A review of the apple sawfly, *Hoplocampa testudinea* (Hymenoptera Ten-thredinidae)

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Abstract

The apple sawfly (ASF), *Hoplocampa testudinea* Klug (Hymenoptera Thenthredinidae), attacks only one host plant, the apple tree (*Malus domestica* Borkh.). It is found in temperate regions of Europe as well as in Eastern North America. The flight of the ASF adults coincides with the bloom of apple trees and larval develop in fruitlets. As the ASF spends approximately 11 months of its life cycle underground as a pre-pupa or pupa, management of the ASF is possible only during 1 month. The ASF is univoltine and has an obligatory diapause that can be extended to 2, 3 or rarely 4 years. Here key publications about the ASF have been selected for their relevance to the application of Integrated Pest Management programs. Because the ASF is dependent on living and developing tissues and because no oviposition or artificial diet is available for laboratory experimentations, research projects have to be conducted in field or semi-field conditions. The main natural mortality factors are the ichneumonid parasitoids *Lathroletes ensator* (Brauns), present in Europe and introduced to Eastern Canada, and *Aptesis nigrocincta* (Gravenhorst) in Europe. The latter also acts as a hyperparasitoid of *L. ensator*. Management of the ASF can be based on monitoring adults with sticky traps and with use of a simulation model. Non-insecticidal methods that can be used deliberately in an ASF management program are reviewed, notably nematodes, entomopathogenic fungi, and physical control methods such as cellulose barriers and exclusion netting. The technical and economic reasons preventing widespread implementation of these approaches are discussed.

Key words: apple sawfly, *Hoplocampa testudinea*, Lathroletes ensator, *Aptesis nigrocincta*, apple orchards, nematodes.

Introduction

Among insect pests associated with apple (*Malus domestica* Borkh.) orchards, the apple sawfly (ASF), *Hoplocampa testudinea* Klug (Hymenoptera Thenthredinidae) (figure 1), has a particular status. The ASF is a pest that directly attacks the fruit and is challenging to manage in commercial orchards because it is vulnerable to control measures for less than a month per year. Adults are diurnal and mainly active during bloom, when conserving pollinators is imperative to apple fruit production and young larvae are vulnerable only during a short period immediately after petal fall, thus restricting possibilities for chemical treatment. Moreover, oviposition and larval development of the species depend entirely on a healthy progress of the apple fruit from pollination to subsequent fruit set. Hence, as no artificial diet or oviposition medium has been developed for laboratory rearing, research has to be done under field or semi-field conditions.

The scientific and technical literature on *H. testudinea* comprises ca. 300 articles. Key early papers on the biology of the ASF presented information from Germany (Velbinger, 1939), England (Miles, 1932; Dicker and Briggs, 1953), Holland (Kuenen and van de Vrie, 1951), Austria (Böhm, 1952), and France (Chaboussou, 1956). A series of papers on natural and biological control were published (notably in Poland in the ‘80s by Jarosława), several of which are not readily accessible because they were written in various languages and were often published in currently rare journals.

Our objective was to critically review the literature on the biology, ecology and behaviour of the ASF, as well as on key antagonists, with particular reference to application in apple protection programs. We aimed to be comprehensive but focused on key information, including details where appropriate. We first discuss the historical perspective, distribution, identification, host plant, life cycle, and rearing of ASF. Next, the occurrence of natural factors such as parasitism and pathogens is discussed. Research and deliberate efforts leading to possible applications within an Integrated Pest Management (IPM) program are treated under the heading “Management”.

Historical perspective on pomiculture

It should be first emphasized that the old literature on the ASF refers to apple orchards quite different from modern ones. The traditionally large trees with tall trunks were difficult if not impossible to sample systematically, while non-insecticidal management tools were limited and fruit thinning was impossible on a commercial scale (hand fruit thinning was impractical at that scale). Alternate fruit bearing was the general situation and levels of fruit damage varied accordingly. Extreme events of various sorts, for example seven ASF larval entries in one fruitlet or ASF larvae crawling over the orchard floor in search of a new fruitlet, are no longer realistic. Currently, observations and pest control practices are much easier on small spindle trees.
Figure 1-10. (1) Female ASF ovipositing in an apple flower; (2) ASF caught on sticky trap, (2a) ventral view of male and (2b) female; (3a) External appearance of fresh oviposition scar shown by red arrow, (3b) tissues of fruitlet receptacle under egg deposition, (3c) as revealed by dissection, (3d) ASF egg in receptacle as revealed by dissection, (3e) ASF egg development (after Kuenen and van de Vrie 1951; see also Trapman, 2016b); (4) ASF mature larva; (5a) ASF primary damage early season, (5b) late season; (6a) Migrating ASF larva and secondary damage showing frass near entry and exit holes, (6b) one ASF larva can damage several nearby fruitlets, (6c) fruitlet cut open showing mature ASF larva and semi-liquid frass plugging hole; (7) Late season appearance of sting damage caused early in the season on apple cultivar Natyra; (8a) L. ensator adult, (8b, 8c) ASF larvae parasitized by L. ensator, red arrow show the endoparasite; (9a) ASF larvae and pupae, (9b) ASF pupa with exit hole of L. ensator; (10) Sticky white trap used to monitor ASF adults. Authors of photos: (1*, 3a*, 5b*, 9a*) Léo-Guy Simard; (2a, 2b) Jacques Lasnier; (3b, 3c, 3d, 3e, 4, 6a, 6b, 10) Weronika Świergiel; (5a, 7) Herman Helsen, (6c) Greg Krawczyk; (8a*) Benoit Rancourt; (8b*, 9b*) Pierre Lemoyne; (8c) Dirk Babendreier.

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The ASF is native to temperate regions of Europe, from Great Britain in the West to the Volga river (Russia) in the East (Fauna Europaea, 2018a). It is rare in Mediterranean countries, and absent in Ireland and Iceland.

The ASF was introduced accidentally to North America, where its common name is European ASF. Its damage was first reported on a crabapple tree in Long Island, New York, in 1939, and positive identification was made in 1942 from specimens collected in a New York State orchard (Pyenson, 1943). Currently, the ASF is present in all major apple-producing regions of New England, Pennsylvania, and in neighbouring States of Delaware, Maryland and West Virginia (Greg Krawczyk, personal communication).

In Canada, the ASF was reported in 1940 on Vancouver Island in Victoria, British Columbia (Downes and Andison, 1942; Downes, 1944). There are no further mentions of the ASF in western North America, probably because it was eradicated there before it reached the continent. In eastern Canada, ASF was found for the first time in 1979 in Hemmingford, Quebec (Paradis, 1980), a few kilometres from the New York State-Quebec border. Subsequently, it was quickly found in all major apple-producing areas of Quebec (Vincent and Mailloux, 1988). Currently, it is found in major apple-producing areas from Port Hope, Ontario, to Nova Scotia (Vincent et al., 2016).

Identification

The genus Hoplocampa Hartig 1837 is a well-defined and stable group within the sawfly subfamily Nematinæ (Prous et al., 2014). Hoplocampa species are associated with Rosaceae, each with one or a few related species of pome- or stone fruits (subfamilies Maloideae and Prunoideae). Their life histories are similar. Keys to adults of the North American species are presented in Ross (1937, 1943), to the British species in Benson (1952) and to most European species in Masutti and Covassi (1980). Wing venation of the ASF is typical for the genus (e.g. Prous et al., 2014). The bodies of male and female ASF adults are black above and orange underneath. H. testudinea is the largest species in the genus and the only one associated with apple trees. Adult female ASF are larger than males. While males have a rounded abdomen extremity (figure 2a), females have a conspicuous brown ovipositor, the saw, that is clearly visible ventrally even when specimens are caught on sticky traps (figure 2b).

Miles (1932) and Lorenz and Kraus (1957) described the larval morphology of the ASF. The neonate larva is whitish with a black head and dorsal black marks on three terminal segments, and clearly visible eyes. The full-grown larva is about 12-13 mm long with a brown head. The larvae of H. testudinea can be easily distinguished from other internal fruit feeders. Like other sawfly larvae, in addition to the three pairs of true legs on the foremost (thoracic) segments (figure 8b), they have another 6 pairs of non-segmented prolegs on abdominal segments 2-7. In contrast, lepidopteran larvae like the codling moth (Cydia pomonella L. Lepidoptera Tortricidae) and the fruitlet mining tortrix - several species, including Pammene rhodiella (Clerck) Lepidoptera Tortricidae - have only 4 pairs of prolegs on segments 3-6 (Alford, 1973). The frass of ASF larvae is wetter, sometimes almost dripping (figure 6b-c), than that of lepidopteran larvae, while fruit with older ASF larvae are easily recognized by a characteristic and nasty smell resembling that of stink bugs. No other fruit-feeding sawfly has been recorded on apple. Occasionally, the pear sawfly, Hoplocampa brevis (Klug) (Hymenoptera Tenthredinidae), has been observed to oviposit and develop in apple ovaries in the laboratory (Velbinger, 1939), and Ametastegia glabrata (Fallen) (Hymenoptera Tenthredinidae) cause infestations in orchards of Sweden (Weronika Świergiel, personal observation). The natural history of sawflies, including the genus Hoplocampa, their habits, and information on curation of specimens are treated by Benson (1950) and Boevé and Pasteeels, 1985; Boëvé et al., 1996). Maxwell (1955) treats the internal larval anatomy of sawflies.

Host plant

H. testudinea is restricted to apple as a host plant. The only attack by this pest on another tree species was reported by Stritt (1943), who found foul-smelling larvae, larger than those of the pear sawfly, in a pear orchard near Stuttgart, Germany. The following year, he reared a few adult female ASF out of infested pears from the same orchard. Velbinger (1939) reported that the ASF did not oviposit on either pear (3 cultivars) or plum (1 cultivar), whereas the pear sawfly accepted apples from 5 out of 6 cultivars.

As apple trees need cross-pollination, orchards are composed of mixes of cultivars planted in a spatial layout with respect to flowering time and pollination compatibility. Several articles mention differences in ASF attack among apple cultivars, and some explain these observations to be the result of ‘preference’. For instance, in the Bordeaux region (France), Roussel and Mansencal (1961) reported 20, 30 and 35% damage caused respectively to cultivars Golden Delicious, Winter Banana and Grand Alexandr. From 14 females caged on the cultivar Gascoyne’s Golden Delicious in a 1.7-5.8 for susceptible cultivars (Briggs and Alston, 1969). The ratio of primary (figure 5a-b) to secondary (figure 6a-c) damage was four times greater, suggesting that larval mortality or slow larval development on cultivar Gascoyne’s.

In conclusion, differences in damage levels between apple cultivars are often due to the reaction of the ASF to factors varying among cultivars such as flower density and colour, flowering period and fruit set.

Life cycle

Drawing mostly on papers by Velbinger (1939; 1948), Miles (1932), Dicker (1953), Böhm (1952), Chaboussou (1956; 1957) and Sjöberg et al. (2015) a summarized life cycle follows.
The ASF is univoltine. The adults emerge before or at the pink stage (phenological stage BBCH 59) of early flowering cultivars (Miles, 1932; Kuenen and van de Vrie, 1951; Babendreier, 1998; Ciglar and Baric, 2002). Peak adult activity is greatest on still, sunny days (Dick- er, 1953; Haalboom, 1983). Within 24 hour of emer- gence, females start laying eggs into the receptacle of open flowers when the temperature is > 11 °C (Graf et al., 1996c). Most eggs are normally laid before the end of bloom (BBCH 65-69) (Sjöberg et al., 2015) (figure 3a-d). Several studies report that egg deposition starts on the king flowers of older branches (Kuenen and van de Vrie, 1951; Gottwald, 1982; Tamosiūnas, 2014; Trapman, 2016b). Neonate larvae mine the fruitlet super- ficially while subsequent larval stages typically migra- te to other fruitlets to eat internal tissues, and eventually their seeds. Last larval instars start the soil to form a cocoon. The ASF overwinters as prepupae which evolve into pupae in spring.

Adults
The emergence of adults is generally studied by con- centrating last-instar larvae on a defined spot where they can enter the soil and by collecting emerging adults in a cage the following spring. Emergence is well synchro- nized with the bloom period e.g., starting 3 days before the pink stage of cultivar McIntosh in Quebec (Vincent and Mailloux, 1988) and extending over approximately 2 weeks (Babendreier, 1998). In some cases, females emerge slightly earlier than males (Stepniewska, 1939; Vincent and Mailloux, 1988; J.-P. Zijp, unpublished). In other cases, both sexes emerge simultaneously (Velbinger, 1939; Niezborala, 1978; Babendreier, 1998).

Estimates of sex-ratios have been done frequently. However, both visual inspection of trees and tapping branches over an umbrella have given highly variable results. For example, the latter method yielded an average of 30% (Dicker, 1953) and 75% (Velbinger, 1939) males. More reliable figures may be obtained by allowing adults to emerge under semi-field conditions. Graf et al. (1996a) reared 68% females (n = 565) from fruit- lets showing secondary damage (figure 6a-c). Babendreier (1998) found sex-ratios of 66, 70 and 79% females (n = 633). J.-P. Zijp (unpublished) recorded emergence of 64-73% females in samples reared in an orchard or in containers in an insectary, with an overall average of 68% (n = 1340) across three years.

ASF adults feed on pollen or nectar of apple flowers and take up droplets of water present on apple leaves (Miles, 1932). They fly during day time only (Gottwald, 1982). As in other sawfly species, pheromones and other chemical stimuli are most likely involved in encoun- ters between males and females, but none have been re- ported so far. Mating occurs soon after emergence (Velbinger, 1939; Böhm, 1952), and lasts on average 3 minutes in field cages (Babendreier, 1998) or approxi- mately 5 minutes in the open field (Miles, 1932). Both sexes spend > 80% of the daylight hours on apple flow- ers (Babendreier, 1998).

In early May in Switzerland, Babendreier (1998) ob- served average lifespans of 11.5 days for females and 10.0 days for males in field cages covering a flowering apple tree. Graf et al. (2001) found the average lifespan of females to be 24.3 days at 10.5 °C and 7.0 days at 20.5 °C.

Oviposition nearly always takes place on open flowers (Miles, 1932; Velbinger, 1939; Dicker, 1953) (figure 1). The females walk over the stamens for some time, then move between the petals to the outside of the receptacle and oviposit in the skin of the receptacle. This causes a small funnel-shaped mark visible on fruits at harvest (figure 7). The total time for oviposition is about 60-120 seconds (Miles, 1932; Soenen, 1952; Roitberg and Pro- kopy, 1980), with an average of 115 seconds determined under field cage conditions (Babendreier, 1998). Oviposition attempts lasting < 50 seconds are unsuccessful (Roitberg and Prokopy, 1984). It was also observed that oviposition was interrupted after ants contacted adult ASF (Babendreier, 1998).

Using traps, Wildbolz and Staub (1986) found that adults were attracted first to the top of the trees and then moved down the trees for egg-laying, particularly on the south side. Hence most eggs were found higher up in the trees. Accordingly, larval distribution across apple trees in an orchard was found to be aggregated (Babendreier, 1998). This is consistent with findings of Tamosiūnas et al. (2015) who demonstrated a strong tendency for aggregation of adult ASF across orchards in Lithuania, with a constant position of the clumps over years.

Eggs
Eggs are laid singly in the base of the receptacle in a pocket-like cavity made by the female saw (figure 3d). Sometimes, eggs are found between stamens. The ovi- position channel is 1-2 mm deep and the insertion mark of about 2 mm in length turns dark within a few days (figure 3a-b) (Velbinger, 1939; Böhm, 1952). Not all in- sertion marks contain an egg. Niezborala (1978) count- ed between 1 and 17.5% empty marks on various culti- vars.

One egg is laid per flower, exceptionally two (Soenen, 1952; Niezborala, 1978; Gottwald, 1982; Weronika Świergiel, personal observation). Direct behavioural ob- servations have shown that females lay one or two eggs per fruit cluster if these have 5 or 6 flowers, but always lay only a single egg per cluster if few flowers are pre- sent in a cluster (Babendreier, 1998). The presence of an egg has no effect on the number of visits to the flowers. However, females spent significantly less time on the receptacle of an uninfested flower before attempting oviposition, or before leaving, than did females on an egg-infested blossom (Roitberg and Prokopy, 1984). Following oviposition, 83% of ASF females inspect the oviposition wound and place their mouthparts on it for a few seconds; only 18% of females show that behaviour when oviposition had been unsuccessful. When the ovi- positor is withdrawn, a droplet that exudes from the oviposition slit is often consumed by the female (Dick- er, 1953). This exudation causes a brownish discolora- tion of the fruitlet skin that can be visually detected by careful examination (Miles, 1932) (figure 3a).

Velbinger (1952) and Chaboussou (1961a; 1961b)
have demonstrated that virgin females lay as many viable eggs as mated females. Whether sex determination is by arrhenotoky, like in most Hymenoptera (Heimpel and de Boer, 2008), is unknown for the ASF. Several researchers reported an average of $< 30$ eggs laid per female under artificial conditions (Soenen, 1952; Böhm, 1952; Dicker, 1953; Chaboussou, 1961a; 1961b; Alford, 1973; Graf et al., 2001). However, as the ASF is synovigenic (i.e., the female continues to produce mature eggs if she is fed adequately), egg laying capacity under field conditions may be greater. Velbinger (1939) found up to 78 eggs in the ovary of one female and cites Kazansky (1935) who found a maximum of 87. Niezborala (1978) reported between 16 and 116 eggs, with an average of 43. Field collected females had 25.4 fully grown eggs on average, plus 33.8 eggs of smaller size with yolk (J.-P. Zijp, unpublished). As these females had been laying some eggs already and had their stomachs filled with pollen, the potential production must have been well over 30 eggs per female. Babendreier (1998) found on average 8.5 eggs in the ovary of freshly emerged females, while females fed honey and water but deprived of apple flowers for oviposition reached a plateau of approximately 35 eggs at about 6 days after emergence.

As illustrated by Kuenen and van de Vrie (1951), there are six egg stages (figure 3e) (Trapman, 2016a). The freshly laid egg is kidney-shaped (Miles, 1932; Böhm, 1952) and measures $1 \times 0.33$ mm (Babendreier, 1998). It is whitish and viscous (yoghurt-like), and the chorion becomes transparent after 2-3 days, allowing observation of larval development. The egg swells and changes form as development proceeds. This causes a rupture in the fruitlet epidermis, leaving the egg partially exposed (Miles, 1932). The embryonic development (from egg deposition until egg hatching) spans 8-20 days, with an average of 12 days (Kuenen and van de Vrie, 1951). Graf et al. (2002) determined that egg development takes 85 DD ($> 6.9 \degree C$). Most eggs survive temperatures as low as $-2.5 \degree C$, but young larvae that have not yet penetrated the fruit are killed at $< 0$ °C (Feytaud, 1924). Fungal infestations were seen to kill eggs laid in cool and humid weather (Noack, 1993).

**Larvae**

There are five larval instars that can be distinguished by the width of the head capsule. Miles (1932) provided the following average (minimum-maximum) widths in mm: first instar 0.392 (0.34–0.42); second 0.500 (0.53–0.57); third 0.786 (0.76–0.82); fourth 1.106 (1.07–1.16); fifth 1.526 (1.49–1.57). Slightly smaller head capsules were found by Babendreier (1998) and by Hey and Steer (1934). Growth of head capsules follows Dyar’s law. The first instars have a light grey-brown head, the second, third and fourth a blackish brown head and anal plates of similar colour, and the fifth a yellowish-brown head and a light anal plate (Velbinger, 1939). These colours develop a few hours after moulting.

The first instars mine the fruitlet superficially, leaving a typical meandering scar on the epidermis of the growing fruitlet (Petherbridge, 1928) (figure 5a), the primary damage, a term coined by Dicker (1953). Like unharmed fruits, such fruitlets remain on the tree until harvest (figure 5b). Neonate larvae that hatch inside a fruitlet generally start mining between or just below the sepals, while those hatching in the open start to mine somewhere on the side of the fruitlet.

Some second but mostly third instars move to a nearby fruitlet and burrow towards the seeds on which they feed. These fruitlets show secondary damage, as termed by Dicker (1953) (figure 6a-c). Chaboussou (1961) observed that about half of these larvae moved to a third fruitlet, while Dicker (1953) observed that 17% of the larvae moved three times (figure 6a-b). Feeding on up to 5 fruitlets, as mentioned by Kuenen and van de Vrie (1951) is quite unlikely in a well-managed orchard. While entering a second fruitlet, the fruit skin is not ingested by larvae, but scraped with the mandibles and put aside. This is why stomach poisons like lead-arsenate have little larvicidal effect (Kuenen and van de Vrie, 1951). Moulting occurs exclusively within the fruitlet (Velbinger, 1939).

Larval frass is frequently found plugging the entry hole made in the fruitlet by older larvae (figure 6a-c). As some ASF larvae might have exited the fruitlet, only dissections of fruitlets showing secondary damage provide a reliable indicator of larval presence (Vincent et al., 2016). More than one ASF larva can be found per fruit, particularly when ASF populations are high, as reported in the early literature (Miles, 1932; Velbinger, 1939). Destruction of the seeds causes premature fruitlet drop, generally in June, well after the larva has descended into the soil.

Development of the egg and through the fifth instar takes between 3 and 5 weeks in the field in central and northern Europe (Velbinger, 1939; Böhm, 1952; Dickler, 1954; Niezborala, 1978; Gottwald, 1982; Babendreier, 1998; Sjöberg et al., 2015). The exact time is difficult to determine because studies must be conducted in fruitlets growing on the tree to obtain a realistic estimate.

The last larval instars produce a characteristic odour, akin to those emitted by several stink bug species (Hemiptera). Boevé et al. (1996) showed that disturbed larvae emit four aliphatic compounds by evertting their ventral glands, but only the fifth instar produces quantities that can be easily smelled by humans. Four butanoic compounds (i.e., 3-hydroxy-2-butanoic; 3-methyl-1-butanol; 2,3-butanediol; 1,2-butanediol) and 2-phenylethanol were found to emanate mainly from the frass of full grown larvae (Boevé et al., 1996). The full-grown larva (figure 4) evacuates its intestines before leaving the fruitlet and burrows immediately into the soil, where it descends into the soil. Sandy soils allow greater survival (Zijp and Blommers, 2002a). In the soil, the larva spins a cocoon and transforms into a prepupa within a few days (figure 9a).
Pupae

The ASF spends approximately 11 months underground as a prepupa or pupa in a cocoon. Velbinger (1939) extensively described the preparation of the cocoon by the larva. The cocoon has two layers, is water impermeable and measures 7-8 mm long by 3-4 mm wide (Velbinger, 1939). In Europe, pupation occurs in March or April, about 3-4 weeks before adult emergence (Miles, 1932; Böhm, 1952; Zijp and Blommers, 1993). As reported for several sawfly species (Danks, 1987), some prepupae have a prolonged diapause for a second or third year (Dicker, 1954; Niezborala, 1978; Zijp and Blommers, 1993). Babendreier (1998) reported proportions of 36.8, 9.2, 8.4 and 1.6% adult emergence after 1, 2, 3 and more years underground, respectively. Prolonged diapause may provide better chances of survival, notably in years with poor fruit set, or when larvae are killed by insecticides (Kuenen and van de Vrie, 1951).

Rearing

Rearing the ASF throughout its life cycle is impeded by its dependence on the healthy growth of apple ovaries. However adults may be obtained from full-grown larvae or cocoons. The latter may be collected by sampling soil from under well infested trees, an or cocoons. The latter may be collected by sampling soil. However adults may be obtained from full grown larvae or cocoons. The latter may be collected by sampling soil from under well infested trees, and by crumbling or by sieving it over water. The cocoons can be easily collected because they float (Velbinger, 1939). It is easiest, however, to collect late instars from fruitlets showing secondary damage (figure 6a-c). These can be laid on the ground (Velbinger, 1939) so that the descending larvae go directly into the soil. They can also be put on wire mesh placed over a bucket, so that descending larvae can first be checked for parasitoids and counted before use (Babendreier, 1998). When ASF larvae are placed on sandy soil, the cocoons can easily be collected by sieving the soil after a few weeks. Sand particles (i.e., quartz < 0.8 mm) should be used to allow successful cocoon spinning and increased survival rate (Weronika Swiergiel, personal observation). The cocoons are drought tolerant; to produce many adults, ASF larvae put into small soil-filled pots stored without covering in an outdoor insectary had to be watered only twice in 10 months. For containment, large earthen flower pots or wide plastic tubes filled with larvae can be buried in the ground to study overwintering in the orchard, while at the same time this will exclude predation by ants or moles. Reared adults can be isolated on branches by means of sleeve cages, and the flowers have to be pollinated by hand, as pollination by the engaged sawflies is insufficient.

Natural control

Parasitoids

Only ichneumonids have been reported to parasitize the ASF (table 1). Lathrostizus ensator (Brauns) (Hymenoptera Ichneumonidae) is the usual larval parasitoid of the ASF in European orchards (Fauna Europaea, 2016).

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<td>Lathrostizus citreus (Briske)</td>
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<td>Aptesis nigrocincta Gravenhorst</td>
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<td>Microcryptus nigrocinctus Gravenhorst</td>
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<td>Microcryptus abdominalis Gravenhorst</td>
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<td>Holocremia bergmanni (Thomson)</td>
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<td>Holocremia areator (Gravenhorst)</td>
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<td>Lathrostizus macrostoma (Thomson)</td>
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*References from Jaworska (1987). **similar parasites found on H. testudinea, H. brevis and H. minuta larvae, which occurred in large numbers on the latter two species.
2018b), notably in Germany (Velbinger, 1939), Switzerland (Carl and Kählert, 1993), The Netherlands (Zijp and Blommers, 1993) and the UK (Cross et al., 1999b).

In Poland, *Lathrolestes marginatus* (Thomson) (Hymenoptera Ichneumonidae), reported by Jaworska (1987; 1992), appeared to be the same species, i.e., *L. ensator* (Barron, 1994; Zijp and Blommers, 2002b). Zerova et al. (1992) refer to *L. ensator* as the major parasitoid of ASF in Ukraine, while a single specimen of the parasitoid was reared from *H. testudinea* larva found in Golden Delicious fruitlets near the village of Tirolo (Alto Adige, Italy) in 1995 by Leo H. M. Blommers (personal observation).

Two other *Lathrolestes* species have been reported as important enemies of the ASF: *Lathrolestes citreus* (Brischke) (Hymenoptera Ichneumonidae) in Central Poland (Niezborala, 1976), and *Lathrolestes luteolus* (Thomson) (Hymenoptera Ichneumonidae) in Moldavia (Tuniekiej, 1966 in Jaworska, 1987). However, these two names cannot apply to parasitoids of the ASF, as to they pertain to tiny parasitoid species of leafmining sawflies of linden and elm, respectively (Reschikov, 2015).

The flight of *L. ensator* starts when the flight of the ASF is almost over, i.e. around mid-May in The Netherlands. Emergence of adults from the host cocoon (figure 9b) in the soil occurs when temperatures at 10 cm below ground level reach 13 °C (Jaworska, 1987). Adult males appear first. Females are pro-ovigenic (they have fully developed eggs at emergence) and have 88 and 120 eggs according to Babendreier (1998) and Zijp and Blommers (2002b), respectively. How *L. ensator* find its host is not known, but Babendreier (1996) observed females hovering above the apple tree canopy and entering fruit clusters infested by the ASF significantly more often than uninfested ones. Females were even seen to land directly on an infested fruit in 22 out of 23 visits to infested fruit clusters.

Although a parasitoid egg is occasionally found in first instars ASF (Zijp and Blommers, 1993; Babendreier, 1998), females oviposit mainly in second instars (Onufreichik, 1974; Jaworska, 1987; Babendreier, 1998), which feed superficially under the fruit skin. Females *L. ensator* rarely oviposit in ASF larvae once these are inside the fruitlet (Babendreier, 1998): in only 1 out of 14 observations did females successfully parasitized a larva inside the fruitlet, which still was a second instar. A delay in parasitoid emergence due to a week of cold weather apparently forced their acceptance of third instar ASF, as the latter had continued growing (Zijp and Blommers, 2002b). Taking into consideration the well synchronized development of apples and the ASF, *L. ensator* has a short period to parasitize ASF larvae, which may be modulated by suitable weather conditions prevailing during that period. Babendreier (1998) showed that, in 6 out of 8 mass collections, higher parasitism rates were obtained for larvae developing later, as parasitism increased from 10 to 40% during the 10-day emergence period from collected fruitlets. This suggested a lack of synchronization of host and parasitoid or a higher performance of *L. ensator* at a later point in time when temperatures are usually slightly higher. For the ASF, this might create a selection pressure to oviposit early.

Female *L. ensator* lay up to 25 eggs per day, and 60 in 4 days (Jaworska, 1987). Superparasitism is common. The ovipositing female apparently does not avoid previously parasitized larvae and at least up to 4 eggs can be found in one ASF larva, although only one egg eventually develops into an adult (Jaworska, 1987; Zijp and Blommers, 1993; Babendreier, 1998). The banana-shaped egg is initially white, but turns black soon after oviposition, so that it becomes visible through the host skin (figure 8b-c). The egg remains visible in the fully grown host larva entering the soil but, about 2-3 weeks later the 0.7-0.9 mm long caudate larva has hatched. In the larval host, the size of encapsulated and non-encapsulated eggs is 0.4 × 0.3 mm and 0.58 × 0.17 mm, respectively (Jaworska, 1987).

The neonate parasitoid larva has a brownish head capsule and a 0.2-0.3 mm long tail. Within a few weeks, by the time the larva entirely fills up the body cavity of the host, it completes its development. Cococon formation starts about 40 days after the host enters the soil (Jaworska, 1987). The filmy cocoon lies against the inner wall of the host cocoon, with the head capsule and other remains of the host in between. In The Netherlands, the pupa of *L. ensator* gradually develops through winter, in contrast to its host (Zijp and Blommers, 1993). In regions experiencing cold continental winters (as in Poland), pupal development starts in early spring (Jaworska, 1987).

Like its host, some prepupae of *L. ensator* do not develop into an adult until after two or three winters; their coconos are located deeper in the soil (Jaworska, 1987). Babendreier (1998) found a strong correlation in the proportions of pupae remaining in diapause after one winter between *L. ensator* and its host, while the rate was consistently higher for the parasitoid than for the ASF (Babendreier, 1998; Zijp and Blommers, 2002b). In Belarus, Onufreichik (1974) found that few parasitoids emerged after one winter, 35-81% after two winters and 19-61% after three winters.

In The Netherlands, *L. ensator* is present in most apple orchards under IPM programs that harbour the ASF (Zijp and Blommers, 1993). In Poland, Jaworska (1987) found that parasitism was < 4% in pesticide-treated orchards, and ranged from 8 to 79% in untreated orchards. Parasitism levels > 80% were reported by Karabash (1967) in Ukraine, Zijp and Blommers (1993) in The Netherlands, and Vincent et al. (2016) in Canada. However, larval parasitism levels between 20 and 40% are more typical (Carl and Kählert, 1993; Graf et al., 1994). Mass collections in 27 orchards, managed organically or according to IPM principles, showed parasitism rates between 0.6 and 40% with a tendency for higher rates in orchards having fewer pesticide treatments (Babendreier, 1998). Based on a tentative life table, Zijp and Blommers (2002b) estimated that the population density of ASF may increase 2.4 times annually, and that 60% larval parasitism must occur in order to achieve regulation of ASF populations.

Another factor detrimental to *L. ensator* is the vulnerability of parasitized ASF larvae to fungal diseases in
the soil. In Poland, Jaworska (1987) observed > 70% mortality of parasitized larvae by a fungus. The highest mortality (52%) occurred during development of the parasitoid larva in the ASF cocoon, compared with about 15% after the parasitoid had spun its own cocoon. Carl and Kähler (1993) found a similar difference between unparasitized (19%) and parasitized (52%) larvae killed by Paecilomyces farinosus. Parasitized ASF larvae were sporadically killed by nematodes in the soil (Jaworska, 1987).

A second ichneumonid parasitoid species of the ASF is Apteis nigrocincta (Gravenhorst) (syn. Microcryptus nigrocinctus) (Hymenoptera Ichneumonidae) (Babendreier, 2000). Few papers have been published on this species, probably due to its cryptic life history, i.e., functioning as a cocoon parasitoid below ground. However, it has been found in several apple orchards in Switzerland (Carl and Kähler, 1993; Babendreier, 1999; 2000) and in the Baltic States (Zajanckauskas, 1963, in Jaworska, 1987). Čoruh et al. (2014) found it in Turkey but it is unclear as to whether this was in apple orchards or other habitats. Females are brachypterous while males are normally winged. As A. nigrocincta females seek to parasitize the cocoons underground, they need cracks or fissures in the soil to reach their host (Carl and Kähler, 1993). Preliminary tests indicate that A. nigrocincta females may follow a chemical trail left on the ground by fifth instars ASF to find hosts (Babendreier, 1998).

A. nigrocincta adult lifespan is on average 2 months when given food and hosts. It is synovigenic and lays an average of 20 eggs during its lifetime (Babendreier, 2000). After penetrating the cocoon, the eggs are laid externally on the host. At 20 °C, larva hatch after a few days and larval development is completed after 11.5 days. The complete cycle is finished after about 39 days at 20 °C. Superparasitism occurs in this species and a major determining factor for the female decision to lay an additional egg seems to be the encounter rate with hosts (Babendreier and Hoffmeister, 2002).

In Switzerland, three emergence periods have been observed for A. nigrocincta: a first period in June, well synchronized with the descending phase of the ASF; a second period observed during August, and; a third one in October (Babendreier, 1999). Hibernation takes place as mature larva in the cocoon or in the adult stage (females only). Rates of parasitism within a single generation ranged from 12.1 to 39.7 % (Babendreier, 2000). Zajanckauskas (1963, in Jaworska, 1987) reported 33% parasitism. The impact of this multivoltine parasitoid accumulates on its univoltine host; consequently, A. nigrocincta may be a major mortality factor of ASF cocoons. Despite seemingly having potential to play a role in controlling ASF populations, A. nigrocincta is not considered as a classical biological control agent because of its lack of host specificity and because it is a hyperparasitoid of L. ensator (Babendreier and Hoffmeister, 2003).

A related species, Microcryptus abdominator Gravenhorst (Hymenoptera Ichneumonidae), was reported by Jaworska (1987), who reported rearing several specimens of Holocremma bergmanni Thomson (now Olesicampe bergmanni). Little information is available on these and other parasitoid species listed in table 1: several were reported only once in Eastern Europe, often in low numbers. In the absence of recent taxonomic work on most of these species, their identification should be treated with caution.

It may be concluded that, as far as is known, L. ensator is the only specific parasitoid of the ASF larva. It occurs over most of the ASF distribution range in Europe, and currently in some regions of Eastern North America.

Predators

Hanne Lindhard Pedersen (personal communication) observed predaceous insects feeding on ASF eggs in a Danish orchard. Predatory bugs like Himacerus apiterus (F.) (Hemiptera Nabidae) were observed feeding on young ASF larvae (Zijp and Blommers, 2002b). Ladybirds and lacewings have also been reported to attack ASF larvae, while ants (Lasius sp.) may kill ASF larvae that seek to enter the soil (Velbinger, 1939). Some holes of about 0.1 mm diameter were found in ASF cocoons collected from the soil in Switzerland, suggesting unidentified arthropod predators acting below ground (Babendreier, 1998). To what extent the pupae are destroyed by moles, shrews and other insectivorous mammals is unknown. Velbinger (1939) mentioned spiders as predators of ASF adults. Nagy (1960) also observed birds taking adult plum sawfly, Hoplocampa flavis L... Pedersen et al. (2004) mentioned the deliberate use of young hens to eat insect larvae on the ground, a method that likely impacts the ASF as well. Overall, the impact of predators is undetermined.

Entomopathogenic fungi

Fungi that kill H. testudinea in its cocoon in the soil can be important mortality factors. More than 70% of the larvae may be killed by Paecilomyces fumosoroseus (Wize) Brown et Smith; Paecilomyces farinosus (Dicks et Fr.) Brown et Smith and Verticillium lecanii (Zimm.) (Jaworska, 1992). Graf et al. (1994) found 8.2-16.2% of ASF killed by P. farinosus. Carl and Kähler (1993) found this fungus on hibernating H. testudinea removed from the soil, while 19% of ASF prepupae and 52% of prepupae parasitized by L. ensator were killed, mostly by this fungus. Onufreichik (1974) found 15-30% of hibernating larvae were killed by the fungi Beauveria bassiana (Bals.) Vuill. and P. fumosoroseus under natural conditions.

Nematodes

In Poland, Jaworska (1986) found dead ASF larvae and pupae infested with mermithid, rhabditid and steinernematid nematodes. Less than 2.3% of the ASF larvae died due to mermithids. Diapausing ASF pupae were also found infested with rhabditid nematodes. In Petri dish trials, rhabditids were not consistently pathogenic to ASF larvae. However steinernematids were highly pathogenic. Their effect was observable 48 hours after infection.
Management

Types of damage

The ASF is a pest that directly destroys the crop by causing three types of damage. First, a mark, the so-called “sting”, is caused by the actual oviposition (figure 3a-b). The tiny slit in the receptacle made by the female saw results in an inconspicuous funnel-like depression near the petals of the growing fruit. In the case of unsuccessful oviposition or egg hatch, this is the only sign of ASF presence that can be recognized on mature fruits (figure 7). The slight deformation of the fruit does not usually lead to quality downgrade. Second, the superficial mining of the young larva leads to the typical ribbon-like scars (Petherbridge, 1928) (figure 5a-b). Fruits with this primary damage (Dicker, 1953) often remain on the tree until harvest and are downgraded. Third, on entering a nearby fruitlet the migrating larvae (figure 6a) feed rapidly and voraciously causing secondary damage (figure 6a-c) (Dicker, 1953). Such fruit, with internal tissues, ovary walls and even seeds having been eaten by the older ASF larvae (figure 6c) fall in June, allowing the ASF to complete its life cycle underground (Miles, 1932).

Basic considerations

Secondary damage visible at harvest (figure 5b) provide a rough estimate of actual ASF density and the risk of damage next year, because several factors are at play between bloom and harvest, notably flower abundance on different cultivars, natural control by predators and diseases, coincidence of flowering and ASF peak flight, and premature fruit drop. An experienced grower or an advisor familiar with the orchard will often be able to make an educated guess and qualitatively assess such conditions, but a quantitative risk assessment for the following year is not feasible.

Before the commercial availability of synthetic insecticides prior to World War II, ASF was one of the major pests of apples because effective control was difficult if not impossible to attain on the large fruit trees with available means. Excessive levels of ASF damage were not unusual, e.g., up to 90% fruit damage (primary and secondary) on cultivar Worcester Pearmain in England (Miles, 1932) and up to 60% in Victoria, British Columbia, orchards (Downes and Andison, 1942). Likewise, Vincent and Mailloux (1988) observed up to 85% of fruit showing secondary damage in an untreated apple orchard in Frelighsburg, Quebec.

Kuenen and van de Vrie (1951) noted that, whereas the ASF is one of the most important direct pests of apple orchards, its damage is unimportant in abandoned orchards. This may be because of alternate fruit bearing or more abundant natural enemies present in neglected orchards. When fruitlets are scarce, necessary resources for the completion of the ASF life cycle are limited: females do not find fruitlets for oviposition and migrating larvae have difficulty finding a new fruitlet nearby. By contrast, sufficient flowers and fruitlets are present annually in well-managed orchards.

In general, when devising ASF management programs, a pest manager has to consider tactics that would have adulticidal, ovicultural or larvicidal effects. It is theoretically possible that adults can be killed or behaviourally impaired by insecticides applied before bloom. ASF eggs and early instar larvae are mostly vulnerable to post-bloom treatments.

Physical control methods

Some physical control methods to manage ASF have been investigated. Hand removal of infested fruitlets and soil tillage were common control practices in the past (Velbinger, 1939). Removal of infested fruits as soon as the superficial mining scars (primary damage) appear, so as to prevent secondary damage, is currently performed in some commercial orchards in Sweden and Denmark (Weronika Świergiel, personal observation).

Benoit et al. (2006) tested cellulose sheets as a physical barrier that could prevent the completion of life cycles of the ASF and the plum curculio (Conotrachelus nenuphar Herbst) (Coleoptera Curculionidae). Available in rolls, the sheets were deployed on the soil under the canopy of apple trees such that apples fall in June would fall on the sheets, preventing larvae to enter the soil for further development. A cage put over experimental quadrats after fruit drop allows determination of the emergence of adults the following spring. Cellulose sheet reduced ASF adult emergence by 60 to 95% compared with the control. But as some prepupae have a prolonged diapause and stay in the soil for several years, complete management of an ASF population would require the use of this tactic for several consecutive years.

Haalboom (1983) showed that ASF damage was lower on trees near zinc-white traps (figure 10) but concluded that mass trapping was too expensive as a management method, although a similar method is currently used in some Danish organic orchards (Weronika Świergiel, personal observation). Cardboard sticky traps are folded and stapled around the wires at intervals of every 2-4 trees, while fruitlets showing primary damage are removed.

The application of kaolin, a hydrophobic particle film of fine white clay marketed as Surround™ in the USA and Europe (Glenn et al., 1999), reduces ASF damage, but it is unclear to what extent. Repeated applications of kaolin against apple scab disease - Venturia inaequalis (Cooke) G.Winter - reduced high ASF damage on cultivar J. Grievie by ca. 75% in insecticide-treated orchards compared with controls (Markó et al., 2006; 2008). However, it also exerted a negative effect on the larval parasitoid L. ensator.

In testing the effect of exclusion nets covering apple trees in studies conducted in Quebec, Chouinard et al. (2017) obtained ambiguous results: in 2012 ASF damage at harvest was 0.28% (covered) vs 0.69% (uncovered), while in 2016 ASF damage was 0.14% (covered) vs 0% (uncovered). Finally, if apple trees are few and small such as in private gardens, successful management can be obtained by removing all infested fruit before the third week of June, i.e. before larvae leave the fruitlets and enter the soil (Alford, 1973).
Monitoring and decision making

The necessity to apply insecticides against ASF adults before bloom is a difficult decision to make, as it chiefly depends on observations from the previous year. However, if a drastic reduction of ASF populations is needed, a pre-bloom application of an adulticide can be made, followed by a larvicidal treatment post-bloom. Under a post-bloom treatment scenario, the full range of action thresholds for control of ASF becomes available. In addition to recording infestation levels in the previous year, a pest manager can score the numbers of ASF adults caught on visual traps and count the numbers of flowers with eggs or fruitlets with incipient primary damage.

Infestation levels from the previous year may be determined by fruit showing primary damage at harvest or, preferably, fruitlets showing secondary damage before June drop. This is a first step to support decision making the following year. For example, van den Ende et al. (1996) proposed monitoring ASF adults with visual traps when damage to the previous year’s harvest was > 1% and no detrimental side effect on ASF eggs or larvae is expected from insecticide applications targeted against other pests.

The use of visual traps to monitor the ASF flight has a long history. Kuenen and van de Vrie (1951) observed that few eggs are deposited in flowers with the petals removed. Chaboussou (1961b) concluded that ovipositing females prefer white over pink flowers. Comparing ASF captures on traps painted with different spectral reflectances ranging from 300 to 650 nm, Owens and Prokopy (1978) found the highest captures on surfaces painted with Zn-white. As Zn-white and apple flower petals have similar reflectance patterns, i.e., white with almost no reflectance of UV, ASF adults appear to be specifically responsive to the colour of the blossoms on which they feed, often mate, and oviposit (Owens and Prokopy, 1978).

In several countries, Owens and Prokopy (1978) inspired research that contributed to the use of sticky traps based on the behaviour of ASF adults (Gottwald, 1982; Haalboom, 1983). In 1975-1979, Gottwald (1982) studied ASF behaviour with cylindrical white sticky traps in a region west of Berlin (Germany). He found that more males than females were captured and that most adults were captured on the South East and South West-sides of the traps; exposure to the sun had a positive effect. Most activity occurred between 9:00 and 11:00, at 18-21 °C (air temperatures), and > 50% of daily captures occurred within 3 hours. Male captures dominated in the morning while female captures slightly dominated in the afternoon. It was concluded that traps should be positioned on the South side of a tree (although tree rows in modern plantings are usually directed North-South), and high enough to be exposed to the sun.

The white plastic ‘cross traps’ type REBEL®™, originally developed by Remund and Boller (1978) and tested by Wildbolz and Staub (1984; 1986), are currently widely used in Europe. Graf et al. (1996c) found three traps per cultivar to be the optimal number for reliable ASF monitoring. Due to the limited range of the traps (only 3% of released ASF were recaptured at 40 m distance), low mobility and heterogeneous distribution of ASF, a distance of 50 m between traps is suggested. Captured specimens should be carefully examined, because white sticky traps attract other sawfly species, such as Hoplocampa species from nearby pear or plum trees, visually similar species like the cabbage or turnip sawfly (Athalia rosae L.) (Hymenoptera Tenthredinidae), and a number of flies and bees from nearby wild vegetation. Unlike plum sawflies adults (Sprengel, 1930), ASF adults are not attracted by fermenting fruit sap or wine (Böhm, 1952).

Graf et al. (1996b) recommended deploying white sticky traps at 8-10 days before bloom. If traps are installed too early, they may lose their visual attractiveness by capturing too many other insects. Zijp and Bloommers (1997) found that in order to capture the first emerging adults with a safety margin, the traps should be deployed at 157 degree-days (DD) (> 4 °C, air temperature) from March 15. Although the model was validated and found acceptable for seven different localities in Sweden (Sjöberg et al., 2015), caution should be taken when adopting the model in other geographical areas, as Graf et al. (1996c) found that the temperature-dependent post-diapause development of prepupae from different European regions differed significantly, while different artificial substrates also had some influence on the time of emergence (Graf et al., 1996a). Graf et al. (1996c) suggest that inclusion of winter dormancy might improve the model, as the severity of winter affects the duration of diapause.

Trap catches provide a reliable estimate of adult emergence as > 95% of released females were caught within 24 hours (Graf et al., 1996c). However, the reliability in forecasting the risks of fruit damage is low, because the traps compete with the attractiveness of open flowers and the attraction of ASF adults is weather dependent (Haalboom, 1983). In spite of these limitations, cumulative trap catches can be used to determine the necessity of a pesticide application. In 19 orchards in Massachusetts, Coli et al. (1985) reported a significant positive relationship between the numbers caught on fewer than one non-UV reflecting white trap per ha and the primary damage scored on the trees shortly before harvest. In Quebec, Vincent and Mailloux (1988) found a similar significant relationship in 13 orchards over 5 years, when the traps were deployed after a pre-bloom insecticide application and the primary damage scored on 1000 fruits at harvest. However, the damage in both studies was low, rarely > 1%, with few and extreme exceptions. Coli et al. (1985) suggested a cumulative threshold of 4.7 ASF captures per trap, so as to attain < 0.7% damage at harvest, while Vincent and Mailloux (1988) reported both false negative and false positive cases, most probably due to the pre-bloom treatment in combination with a low trap density. In Ontario, Canada, the action thresholds for post-bloom treatments are based on trap captures, i.e. 6 ASF adults per trap if an insecticide has been applied pre-bloom, and 3 ASF adults per trap if no insecticide has been applied pre-bloom (OMAFRA, 2018).

Greater action thresholds have been suggested in Europe. After several years’ experience, Höhn et al. (1993)
stated that 20-30 ASF adults captured per trap indicate a risk if the flowers are abundant and the ASF flight coincides with the flowering period.

When interpreting trap captures, factors such as prevailing weather conditions and blooming intensity should be considered. Activity of ASF adults increases during sunny days (Dicker, 1953) and decreases due to unfavourable weather conditions, e.g. rain and cloud cover (Haalboom, 1983). Several studies have shown that, after a steady increase, trap catches decrease during peak bloom due to visual competition with flowers, and increase again at petal fall (Gottwald, 1982; Haalboom, 1983; Coli et al., 1985; Noack, 1993; Graf et al., 1996c; Zimmer, 2000; Sjöberg et al., 2015). Sjöberg et al. (2015) found that 85% of the total oviposition, but only 60% of total female captures occurred up until full bloom (BBCH 65). They suggest that, if this finding is confirmed in other localities, the variation in the relationship between trap catches and damage levels might decrease using only trap catches until full bloom. In summary, the most important parameter to implement a control threshold is trap captures before peak bloom because they represent the great majority of the oviposition, while captures scored during and after peak bloom (after BBCH 64) are less reliable estimates with respect to oviposition.

It is noteworthy that the use of these parameters depends on local factors and the experience and insight of the grower or advisor with respect to such elements as hand thinning, premature fruit drop, or market destination of the crop. Control thresholds based on cumulative trap catches mainly concern the decision whether to count eggs in quasi-real time or primary damage later on. For example, in The Netherlands a few traps are positioned in orchards and cultivars where damage is expected (Marc Trapman, personal communication). Trap catches > 50 ASF adults per trap always require treatment. When cumulative captures range between 20 and 50 ASF adults per trap, a monitoring of 50 flower clusters per orchard and cultivar for eggs is performed. The decision for treatment is based on knowledge of previous damage in the orchard, the intensity of flowering, and is always advised when eggs are present in > 10% of flower clusters. Using white sticky traps in northern Germany, Noack (1993) advised counting ASF eggs when > 2 ASF adults have been captured per trap.

Counting eggs (figure 3d) or oviposition scars (figure 3a-b) is the oldest and most direct way to determine the threat of ASF damage (Miles, 1932). It must be done right after bloom. It is labour intensive but was adopted widely in Europe in the 1970s under so-called ’Supervised Control’ programs. A control threshold of ten scars (primary damage, figure 5a) per 100 flower clusters was recommended in The Netherlands (van Frankenhuyzen and Gruys, 1978; Gruys, 1980; Blommers, 2005), and 3-5% infested flowers in Germany (Heinze, 1978; Freier et al., 1992). Noack (1993) noted that ASF could have a useful fruit thinning effect at lower infestation levels and recommends a threshold from 15-30 scars per 100 clusters when flowering is abundant down to 5-10 in years with flower losses due to late spring frosts. However, the selection of apples to thin will not be based on the same criteria as the grower would choose (Marc Trapman and Henrik Stridh, personal communication).

For visual observations of egg development, six stages were described in Dutch by Kuenen and van de Vrie (1951) (figure 3e). Trapman (2016b) provided an English translation of key elements of this publication as well as practical insights. Visual observations should focus on the most vulnerable cultivars in correlation with intensity and duration of the flight, as indicated by daily trap catches. As the first ASF adults usually emerge just before the first flowering cultivars, these cultivars tend to suffer most attack. When monitoring for ASF eggs, the egg laying behaviour of the adults should be considered. The first eggs should be sought on the king flowers of older branches (Kuenen and van de Vrie, 1951; Gottwald, 1982; Tamošiūnas, 2014; Trapman, 2016a). Southern and top parts of the tree as well as isolated branches and distal parts of branches are most attacked (Soenen, 1952).

Modelling

The first attempts to improve timing of monitoring and control of the ASF with help of biologically-based algorithms were initiated in Switzerland and The Netherlands (van den Ende et al., 1996; Graf et al., 1996a; 1996b; Zipp and Blommers, 1997). These algorithms assume that the time spent in a developmental stage (egg, larva, pupa, adult) is inversely related to ambient temperature above a fixed threshold (Andrewartha and Birch, 1954). After determining post-diapause development times at various constant temperatures in the laboratory, Graf et al. (1996a) constructed a soil temperature-driven model for adult emergence. A threshold of 4.5 °C and an average temperature sum (thermal constant, TC) of 205 and 220 day-degrees (DD), for females and males, respectively, yielded the best fit both in emergence cages and with captures on white sticky traps positioned in apple trees. In a Dutch orchard, the first trap captures of adults could be described by a simple TC based on temperatures taken at 5 cm depth in the soil. The most accurate was 134 DD (> 4 °C) accumulated from April 1st until the first capture of adults (Zipp and Blommers, 1997). Similar figures were obtained in two orchards (one organic and one conventional) in Lithuania (Tamošiūnas and Valiuškaitė, 2013), and in 12 assessments (i.e. orchards or years) in a few organic orchards in Sweden (Sjöberg et al., 2015).

Graf et al. (1996c) found that the temperature-dependent post-diapause development of prepupae from different European regions differed significantly. The TC increased from South to North, from 194 DD in South Tirol (Italy) to 228 DD in Schleswig-Holstein (Germany), while the development threshold appeared to be the same everywhere (i.e. 4.5 °C). Inclusion of winter dormancy to improve the models was recommended by Graf et al. (1996c) because, while the lower temperature threshold for post-diapause development is rarely reached under natural conditions before the end of diapause (in early March), earlier exposure to higher temperature appeared to reduce the duration of post-diapause development. Tauber and Tauber (1986) dis-
cuss this apparent conflict between the effects of low versus elevated temperature around the end of winter diapause.

Comparing various approaches, Tamošiūnas and Valiukšaitė (2013) noted great differences in temperature sums based on air temperature between years. They found that a TC > 4 °C at a soil depth of 10 cm gave the best fit with the flight curve based on white trap captures, while a TC of 160 DD of air temperature > 4 °C starting on April 1st should be the best choice in practice.

Trapman (2016a) constructed a Dynamic Simulation Model (DSM) by collecting and analysing large data sets on temperature-related development and activity of ASF adults in The Netherlands and Belgium, from the emergence of ASF adults to the time of pesticide application, notably Quassia®; targeting young larvae. The first capture of adults on white traps varied between April 5 and May 2 in 42 observation events in 2003-2015 and the average temperature sum from March 15 to flight initiation was 181 DD > 4 °C (Standard deviation = 4.2 days). This was slightly higher than the 177 DD reported by Zijp and Blommers (1997), and also higher than the 169 DD > 4 °C found by Sjöberg et al. (2015). Trapman (2016a) used life-table data for post-diapause development, female lifespan and the duration of the fecundity period determined by Graf et al. (2001; 2002). He also estimated and roughly validated temperature sums for the migration of larvae from the initial affected fruitlet to the second one. Weather conditions suitable for flight and egg deposition were assumed to be similar to those for plum sawflies (Wildbolz and Staub, 1986) and the female egg stock was assumed to be a non-limiting factor. The simulation model uses ‘first flowers open’ (BBCH60) as ‘cultivar-local’ biofix for the start of egg deposition on that cultivar.

To validate the ASF-DSM, the outcome was compared with the actual situation in up to 44 orchards annually in four European countries from 2010 to 2015 (Trapman, 2016b). The difference between a simulated 2% egg hatch (the suggested time for treatment) and the application date of Quassia® as advised by an expert was 0.69 days on average, and rarely exceeded ± 2 days. Therefore, the modelled estimate was precise enough for decision making and might reduce the need for field observations of ASF egg hatching.

Chemical control

The ASF is susceptible to a broad range of pesticides. Organic insecticides like rotenone and quassia were the first used in the 1940s, followed by organochlorines, notably DDT and lindane. Nicotine was demonstrated to exert larvicidal effects by McKinlay (1950). The organophosphates and carbamates were dominant options from the 1950s to the 2000s. For example, up to 15 of these insecticides (azimphos-methyl, bromophos, carbaryl, chlordimeform + formetanate, dichlorvos, dime thoate, endosulfan, methidathion, parathion, phenthoate, promecarp, propoxur, trichlorphon, vani diothion) were listed against ASF in Germany (Heinze, 1978). Some of these insecticides became instrumental in ‘supervised control’ in the 1970s and IPM in the 1980s, as they allowed some fine tuning because of their different toxicities for various pests and natural enemies (Blommers, 1994; 2005). Following the ban of organophosphates and carbamates in the European Union in the 1990s, neonicotinoids (imidacloprid, thiacloprid, acetamiprid) became the most commonly used insecticides for ASF control. Field experiments in organic orchards in Poland conducted with extracts from the wood of Quassia amara and from the seeds of Azadirachta indica (commercial formulation NeemAzal-T/S) gave variable results (Danelski et al., 2014).

In general, the literature shows that the best application time is shortly after bloom, before the eggs start to hatch. For the most part, pesticide applications during bloom are forbidden or not recommended because of potential detrimental effects on pollinators. However, some compounds have been reported to be effective while reasonably safe for honeybees. For instance, the nereistoxin thiocyclam hydrogen oxalate (Evisect™), while not harmful to honey bees (Gerig, 1977), gave adequate control of the ASF in field tests (Helsen and Blommers, 1988) and is registered for this use in Switzerland. In Hungary, sprays with the insecticide g-BHC after petal fall reduced fruit damage by 82% compared to the control (Nagy, 1954).

Applied immediately before flowering, the systemic fungicide Topsin M (thiophanate-methyl) completely inhibits larval hatching (Predki and Profic-Alwasia k, 1976). Its breakdown product, methyl benzimidazol-2-yl carbamate (Vonk and Sijpestein, 1971), is accumulated in the fruit skin. This was confirmed by applications against apple scab and powdery mildew in the rosy-bud stage in IPM practice (Leo H. M. Blommers, personal observation). Applied at the peak of the ASF adult flight (i.e., at the pink bud stage), the fungicides fenarimol, cyproconazole+captan and thiophanate-methyl were found to be effective in reducing fruit damage (Olszak and Maciesiak, 1996). Partial or even full control of the ASF may also be achieved by treatments against other pests. For instance, differbenzuron applied against winter moth, Operophtera brumata (L.) (Lepidoptera Geometridae), or noctuids (Orthosia sp.) (Lepidoptera Noctuidae) and thiacloprid against aphids will decimate ASF populations (Erdelen, 2001; Galli and Nikusch, 2005; OMAFRA, 2017; DEFRA/ADHB, 2018).

In organic orchards in Pennsylvania, the ASF is a serious concern. The best option for organic orchards is to spray Surround (active ingredient = kaolin clay) mixed with either Pyganic® (active ingredient = 5% pyrethrins) or Venerate® (active ingredient = heat-killed Burkholderia). These two mixtures should be applied before and immediately after bloom (Greg Krawczyk, personal communication).

In European organic orchards, the most commonly used insecticide is an extract of “Quassia wood”, originating either from Quassia amara or Pteroceras excelsa (Wijnen et al., 1994; Kienzle et al., 2008). The main active ingredient, quassin, has a short residual life and works best on the neonate larvae, which must feed on the product before they enter the fruit (Kienzle et al., 2005). As a result, correct timing of the application and
good coverage of the receptacles is crucial to effect optimal larval mortality. Another obstacle to reliable efficacy is the variability in active ingredient contents of the base product, traditionally leading to erratic efficacy of home-made extracts. Standardization of the quassin contents in commercial products has greatly improved the reliability of these formulations (Kienzle et al., 2008). Quassia* was submitted for registration in the EU in 2012.

Occasionally, natural pyrethrum, synergized with piperonyl butoxide, is used for ASF management (Kienzle et al., 2008). Self-made concoctions of common tansy (Tanacetum vulgare), also containing pyrethrum-like chemicals, or common wormwood (Artemisia vulgaris), are recommended against ASF larvae in France. Lack of exclusivity precluded development, registration and marketing of these insecticidal plant extracts (e.g., EFSA, 2014). Some may have a small local and temporary market, but as different plant species might be involved, the quality of the plant source material is generally poorly defined in terms of insecticidal and health properties (Zimmer, 2000; Sjöberg et al., 2015).

Side effects of insecticides on biocontrol agents

The statement that parasitism by L. ensator is higher in orchards where less insecticide has been used (Babendreier, 1998) is not surprising because adult L. ensator emerge soon after flowering and may be affected by post-bloom application of pesticides. In fact, well-timed application of a selective or short-lived compound like Quassia should be recommended, as it resulted in high level of parasitism in The Netherlands (L. H. M. Blommers, unpublished).

Studies suggest that applications of synthetic pyrethroids, neonicotinoids and sulphur should be avoided during the flight of L. ensator. In the 1990’s, the near absence of L. ensator in organic orchards was probably due to the application of large amounts of wettable sulphur against apple scab in organic orchards in The Netherlands (Zijp and Blommers, 2002a).

Biological control

Parasitoids

In a classical biological control program from 1995 to 2001, L. ensator (figure 8a-c) was first established in Freilighsburg, Quebec, following yearly releases of adults (figure 8a) that emerged from parasitized cocoons (figure 9b) collected in Western Europe (Vincent et al., 2001; 2002). From there it has been successfully disseminated in five localities of Quebec and Ontario (Vincent et al., 2013; 2016) and in other orchards of southern Quebec (Jacques Lasnier, personal communication). As of 2018, it is the only documented natural enemy of ASF in North America.

Nematodes

In Poland, Jaworska and Stanuszek (1986) applied four doses of Heterorhabditis sp. (5 - 50 per pupa) on filter paper rolled around ASF pupae and found infection rates of 100%.

In Quebec, Vincent and Bélair (1992) conducted bioassays with Steinernema carpocapsae (Weiser) DD 136 and All strains, Steinernema feltiae (Filipjev) and Heterorhabditis bacteriophora Poinar. The DD 136 strain caused highest mortality of ASF larvae after 24 hours (86% mortality), while all nematode species caused 100% larval mortality after 72 hours. A single treatment with S. carpocapsae All strain caused significant larval mortality (> 82% vs 5.8-9.5% control). The S. carpocapsae All strain applied in May-June as foliar sprays was evaluated against the ASF and plum curculio, C. nenuphar (Bélair et al., 1998). Inconsistency of results and high costs for production and application so far preclude the use of this nematode against these pests in commercial apple orchards. Nematodes can be an insecticide-free option to manage the ASF in small orchards or private gardens where the use of pesticides is prohibited.

Fungi

Laboratory tests gave promising results for fungi as a control agent against H. testudineae. Jaworska (1979a) tested the pathogenicity of eight entomopathogenic fungi by spraying spores on fifth instars (parasitized or not by Lathroletes sp.), and cocoons containing prepupae on filter paper discs in Petri dishes. The fungi P. farinosus, P. f. Sinaius, C. callosum, A. flavus Link ex Fries, B. bassiana, Beauveria, metatarsius (Metsch.) Siem. and Metarrhizium anisopliae (Metsch.) Sorok caused greater mortality (= 58% vs 13%) among unparasitized and parasitized fifth instars. In contrast, Scopulariopsis brevicaulis Bainier caused no statistically greater mortality than the control. Up to 100% mortality of fifth instars within 7 days after treatment was caused by P. f. farnosus, P. f. Sinaius and C. lecanii. However, treatment of cocoons with fungal spores did not cause significant differences in mortality compared with the control.

During 4 years of field experiments, Jaworska (1979b) studied the pathogenicity of eight species of entomogenous fungi in the soil. P. f. farnosus and P. f. Sinaius caused the highest mortality of ASF larvae during their diapause. Lower mortality, but still significantly more than in control, was caused by C. lecanii, A. flavus, B. bassiana, B. tenella and M. anisopliae. Scopulariopsis brevicaulis caused no greater mortality than the control. In addition, adult female ASF that survived treatment with the fungi A. flavus, B. bassiana and B. tenella had fewer developed eggs on the first day of flight (Jaworska, 1979c) and their fertility and lifespan was significantly reduced compared with control females.

In a laboratory study, B. bassiana or M. anisopliae caused high ASF larval mortality (49.4-68.4%) (Świergien et al., 2016). However, Świergien et al. (2016) could not replicate these results in full scale field experiments in a Swedish organic orchard using the highest recommended soil application dose of B. bassiana (5.37 × 10^10 CFU per m²), as they observed only 17% mortality of the recovered cocoons. They suggested that low humidity in drip irrigated orchards, and pos-
sibly fungistatic effects by either antibiosis or frequent sulphur applications, may have contributed to lower mortality rates.

In conclusion, the effectiveness of fungi applied to the soil to reduce ASF populations depends on soil moisture, antibiosis and the period with temperatures favourable for infection (Jaworska, 1979a; 1979b; 1979c; Świergiel et al., 2016). The importance of some factors such as the critical temperature at the depth underground of the descending prepupae is unclear (Zimmermann, 1986; Jaronski, 2007).

Little is known about pathogens applied against the immature stages of ASF while on the tree. Priedits and Rituma (1974) tested a mixture of B. bassiana (1.3-1.8 kg per ha) and carbaryl or trichlorphon which resulted in 73-86% control of H. testudinaria. Bacillus thuringiensis applied at 0.4-0.7% mixed with carbaryl or tri-chlorphon was ineffective. Applied before bloom, the formulation Thuricide 90 TS (Bacillus thuringiensis ser. kurstaki) had no significant effect on the ASF (Niezborala, 1972, in Jaworska, 1987). A preparation of P. fumosoroseus of homopteran origin and devised for whitefly control (Preferal™), applied during both flight and egg hatch of ASF had no effect (L. H. M. Blommers, unpublished).

Other pathogens
In their review, Cross et al. (1999a) did not mention other microbials or viruses that were researched as tools to manage the ASF.

Concluding remarks
Published information about ASF outbreaks and management shows that H. testudinaria needs to be managed in most commercial orchard in which it has established, both in its native area of Europe, and in regions it has invaded like eastern North America. The explanation of ASF outbreaks remains difficult and preventive action a distant hope.

Consideration for the fruit is as important as the ASF itself with respect to monitoring and damage forecasting. In contrast to other pests like leafrollers or scales which appear and attack irrespective of host phenological stage, the ASF begins its life when the fruitlet is available. Instead of calculating the day of first adult appearance, one may consider, or estimate as did Trapman (2016b), the opening of first apple flowers as the beginning of the new ASF generation.

At the time of adult emergence, it would be useful to know the density of female ASF. However, this is difficult as some pupae will stay in diapause underground for another year at least, while others have been or are being killed underground by parasitoid, disease or both. Observations in The Netherlands have shown that, in absence of control measures, ASF populations may double each year in well-managed orchards (Blommers, 2005), while observations in Denmark in unsprayed commercial orchards indicate both smaller and larger yearly increases possibly due to shifting local conditions such as presence of natural enemies (Weronika Świergiel, personal observation). This situation could be worse in North America, where the ASF is an exotic pest. Fortunately, adult densities estimated by means of white sticky traps can be used to assess whether later field counts of eggs or stings to fruitlets would be sensible.

The interpretation of trap captures tends to be complicated, as commercial apple orchards are typically mixes of cultivars positioned in particular spatial arrangement with respect to flowering time and cross-pollination compatibility. As flowers are abundant normally in commercial plantings and the ASF have limited mobility, population density in any part of an orchard should be determined mainly by the history of ASF attack and management in that part.

As a rule, ASF adults start to emerge just before early cultivars begin flowering, and plots of these early cultivars tend to remain the most infested over years. However, clear differences in susceptibility to ASF attack between cultivars have never been shown. In fact, if they exist, they are almost impossible to establish, as the attack itself takes only a few days during an outburst of flowers under otherwise unpredictable conditions, while most eggs and young larvae disappear, due to natural control of some kind, within about two weeks (Zijp and Blommers, 2002b). The impossibility to relate egg production with available protein in the food is one important handicap in field research of the ASF. This might perhaps be partially overcome by researching the causes of this high mortality of eggs and larvae.

As far as is known, two larval parasitoids exert most natural control of ASF: the specialized larval parasitoid L. ensator and, in Europe, the more polyphagous coccinellid parasitoid A. nigrocincta. These species, when present, may eliminate substantial numbers of host, although L. ensator has only a brief post-bloom period available to attack its larval host. During that critical period, L. ensator may be affected by unfavourable weather conditions and by chemical treatments. Development of sprayable disease agents is hindered by the difficulty of rearing the ASF. In summary, there is currently no biological agent known that can be deliberately managed to achieve substantial control the ASF. So far, most published information concerns situations where ASF reached high densities. Studies in situations where ASF densities are low and in absence of chemical control are clearly missing.

While control of ASF in Europe was straightforward for several decades when broad-spectrum insecticides were in general use, development of orchard IPM as well as the increase of organic fruit growing restored ASF’s pre-World-War-II pest status. Moreover, due to increased consumer awareness, increased scrutiny and standards of regulatory agencies such as the EU, and marketing criteria implemented by supermarkets, the choice of broad-spectrum pesticides is decreasing.

Most studies on biocontrol of ASF with entomopathogenic nematodes were published more than 20 years ago. Recently, projects were undertaken in Germany to target ASF larvae that search for pupation sites or ASF females before they lay eggs (Ralf Udo Ehlers, personal communication). It might also be worthwhile to re-
search the use of entomopathogenic fungi, following up on Jaworska (1979b; 1992) who reported high ASF pupal mortality in semi-field trials. However, as the outcome of field studies by Świergierl et al. (2016) were less positive, it would be interesting to test the hypothesis that the fungicidal effect of sulphur accumulating in the soil after frequent high dose applications of this element in organic orchards is a major factor for reduced effectiveness of fungal agents.

While a decreasing choice of chemical control options is expected to promote the ASF as major pest, recent developments towards plantings of supercolumn/columnar apple trees in combination with mechanical/cultural protection against hail, storms and replant disease, might open opportunities to exclude ASF from the orchards. As the duration of adult ASF flight is less than 2-3 weeks, such a “greenhouse approach” might be promising.

Acknowledgements

An early draft of this paper has been written by Jan-Piet Zijp, with the help of Charles Vincent and Leo Blommers in 1995, but remained unfinished. We thank the State Department of Canada for translating Tchakstynia (1968) and Dulak-Jarworska (1976) respectively from Russian and Polish. Benoit Rancourt and Jérémie Côté (Agriculture and Agri-Food Canada, Saint-Jean-sur-Richelieu, Québec, Canada) are thanked for their technical input. We thank Greg Krawczyk (Penn State University, Biglerville, Pennsylvania, USA), Jacques Lassnier (Co-Lab R & D, Granby, Québec, Canada), Chris Bergh (Virginia Tech, Blacksburg, Virginia, USA) and Leslie Farmer (Pest Management Centre, Agriculture and Agri-Food Canada, Ottawa, Ontario) for comments of the manuscript, and Marko Prous (Senckenberg Deutsches Entomologisches Institut, Munich, Germany) for information on ASF identification. We have greatly benefited from the vast experience of Marc Trampen (Private advisor, The Netherlands) in the management and control of ASF, also in connection with other pests and diseases, in the context of integrated pest management and organic pest control of pome fruit in The Netherlands and neighbouring countries during three decades. Charles Vincent acknowledges a Fellowship from the Programme of the Netherlands Ministry of Agriculture, Nature Management and Fisheries as well as financial support by the Pest Management Centre, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.

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Hoplocampa testudinea

Population dynamics of Hoplocampa testudinea (Klug) with the use of visual traps.

Reviews on the biology and control of the apple sawfly Hoplocampa testudinea (Klug).


Observations on the apple sawfly Hoplocampa testudinea (Klug) with the use of visual traps.


- Observacje nad Lathrolestes marginatus (Thompson), paszytom owocnicy jabłkowej Hoplocampa testudinea (Klug) (Hymenoptera, Tenthredinidae) [Observations on Lathrolestes marginatus (Thompson), a parasite of apple sawfly, Hoplocampa testudinea (Klug) (Hymenoptera, Tenthredinidae)]. Polskie Pismo Entomologiczne, 57: 553-567.


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Received October 16, 2018. Accepted February 4, 2019.