Biology of Trioza apicalis - A Review

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Abstract

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The morphology and biology of immature stages and the distinguishing characters of generations in summer are briefly reviewed. The time of migration of the overwintered generation and the use of the median flight time are given. The longevity of overwintered adults, and the start and course of oviposition by overwintered females were observed mainly during June and July. The interval between adult emergence and flights from carrots appears to be very short, 2–3 days. Departure from developmental summer host plants culminates at the beginning of September. The sex ratio of the overwintered generation is not persistent, since it is usually female-biased. In emerged adults in summer the ratio is 50:50, with weak protandry. The systemic action of sucking for the curling of leaves was found by Láska already in 1964. In literature records, both subspecies of Daucus carota dominate as developmental hosts, more recently Coriandrum sativum was shown to be more suitable than Petroselinum hortense. Norway spruce, and to a lesser extent other conifers, are predominantly mentioned as overwintering shelter plants. It is not clear how overwintering occurs in regions without coniferous forests, and only undefined shrubs or trees are given in the literature. The first damage was reported in Denmark about in 1896, spreading from about 1918 over just a few years to the other Fennoscandian countries, and later in some other European countries. The spring migration is discussed, which occurs in central and northern Europe on the same date, perhaps explicable by the orientation of this pest or its particular populations to long days, despite the climate and phenology of each region. It is hypothesised that a particularly aggressive race evolved in Sjaelland (Denmark) at the turn of the nineteenth and twentieth century, which later spread to other regions of northern and central Europe.

Keywords: *Trioza apicalis* Förster; *Daucus carota* L.; immature stages; migration; systemic action of sucking; photoperiod; population

Trioza apicalis is a serious pest of carrots in northern and occasionally in central Europe. The literature dealing with this pest was mostly published in less-known journals and languages in the first half of the 20th century. A comprehensive review of its biology is lacking and the present paper summarises published information on this species. I add descriptions of the immature stages, together with the distinguishing characters of old and new generations in summer.

History of knowledge of Trioza apicalis

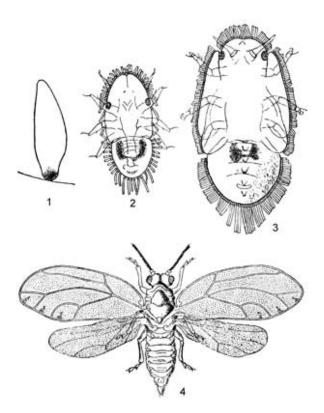
The original description of *Trioza apicalis* by FOERSTER (1948) is short. The collecting localities

were Aachen, Boppard and the Harz mountains; it was described as rare, and there was no mention of carrots or any other host plant. The description of *T. apicalis* followed that of *T. urticae*, which was noted as "very abundant on Urtica dioica". The first published record of the curling of carrot leaves dates before 1896. The correct cause of this damage was unknown for a long time, in fact until 1908, when H. J. Palesen (ex ROSTRUP 1921) determined the pest as Trioza viridula. At the beginning of the 20th century, ROSTRUP (1921) observed similar damage on the Danish island of Sealand (Sjælland), and was the first to describe the biology and figure the first and fifth larval instars. Ozols (1925) published a large paper on T. apicalis in Latvian, with a short English summary, reporting damage to carrots in

some regions of Latvia in 1919 and almost in the entire country in 1921. In 1922 almost the entire carrot crop was destroyed.

Another important author was Lundblad (1929), who studied carrot psylla in southern Sweden. He published drawings of the eggs of *Bactericera nigricornis* (as *Trioza*) and *Trioza apicalis* (as *viridula*), but as the figure legends were confused, some later papers illustrated the eggs of *B. nigricornis* as those of *T. apicalis*. Bey (1931) also dealt with *T. apicalis* (as *viridula*) and *B. nigricornis*, recording their abundances sampled by sweep net. Husås (1940) gave some notes from Norway.

In revising Zetterstedt's psyllid types, Ossianilsson (1941) showed that the name *Trioza viridula* was misinterpreted and that the name *T. apicalis* should be used for the carrot psylla. Ozols (1962) suggested that the annual periodicity of population fluctuations of carrot psyllid is connected with climate via sunspot activity: this was later refuted by Láska and Rogl (2008). Láska (1964) gave some biological remarks and noted the existence of systemic damage to the plant caused by the insect's feeding activities, later confirmed by Markkula *et al.* (1976). Trials testing the effectiveness of insecticides (Krumrey & Wendland 1973) also



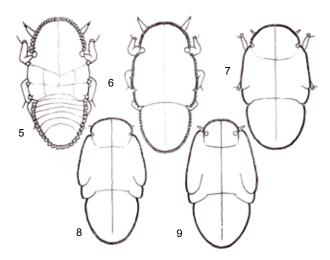
Figures 1–4. *Trioza apicalis*: (1) egg; (2–3) larvae in translucent light; (4) imago – female (Ozols 1925)

dealt with alighting behaviour of *T. apicalis* on carrot. Láska (1974) then published an extensive study about several aspects of the biology. Similar work was published by RYGG (1977).

BURCKHARDT (1986) published a taxonomic revision of the *Trioza apicalis* group, producing a key to the eight recognised species, three of which were new. Nehlin *et al.* (1994) used sawdust and conifer volatiles for reducing the alighting of *T. apicalis*, and started olfactory studies on the volatiles of host plants (Nehlin *et al.* 1996; Valterová *et al.* 1997; Kristoffersen et al. 2007). Monitoring of the flight period in carrot fields (Tiilikkala et al. 1995; Fischer & Terrettaz 2002) was aimed at improving the control. The effect of short periods of feeding on plants was studied by Nissinen *et al.* (2007), while Kristoffersen and Anderbrant (2007) studied the winter shelter plant preferences.

Egg (morphology and biology)

The eggs are white, later weakly yellowish, long and oval, slightly asymmetric, almost pointed and without a visible stalk. The best figure is by Ozols (1925), who also gave measurements of more than 60 eggs: length 0.357 (0.336–0.385) mm, width 0.180 (0.133–0.104) mm. Lundblad's (1929) confusion of figure legends, already mentioned above, caused some subsequent authors to give a long stalk to the eggs of *T. apicalis*.



Figures 5–9. *Trioza apicalis* larvae (length in mm): (5) instar 1 (0.40); (6) instar 2 (0.59); (7) instar 3 (0.82); (8) instar 4 (1.30); (9) instar 5 (2.00) (Láska 1974)

In a glasshouse at 23.5°C, BEY (1931) observed the embryonic development to take 5 days, while Husås (1940) reported 3 weeks in southern Norway. According to Láska (1974), embryonic development in the laboratory at temperatures from 23.5°C (22–26°C) lasts for 9.22 days (8–10 days). In outdoor experiments involving fluctuating temperatures averaging 16.8°C, egg development took 14 days on average; in similar outdoor observations at an average temperature of 17.4°C, embryonic development generally took 12 days. According to RYGG (1977), egg development lasts for 10.6 days (7–14 days) on average in laboratory conditions of 21°C.

The occurrence of eggs on plants in the field in Norway (RYGG 1977) peaked mainly in the second half of July. The last eggs were observed on August 20.

The optimal relative humidity for hatching was investigated in studies using saturated solutions of several salts. Optimal hatch occurred at a relative humidity of 90% above the salt $\rm ZnSO_4$ (Láska 1974).

Larva (morphology and biology)

The first drawing of the larva was by ROSTRUP (1921). OZOLS (1925) presented detailed figures of the first and fifth instars under the compound microscope, while Lundblad (1929) showed general views (omitting the 1st instar). Detailed descriptions and figures of all instars were made by Láska (1974), who also provided measurements of body sizes and the numbers of sectasetae around the body (seen in the figures). Some details of the fifth instar were described and figured by Ossianilsson (1992) and other authors such as Burckhardt (1986) and Burckhardt and Freuler (2000). The last publication also provides diagnoses for

separating the fifth instars of *Trioza apicalis* and *T. anthrisci* Burckhardt, 1986. The sizes of the instars of *T. apicalis* (LÁSKA 1974) and their duration under constant laboratory conditions of 21°C (RYGG 1977) are shown in Table 1.

The total larval development lasts for 42.6 days (32–58 days) (n = 28) at 21°C (RYGG 1977). LÁSKA (1974) investigated the duration of the entire larval period in natural conditions: in the first trial (mean temperature 17.3°C) it took a median of 40 days (34–88 days) (n = 34), while in the second trial (mean temperature 16.3°C) the median was also 40 days, but only 11 specimens completed development.

RYGG (1977) provided an interesting table of the frequencies of the different instars in a field near Jonsberg from May to October (Table 2).

The total development time (including eggs) in a glasshouse at 21°C was about 35 days (Schewket 1931), but in a laboratory at the same temperature it took longer, 53 (42–68) days (Rygg 1977). In field conditions (mean 17°C), it took a median of 54 days (Láska 1974).

Distinguishing characters of new and old generations in summer

Newly emerged adults have the light green head except for the antennae (which have a yellowish-white base and brown to black apical segments), the eyes and two reddish lateral ocelli next to the eyes. The thorax is mainly light green with the clear-cut yellow dorsal pattern. The pattern is created by a median yellow spot in the anterior part and two longitudinal stripes. The legs are yellowish, but the femora have a slightly greenish hue. The abdomen is greenish, a little lighter at the tip.

One-year-old overwintered adults are more variable. Bluish-green specimens predominate. The

Table 1. Trioza apicalis – measurements of instars (LÁSKA 1974) and duration of development at 21°C (RYGG 1977)

Instar	Morphology (mm)		Duration (days)	
	length	width	mean	range
1 st	0.35-0.43	0.17-0.21	7.2	5–9
2^{nd}	0.55-0.63	0.26 - 0.34	6.9	6–8
$3^{\rm rd}$	0.77-0.88	0.36-0.48	9.2	7–13
4^{th}	1.22-1.37	0.59-0.70	10.4	8–17
5 th	1.75-2.15	0.89-1.07	8.9	6–11

abdomen and most of the thorax are dark green or bluish-green. The thorax is without or with indistinct pattern. The head is light yellowish brown, often with an orange spot. The legs are light yellowish brown, the femora have a very slight greenish hue. Light specimens are rarer: in extreme cases, the entire insect is pale, or the abdomen is greenish; sometimes the thorax is also greenish. The head and legs are always without any green hue.

Flights and phenology

Immigration into crop fields is one of the most relevant aspects in plant protection, and most authors dealing with carrot psylla give at least some short notes on the first occurrence in fields. In Latvia, Ozols (1925) observed the first occurrence in 1920 (May 31), 1921 (May 24) and 1922 (May 27); Husås (1940) observed the first adults on May 31. In Germany (Munich) KRUMREY and Wendland (1973) found the first adults on May 14, 1971 and May 19, 1972. Láska (1974) recorded the first adults in Olomouc (Czechoslovakia) on June 20, 1962, May 28, 1963, June 2, 1964, June 10, 1965, May 27, 1966) (a single adult on May 16, 1966) and June I, 1967. In Norway, Rygg (1977) first caught adults during the first ten days of June in the years 1969, 1970 and 1971. According to ROSTRUP (1921) in Denmark the first curling of leaves was observed on May 20, 1912, May 21, 1915, and June 16, 1918 (a year when the carrot had set seed by May 15); in these records the first flight must have begun some days before.

Most authors represent the course of the flight period graphically, making it difficult to compare across various years, countries and authors. The beginning of flight is rather accidental, with often one specimen being decisive for reporting the date. It is better to use the median flight date, i.e. the date by which a half of the annual total is reached. Láska (1974) presented graphs but he also calculated the median flight date directly from the actual numbers. Thus at Olomouc the median flight dates were June 17, 1963, June 21, 1964, June 13, 1965, and June 19, 1966. Ozols (1925) reported almost the same dates for the main occurrence in Latvia, June 5–June 20, even though Latvia is about 1000 km north of Olomouc. The median dates from various latitudes are surprisingly similar, as discussed by Láska *et al.* (2011).

Longevity of overwintered adults

The longevity of overwintered *T. apicalis* on carrot plants was measured by RYGG (1977) in the laboratory. From his table, about a half of the adults were alive after 6 weeks, and only three percent after 10 weeks (= 70 days). The date of the start of his experiment is not clear. Láska (1974) observed the longevity in the field in 1966: the last adult was found on August 22. In laboratory conditions (Láska 1964), one female lived until October l.

Short flights during summer

Monitoring involves counting the number of alighting psyllids on plants. The accuracy of this method is reduced by the occurrence of short flights among plants. For example, Láska (1974) placed four plants at a 60-cm distance from one another in two large cages, releasing one female with two males in each. After 8 days the female attacked one and two plants in each cage, respectively, judging from eggs laid. Based on these data, subsequent monitoring in 1966 and 1967 used

Table 2. Instars (in %) on different sampling dates of *T. apicalis* larvae in Norway in the field Jonsberg 1975 – part of the table of RYGG (1977)

Instar	1 st July	1 st August	1 st September	1 st October
1 st	100	46	4	0
2 nd	0	35	7	0
$3^{ m rd}$	0	9	11	2
$4^{ m th}$	0	5	36	4
5 th	0	5	42	94

plots 8 m apart in order to eliminate the effect of short flights.

Start of oviposition

Monitoring data suggest that oviposition starts in June, e.g. June 12 to July 7 in Denmark (Rostrup 1921), June 12 in Germany (Aschersleben) (Bey 1931), and June 10 in Norway (Husås 1940). Láska (1974) observed the eggs laid by the first females to alight. In 1964, the earliest females were found on June 4, and the first oviposition on June 6; in 1966, the first female was caught on May16, and the first eggs laid on May 19. Two females caught in the same plot on May 27 laid eggs on May 28.

It is clear from Láska's (1974) trials that previous authors reported dates that were too late because finding eggs is difficult, whereas the first adults are easy to determine from trap catches. The time between the appearance of the first adult and the first egg laid is actually only about 3 days.

Oviposition of overwintered females

OZOLS (1925) found the number of eggs laid by one female to be 420–761. Husås (1940) reported about 700 eggs, but it is not clear whether this number was estimated or actually counted. In the laboratory at 18–22°C, Láska (1964) counted totals of 834–946 eggs on plants that were renewed every week. During the period from June 22 to July 27, one female laid about 18–22 eggs each day, according to temperature (in total over 2400 eggs): at 20.5°C an average of 22.6; at 18°C 18.4; and at 19.5°C 20.5. (Table 3).

Emergence of adults during a day

At 20°C in the laboratory, most adults emerged before 6 a.m. Peak emergence under field conditions was observed between 6 a.m. and 8 a.m. – Table 3 (LÁSKA 1974).

The interval between adult emergence and emigration from carrot

OZOLS (1925) stated that emerging adults do not damage carrot plants because they leave the plants within a short time. This phenomenon was observed in detail by Láska (1974) using two methods in the field. The first method observed adults on the netting of field cages covering the plants, and showed that adults left the plants mainly on the 2nd (30%) and 3rd (36%) day after eclosis, with only 11% leaving when older than four days. In the second method, adults were observed in the field on non-caged plants, which is much harder because they must be counted without disturbing the plants: this confirmed that adults left the plants two to three days after eclosion.

Low temperatures appear to depress the propensity to fly. No flight was seen at 16°C; during days with temperatures of 29°C, four adults already left the carrot plant on the same day they emerged (Láska 1974 published a table with the numbers and temperatures).

Departure from summer host plants

The departure of adults can be monitored by collecting the new generation on the netting of

Table 3. Emergence of adults during day under field conditions (LÁSKA 1968)

Hours	1965-09-09		1967-08-20	
	temperature (°C)	number	temperature (°C)	number
0-6	9.0	0	10.0	2
6-8	14.5	10	15.0	6
8-10	19.0	2	18.6	0
10-12	22.5	1	18.5	2
12-14	23.5	1	20.2	1
14-16	23.0	0	21.4	0

Table 4. Departure of new adults of Trioza apicalis from carrots during two different days (Láska 1974)

Hours	1966-08-29		1967-08-21	
	temperature (°C)	number	temperature (°C)	number
6–7	13.6	0	14.4	0
7–8	15.6	0	15.0	0
8-9	18.6	30	15.2	0
9–10	20.0	351	18.6	1
10-11	18.8	621	20.4	84
11-12	19.5	287	18.5	117
12-13	20.8	141	20.0	50
13-14	21.0	141	20.2	70
14-15	19.2	21	20.5	46
15–16	18.2	3	21.4	8
16–17	17.9	2	_	-

a cage. Using this method, 3274 individuals were collected from a single cage in 1965 and 9521 individuals from two cages in 1967. Láska (1974) presented the detailed data. The first new adults appeared on August 11 in 1965, and on July 25 in the warmer year 1967. The median date of departure was September 8, 1965 and September 1, 1967. The last departure of adults was observed on November 8, 1967.

The diurnal rhythm of flights was monitored on two days in August in 1966 and in 1967. The peak was in the middle of the day, with 81% (1966) and 54% (1967) caught before 2 p.m. (Table 4).

Sex ratio

In the migrating overwintered generation, most individuals are females. From a total of 2496 specimens from all years, only 37.6% were males. In the new generation, in contrast, the sex ratio overall is about 1:1 (Láska 1974). At the beginning of the flight period males are more frequent (typically 56%), but females are more numerous at the end. In Landvik in Norway (Rygg 1977), the sex ratio of alighting psyllids was close to 1:1, only 51.4% females in 1970-1972 (n=4388 individuals), much less than was found by Láska (1974). This discrepancy may be due to geographical differences or different monitoring methods (on plants or in yellow dishes).

Systemic action of sucking

Láska (1964) found out that in plants attacked by *T. apicalis* the new leaf is curled even if not in contact with the insect. This means that there is a systemic effect of sucking, confirmed by Markkula and Laurema (1976). Overwintered adults exert the strongest curling effect, followed by that of larvae, while new adults have no effect on plants. Overwintered males curl leaves less than overwintered females (Láska 1974).

Developmental host plants of *Trioza apicalis*

The main developmental host is *Daucus carota sativus* (cultivated carrot) and *Daucus carota carota* (wild carrot). In trial plots, both subspecies have similar performance in all aspects, even though the values for wild carrot are better than for cultivated carrot (although not significantly; Láska 1974). This means that both types stimulate similar alighting and oviposition, and result in similar numbers of developed adults. An additional host plant is parsley (*Petroselinum hortense* Hoffm.) but it is less suitable in all aspects: in parallel trials cultivated carrot produced 365 adults, while parsley produced only 20; development on parsley was also longer than on carrot (Láska 1974).

In the laboratory, 16 adults were reared from eggs on cumin (*Carum carvi* L.) leaves but in field trials no adults developed on cumin planted in parallel with carrots, whereas more than 800 adults developed on neighbouring carrot plots (LÁSKA 1974). VALTEROVÁ *et al.* (1997) confirmed that cumin is a poor host.

Láska (1974) reported other host plants from literature sources but since they dated from before Burckhardt's (1986) revision of the *Trioza apicalis* group, some might in fact refer to other *Trioza* species.

Valterová et al. (1997) listed 16 species of Apiaceae from successful oviposition trials in laboratory conditions. It is very surprising that Coriandrum sativum, which was not tested before, appeared as a better host plant than parsley, followed by Pimpinella saxifraga, Pastinaca sativa, Foeniculum vulgare, and Anthriscus cerefolium. At the end of this list were Angelica archangelica, Levisticum officinale, Aethusa cynapium, Pimpinella anisum, Anthriscus sylvestris, Anethum graveolens, Carum carvi, and Aegopodium podagraria.

In summer adults of *T. apicalis* can live also on spruce (Ozols 1925). Valterová *et al.* (1997) reported that carrot psyllids survived on spruce for 30 weeks.

Damage to carrots by carrot psyllids

In a very careful trial, NISSINEN et al. (2007) found out that even a very short period of sucking (3 days) on young plants lowered the final yield by about 35%, discolouring the leaf right up to harvest. Thus the potential for damage is great.

In some years in northern Europe carrots cannot be grown without application of insecticides, as is illustrated by the low yield of control plots in trials with insecticides. In Finland (TIILIKKALA et al. 1995) protected plots yielded 70 t, while most control plots yielded about 5 tonnes. Insecticide treatment is an economic necessity in Norway, Sweden, Denmark (where carrot growing was impossible in the 1920s), and Latvia (where about 70% of the crop was lost in 1922; Ozols 1925). In central Europe damage is lower: about 50% in Germany and up to 83% in some districts of Czechoslovakia (Láska 1974). In Switzerland (FISCHER & TERETTAZ 2002), however, the recommendation is that one spray during the season is sufficient.

Overwintering of carrot psylla

In Fennoscandia all authors agree that the overwintering plant is spruce (Ozols 1925, 1960; Lundblad 1929; Rygg 1977; Tiilikkala et al. 1995). Kristoffersen and Anderbrant's (2007) study was devoted to an inventory of overwintering plants in Sweden. Out of 365 samples collected over two winters from *Picea abies*, *Pinus silvestris* and *Juniperus communis*, only 67 were positive, yielding a total of 236 carrot psyllids. In one locality (Gotland), the psyllids were equally prevalent on all three hosts, but in two other areas *Picea abies* was attacked more frequently.

Studies were also conducted in countries where coniferous forests are virtually absent. It is interesting that the first studies on psyllid damage (ROSTRUP 1921) originated from Denmark, where pine or spruce forests are practically absent, or have been planted only in the last 100 years. Rostrup found only a single adult on harvested carrot in December, but commented on the findings of previous authors.

Non-coniferous shrubs and trees were mentioned in central European literature (BAUDYŠ 1936; SCHMIDT 1944; MÜHLE 1953) but the particular species were not identified. LÁSKA (1974) did not know the local shelter plants, since the spruce forest was at least 5 km away.

DISCUSSION

Monitoring: yellow traps or inspecting plants? Most authors used yellow traps, even if RYGG (1977) wrote: "For the determination of threshold values, a direct counting method would be necessary". Alighting adults are directed at a distance by odour (Kristoffersen et al. 2007) and apparently by colour in the proximity of plants. It is not clear why exclusively yellow traps are used rather than any other colour. It is possible that germinating plants provide odour, but have a much smaller surface area than the striking yellow traps observed by the eyes of the insect. No comparison of yellow traps with actual counts on plants has been carried out.

Dates of flights onto carrots. A comparison of the median dates of alighting shows that it occurs approximately on the same date from central Europe to Finland, despite very different climate and plant phenology. Clearly it is determined mainly

by the photoperiod, as was stated by Láska et al. (2011). When comparing the plant phenological data, they are delayed in Finland by about one month (Láska et al. 2011). If the *Trioza* population in the Czech Republic were fully adapted to plant phenology, then the flight median date would not be June 17, but May 17, when the carrot plants are mostly in the cotyledon phase (like in Finland on about June 17).

Origin of the pest race. The transition from wild carrot (or another wild host) was not fast and simple. The carrot psyllid apparently existed at least for several thousand years in temperate and northern Eurasia, but surely about 1848 (FOERSTER 1848) in three localities in Germany. No carrot damage was recorded in Europe except for that caused by aphids in Germany (FRANK 1893). The first observation of the curling of carrot leaves dates back to 1896 on the Danish island of Sjaelland, later identified as having been caused by the carrot psyllid. A slow expansion followed, and the carrot psyllid did not reach continental Denmark until about 1912 (ROSTRUP 1921). During the next about ten years outbreaks appeared in neighbouring countries: Latvia, Sweden, and Norway. Three outbreak populations could not arise independently (probably more countries were involved, but we have no reports). It is much more probable that outbreak populations had one source - Sjaelland. A slow spread southward followed, reaching the middle of Germany (Aschersleben) by 1929 (BEY 1931). Its first appearance in Czechoslovakia is not known, but BAUDYŠ (1936) wrote that the carrot psyllid was a common pest. The spread southwards slowed down and damage in South Germany (München) was reported only in 1973 (Krumrey & Wendland 1973), and no substantial carrot damage in Switzerland was observed until 1996, 1997 (Burckhardt & Freuler 2000; FISCHER & TERRETAZ 2002).

HODKINSON (2009) postulated a high degree of phenological synchrony between the psyllid and host-plant growth both in temperate and tropical conditions. In the case of the carrot psyllid, the phenologies match for Sjaelland or Latvia, where the carrot plants are young during the main migration flight, whereas in southern Czechoslovakia (Olomouc) (Láska *et al.* 2011) the maximal flight occurs at the time when the carrot plants are rather old.

Based on the above facts, I hypothesize that an aggressive outbreak race evolved in the turn of the

19th and 20th century in Sjaelland, which gradually replaced the original local populations in a considerable part of the area inhabited by carrot psyllid. This race is still adapted to the photoperiod conditions of northern Europe.

CONCLUSIONS

The biology of *Trioza apicalis* from the time of description up to the present is briefly reviewed according to the known literature; the author has been studying this pest for half a century. To assess the flights of the psyllids onto carrots in research works, counting of individuals on plants is recommended: yellow traps may, however, be useful for tentative monitoring. It is important to understand why the invasion of the carrots culminates approximately at the same time, about mid-June, at latitudes ranging from 42°N (Switzerland) to 62°N (Finland), despite the great temperature and phenological differences of these localities. In Finland the effect of the extremely long day is compensated by the very low temperature. The same day length response could arise if all pest populations were derived from the same initial outbreak at the end of the 19th and beginning of the 20th century on the Danish island of Sjaelland. T. apicalis before outbreak in Sjaelland probably lived everywhere in northern and central Europe as wild populations not strongly affecting the cultivated carrot.

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