboratory, the beetles caused severe damage also to the fine cortex of freshly budded *Tilia cordata* sprouts. According to Becker (1954), the beetles may occasionally injure also young berries on *Vitis*.

Closer data on the feeding notches and food consumption of *B. betulae* do not exist in literature. The author's own research indicates that fresh feeding notches are 1–60 (on average 8.0) mm long and 1–1.6 (on average 1.2) mm wide. On growing and grown-up leaves, the nervation at the site of notches becomes as a rule necrotic later, and the epidermis (including small veins) is torn off. Dimensions of notches increase with the increasing leaf blade size. Especially the width of notches on grown-up leaves increases up to 2 mm and even more. The notches use to be localized between lateral veins in various parts of the blade (namely in its basal and middle third). Approximately 62%, 25% and 13% of notches run parallel to lateral veins, parallel to the main vein and perpendicularly to lateral veins, respectively. The beetles intensively damage namely leaves at the base of one-year shoots, which are usually not included in leaf rolls. The damage of leaves caused by the maturation and regeneration feeding of the beetles is very uneven. The most damaged leaves may lose as much as up to 30% of their assimilation area.

After wintering, females live on average seven (males five) weeks. During that time, the females and males can damage on average 40 cm^2 (25 cm^2) of *Tilia cordata* leaves. During the feeding, the beetles secrete abundant tiny frass pellets, which are 0.4–1.3 (on average 0.9) mm long and 0.17–0.25 (on average 0.22) mm wide. Immediately after defecation, these are dark green, later brown to black. At feeding on the adaxial face of leaves, some frass pellets stick to the upper epidermis for some time before they are taken down to the ground by wind and rain.

Adults of *B. betulae* are heliophilous, which is documented among other things also by their body of bright metallic lustre. They are most active at temperatures from 20 to 25 °C. In warm and sunny weather, they use their relatively good flying capacity for spreading into both near and more remote surroundings. In rainy weather, they hide mainly under the leaves of host trees. They consume only dried-up leaves, according to Dobrovoľskij (1950) largely in May.

The beetles mate first after several days of intensive feeding. Copulating couples can be observed mainly in May, rarely in June. Prior to egg laying, fertilized females bite out oval mines (lodges) in the basal parts of annual shoots the size of which ranges from 1.0×0.5 mm to 2.0×1.8 mm (on average 1.2×1.0 mm). The mines reach deep into the shoots and end as a rule at the opposite epidermis. In the Brno region, 92.5% of *Fagus sylvatica* shoots exhibited one mine, 3.7% of shoots showed two mines, 0.5% of shoots three mines and 0.3% of shoots had four mines. Only some 3% of shoots with leaf rolls were not damaged with mines at all, but on the other hand, petioles of the rolled leaves were bitten (sometimes even bitten through). The stems were at all times injured on leaf rolls occurring on shoots not damaged by mines and sometimes even on shoots with mines. In total, 20.5% of leaf rolls exhibited injury to 1–4 (exceptionally more) leaf petioles. Damaged petioles were recorded only on 11% of *F. sylvatica* annual shoots, 27% of *Tilia* annual shoots, and on 13% of *S. caprea* annual shoots. According to some, particularly older, authors (Ratzeburg, 1839; Schaufuss, 1916; Escherich, 1923; Dosse, 1954; Becker, 1954; Miller, 1956; Brauns, 1964; Foltýn *et al.*, 1965), the vine leaf roller harms only the leaf petioles.

The females of *B. betulae* prick (bite out) annual shoots with 1–12 (exceptionally even more) leaves. Biting out a mine in the shoot or petiole takes them ca. 15 and 10 min., respectively. In 2013, females colonized the early sprouting *F. sylvatica* and *Tilia* spp. in the Brno region towards the end of April and at the beginning of May (Tabs. I and II). The later

I: *Average length of annual shoots on Fagus sylvatica damaged by Byctiscus betulae and average size of leaf rolls. Brno region (Vsetín region*), 2013*

Date	Locality	Number of damaged shoots		Average length of annual shoots (cm)		Average size of leaf rolls (mm)	
		with leaf rolls	without leaf rolls	below puncture	above puncture	length	width (maximum/middle)
1 May	Bílovice n. Sv.	5	1	0.2	4.7	60.2	9.2/8.5
8 May	Vranov	6	0	0.3	5.5	80.0	10.8/9.9
15 May	Vranov	7	2	0.5	6.6	57.7	10.4/9.5
19 May	Bystřička*	1	2	0.8	3.1	60.0	10.0/9.0
22 May	Horákov	7	3	3.0	8.8	74.3	13.0/12.2
26 May	Vranov	5	2	3.1	6.4	63.0	9.6/8.7
9 June	Komín	4	3	2.0	6.3	66.4	7.2/7.2
19 June	Horákov	5	3	1.0	5.9	55.0	9.8/7.6
22 June	Žabovřesky	7	3	1.0	7.1	52.9	8.3/7.7
5 July	Vranov	5	2	1.8	6.2	81.0	10.0/8.0
15 July	Vranov	3	4	0.8	3.1	50.0	10.3/10.3
20 July	Bílovice n. Sv.	2	3	3.2	3.4	60.0	6.5/5.5
Total (mean)		57	28	(1.5)	(6.0)	64.3	9.9/8.9
(%)		67.1	32.9	(20.0)	(80.0)	-	-

II: *Average length of annual shoots on Tilia spp. damaged by B. betulae and average size of leaf rolls. Brno region, 2013*

Date	Locality	Number of damaged shoots		Average length of annual shoots (cm)		Average size of leaf rolls (mm)	
		with leaf rolls	without leaf rolls	below puncture	above puncture	length	width (maximum/ middle)
5 May	Bílovice n. Sv.	2	1	0.5	4.0	87.5	13.5/10.0
8 May	Vranov	1	1	0.3	4.3	70.0	13.0/13.0
15 May	Vranov	2	0	0.5	4.2	90.0	16.5/15.2
22 May	Horákov	13	2	11.7	6.9	71.9	12.8/11.4
29 May	Podkomorské lesy	10	0	15.6	4.8	70.0	11.8/10.6
5 June	Horákov	10	1	22.5	5.3	75.8	12.0/11.2
12 June	Bílovice n. Sv.	4	4	15.4	4.4	73.8	13.8/11.0
19 June	Horákov	7	1	32.7	4.0	74.6	9.9/9.6
28 June	Horákov	9	4	30.7	5.3	68.7	11.9/10.4
10 July	Horákov	13	1	45.3	3.3	62.5	10.0/8.8
15 July	Vranov	1	2	20.0	2.5	65.0	12.0/12.0
20 July	Bílovice n. Sv.	6	2	32.1	3.4	76.7	12.7/11.3
25 July	Doubravník	5	1	23.5	4.7	80.0	12.2/10.2
31 July	Horákov	7	0	35.0	3.7	58.9	11.0/10.1
20 August	Bílovice n. Sv.	3	0	30.7	4.7	57.3	6.3/6.3
Total (mean)		93	20	(24.7)	(4.6)	70.7	11.7/10.4
(%)		82.3	17.7	(84.3)	(15.7)	-	-

III: *Average length of annual shoots on Salix caprea damaged by B. betulae and average size of leaf rolls. Brno region, 2013*

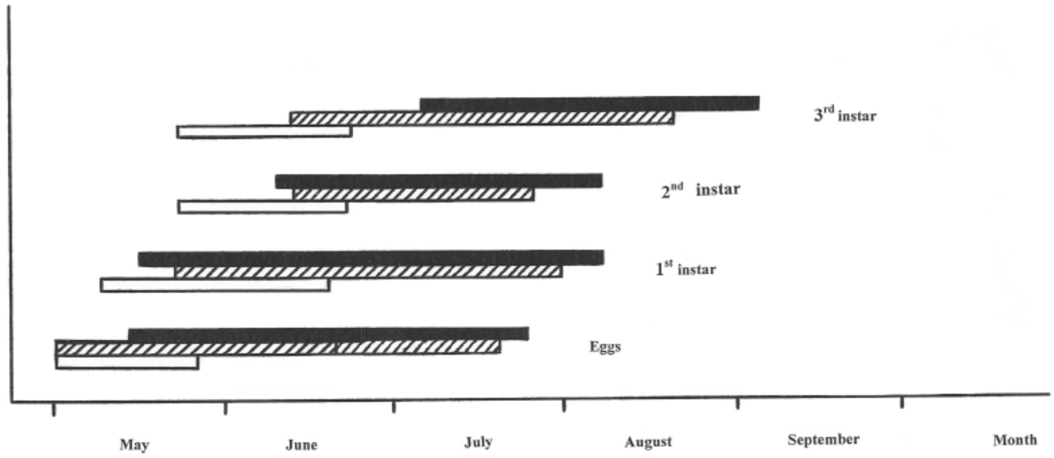
Date	Locality	Number of damaged shoots		Average length of annual shoots (cm)		Average size of leaf rolls (mm)	
		with leaf rolls	without leaf rolls	below puncture	above puncture	length	width (maximum/middle)
15 May	Vranov	2	0	0	2.5	40.0	9.5/9.2
22 May	Horákov	2	0	5.5	6.0	65.0	10.0/9.8
26 May	Vranov	12	2	5.5	4.6	73.3	9.1/8.8
29 May	Podkomorské lesy	6	0	7.3	4.9	75.0	10.3/9.5
9 June	Komín	4	1	3.2	5.2	85.0	8.7/8.7
12 June	Bílovice n. Sv.	6	1	17.8	3.8	56.1	6.1/6.1
28 June	Horákov	9	2	17.1	4.5	84.8	10.4/9.2
5 July	Vranov	19	4	20.0	3.6	79.3	11.0/9.6
10 July	Horákov	8	2	23.7	4.4	68.1	10.1/9.0
15 July	Vranov	9	1	16.8	3.8	78.3	11.3/9.4
20 July	Bílovice n. Sv.	16	3	24.7	3.6	76.8	8.8/8.4
25 July	Doubravník	15	4	31.6	4.0	76.7	9.5/8.3
31 July	Horákov	2	2	20.0	4.0	70.0	8.0/8.0
7 August	Podkomorské lesy	11	3	21.6	3.6	85.9	12.0/11.2
15 August	Vranov	14	6	24.4	3.4	72.5	8.9/8.7
20 August	Bílovice n. Sv.	11	4	22.6	3.6	73.5	10.4/9.3
28 August	Bílovice n. Sv.	7	4	12.8	4.1	74.3	10.4/9.8
30 August	Podkomorské lesy	13	4	24.9	3.8	77.0	10.9/9.3
4 Sept.	Podkomorské lesy	13	4	20.5	3.7	74.0	9.2/8.5
11 Sept.	Podkomorské lesy	11	2	14.0	3.2	73.5	12.7/10.4
15 Sept.	Vranov	12	3	19.9	3.4	76.8	9.4/8.4
Total (mean)		202	52	(19.4)	(3.8)	75.4	10.0/9.1
(%)		79.5	20.5	(83.6)	(16.4)	-	-

sprouting *S. caprea* was colonized by them only from mid-May (Tab. III). In 2014, leaf rolls on *F. sylvatica* appeared as early as in mid-April. The first damaged shoots on *F. sylvatica* were long on av. 4.9 cm, on *Tilia* spp. 4.5 cm, and on *S. caprea* only 2.5 cm. The punctures were localized at all times at the very base of shoots; thus, the total length of shoots was in fact identical as the length of shoots above the puncture. The tables indicate that annual shoots above the puncture on *F. sylvatica*, *Tilia* spp. and *S. caprea* were on average 6.0 cm, 4.6 cm and 3.8 cm long. Leaf rolls did not occur on average on 32.9% of the injured shoots of *F. sylvatica* (17.7% of *Tilia* spp. and 20.5% of *S. caprea* shoots, resp.). On *F. sylvatica*, the females harmed the shoots for the shortest time (only in the first half of May). The average length of shoots below the puncture (1.5 cm) and above the puncture (6.0 cm) was not generally changing during the period from May to July. On *Tilia* spp., the females bit out the shoots from the beginning of May to the end of June, and on *S. caprea* only from 10 May to the end of June (Fig. 1). It follows from the above facts that the beginning and duration of period in which the shoots are damaged (and the leaf rolls created) depend largely on the course of the flushing of leaves.

Creation of Leaf Rolls and Their Characteristics

Females of *B. betulae* create leaf rolls on young woody plants up to 2 metres in height, more scarcely on the low and medium branches of grown-up trees. In the Brno region, the rolling usually takes place from the end of April to the beginning of July (largely in May and June) (Fig. 1). In this region, some 98% of leaf rolls are created on annual shoots that have been bitten into and only 2% of leaf rolls are created on intact annual shoots. After the interruption of vascular tissues in annual shoots (or in petioles), the leaves start gradually wilting. The females return to the wilted, pliable and somewhat drooping leaves within several hours and start rolling them lengthwise into loose cigar- to cone-shaped rolls with open ends. At all times, they start rolling from the lateral margin of the medium-sized and large leaf, usually in the abaxial direction. The first rolled leaf is usually situated in the central part of the annual shoot. The rolls often include (in addition to the apical parts of annual shoots) also the tiny apical leaves (in *Vitis* sometimes even entire inflorescences).

In rolling a leaf blade, the females use namely their strong legs and rostrum, firmly holding and pulling



1: *Period of the occurrence of vital Byctiscus betulae eggs and larvae in leaf rolls on Fagus sylvatica (light), Tilia spp. (dashed) and Salix caprea (dark). Brno region, 2013*

IV: *Relation between the average number of eggs of B. betulae and the average number (area) of rolled/completely destroyed leaves in the leaf rolls on F. sylvatica, Tilia spp. and S. caprea. The last row presents the average % increase in the number/area of completely destroyed leaves as compared with the rolled leaves. Brno region (Vsetín region), 2013*

Number of eggs in leaf rolls	Average number of rolled/destroyed leaves in the leaf roll				Average area of rolled/destroyed leaves in the leaf roll (cm^2)			
	Fagus sylvatica	***Tilia* spp.**	***Salix caprea***	**(Mean)**	***Fagus sylvatica***	***Tilia* spp.**	***Salix caprea***	**(Mean)**
0	-	-	2.3/3.0	(2.3/3.0)	-	-	32.0/44.7	(32.0/44.7)
1–3	3.9/5.5	2.7/3.1	2.7/3.6	(2.8/3.6)	32.5/40.9	44.6/52.3	31.4/39.6	(34.4/42.5)
4–6	5.1/6.3	3.0/3.3	3.9/4.5	(3.8/4.4)	44.8/50.6	65.3/68.7	44.9/49.9	(52.2/56.8)
7–9	7.4/10.4	4.6/5.1	3.9/4.7	(5.0/6.0)	79.2/95.0	74.5/86.6	48.1/57.7	(68.0/80.2)
≥ 10	10.3/14.0	9.0/10.0	6.8/8.3	(8.4/10.6)	82.7/85.3	157.5/180.0	56.5/68.3	(87.7/98.8)
Mean	5.6/7.0	3.3/3.7	3.3/4.1	(3.6/4.4)	49.5/58.0	63.2/69.9	38.3/45.5	(47.6/54.8)
(%)	+ 25.0	+ 12.1	+ 24.2	(+ 22.2)	+ 17.2	+ 10.6	+ 18.8	(+ 15.1)

the pliant leaf blade by their legs and pressing it with using their rostrum. They also use their abdomen in shaping the roll. Less elastic parts of the leaf, leaf edges and leaf folds they stick together at multiple (up to 40) points by using the secretion of their abdominal glands. The secretion is not apparent after having dried up and the rolls keep their shape. The rolling is facilitated by glutinose leaf margins, which are provided with glands producing sticky secretion. The youngest (i.e. partly extended) terminal leaves are usually included in the rolls but not rolled by the females. The leaf rolling and the concurrent oviposition (see the next chapter) lasts to a female usually 1.5–6 hours, according to Ratzeburg (1839) 5–6 hours. Exceptionally, there are two or even more females participating in the rolling (and even in oviposition).

The leaf rolls are longitudinal because the main veins of the rolled leaves are in the longitudinal axis of the rolls. A few leaves are rolled obliquely (as a rarity perpendicularly) to the longitudinal axis of the leaf roll. This applies rather to smaller leaves situated at the roll perimeter. The number of leaves in one roll depends mainly on the leaf size. On large-leaved trees, the rolls are usually formed of one leaf only; on small-leaved woody plants, the rolls consist of more leaves (Kôno, 1930; Baudyš, 1952; Stejskal and Trnka, 2013 and others). According to Escherich (1923) and Francke-Grosmann (1974), rolls are largely created of several leaves. Dobrovoľskij (1950), for example, informs about the specific number of leaves; according to him, the rolls on *Vitis* are produced from a single leaf and those on *Pyrus pyraster* from 5–15 leaves.

In the Brno region, the rolls on *F. sylvatica* consisted of 1–13 (on av. 5.6) leaves the total area of which was 8–144 (on av. 49.5) cm^2. The rolls on *Tilia* spp. consisted of 1–14 (on av. 3.3) leaves the total area of which was 10–207 (on av. 63.2) cm^2. The rolls on *S. caprea* included 1–10 (on av. 3.3) leaves the total area of which was 8–96 (on av. 38.3) cm^2. Leaf area rolled on the damaged annual shoots of *F. sylvatica* was on average 75.0%. Approximately 25% of leaves died without having been rolled. Leaf area unrolled on the damaged annual shoots of *Tilia* spp. was 12.1% (and on *S. caprea* 24.2%). Thus, the total average leaf area on the damaged shoots of *F. sylvatica* increased to 58.0 cm^2 (by 17.2%), on *Tilia* spp. to 69.9 cm^2 (by 10.6%), and on *S. caprea* to 45.5 cm^2 (by 18.8%) (Tab. IV).

V: *Leaf-rolling direction in B. betulae rolls on F. sylvatica, Tilia spp. and S. caprea. Leaves are ordered from the centre of rolls to the rim (i.e. in the order of their rolling). Numerator is the number of leaves; nominator is the percentage. Brno region, 2013*

Order of leaves in rolls	***Fagus sylvatica***			***Tilia* spp.**			***Salix caprea***		
	abaxially	**adaxially**	**combined**	**abaxially**	**adaxially**	**combined**	**abaxially**	**adaxially**	**combined**
1st	32/82.1	5/12.8	2/5.1	38/59.4	5/7.8	21/32.8	180/94.3	6/3.1	5/2.6
2nd	25/65.8	8/21.1	5/13.1	16/29.6	8/14.8	30/55.5	99/59.3	62/37.1	6/3.6
3rd	15/50.0	10/33.3	5/16.7	22/52.4	2/4.8	18/42.8	75/60.5	42/33.9	7/5.6
4th	14/63.6	6/27.3	2/9.1	7/36.8	1/5.3	11/57.9	57/67.8	25/29.8	2/2.4
5th	11/64.7	3/17.6	3/17.7	5/45.5	1/9.1	5/45.4	25/51.0	20/40.8	4/8.2
≥ 6th	24/70.6	5/14.7	5/14.7	7/50.0	3/21.4	4/28.6	20/55.6	13/36.1	3/8.3
Total (mean)	121/67.2	37/20.6	22/12.2	95/46.6	20/9.8	89/43.6	456/70.0	168/25.8	27/4.2

Young smooth leaves with thinner lateral veins are usually rolled in one direction. On the cross section, such leaf rolls show a spiral curving as a rule (according to Lengerken, 1959 at all times) to the abaxial face. However, the scheme has a number of exceptions. For example on *F. sylvatica* the females would often fold a smaller or larger marginal part of the blade along some of lateral veins first (rarely they fold the leaves in half along the main vein), usually on the abaxial face. The folding of leaves may also be bilateral, as a curiosity even apical. Only then would the females roll the pre-treated leaves into a leaf roll. Far more complicated are the rolls on *Tilia* spp., which has relatively large leaves with thick veins. As soon as the females meet with some greater resistance in rolling the leaf, they reverse the rolling direction. After the reversion (leaf folding), they either complete the rolling in one direction or make other two – three turns (on the above-average sized leaves of *Vitis* up to 10 turns). Relatively few deviations were found in the rolling of *S. caprea* leaves, which obviously has to do with their smaller size and tiny nervature (Tab. V). The table shows that leaves most frequently rolled on the abaxial face are those of *S. caprea* (70%), less frequently those of *F. sylvatica* (67.2%), and least often those of *Tilia* spp. (46.6%). Adaxially rolled were 25.8% of *S. caprea* leaves, 20.6% of *F. sylvatica* leaves, and 9.8% of *Tilia* spp. leaves. 43.6% of *Tilia* spp. leaves, 12.2% of *F. sylvatica* leaves and 4.2% of *S. caprea* leaves were rolled in a combined way (i.e. with folds onto both faces). In all studied tree species, the first leaves to be most frequently rolled on the abaxial face were the innermost leaves into whose folds the females deposit eggs most often.

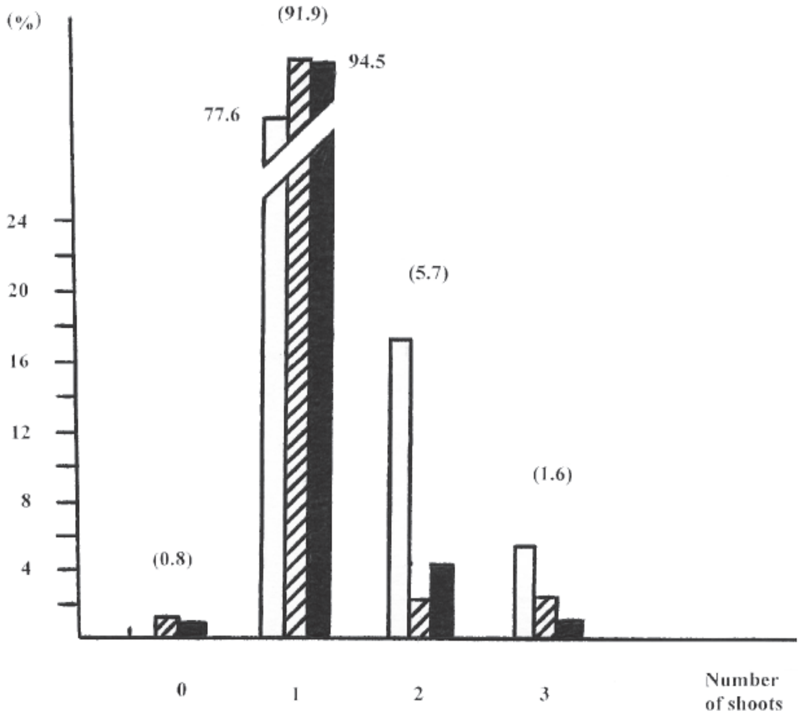
Overwhelming majority of the rolls (98%) was created on annual shoots damaged by feeding mines (punctures). Only a negligible part (2%) was localized on leaves with damaged petioles. The females sometimes include in the rolls also leaves from one or two neighbouring punctured shoots; in such a case, leaves from two to three shoots participate in such rolls. The phenomenon was most frequently observed in *F. sylvatica*, on which on average 77.6% of rolls were created from leaves on a single shoot, 17.2% of rolls were created from leaves on two shoots and 5.2% rolls were produced from leaves on three shoots (Fig. 2). Included in the rolls comprising leaves from two or three punctured shoots were usually all leaves of one shoot and one or a few leaves of the second and/or third shoot. A greater part of the leaf rolls (on average 91.9% on *Tilia* spp. and 94.5% on *S. caprea*) was localized on a single shoot.

Unlike the compact and usually single-leaf cigar-shaped rolls of *Byctiscus populi* (L.), rolls of *B. betulae* are soft (loosely coiled), severely crimped on the surface. They are as a rule multifoliate, spindle-shaped (70%) or funnel-shaped (30%). On the basal end (near petioles), they are entirely open. On the apical end, they are imperfectly closed by conical taper. The size, shape and general appearance of the rolls depend largely on the tree species, i.e. on the size and shape of leaves. Average dimensions of leaf rolls on the main studied tree species (i.e. length and width at half-length of the roll) are presented in Tabs. I, II and III. The smallest leaf rolls were found for example on *Pyrus pyraster* (45.0×6.3 mm), *P. tremula* (43.3×6.8 mm) and *P. alba* (50.0×7.0 mm). Average-sized rolls were observed on *C. avellana* (60.0×9.0 mm), *F. sylvatica* (64.3×8.9 mm), *S. caprea* (75.4×9.1 mm) and on *Tilia* spp. (70.7×10.4 mm). The largest rolls were found on *Vitis vinifera* (76.1×14.6 mm) and *Rubus idaeus* (110.0×10.0 mm). In available literature, the size of leaf rolls is mentioned by Trdan and Valič (2004), who claim that leaf rolls on *Vitis vinifera* are 5–12 (on average 8.5) cm long.

A tiny leaf roll of *B. betulae* (diameter ca. 6 mm) on *F. sylvatica* was formed by ten layers of leaves on the cross-section (at mid-length of the roll). A large leaf roll on *Tilia* spp. (diameter ca. 15 mm) consisted of eighteen layers of leaves. This shows that in the multiwall leaf rolls, the eggs and the larvae have relatively favourable conditions for their evolution.

Egg Laying

In the first stages of rolling, the females of *B. betulae* crawl under leaf folds to lay eggs. The eggs are placed loosely between the leaves, not under the leaf epidermis. In the leaf rolls on *S. caprea*, the eggs are laid into dense hairs on the abaxial face of leaves, sometimes into bitten out tiny feeding mines on the leaf surface. According some few authors (e.g. Miller, 1956), the females may lay eggs also in



2: *Percentage representation of B. betulae leaf rolls on intact shoots, and on one to three damaged (gnawed) shoots (F. sylvatica – light, Tilia spp. – dashed, S. caprea – dark). Mean representation on all three examined tree species is in brackets. Brno (Vsetín) regions, 2013*

VI: *Length and width of B. betulae eggs (1 division = 0.0357 mm)*

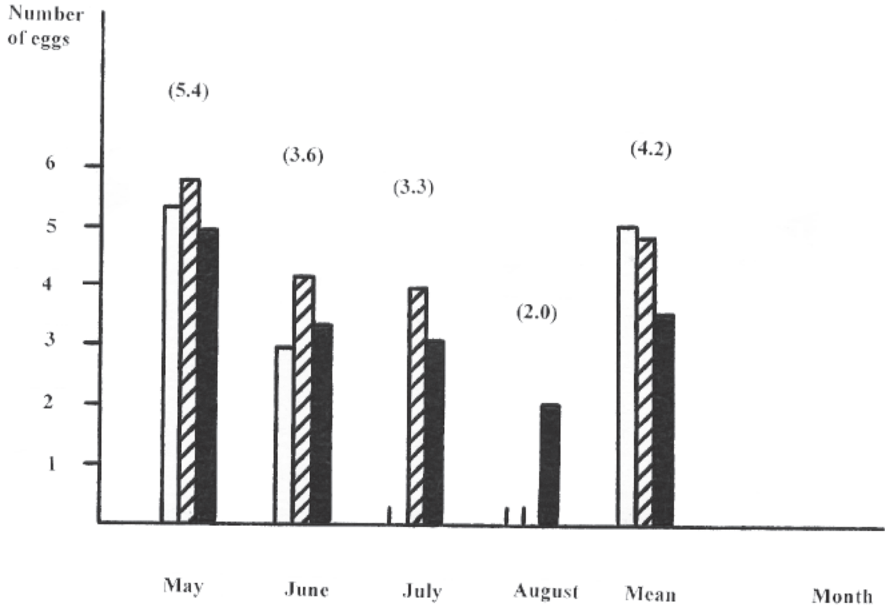
Length of eggs	Number	(%)	Width of eggs	Number	(%)
23	3	0.6	16	4	0.8
24	9	1.9	17	30	6.2
25	52	10.7	18	60	12.3
26	87	17.9	19	170	34.9
27	154	31.6	20	169	34.7
28	91	18.7	21	48	9.9
29	46	9.4	22	5	1.0
30	39	8.0	23	1	0.2
31	4	0.8	Total	487	100.0
32	2	0.4			
Total	487	100.0			

the completed leaf rolls, into perpendicular small shafts bitten out in the rolls. The eggs have a shape of rounded cylinders and are 0.8–1.1 (on av. 0.96) mm long and 0.5–0.9 (on av. 0.69) mm wide (Tab. VI). Their colour is glassy to dull white at first, later light yellow, grey to light yellow-green with the slightly transparent embryo. The surface of the eggs is semi-glossy to glossy, and slightly sticky at the beginning. Gum, which is according to Lengerken (1959) apparently of the same origin as the secretion used for glueing leaf rolls, binds the egg to the blade during the rolling.

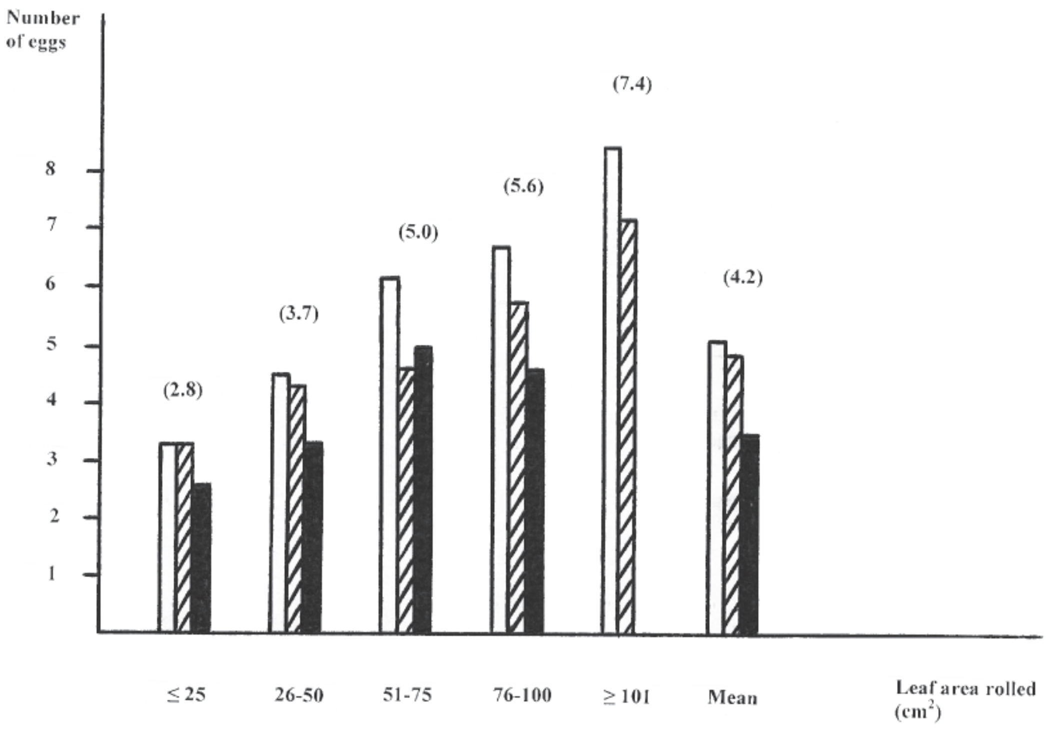
Females of the Byctiscini tribe from the family of Rhynchitidae (in contrast to females from the subfamily of Apoderinae, family of Attelabidae) lay often more than three eggs into one roll (Park, Lee and Park, 2012). Ratzeburg (1839), for example, mentions 4–8 eggs in the leaf rolls of *B. betulae*, Taschenberg (1874) 1–4 eggs, Schaufuss (1916) 5–8 eggs, Kôno (1930) 1–10 eggs, Perepechai (1930) 2–12 eggs, Ruiz Castro (1946) 5–6 eggs, Baudyš (1952) 3–10 eggs, Miller (1956) 4–15 eggs, Scherf (1964) and Trdan and Valič (2004) 1–8 eggs, Konopleva (1974) 3–9 eggs, Francke-Grosmann (1974) 1–14 eggs and Antonie, Todorescu and Oprean (2006) on average 4.3 eggs.

In the Brno region, the leaf rolls of *B. betulae* contained 0–16 eggs. Leaf rolls on *F. sylvatica* contained 1–14 (on av. 5.1) eggs, on *Tilia* spp. 1–13 (on av. 4.9) eggs, on *S. caprea* 0–12 (on av. 3.5) eggs, on

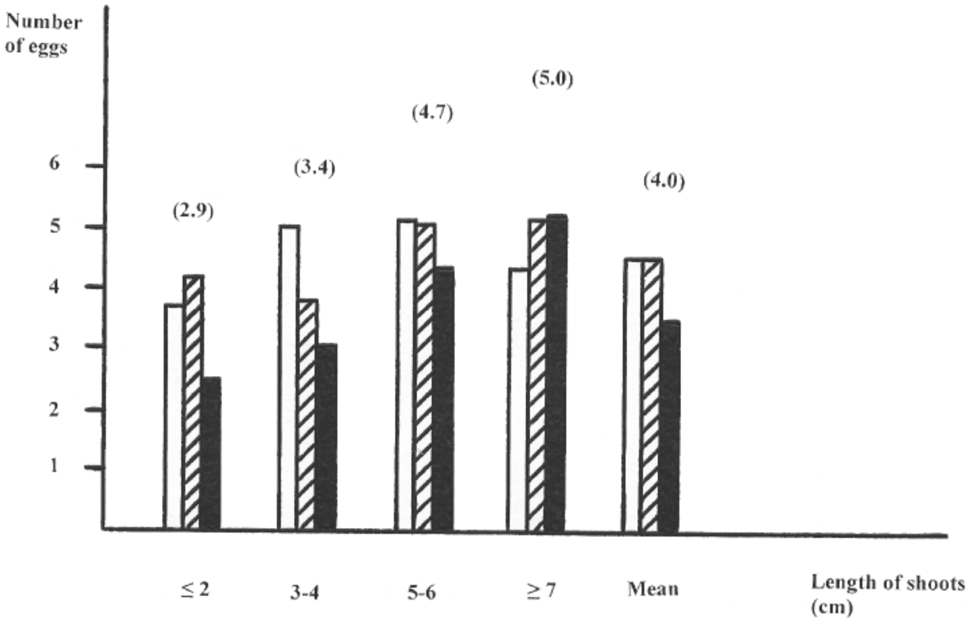
Pyrus pyraster 2–5 (on av. 3.6) eggs, on *P. tremula* 1–10 (on av. 3.4) eggs. The highest number of eggs (3–16 /on average 8.0/) was laid in the leaf rolls on *Vitis vinifera*. Ovaries of naturally dead females kept in the laboratory contained 1–15 well-developed eggs. Females laid the highest average number of eggs into the leaf rolls in the month of May, i.e. in the period of the peak breeding. From this month, the average number of eggs in the rolls was decreasing until the end of the egg laying period (Fig. 3). The average number of eggs in the leaf rolls demonstrably increased with the increasing total surface area of the rolled leaves, and rather surprisingly also with the increasing average length of the damaged



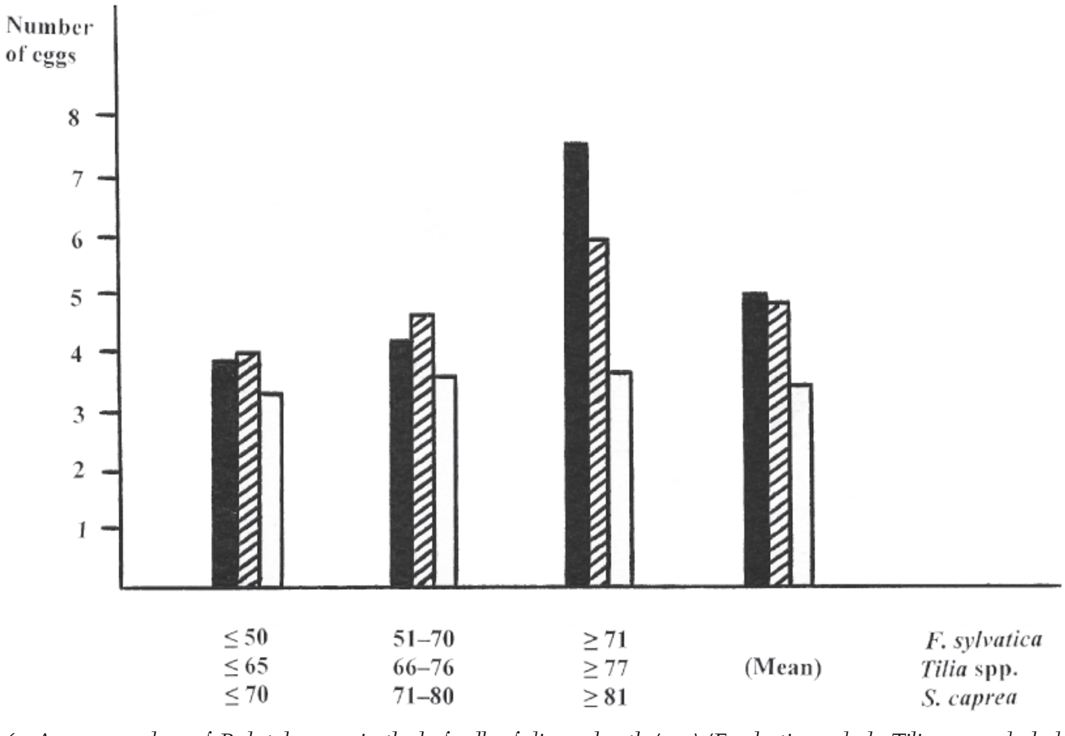
3: *Average numbers of B. betulae eggs in leaf rolls on F. sylvatica (light), Tilia spp. (dashed) and S. caprea (dark) according to the date of their deposition. Mean numbers of eggs on all three tree species are in brackets. Brno (Vsetín) regions, 2013*



4: *Average numbers of B. betulae eggs in leaf rolls on F. sylvatica (light), Tilia spp. (dashed) and S. caprea (dark). Mean numbers of eggs on all three tree species are in brackets. Brno region, 2013*

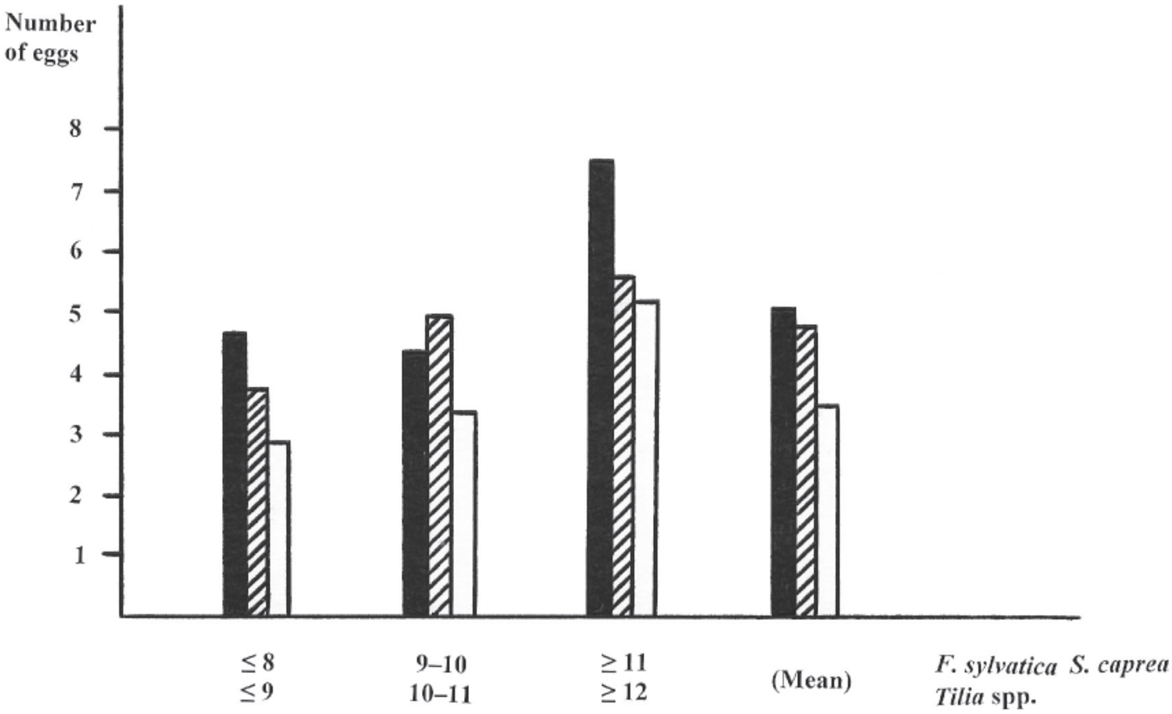


5: *Average numbers of B. betulae eggs in leaf rolls on F. sylvatica (light), Tilia spp. (dashed) and S. caprea (dark) according to the length of shoots damaged above the puncture (cm). Mean numbers of eggs on all three tree species are in brackets. Only leaf rolls created on one shoot were evaluated. Brno (Vsetín) regions, 2013*

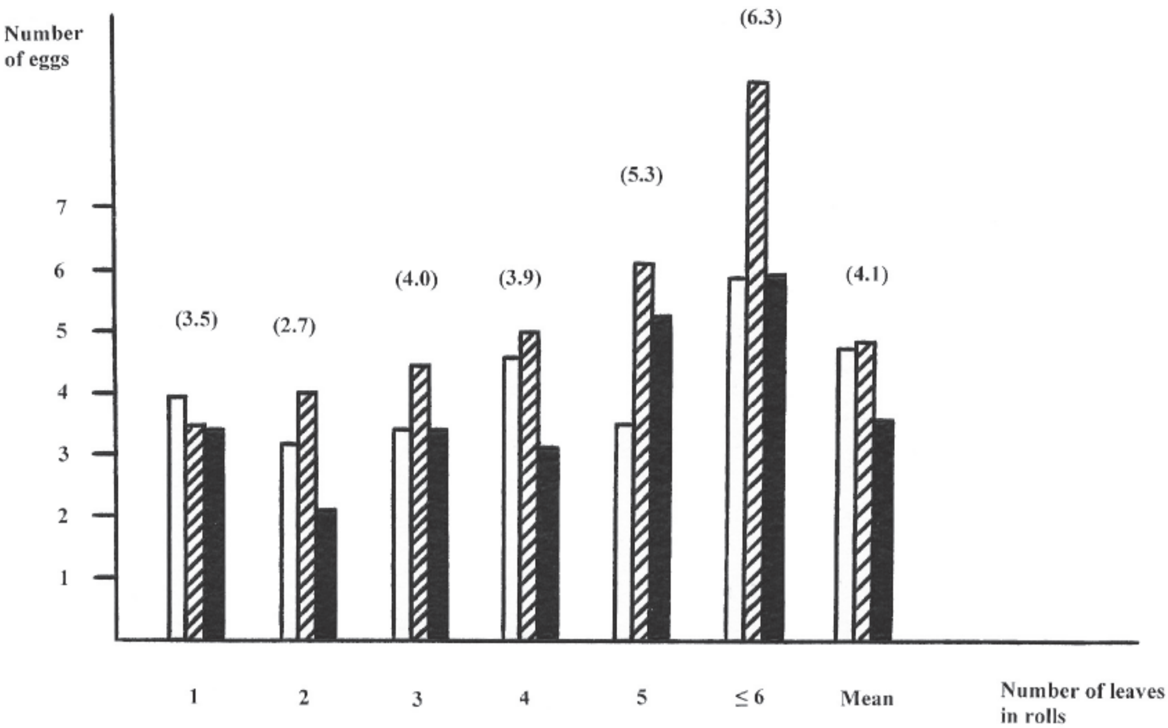


6: *Average numbers of B. betulae eggs in the leaf rolls of diverse length (mm) (F. sylvatica – dark, Tilia spp. – dashed, S. caprea – light). Brno (Vsetín) regions, 2013*

shoots (Figs. 4 and 5). Females were found to tend considerably to the rolling of larger leaves. This is also why they colonize early succession stages of trees on which the leaves are larger and softer (more elastic) than on older trees. An unambiguously positive relation exists between the average number of eggs and the size (length and width) of the leaf rolls (Figs. 6 and 7). Trdan and Valič (2004) mention a weak positive correlation between the length of leaf rolls and the number of eggs. The number of eggs laid by females into rolls consisting of three and more leaves was conspicuously higher (Fig. 8). Nevertheless, the average number of eggs falling to one rolled leaf continually decreased with the increasing number of rolled leaves (Fig. 9). A survey focused on the localization of eggs in

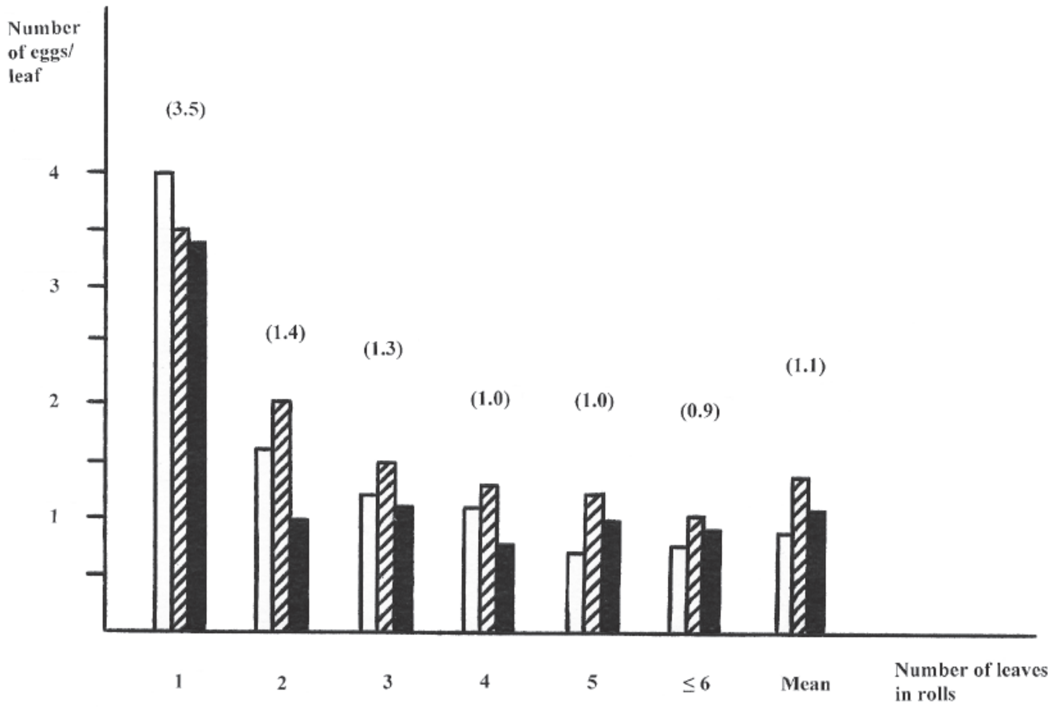


7: *Average numbers of B. betulae eggs in the leaf rolls of diverse width (mm) (F. sylvatica – dark, Tilia spp. – dashed, S. caprea – light). Brno (Vsetín) regions, 2013*

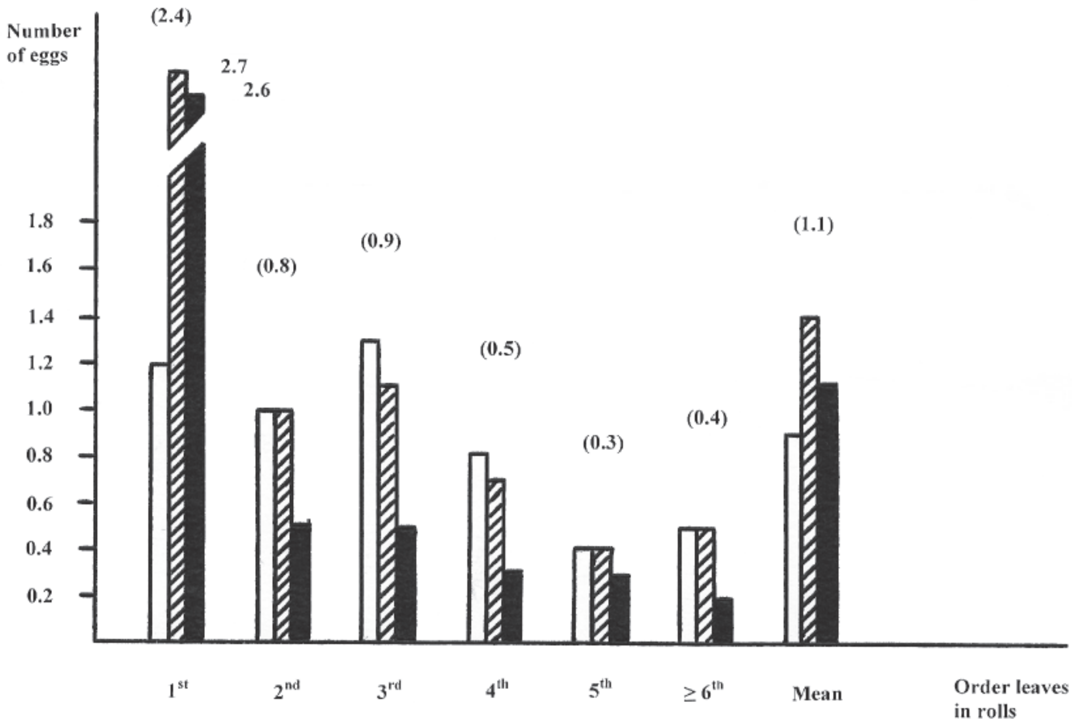


8: *Average numbers of B. betulae eggs in leaf rolls in dependence on the number of rolled leaves (F. sylvatica – light, Tilia spp. – dashed, S. caprea – dark). Mean numbers of eggs on all three tree species are in brackets. Brno (Vsetín) regions, 2013*

rolls created from one and more leaves brought interesting results. In single-leaf rolls, all eggs were laid into the first leaf folds, i.e. as near to the leaf roll centre as possible. In multiple-leaf rolls on *Tilia* spp. and *S. caprea*, the highest average number of eggs was laid into the folds of the first rolled leaf, i.e. into the earliest rolled leaves in the middle of the leaf roll. In leaf rolls on *F. sylvatica*, eggs were found in abundance also in the folds of other leaves occurring near the central leaf (Fig. 10).



9: *Average numbers of B. betulae eggs converted to one rolled leaf (F. sylvatica – light, Tilia spp. – dashed, S. caprea – dark). Mean numbers of eggs falling to one leaf on all three tree species are in brackets. Brno (Vsetín) regions, 2013*



10: *Average numbers of B. betulae eggs localized on individual leaves in leaf rolls on F. sylvatica (light), Tilia spp. (dashed) and S. caprea (dark). The leaves are ordered from the centre of leaf rolls to their perimeter. Mean numbers of eggs on the individual leaves of all three tree species are in brackets. Brno (Vsetín) regions, 2013*

In the Brno region, females lay eggs in the period from May to July. Escherich (1923) and Francke-Grosmann (1974), for example, mention the same period. However, most authors mention a considerably shorter egg laying period (e.g. Ratzeburg, 1839 – mostly June, Jäger, 1876 – May and June, Perepechai, 1930 – May, Dobrovoľskij, 1950 – from the end of April or beginning of May to mid-June, Vasiljev *et al*., 1974 – May, less often June, and Mellings, 2002 – June and July). According to the author's own findings, females and males live after wintering on average one and a half month and only a month, respectively. Females lay eggs into rolls created from the leaves of suitably sprouted trees, which they actively look after in the stands. Leaves that were rolled earliest (already at the end of April and in the first two decades of May, in 2014 even from mid-April) in the Brno region were those on *F. sylvatica*. Leaves on *Tilia* spp. were rolled from the beginning of May to the beginning of July. On *S. caprea*, females appeared as late as in mid-May and produced leaf rolls until the end of the first decade in July (Fig. 1). There are no findings in the literature about the change of host trees in the breeding period of *B. betulae*.

Literature data about the total number of leaf rolls produced by one female and about the total fertility of females are sparse and inaccurate. According to Baudyš (1952), Dosse (1954) and Francke-Grosmann (1974), females create 20–30 leaf rolls, according to Miller (1956) and Brauns (1964) up to 30 rolls and according to Trdan and Valič (2004) more than 10 rolls. According to the author's own observations, the number of leaf rolls created by one female depends largely on actual fertility of the females and on the average number of eggs in leaf rolls on different host tree species. Results from guidance breedings showed that females lay about 50 eggs during their life (according to Krieg, 1924: 35–40 eggs, according to Scherf, 1964: 40–65 eggs). On *P. tremula*, *S. caprea* and *Pyrus pyraster* they produce on average only 15 leaf rolls, on *F. sylvatica* and *Tilia* spp. only 10 rolls and on *Vitis vinifera* even only 8 rolls. These findings are in stark contrast to the hitherto published literature data.

On the cross-section, the rolls of *B. betulae* are formed by 8 to 18 layers of leaves. Being open on both ends, they are less compact than leaf rolls created by *B. populi* and by most other leaf-rollig weevils. They dry out and turn brown and black relatively quickly. Leaf tissues inside the rolls keep certain moisture and green colour for some time though. The rolls usually hang on declining and dead annual shoots, and after several weeks, they begin to fall down from the trees due to wind and rain. On the ground, they become wet and gradually disintegrated.

Embryogenesis and Post-embryogenesis

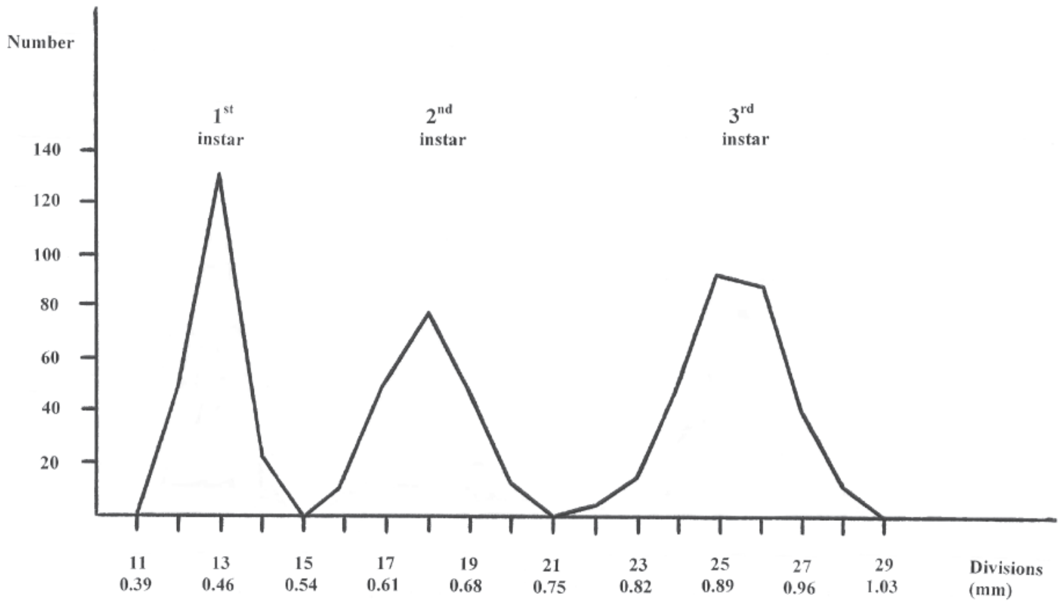
Larvae emerge from the eggs of *B. betulae* usually in 8–10 days (Ratzeburg, 1839; Dobrovoľskij, 1950; Scherf, 1964; Vasiljev *et al*., 1974 and others). According to Schaufuss (1916), larvae develop in the eggs only 5–6 days, according to Ruiz and Castro (1946) 10 days, according to Baudyš (1952) 8–16 days and according to Aslan and Calmasur (2002) 10–12 days. Duration of embryogenic development depends mainly on temperature and less on relative humidity (Becker, 1954). This author claims that at 29 °C and relative humidity 92%, the larvae emerge already in 3–4 days after oviposition. At a very low humidity and temperature of 5 °C, the larvae do not emerge, and at a temperature of 32 °C, the larvae die. In the author's laboratory with a temperature ranging from 20 to 25 °C and relative humidity 90%, the larvae emerged from the eggs as late as in 8–9 days. At the time of egg larvae eclosion, leaf tissues inside the rolls were withered but still green.

Larvae of the 1st instar do not consume the chorion of eggs, and after a short rest they start ingestion. At the beginning, they bite out tiny mines into the leaf blade, reaching as far as to the opposite epidermis; later they make irregular windows in the leaves. In several days of feeding on *F. sylvatica*, they damage 10 mm^2 of the leaf blade. Undigested food is excreted in the form of black filamentous (cross strangulated) frass pellets which are 0.07–0.36 (on average 0.18) mm long and ca. 0.036 mm wide. In the larvae of this instar, the head case (cranium) width is 0.4–0.5 mm. The larvae are 1.25–2.9 (on average 2.0) mm long and 0.53–1.1 (on average 0.8) mm wide. Grown-up larvae of the 1st instar moult at the site of feeding.

Larvae of the 2nd instar make windows into the leaves and damage in total ca. 40 mm^2 of the leaf blade. They defecate black filamentous frass pellets, which are 0.17–1.4 (on average 0.5) mm long and ca. 0.07 mm wide. Their head is 0.57–0.7 (on average 0.64) mm wide. They are 1.6–4.6 (on average 3.1) mm long and 0.9–1.8 (on average 1.35) mm wide. Grown-up larvae of the 2nd instar moult at the feeding site, too.

Larvae of the 3rd instar continue irregular feeding on inner parts of the leaf roll. They consume the blade including small to medium-sized veins, and they destroy in total ca. 250 mm^2 of the leaf. The larvae produce black filamentous frass pellets, which are 0.3–3.0 (on average 1.2) mm long and ca. 0.18 mm wide. Their head is 0.8–1.0 (on average 0.9) mm wide (Fig. 11). They are 4.0–7.0 (on average 5.5) mm long and 1.4–2.5 (on average 2.0) mm wide. Grown-up larvae are 5–8 (on average 6.5) mm long and 2.0–3.0 (on average 2.5) mm wide. They have a yellow-brown head, dark mandibulae, white legless body with individual yellow setae. They are thickset, slightly dorsoventrally flattened, ventrally mildly arcuated, tapered at both front and rear end. On *F. sylvatica*, the larvae of all three instars consume approximately 300 mm^2 of the leaf blade.

The larvae of *B. betulae* do best at a temperature of 25 °C and 100% of relative humidity; they die at temperatures above 30 °C and below 5 °C (Becker, 1954). They are considerably resistant to drought. Under a drought spell, the rolls dry out and the feeding of the larvae gradually ceases. Ingestion is usually restored after repeated moistening of the leaf rolls. However, under long-lasting very warm and dry weather, the larvae (and eggs) would die. Since the wintering places are left unevenly and the period of egg deposition is long, the larvae can be found in the leaf rolls from 10 May to the beginning of September (Fig. 1). Duration of their development depends on temperature and humidity. According



11: *Head case width of the B. betulae larvae of the 1st–3rd instars (1 division = 0.0357 mm)*

VII: *Mortality of B. betulae in leaf rolls on F. sylvatica. From 5 July, the analyses were made more difficult due to natural disintegration of leaf rolls. Brno region (Vsetín region*), 2013*

Date	Number of live individuals			Number of dead individuals			Total
	eggs/1st instar	2nd/3rd instar	abandoned/total	eggs/1st instar	2nd/3rd instar	total	
1 May	17/-	-	-/17	-	-	-	17
8 May	19/6	-	-/25	-/1	-	1	26
15 May	29/5	-	-/34	-	-	-	34
19 May*	4/-	-	-/4	-	-	-	4
22 May	17/10	13/2	-/42	2/2	9/-	13	55
26 May	10/13	2/-	-/25	1/-	-	1	26
9 June	-/1	10/3	-/14	-/7	2/-	9	23
19 June	-/1	1/-	2/4	1/2	3/-	6	10
22 June	-	4/2	-/6	1/3	1/-	5	11
(5 July)	?	?	?	?	?	?	?
(15 July)	?	?	1/1	?	?	?	1
(20 July)	?	?	?	?	?	?	?
Total	96/36	30/7	3/172	5/15	15/-	35	207
(%)	46.4/17.4	14.5/3.4	1.4/83.1	2.4/7.2	7.3/-	16.9	100.0
Total (from 19 June)	-/1	5/2	3/11	2/5	4/-	11	22
(%)	-/4.6	22.7/9.1	13.6/50.0	9.1/22.7	18.2/-	50.0	100.0

to the author's own observations, the larvae grow up in 4–7 weeks, in the laboratory already in 3 weeks. According to Ratzeburg (1839), the larvae eat 5 weeks, according to Taschenberg (1874) and Schaufuss (1916), 4–5 weeks, according to Ruiz and Castro (1946), Baudyš (1952) and Dosse (1954) 3–5 weeks, according to Dobrovoľskij (1950) 20–30 days and according to Aslan and Calmasur (2002) only 15–18 days.

In 2013, the grown-up larvae in the Brno region were leaving the eaten out inside of the leaf rolls on *F. sylvatica* in the second half of June (Tab. VII), on *Tilia* spp. from 15 July to 20 August (Tab. VIII) and on *S. caprea* from the beginning of August to the beginning of September (Fig. 1, Tab. IX). Nevertheless, the rolls persisted on the trees usually until the end of summer and the beginning of autumn. At the beginning of the leaving period, most leaf rolls were on the trees. The larvae were biting their way out through oval holes of 1.7–2.2 mm in diameter and were falling onto the ground. There, they created oval pupal chambers at a depth of 2–5 cm, in which they pupated. Stejskal and Trnka (2013) inform that falling onto the ground towards

VIII: *Mortality of B. betulae in leaf rolls on Tilia spp. From 20 July, the analyses were made more difficult due to natural disintegration of leaf rolls. Brno region, 2013*

Date	Number of live individuals			Number of dead individuals			Total
	eggs/1st instar	2nd/3rd instar	abandoned/total	eggs/1st instar	2nd/3rd instar	total	
5 May	17/-	-	-/17	-	-	-	17
8 May	3/-	-	-/3	-	-	-	3
15 May	18/-	-	-/18	-	-	-	18
22 May	44/23	-	-/67	3/1	-	4	71
29 May	39/3	-	-/42	2/-	-	2	44
5 June	27/11	-	-/38	7/-	-	7	45
12 June	7/1	2/5	-/15	1/4	-	5	20
19 June	8/7	-/3	-/18	27/-	1/-	28	46
28 June	5/5	5/-	-/15	14/-	-	14	29
10 July	11/10	2/1	-/24	21/-	-	21	45
15 July	-	-	-	-	-	-	-
(20 July)	1/1	2/5	-/9	5/2	-	7	16
(25 July)	-	3/-	-/3	9/-	-	9	12
(31 July)	-/4	-/2	1/7	19/1	1/-	21	28
(20 Aug.)	-	-/1	-/1	-	-	-	1
Total	180/65	14/17	1/277	108/8	2/-	118	395
(%)	45.6/16.4	3.5/4.3	0.3/70.1	27.4/2.0	0.5/-	29.9	100.0
Total (from 15 July)	1/5	5/8	1/20	33/3	1/-	37	57
(%)	1.8/8.8	8.8/14.0	1.7/35.1	57.9/5.2	1.8/-	64.9	100.0

the end of summer are leaf rolls with the larvae. Pupae are 5–6 mm long, white at first, later dark with metallic lustre. They have an arcuated body, brown eyes, protruding bases of wings and long setae on the back. They are stenohygric because they develop only at a relative humidity of about 50–55% (Antonie, Todorescu and Oprean, 2006). In the Brno region, the larvae pupated from the beginning of July to the end of September. Beetles started to emerge after 1–2 weeks of pupal rest. The beetles stayed in the pupal chambers until the next spring (see chapter Wintering stage). Development is obligatorily univoltine.

Mortality

Main factors participating in the regulation of the abundance of *B. betulae* are weather and insect parasitoids. According to Krieg (1924), weather is (unlike natural insect enemies) a factor able to end the pest gradation. By contrast, Scherf (1964) considers the insect parasitoids and predators as important regulators of abundance.

At the time of their occurrence on woody plants, beetles are considerably resistant to harsh weather. However, many beetles wintering in heavy or sandy soils may die during the long period of hibernation (Miller, 1956). Eggs and larvae may die during extremely cold and rainy weather, and particularly in tropical heats and during drought spells.

In the Brno region, on average 50.0% of *B. betulae* population died in the leaf rolls on *F. sylvatica* in 2013 (Tab. VII), 64.9% of the population died in the rolls on *Tilia* spp. (Tab. VIII) and 85.0% of the population died in the rolls on *S. caprea* (Tab. IX). Following the cold and rainy May and the first half of June in 2013, the weather in July and in the first half of August was extremely warm and dry. The leaf rolls were rapidly drying out due to high temperatures (30–38 °C) and the absence of precipitation (even dew). However, the larvae of *B. betulae* in the leaf rolls on *F. sylvatica*, which had completed their evolution in the rolls before the onset of the unfavourable weather (i.e. before the beginning of July), escaped from the adverse effect of heat and drought (Tab. VII). On the other hand, the leaf rolls on *Tilia* spp. and *S. caprea* contained abundant eggs and larvae of all three instars at that time (Tabs. VIII, IX). The extreme weather killed about 10% of eggs and 5% of larvae in the leaf rolls on *Tilia* spp. and *S. caprea*.

The rich generic spectrum of *B. betulae* insect enemies is dominated by representatives from the family of Braconidae. Species mentioned in the available literature include *Apanteles laevigatus* (Ratz.), *Bracon admotus* (Papp), *B. discoideus* (Wesm.), *B. rhynchitii* Gr., *Diospilus capito* (Nees), *Dolichogenidea laevigata* (Ratz.), *Embasus ruficollis* (Wesm.), *E. tibialis* (Hal.) and *Sigalphus caudatus* Nees. Species from the families of Eulophidae and Ichneumonidae taking part in parasitization are *Elachertus idomene* Walk. and *E. lateralis* (Sp.), and *Gregopimpla inquisitor* (Scop.), *Pimpla brunnea* (Br.) and *P. rufipes* (Mill.), resp. Important parasitoids are representatives from the oophagous family of Trichogrammatidae

IX: *Mortality of B. betulae in leaf rolls on S. caprea. From 28 July, the analyses were made more difficult due to natural disintegration of leaf rolls. Brno region, 2013*

Date	Number of live individuals			Number of dead individuals			Total
	eggs/1st instar	2nd/3rd instar	abandoned/total	eggs/1st instar	2nd/3rd instar	total	
15 May	3/4	-	-/7	-	-	-	7
22 May	11/3	-	-/14	-	-	-	14
26 May	56/14	-	-/70	-	-.	-	70
29 May	27/-	-	-/27	-	-	-	27
9 June	1/6	4/-	-/11	1/-	-	1	12
12 June	17/-	-	-/17	1/-	-	1	18
28 June	-/5	7/-	-/12	11/5	-	16	28
5 July	6/12	30/2	-/50	15/5	1/1	22	72
10 July	2/-	-	-/2	13/1	4/5	23	25
15 July	4/2	7/4	-/17	1/5	2/-	8	25
20 July	2/6	16/1	-/25	31/3	1/-	35	60
25 July	5/6	6/2	-/19	19/6	2/3	30	49
31 July	-	-	-	2/2	-/1	5	5
7 August	-/1	2/2	1/6	10/2	4/7	23	29
15 August	-	-/3	2/5	6/3	1/6	16	21
20 August	-	-	1/1	12/3	1/2	18	19
(28 August)	-	-/1	-/1	4/1	-	5	6
(30 August)	-	-/1	-/1	12/1	-/1	14	15
(4 Sept.)	-	-/1	1/2	1/3	4/2	10	12
(11 Sept.)	-	-	-	-	-	-	-
(15 Sept.)	-	-	-	-	-	-	-
Total	134/59	72/17	5/287	139/40	20/28	227	514
(%)	26.0/11.5	14.0/3.3	1.0/55.8	27.1/7.8	3.9/5.4	44.2	100.0
Total (from 31 July)	-/1	2/8	5/16	47/15	10/19	91	107
(%)	-/0.9	1.8/7.5	4.8/15.0	43.9/14.0	9.3/17.8	85.0	100.0

X: *Mortality of B. betulae eggs and respective instars of larvae in leaf rolls on F. sylvatica, Tilia spp. and S. caprea (overall survey in %). Brno (Vsetín) regions, 2013*

Period (from–to)	% of live individuals			% of dead individuals			Total
	eggs/1st instar	2nd/3rd instar	abandoned/ total	eggs/1st instar	2nd/3rd instar	total	
1–15 May	86.9/12.3	-	-/99.2	-/0.8	-	0.8	100.0
16–31 May	66.9/21.2	4.8/0.7	-/93.6	2.6/0.9	2.9/-	6.4	100.0
1–15 June	44.1/16.1	13.5/6.8	-/80.5	8.5/9.3	1.7/-	19.5	100.0
16–30 June	10.5/14.5	13.7/4.1	1.6/44.4	43.5/8.1	4.0/-	55.6	100.0
1–15 July	13.7/14.3	23.2/4.2	0.6/56.0	29.8/6.5	4.1/3.6	44.0	100.0
16–31 July	4.7/10.0	15.9/5.9	0.6/37.1	50.0/8.2	2.3/2.4	62.9	100.0
1–15 Aug.	-/2.0	4.0/10.0	6.0/22.0	32.0/10.0	10.0/26.0	78.0	100.0
16–31 Aug	-	-/7.3	2.5/9.8	68.3/12.2	2.4/7.3	90.2	100.0
1–15 Sept.	-	-/8.4	8.3/16.7	8.3/25.0	33.3/16.7	83.3	100.0
Total	36.7/14.3	10.4/3.7	0.8/65.9	22.6/5.7	3.3/2.5	34.1	100.0

(*Poropoea defilippii* Silv., *P. minkiewiczi* Now. and *Ophioneurus signatus* Ratz.). The predator of imagos is reportedly *Dromius linearis* (Ol.) from the Carabidae family.

In the Brno region, endoparasitoids of eggs from the family of Trichogrammatidae represented the main factor causing the mortality of *B. betulae* in the leaf rolls (on *F. sylvatica*, *Tilia* spp. and *S. caprea*, they killed about 9%, 40% and 30% of the population, respectively). Characteristic symptoms of their attack (i.e. browning to blackening of eggs) showed first (from 22 May) in the rolls on *F. sylvatica* and

Tilia spp. The first adults of the parasitoids emerged towards the end of June and the last ones at the end of August. In the period from June to August, the percentage of dead eggs increased up to 68.3% (Tab. X). The decisive share on this mortality was that of endoparasitoids (in the rolls on *Tilia* spp. and *S. caprea* partly drought too). A small portion of eggs was killed by the saproparasitic larvae of Cecidomyiidae and sporadically also by the nymphs of Heteroptera and larvae of Neuroptera. The larvae of Cecidomyiidae were found in the leaf rolls from mid-June to mid-September their number ranging from 1 to 15. Several larvae were observed sucking on the dead larvae of *B. betulae*.

The ectoparasitoid larvae of Braconidae were found in the leaf rolls of *B. betulae* from mid-May. From mid-June, light brown cocoons of gregarian Braconidae began to occur on the dead larvae of the 3rd instar in the number of up to 5 pieces per a leaf roll. The first abandoned cocoons (4–6 mm long and 1.5–2 mm wide) were recorded in the rolls on *F. sylvatica* on 5 July. In August and September, the leaf rolls on *Tilia* spp. and *S. caprea* exhibited abundant occurrence of small cocoons 2–4 mm long and 1–1.5 mm wide. In the Brno region, the larvae of Braconidae killed about 5–20% of the total *B. betulae* population in the leaf rolls.

From the end of August to mid-September, the rolls of *B. betulae* on *S. caprea* were damaged by the feeding of *Anacampsis populella* (Cl.) (Gelechiidae) caterpillars. Unspecified caterpillars of Lepidoptera were found sporadically in June also in the leaf rolls on *F. sylvatica* and *Tilia* spp.

Economic Importance

Byctiscus betulae is an abundant, widely spread and relatively well-known polyphagous species of leaf-rolling weevils (Rhynchitidae). Its most favourable host woody plants are *Vitis vinifera* and some fruit tree species (e.g. *Pyrus* spp. and *Malus* spp.). It frequently occurs also on forest trees (in the Brno region mainly on *F. sylvatica*, *Tilia* spp., *S. caprea* and *P. tremula*). Wintering beetles appear on the trees usually from the end of April. They damage young buds first, later freshly opened leaves. After wintering, females live on average seven (males five) weeks and damage on average 40 cm^2 (males 25 cm^2) of leaves.

After several days of ingestion, beetles mature sexually. Fertilized females then bite out one (exceptionally up to four) oval mines (diameter ca. 1.1 mm) into the base of annual shoots long on av. 5 cm, which usually reach up to the opposite epidermis. Due to the interruption of vascular tissues, the leaves gradually begin to wilt and the shoots bend. The females roll the wilted leaves lengthwise into spindle- or funnel-shaped rolls and lay eggs into leaf folds during the first stages of the rolling. To produce the rolls, they use only the part of shoots with the feeding mines (on *F. sylvatica* on average 67.1%, on *Tilia* spp. 82.3% and on *S. caprea* 79.5%) (Tabs. I, II, and III). On the damaged annual shoots of *F. sylvatica* the total average leaf area was 58.0 cm^2, the females rolled 1–13 (on average 5.6 of 7.0) leaves, the total average area of which was 49.5 cm^2. On the damaged annual shoots of *Tilia* spp. the average leaf area of which totalled 69.9 cm^2, the females rolled 1–14 (on average 3.3 of 4.1) leaves, the total average area of which was 63.2 cm^2. On the annual shoots of *S. caprea* whose average area totalled 45.5 cm^2, the females rolled 1–10 (on average 3.3) leaves, the total average area of which was 38.3 cm^2 (Tab. IV). It follows that on average 25.0% of the number of leaves and 17.2% of the leaf area were not included into the rolls on the damaged annual shoots of *F. sylvatica*. On the annual shoots of *Tilia* spp. and *S. caprea*, 12.1% (24.2%) of the number of leaves and 10.6% (18.8%) of the leaf area were not included in the rolls (Tab. IV).

Only a negligible portion of the leaf rolls was created on intact shoots (1–3%). In such rolls, the females damaged petioles of the rolled leaves instead of shoots. In order to speed up the wilting of leaves, they bit up to 20% of the stems of leaves in rolls on the damaged shoots. Most leaf rolls (on *F. sylvatica* 77.6%, on *Tilia* spp. 91.9% and on *S. caprea* 94.5%) were situated on one annual shoot (Fig. 2).

The larvae of *B. betulae* live inside the dying and dead leaf rolls. They are completely harmless and by consuming the leaf tissues, they contribute to more rapid disintegration of the leaf rolls.

Trees endure defoliation caused by the beetles much better than the mining of shoots. Inquiries conducted in the Brno region showed that overwhelming majority of leaf rolls are created on gnawed out shoots and that the shoots always die. At an outbreak, the damage to shoots may be considerable. The disturbed balance between roots and assimilatory organs activates dormant buds and facilitates the growth of new young sprouts. Various growth anomalies are observed (crown densification and spreading, bayoneted growth, forked branches etc.). Noticeable may also be the loss of increment, namely when the lead is destroyed. Damaged trees are much more succeptible to infections caused by various rot agents.

Most authors consider *Byctiscus betulae* a pest of vineyards and fruit orchards, less a pest of forest trees. For example, Formánek (1911), Stellwaag (1918), Pfeffer *et al.* (1961), Francke-Grosmann (1974), Konopleva (1974), Stolina *et al.* (1985) and others take it for a pest of young *Populus* spp. Much sought hosts are also *Salix* and *Fagus* (Stellwaag, 1918), *S. caprea* (Vasiljev *et al.*, 1974) and *Tilia* (Henschel, 1895). In the last decades, damages caused by *B. betulae* in vineyards and fruit orchards receded into the background. Nonetheless, this fact does not exclude a possibility of its occasional outbreaks and the related damage of trophically expedient species of both non-forest and forest woody plants.

Possibilities of Protection and Counter Measures

The vine leaf roller (*B. betulae*) often multiplied excessively in vineyards in the past, where its populations were responsible for considerable economic losses. Until the beginning of the 20th century, vinegrowers tried to reduce losses in grape vine production mainly by the manual collection of the beetles or by shaking (tapping) them down and by collecting the leaf rolls. In favourable weather, the beetles occur largely on the upper face of the leaves of low woody plants where they are well visible and easy to reach. Their collection is efficient only on cold and cloudy days or early in the morning when their activity is low (Ratzeburg, 1839; Taschenberg, 1874; Smolák, 1941; Francke-Grosmann, 1974). In good weather, the beetles are very alert and agile, recording even the slightest movement in both near and more distant surroundings including the movement and shaking of the host woody plant. Due to external impulses signalling danger, they frequently fall into the status of a so-called akinesis, when they pull legs and antennae to the body and fall onto the ground. Sometimes, under warm and sunny weather, they try to escape from the enemy by relatively quick run or fly-off. This is why Plavil'ščikov (1963) states justly that the observation of leaf-rolling weevils is a good school of patience. In the past, schoolchildren were often used to collect the beetles and the leaf rolls (Escherich, 1923). Open umbrellas turned upside down or canvases were used to catch the shaked-off (tapped-off) beetles from the tree crowns. The collected beetles and leaf rolls had to be safely liquidated (by burning at the best). Perepechai (1930) maintains that the manual collection of the pest has to be done three to four times a year, in mid-June and during the summer period. From a practical viewpoint, however, the measure is not efficient enough (Krieg, 1924).

Mechanical soil cultivation in the autumn by which hibernating beetles are destroyed brings good results. Appropriate agronomic measures include the sound establishment of vineyards at suitable localities and the cultivation of grapevine varieties and hybrids with a certain resistence to infestation (Antonie and Todorescu, 2008). One of environment-friendly methods for controlling pest abundance is the protection of insectivorous birds (including pheasants) and ants from the family of Formicidae. An important role in the future integrated protection of vineyards against the pest may have the promotion and perhaps also the efficient employment of oophagous parasitoids from the family of Trichogrammatidae.

In the open, beetles and larvae in leaf rolls can be killed by means of insecticides. In the first half of the 20th century, the pest was liquidated namely by arsenates in the form of repeated spring spraying or dusting (Krieg, 1924; Lederer, 1928–1932; Ruiz Castro, 1946 a.o.). In the 1930–1970s, nicotinic preparations and DDT- or HCH-based preparations were recommended (Ruiz Castro, 1946; Baudyš, 1952; Dosse, 1954 a.o.). In the second half of the 20th century, agents most used in plant protection were organophosphates (esters of phosphoric acid), which are used until today together with pyrethroids, neonicoticoids and carbamates. Organophosphates have (similarly as the formerly applied HCH-based preparations) a systemic effect and so they are able to liquidate larvae living in leaf rolls (Dose, 1954; Foschi, 1960). Good results were recorded for example after the treatment of young aspen plantations with malathione (carbophos) (Konopleva, 1974). Chemicals can be applied in the autumn to kill larvae and beetles wintering in the soil. Advised disinsectants were caustic fertilizers (Baudyš, 1952) and lindane (Dosse, 1954).

The protective and counter measures against *B. betulae* are usually not used in forest biocoenoses. In the case of mass outbreak (e.g. in young aspen plantations), the pest can be liquidated by insecticides. Agents applicable in the Czech Republic are only those included in the list of permitted preparations, issued periodically by the CR Ministry of Agriculture upon approval of the main environmental health officer. Dates of treatments depend on the course of spring weather. The first treatment aims at a liquidation of the highest possible number of beetles at the time of their feeding on leaves, i.e. before they begin to damage sprouts (in the Brno region usually at the end of April). Other two to three treatments are to be made as needed at an interval of about two weeks.

CONCLUSION

The monograph presents results of study of the occurrence, biology and harmfulness of *Byctiscus betulae* (L.) on forest trees in the Brno region. Main results obtained from field and laboratory surveys in 2012–2013 are as follows:

1. Leaf rolls were found on 13 species (and 10 genera) of woody plants. Most frequently damaged were *Fagus sylvatica*, *Tilia* spp. (predominantly *T. cordata*), *Salix caprea* and *Populus tremula*. The leaf rolls were not found for example on *Alnus glutinosa*, *Betula pendula*, *Carpinus betulus* and *Quercus* spp.
2. Beetles winter in ground pupal chambers. After 6–8 months of hibernation, the first beetles appear on trees, usually in the last decade of April. They feed on freshly expanded leaves, which are skeleted or windowed by them from the adaxial (less from the abaxial) face of the leaf.
3. After wintering, females live on average 7 (males 5) weeks, and damage on average 40 (males 25) cm^2 of leaves. After fertilization, the females bite out usually 1 (max. 4) mines (diam. 1.2×1.0 mm)

into annual shoots, which reach up to the opposite epidermis. Average length of shoots above the puncture on *F. sylvatica*, *Tilia* spp. and *S. caprea* was 6.0, 4.6 and 3.8 cm, respectively. The females damaged the shoots on *F. sylvatica* in the first half of May, on *Tilia* spp. from the beginning of May to the end of June, and on the later flushing *S. caprea* from 10 May to the end of June.

4. Females create up to 99% of leaf rolls on shoots of which they took a bite. They sporadically roll leaves also on intact shoots on which petioles of the rolled leaves are eaten instead of shoots. In 32.9% of rolls on *F. sylvatica* (17.7% of rolls on *Tilia* spp. and 20.5% of rolls on *S. caprea*), they damaged petioles on damaged shoots too. For the creation of leaf rolls, they use only a part of damaged (punctured) shoots (on average 67.1% on *F. sylvatica*, 82.3% on *Tilia* spp. and 79.5% on *S. caprea*).
5. Leaf rolls on *F. sylvatica* comprised 1–13 (on average 5.6) leaves the area of which totalled 8–144 (on average 49.5) cm^2. Leaf rolls on *Tilia* spp. comprised 1–14 (on average 3.3) leaves the area of which totalled 10–207 (on average 63.2) cm^2. Leaf rolls on *S. caprea* comprised 1–10 (on average 3.3) leaves the area of which totalled 8–96 (on average 38.3) cm^2.
6. Leaves are rolled on the abaxial face, adaxial face or on both. The rolling direction depends on the size of the leaf and elasticity of lateral veins. On *F. sylvatica*, *Tilia* spp. and *S. caprea*, 67.2%, 46.6% and 70.0% of leaves, resp. was rolled on the abaxial face. In all tree species, the first (i.e. innermost) leaves are rolled on the abaxial face, into which the females lay eggs most frequently.
7. Females of *B. betulae* lay eggs in the period from May to July, most often in May. Leaf rolls on *F. sylvatica* contained 1–14 (on average 5.1) eggs, leaf rolls on *Tilia* spp. contained 1–13 (on average 4.9) eggs and leaf rolls on *S. caprea* contained 0–12 (on average 3.5) eggs. The highest number of eggs (3–16 / on average 8.0/) was found in the leaf rolls on *Vitis vinifera*. The average number of eggs in the leaf rolls grows with the increasing total leaf area rolled. In total, the females lay on average 50 eggs. On *P. tremula*, *S. caprea* and *Pyrus pyraster* they create on average 15 leaf rolls, on *F. sylvatica* and *Tilia* spp. 10 leaf rolls and on *V. vinifera* only 8 leaf rolls.
8. Larvae emerge from the eggs in 8–9 days. Their development goes through three instars and they damage in total about 300 mm^2 of leaves. They grow up in 4–7 (in the laboratory in 3) weeks, leaving the leaf rolls on *F. sylvatica* in the second half of June, on *Tilia* spp. from 15 July to 20 August, and on *S. caprea* from the beginning of August to the beginning of September. The grown-up larvae bite outwards through oval holes of 1.7–2.2 mm in diameter and fall onto the ground. There, they create ground pupal chambers at a depth of 2–5 cm. They pupate from the beginning of July to the end of September. After 1–2 weeks of pupal rest, beetles emerge, which stay in the pupal chambers until the next spring.
9. The percentage of *B. betulae* population perished in the leaf rolls on *F. sylvatica* was on average 50% (65% on *Tilia* spp. and 85% on *S. caprea*). The main mortality factor are oophagous parasitoids from the family of Trichogrammatidae, which killed in the leaf rolls on *F. sylvatica*, *Tilia* spp. and *S caprea* on average 9%, 40% and 30% of the *B. betulae* population. Parasitoids from the family of Braconidae liquidated 5–20% of the population. Extreme drought killed 5–20% of the population in the leaf rolls on *Tilia* spp. and *S. caprea*.
10. Woody plants endure defoliation caused by beetles without major consequences. On the other hand, the damage to shoots (gnawing) can be very harmful. Shoots that have been bitten always die, which results in the loss of increment, growth anomalies and/or fungal infections. Protective and counter measures are usually not adopted in forest ecosystems.

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