

Influence of species, sex, age and food on the accumulation of toxic cadmium and some essential metals in Auchenorrhynchous Homoptera

Pekka Nuorteva, Martin Lodenius, Sumio Nagasawa*, Esa Tulisalo & Sirkka-Liisa Nuorteva

*Nuorteva, P., Lodenius, M., Tulisalo, E., & Nuorteva, S.-L., Department of Limnology and Environmental Science, Helsinki University, PB 65, FI-00014 Helsinki University
Nagasawa, S., 19-45 Utoosaka, Shimizu 424-0873, Japan*

Occurrence of toxic Cd and the essential, partly antagonistic metals Fe, Zn, Mn and Cu in the Homopteran suborder *Auchenorrhyncha* was studied through AAS analyses. 22 species from 5 families were analysed through 217 samples including 4360 specimens. The main material was from the unpolluted Finnish SW archipelago, and was complemented with cicadas (*Cicadidae*) from a city garden in Shimizu, Japan, and with leafhoppers (*Typhlocybidae*) from parks of Helsinki city, Finland. The lowest adult levels (below 0.21 ppm) were found in the mesophyll-feeding *Typhlocybidae*, the highest levels in the xylem-feeding *Cicadidae* and *Cercopidae*. Averages as high as 5.5 and 3.6 ppm ppm/dwt occurred in *Meimuna opalifera* and *Philaenus spumarius* respectively. A clear sex difference existed in the Cd levels of *Cicadidae* (males 1.20–11.0 ppm; females 0.06–0.51 ppm). The opposite situation was present for two cercopid and two cicadellid species. During development, the Cd-levels of *Cicadellidae* reached peak concentrations in adults, typically in hemimetabolous insects. In xylem-feeding *Cercopidae* the peak level occurred, however, at the end of the larval stage and was extremely high (up to 30–38 ppm in total, 33 ppm in Malpighian tubules and 180 ppm in the intestine). The necessary reproduction saving Cd decrease in adults was accelerated in *Aphrophora alni* through a change of host plant species. The Cd levels in various species of food plants mirrored itself clearly in the larvae of *Philaenus spumarius*. The high Cd levels in cercopid larvae reflected itself in the sphecid wasp *Argyrostes mystaceous*.

1. Introduction

Mining and industry continuously transfer metals from the interior of rocks to the biosphere. Acid rain supports the transformation of metals into a bioavailable form. Elevated levels of bioavailable metals in the biosphere have the potential to disturb the ecophysiology of living organisms as well

as the functions of the entire life-supporting global machinery. Anomalous metal accumulations and ecophysiological disturbances in various organisms have been described in thousands of scientific papers. Adequate evidence does, however, cover only a few systematic groups of organisms. In fact, systematical categories with tens of thousands of species, have been studied very superficially or not at all.

The insufficiently studied groups include the

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insect order *Homoptera*, consisting of more than 40,000 species, all with piercing-sucking mouthparts. Within this large order too, the existing metal evidence is distributed unevenly. Practically no evidence exists for the suborder *Auchenorrhyncha* consisting of 30,000 species. All available evidence is concentrated to a couple of superfamilies in the smaller suborder *Stenorrhyncha* (consisting of about 10,000 species). This restricted evidence does, however, illustrate some basic features which are valid for the metal biology of the whole order.

1.1. Metal biology in Homopteran suborder *Stenorrhyncha*

1.1.1. Metals in Psyllids

Among psyllids, Al, Fe, Ni, Mn, Cu, Zn, Cd and Hg levels have been determined in 14 out of about 1,000 existing species (Glowacka et al. 1997). Generally psyllids accumulate low amounts of metals, but their metal burdens increase with age. Exuvia were important for the elimination of Al, Ni and Mn, larval wax for Al, Cu and Ni. In polluted areas *Psyllopsis fraxini* eliminated large amounts of Al, Fe, Cu and Cd with honeydew. This way of metal elimination was less important in species living in unpolluted sites. Biomagnification of metal levels from food plants to psyllids (expressed as the concentration factor) was low for Mn, Al and Ni (cf: 0.56–1.08), but high for the toxic Cd (cf: 5.86).

1.1.2. Metals in aphids and their honeydew – a danger for ants

Of the 2,000 aphid species, tentative analyses exist for only 6. Their Cd levels are not very high: 0.04 ppm in the pemphigid *Pachypappa populi* (Nuorteva et al. 1997), 0.3–0.6 ppm in the others (Nuorteva et al. 2001). The corresponding levels for Cu are 9 and 9–25 ppm and for Zn 67 and 220–1,010 ppm, respectively.

Superficial consideration of such low levels gives an impression of minimal influence of aphids on the biotic metal circulation. Such an impression is, however, erroneous. This was found

when Sary and Kubiznakova (1987) detected high metal levels in red wood ants, which consume aphid honeydew. They noted maximal metal levels in such ant workers which had freshly collected the liquid excrements (= the honeydew) of aphids and were on their way back to the nest. This observation has later been confirmed and expanded upon through the studies of several authors (Martin 2000).

Aphids are really able to produce such huge amounts of Cd-loaded honeydew that it is capable to elevate the huge biomass of red wood ants to the highest level among forest animals (Yl.,-Mononen et al. 1989, Nuorteva 1990, 1999, Maavara et al. 1994, Martin 2000). This kind of situation has developed because the red wood ants are really strong honeydew consumers. More than 90% of the red wood ant's food consists of honeydew (Rosengren and Sundström 1991). It is possible to understand the tremendous impact of this Cd transfer process, when one considers that the ant biomass may under optimal conditions exceed that of all other forest invertebrates (Hölldobler and Wilson 1990).

It has been demonstrated (Migula et al. 1993, 1997, Maavara et al. 1994, Martin and Nuorteva 1997, Rabitsch 1997, Martin et al. 1999, Martin 2000) that red wood ant colonies does resist high Cd load by aid of 1) a normal physiological tolerance system, 2) a special social tolerance system based on negative bioaccumulation in the feeding chain (including partial metal transfer inhibition by the postpharyngeal and mandibular glands) and 3) a supercolony system to compensate mortality. However, when anthropogenic environmental pollution elevates the Cd level in ants ten-fold over the normal, the tolerance systems does not more protect the ant colonies. This results to decline of ant populations, which may in turn endanger forest health because red wood ants control effectively the populations of several species of forest pest insects.

1.1.3. The role of aphids as pollution damage exacerbators

Metal pollution in biota is not a simple toxicological problem where the health of certain organisms deteriorates because their tolerance limits are sur-

passed. In many cases, the pollutants only decrease the pest resistance of plants. In such cases, herbivores act as pollution damage exacerbators.

In general, plant suitability for aphids increases through elevated flow of amino acids in the sieve tubes from which most aphids imbibe their food. Because amino acids are the most necessary dietary ingredients for the parthenogenetically reproducing and rapidly growing aphids, any kind of amino acid elevations are beneficial for them. Regularly, aphids benefit from amino acid mobilizations in spring and autumn. In addition, amino acid mobilizations released in the host plant by stress and disease are beneficial for aphids.

On this way air pollution stress with SO₂, NO₂ and acid mist elevates aphid populations on roadsides (Walther et al. 1984, Braun and Flückiger 1985, Bolsinger and Flückiger 1984, 1987, 1989), on agricultural crops (Dohmen 1985, Culliney and Pimentel 1986, Warrington 1987, Warrington et al. 1987, Houlden et al. 1990, 1991) and on forest trees (Villemant 1981, Braun and Flückiger 1989, Warrington and Whittaker 1990, Holopainen et al. 1991, 1995, 1997 Neuvonen et al. 1992, Holopainen and Oksanen 1995).

SO₂ has been noted to more clearly affect aphid performance than O₃ and NO₂ (Holopainen et al. 1995, 1997, Holopainen and Kössi 1998, Kainulainen et al. 2000). Elevation of aphid populations at roadsides may thus be more due to host plant stress than use of NO_x as a nitrogen source (Viskari & al. 2000a). Moreover, aphid performance does not appear to be sensitive to exhaust gas exposure during the shoot elongation period of spruce (Viskari et al. 2000b) – obviously because amino acid mobilization has been fulfilled in advance. It is obvious that acidity-related metal activation plays a role in these pollutant-related and aphid population-enhancing processes, but the role of metals has been specified only by Walther et al. (1984).

Pollution-elevated aphid populations aggravate plant disease because aphid saliva is phytotoxic and may contain various pathogenic viruses (Maramorosch 1958, Kloft 1960, 1961, Nuorteva 1962, Miles 1968, 1978, 1987, 1989 a,b, Schaller 1968, Fritzsche et al. 1972, Srivastava 1988). Thus aphids do essentially increase the plant-injuring potential of pollutants. In fact, elevation of the aphid population often appears to be

the first visible phase of a gradual forest decline process (Carle 1968, Carle and Pontivy 1968, Villemant 1981, Walther et al. 1984, White 1984, Führer 1987, Nuorteva 1990). Although pollution damage aggravation by insect pests is well documented, it has rarely been taken into account by environmentalists (Nuorteva 1997, Nuorteva et al. 1999, 2001).

1.2 Biological background for metal circulation in the Homopteran suborder *Auchenorrhyncha*

Some principles of the pollution biology observed in the Homopteran suborder *Stenorrhyncha* may be valid when one tries to understand the Cd biology in the suborder *Auchenorrhyncha*, where metal pollution biology is practically unknown. Because considerable differences exist in the bionomics between the two suborders, one may also expect some dissimilarities in the pollution biology. Some dissimilarities are described below:

One essential difference is the much more active locomotion (jumping, running and flying) of the auchenorrhynchous *Homoptera* (Fritzsche et al. 1972). Consequently, substantial proportion of the dietary sugars is needed to cover the energy loss, which results in a more diluted honeydew (Schefer-Immel 1957, Mitsuhashi and Koyama 1969, 1971, 1975).

Absence of parthenogenetic reproduction is a second differing feature of the auchenorrhynchous *Homoptera*. As a consequence of this absence the auchenorrhynchs do not respond to plant disease with such a prompt population increase as do the aphids.

While the great majority of aphids use their piercing-sucking mouthparts to take their food from the phloem, only a fraction of the auchenorrhynchous *Homoptera* do the same. Three biological categories can be recognized, the feeding sites of which determine the principles of their life. The divisions are for the most part clear, but in few cases two modes of food intake may occur simultaneously. Sometimes young larvae (nymphs) represent other mode of feeding than older larvae and adults. The three main feeding modes are the following:

1.2.1. Phloem feeding

Phloem feeding characteristic of stenorrhynchous aphids occurs among *Auchenorrhyncha* by most cicadellids (family *Cicadellidae*) and a few leafhoppers (family *Typhlocybidae*). Host plants with an excessively low level of essential amino acids in their phloem are unsuitable as a food source for several auchenorrhynchs (Sogawa and Pathak 1970, Sogawa 1970, 1971, 1973, Oya and Sato 1981). Seasonal variation in amino acid availability drives some species to host plant changes (Prestidge and McNeill 1983).

Like aphids, phloem-feeding auchenorrhynchs are able to secrete salivary phytotoxins and plant pathogenic viruses that increase the flow of solubilized food constituents in the phloem (Maramorosch 1958, Maramorosch and Jensen 1963, Nuorteva 1962, Laurema et al. 1966, Maramorosch et al. 1968, Fritzsche et al. 1972, Prestidge et McNeill 1983). Because the food constituents in the phloem are solubilized to a diffusible form, the digestive enzymes amylase, proteinase, lipase and chlorophyllase are unnecessary and absent (Saxena 1954, Ricou 1962).

In phloem-feeding cicadellids, the food production performed by symbiotic intracellular microbes in mycetomes is effective to such a degree that only 2–3 of the dietetic amino acids remain essential, whereas several of them remain necessary for aphids (Buchner 1965, Mittler 1971 a,b, Koyama and Mitsuhashi 1975, Noda et al. 1979, Schwemmler 1980, Tiivel 1984).

1.2.2. Xylem feeding

Xylem feeding is characteristic of singing cicadas (*Cicadidae*) and spittle bugs (*Cercopidae*), whose larvae often live in or near the ground (Wiegert 1964, Fritzsche et al. 1972, Marchall and Cheung 1973, Halkka 1978, Horsfield 1978, White and Strehl 1978, White et al. 1979, Schaefer 1988, Rossi et al. 1996, Crews et al. 1998).

Their nutritional biology is essentially dissimilar to that of the phloem feeders because the xylem fluid consists mainly of water and dissolved minerals and contains only traces of substances with nutritional value. The dilute xylem fluid is hypotonic in relation to the haemolymph, which

causes some osmoregulatory problems.

The low level of nutrients in the xylem fluid is compensated by two dissimilar modes. Singing cicadas prolong development time of the larvae considerably, up to 17 years (Cheung and Marshall 1973, White et al. 1978, 1979, Karban 1986). In warm environments, part of the ingested water is used in evaporative cooling, which may be necessary to protect the symbiotic intracellular microbes (Noda and Saito 1979, Toolson and Hadley 1987, Sanborn et al. 1992).

The compensation mode of the spittle bugs is to drive enormous amounts of xylem fluid through their intestine – each day they consume an amount of xylem fluid that is 600–1,200 times their body weight (Horsfield 1978). The foam, produced by the thin-skinned larvae from the excreted xylem sap, confers effective protection against desiccation (Brooks and Whittaker 1999)

The xylem feeders too are capable of improving their food quality through the action of intracellular symbiotic microbes (mycetocyte organelles) in their mycetomes (Buchner 1925, 1965, Müller 1949, Mitsuhashi and Kono 1975, Tiivel 1984).

1.2.3. Mesophyll feeding

The mesophyll feeders in our material are represented by some members of the family *Typhlocybidae*. The members of this family are among the smallest of the auchenorrhynchous Homoptera. Some of them (especially members of the genus *Empoasca*) are phloem feeders, but most are mesophyll feeders on leaves, where they empty one cell after another (Smith 1926, Naito 1976). Empty, air-filled cells or groups of cells are seen as white spots on the leaves. Mesophyll feeding typhlocybrids have digestive enzymes that act upon starch, proteins, polypeptides, chlorophyll and fat globules to yield diffusible substances (Nuorteva 1954, Saxena 1954).

Typhlocybrids have no mycetomes but possess free-living symbiotic microbes in their intestine (Buchner 1925, 1965). Their excrement contains only 5.6–17% of the ingested sugars and thus cannot be considered to be real honeydew (Koblet-Günthardt 1975). The same is true for the exceptional mesophyll-feeding adelgid aphids (Kloft

1955 a,b, 1957). When the mesophyll-feeding leafhopper population is high, the surface of the leaves in their food plant is commonly covered by sticky excrement to which pollution particles and microfungi adhere (Choudhury 1985, Reijonen and Nuorteva 1993).

The present study is the first comprehensive attempt to test the metal levels in the suborder *Auchenorrhyncha*, which consists of 30,000 species and thus is the larger of the two homopteran suborders. Only a few scattered metal analyses had been performed on the auchenorrhynchous *Homoptera* when we started our study. Some of our preliminary results were mentioned in an opening lecture presented by the XXIV Nordic Congress of Entomology in Tartu 1997 (Nuorteva 1999) and repeated in Finnish by Nuorteva et al. (2001). These preliminary findings are included among the more extensively documented results of the present paper.

2. Material and study areas

In our study 22 species from 5 families of *Homoptera Auchenorrhyncha* were analysed through 217 samples including 4,360 specimens.

Most of the material was collected in an sterile archipelago area on the northern shore of the Baltic Sea, in Wättlaxvik, Bromarv, Southwestern Finland (665-27). While this region can be considered to be virtually unpolluted background area, it receives the highest rate of Finnish long-distance Cd deposition from industries of Central Europe (Kubin et al. 2000). In our study area, this deposition has been responsible for the population decline of the Cd-sensitive butterfly *Parnassius apollo* (L.) (Nieminen et al. 2001). To some degree, this area is also influenced by airborne acid pollution from some metal industries situating at a distance of 15–50 km:s on the Hanko promontory.

In the study area, granite rocks and the sterile glacialfluvial moraine ground are mainly covered by mixed forest dominated by pine, spruce, birches and poplar. No forest cultivation or clearcuts have been performed. Human impact (including war damage) has, however, occurred in such extent that the biodiversity is deficient. Out of the 263 indicators for virgin forest biodiversity listed by Junninen (2002) only two have been detected in

our study area. The health of the forests in the study area was about normal until the year 1995. Later the mortality of spruces (all age classes) and birches has increased drastically. It exists some reasons to think that long distance Cd pollution has decreased drought resistance of trees and other vegetation (Barcelo et al. 1986 a,b). Drying in turn has weakened the pest resistance and the trees have been forwarded to death by pests. Two bracket fungi (*Fomes fomentarius* and *Piptoporus betulinus*) have been the final killers for birches. The bark beetle *Polygraphus poligraphus* (L.) and the wood wasps *Urocerus gigas* (L.) and *Sirex juvencus* (L.), in the role of supporters, have been the final killers for spruce.

In the study area, it exists some forest-surrounded small agricultural fields, which were still under cultivation 10–15 years ago. At present, they are covered by semicultural and wild herbaceous plants and some grass. On the sea shore two meadows are present. The study area is inhabited by four fishermen families and eight families in summerhomes.

One treeless rock islet in the open Baltic (Stora Läggagrund) was included in the study area in order to control the influence of alkaline brackish water spray on the metal levels in the biota.

The abundance of typhlocybrids in the study area has decreased to such a degree that it was only possible to obtain one sample with a sufficient number of specimens. The disappearance of the earlier abundant populations of froghoppers (*Delphacidae*) is also evident. This disappearance includes the oat pest *Javesella pellucida* which was once studied intensively in this area (Nuorteva 1962). Stagnation of agricultural activities has obviously been the main factor for this disappearance. Thermal elimination of the intracellular symbionts may have supported the froghopper disappearance (Noda and Saito 1979, Toolson and Hadley 1987, Sanborn et al. 1992), because some exceptionally hot spring and summer temperatures have occurred in recent years.

The typhlocybrids, practically absent in Bromarv, were collected from park trees growing on streets or backyards in the centre of the Finnish capital Helsinki, at the northern shore of the Gulf of Finland. The city air is polluted by traffic and fossil energy production. On the leaves inhabited by typhlocybrids, in late summer, it occurred a visi-

ble black cover known to consist of honeydew, microflora and city pollutants including metals (Choudhury 1985, Reijonen and Nuorteva 1993).

The fauna of Bromarv includes no singing cicadas (*Cicadidae*). These were collected in the Nagasawa garden in Shimizu, Shizuoka prefecture, Japan. The garden on the hillside slope facing Suruga Bay was developed for dwelling in the 1960s. Until that time, the land was cultivated for tea gardens and mandarine orange plantations, and abundant amounts of agricultural chemicals and fertilizers had been applied over a long period. Thus, the soil in the garden is very fertile and the vegetation rich.

Although Shimizu is a large city and an international trade port, its traffic and industry produces pollution to the outskirts on a rather moderate scale. Environmental pollution in cities may be beneficial to cicadas because their fungal enemies may be less resistant to it (White et al. 1979, Shimazu 1989). Pesticide use may also benefit cicadas through elimination of predatory ants, which in a non-polluted environment kills cicada larvae before they reach their underground feeding places (Nagamine et al. 1975). In fact, one may today meet very dense populations of cicadas in badly polluted city centres (Zhong and Nianli 1985). – In addition to cicadas, a selection of their host plants and non-host plants was collected in the Nagasawa garden for metal analyses.

With the exception of the extremely large *Cicadidae*, each of our samples consists mainly of 4–170 specimens. Thus each analysis gives a result that is the mean for numerous specimens. The number of specimens as well as the number of replicate samples analysed are presented in tables. As usual, in biological materials, the variation between replicates may be considerable. It is therefore necessary to consider this when one is inspecting the tables. Our material on *Homoptera Auchenorrhyncha* consists of 217 samples, including 4360 specimens belonging to 22 species. In some few special instances analyses were performed separately for different parts or various organs of the specimens.

3. Methods

It is easiest to collect cicadids and spittle bugs by using a sweep net. If one collects material from

trees and bushes, it is possible to recognize their food plants. However, when material is collected through sweep netting from grass fields, the food plants remain obscure. In the case of foam-protected cercopid larvae, it is, however, possible to collect material separately from various species of host plants. This method was used for the polyphagous *Philaenus spumarius*.

In addition to auchenorrhynchous *Homoptera*, analyses were performed on their host plants through analyses on leaves in total. Each sample consisted of several leaves from several plant specimens. The results illustrate the specific metal level differences occurring between different species of host plants. As one may realize from our findings, leaf analyses also provide relevant information on species feeding on plant stems or leaf petioles.

We did not wash our samples, except in the case of spittle bug larvae, where it was necessary to control for a source of error caused by strong contamination of the larval skin by foamed excrements. Three types of washings were used: distilled water washing consisted of immersion for 30 minutes and shaking performed twice; 70% ethanol and 1% ether-water washings consisted of a 12 hour immersion and six one minute shakings.

In handling the material, we used no metal instruments. In two cases, however, we tested the influence of metallic instruments by sorting wet material with metallic tweezers. When compared with non-metallic control sorting, no difference was found. Possibly, our precautionary measure against metal instruments was unnecessary, but we undertook to err on the side of prudence.

Analyses were performed using flame atomic absorption spectrophotometer or a graphite furnace AAS as described in detail in Nuorteva (1990). Our main study object was toxic Cd. In addition, we studied Fe, Mn, Zn and Cu, all of which are essential metals in nutrition and participate in detoxification processes (Dadd 1967, Dadd and Krieger 1967, Bettger et al. 1978, Williams 1984, Soukupov and Oliveriusova 1988, Migula et al. 1989, Christophersen 1993, Pais 1994). We give the metal content as ppm (= mg/kg) of dry weight. During the years 1997–2001 we were unable to analyze Al, because our instrument failed to function.

To find the site of Cd accumulation in cerco-

pids, various organs were selected up for analysis from larvae and adults of *Aphrophora alni*. The work was performed under preparation microscope, in distilled water and by using plastic-covered needle tweezers. The organs were placed and dried on a microscopic cover glass, weighed after drying and dissolved in acids for AAS analysis. Dissection of about 50 larvae and 35 adults produced sufficient material.

To calibrate our study area with the extensive survey on metal deposition in northern Europe done by Rühling et al. (1996), we analysed several samples in Bromarv of the same two bioindicator mosses, that had been used in the more extensive survey. The mean metal levels in Bromarv for *Pleurozium schreberi* (n=17) were: Al 456, Fe 1226, Zn 61, Mn 347, Cu 6.6 and Cd 0.41 ppm/dwt. For *Hylocomium splendens* (n=11), the means were: Al 454, Fe 1406, Zn 57, Mn 356, Cu 9.1 and Cd 0.34 ppm/dwt. Our results are consistent with those of Rühling et al. (1996) for our area during the period in question.

4. Results and Discussion

4.1. Metal levels in adults of various species

Results of analyses on adults of 21 species of *Homoptera Auchenorrhyncha* are presented in Table 1. For the singing cicada *Graptopsaltria nigrofusca* (Motschl), the metal levels are given separately for the head, prothorax, abdomen, wings and legs.

The observed metal concentrations in adult *Auchenorrhyncha* are in general high when compared with those of other adult phytophagous insects. The high concentration is obviously linked with the hemimetabolous mode of metamorphosis occurring in *Auchenorrhyncha*. They do not have the opportunity to eliminate, through pupal meconium formation, the metals accumulated during larval stages. In holometabolous insects, by contrast this elimination system is common and effective (Bicj;k 1984, 1988, Bicj;k and Kaspar 1986, Vogel 1986, Reijonen 1988, Hopkin 1989, Kowalczyk and Watala 1989, Andrzejewska et al. 1990, Migula and Wawrzyczek 1999, Nuorteva 1990, Gintenreiter et al. 1993).

The highest adult Cd levels occurred in the xy-

lem-feeding families *Cicadidae* and *Cercopidae*. Averages as high as 5.5 and 3.6 ppm occurred in *Meimuna opalifera* and *Philaenus spumarius*, respectively. When the metal levels were analysed separately in the head, prothorax, abdomen, wings and legs of the cicadid *Graptopsaltria nigrofusca*, a clear accumulation of all metals except Al was observed in abdomen.

Interestingly, the Cd and Zn levels in our samples of *Cicadidae* from the Japanese city garden were about the same as those reported by Beyer et al. (1985) for *Magicicada septemdecim* (L.) collected near two zinc smelters in eastern Pennsylvania. Obviously the singing cicadas have a strong capability to excrete Zn when its level exceeds a suitable level. Strengthened Zn excretion tears with it Cd (Migula et al. 1989). The functions of Zn and Cd are united in this way. Therefore enhanced nutritional intake of Zn increases excretion of Cd. On the contrary one may note that Cu levels in all three Japanese species of *Cicadidae* were 2–4 times higher than those in Pennsylvania.

The lowest levels of Cd, Zn and Mn in our material occur in the minute-sized, mesophyll-feeding species of the family *Typhlocybidae*. The levels were below 0.12, 14 and 123 ppm, respectively. This was true despite the material mainly being collected from the Helsinki city centre, from trees having leaves with a “black mould complex on honeydew” described by Vereijken (1979) and Choudhury (1985). Washing of such leaves results to decrease of Al and Fe – common pollutants in road dust (Reijonen and Nuorteva 1993).

Nothing is known about the mechanism by which the *Typhlocybidae* maintain exceptionally low levels of Cd, Zn and Mn. Possibly, the low levels are in some way linked with the symbiotic micro-organisms *Typhlocybidae* not being embedded in the cells of mycetomes, but occurring freely in the intestine (Buchner 1925, 1965). Other anatomical features that may be connected with low metal concentrations in *Typhlocybidae* include: 1) the lack of a filter chamber and a suspensory ligament, 2) the occurrence of a longitudinal layer of muscle fibres in the midgut and 3) the joining of the distal ends of the Malpighian tubules (Saxena 1955). This cluster of anatomical, physiological and metal level features speaks against the present idea of taxonomists to adjoin the family *Typhlocybidae* to the family *Cicadellidae*. The importance of in-

Table 1. Mean metal levels in adult aucherorrhynchs (*Cicadidae* from Shimizu, Japan, *Ribautiana* and *Alnetoidia* from Helsinki, Finland, the others from Bromarv, Finland). n = number of specimens/number of samples. For Al, data are based on fewer replicates than for other metals.

Cicadidae	n	(Al)	Fe	Zn	Mn	Cu	Cd
<i>Graptopsaltria nigrofuscata</i> (Motschl) (= <i>colorata</i> Stål)	30/30	9	190	190	—	92	2.30
In toto	15/15	7	210	210	—	100	0.51
Head	5/5	10	50	110	—	7	0.07
Prothorax	5/5	6	140	66	—	20	0.09
Abdomen	5/5	14	350	870	—	270	15.00
Wings	5/1	14	26	18	—	8	0.03
Legs	5/1	24	33	190	—	9	0.10
<i>Cryptotympana facialis</i> (Walker) (= <i>japonensis</i> Kato)	2/2	5	300	250	—	73	0.64
<i>Meimuna opalifera</i> (Walker)	4/4	10	550	400	—	56	5.50
Cercopidae							
<i>Neophilaenus lineatus</i> (L.)	114/6	120	432	160	321	38	0.50
<i>Aphrophora alni</i> (Fall.)	136/14	105	234	212	131	47	1.52
<i>Philaenus spumarius</i> (L.)	410/13	78	402	202	133	33	3.60
Membracidae							
<i>Centrotus cornutus</i> (L.)	7/2	35	240	205	61	27	1.06
Cicadellidae							
<i>Oncopsis alni</i> (L.)	108/2	33	152	127	25	46	0.10
<i>Oncopsis flavicollis</i> (L.)	15/1	11	92	133	13	20	1.51
<i>Populicerus populi</i> (L.)	192/8		79	112	19	18	1.07
<i>Aphrodes makarowi</i> (Zachw.)	32/1	46	212	294	55	29	1.35
<i>Anoscopus flavostriatus</i> Don.	59/5	120	185	123	43	22	0.52
<i>Evacanthus interruptus</i> (L.)	20/3	64	56	323	57	45	0.90
<i>Cicadella viridis</i> (L.)	27/4	75	67	190	27	22	0.68
<i>Sonoronius dahlbomi</i> (Zett.)	153/6	132	156	170	89	32	0.55
<i>Elymana sulphurella</i> (Zett.)	15/1	6	67	93	53	9	0.12
<i>Speudotettix subfuscus</i> (Fall.)	8/1		150	300	410	40	0.98
<i>Athymanus argentatus</i> (Metcalf)	11/1	110	140	160	150	43	0.46
Typhlocybidae							
<i>Empoasca smaragdula</i> (Fall.)	35/1	64	132	90	9	48	0.09
<i>Ribautiana ulmi</i> (L.)	370/3	—	89	123	14	52	0.10
<i>Alnetoidia alneti</i> (Dahlb.)	850/5	228	89	90	13	56	0.12

ternal anatomy and biochemistry for the systematic classification of *Homoptera* has been stressed by Klimaszewski et al. (1973, 1974) and by Migula et al. (1980).

4.2. Influence of sex on metal levels

In many instances, it was possible to analyse the sexes separately (Table 2). Sex separation of larvae was performed only for *Populicerus populi*, where black lateral spots indicate the male sex.

A clear sex difference existed in the Cd levels of the singing cicadas (family *Cicadidae*): Male levels varied between 1.20 and 11.0 ppm, whereas

female levels varied from 0.06 to 0.51 ppm. No significant difference is present in the general plan and arrangement of the digestive organs of the sexes. In females, however, the crop is much smaller, and its walls are adjoined by fat to the reproductive organs (Hickernell 1920).

Because practically all Cd of singing cicadas exists in the abdomen (Table 1), the explanation of the sex difference must also lie there. More than half of the abdominal biomass of females may consist of eggs, possibly providing a partial reason for the low abdominal Cd level.

The opposite situation existed for two cercopid species. Here the females had higher levels, not only of Cd but of all metals analysed. The same

Table 2. Sex-related metal levels (ppm/dwt) in mature males and females. Metal levels in ppm/dwt. For taxonomical species identification and generic names see Table 1. M= adult males, F= adult females, LM = male larvae, LF = female larvae, n =number of specimens/number of samples.

Species	M/F	n	Fe	Zn	Mn	Cu	Cd
Cicadidae							
<i>G. nigrofuscata</i>	M	15/15	170	180	–	83	4.00
	F	15/15	210	210	–	100	0.51
<i>Cr. facialis</i>	M	1/1	340	190	–	97	1.20
	F	1/1	260	310	–	49	0.08
<i>M. opalifera</i>	M	2/2	760	360	–	70	11.00
	F	2/2	550	400	–	56	0.06
Cercopidae							
<i>N. lineatus</i>	M	30/1	320	170	44	31	0.65
	F	44/1	320	150	58	31	0.61
<i>Aphr. alni</i>	M	62/6	173	218	44	35	0.73
	F	35/4	350	225	281	73	3.32
<i>Ph. spumarius</i>	M	77/2	325	165	44	24	3.95
	F	91/2	430	230	73	28	4.60
Cicadellidae							
<i>P. populi</i>	M	107/4	80	116	18	17	1.09
	F	85/4	78	109	21	19	1.05
	LM	45/1	98	110	15	17	0.74
	LF	96/2	99	91	17	17	0.68
<i>A. flavostriatus</i>	M	19/2	200	113	43	21	0.67
	F	40/3	175	130	44	23	0.42
<i>E. interruptus</i>	M	9/1	55	290	35	38	0.93
	F	20/3	57	340	68	77	0.89
<i>C. viridis</i>	M	6/1	32	130	16	23	0.28
	F	21/3	78	210	30	21	0.82
<i>S. dahlbomi</i>	M	86/3	213	140	107	33	0.68
	F	67/3	99	200	106	31	0.41
Typhlocybididae							
<i>Aln. alneti</i>	M	243/2	85	88	14	56	0.13
	F	166/2	89	96	12	52	0.12

was true for the cicadellid *Cicadella viridis* (L.) and to some degree also for *Evacanthus interruptus* (L.). The other species had no sex differences.

4.3. Influence of developmental stage on metal levels

Larvae (nymphs) of 7 species were available for analyses. The observed levels, including in comparison the levels of young and mature adults are given in Table 3.

In the family *Cicadellidae*, the Cd levels begin to rise during the development and reach top levels in adults. For other metals, such elevation was less clear, except for Fe in *Populicerus populi*. Such gradual metal elevation during development is typical of hemimetabolous insects.

Among the xylem-feeding spittle bugs (*Cercopidae*), the situation was different. Their larvae surpass the Cd and Mn levels of mature adults, being nearly tenfold higher (except Cd in *Neophilaenus lineatus*). In *Philaenus spumarius*, the abnormally high larval levels of Cd and Mn occur still in recently emerged adults but drop gradually during adult maturation. In *Aphrophora alni*, the Cd level drops more abruptly after adult emergence.

The levels of Cd and Mn show similar behaviour in the ecosystems because acidity elevates their bioavailability (Mahler et al. 1982, Tervahattu et al. 2001). Cd is, however, toxic to all organisms, whereas Mn is essential. Consequently, the toxic effects of Cd may be diminished by increasing environmental alkalinity, but simultaneously one must face the harmful deficiency of

Table 3. Influence of developmental stage on metal levels in *Homoptera Auchenorrhyncha*. L = larvae, YA = young adults, A = mature adults, n = number of specimens/number of samples.

Species	L/YA/A	n	Fe	Zn	Mn	Cu	Cd
Cercopidae							
<i>N. lineatus</i>	L	80/2	2,100	255	2150	35	1.06
	YA	19/2	570	955	525	68	7.60
	A	114/6	432	160	321	38	0.50
<i>Ph. spumarius</i>	L	630/16	2141	354	1,406	25	18.90
	YA	102/6	1,800	245	1,493	32	25.67
	A	410/13	402	202	133	33	3.60
<i>Aphr. alni</i>	L	186/9	794	293	5,633	20	21.88
	YA	19/2	570	250	1,230	68	7.60
	A	136/14	234	212	131	47	1.52
Cicadellidae							
<i>P. populi</i>	L	153/4	21	100	22	17	0.83
	YA	59/3	84	117	19	19	0.93
	A	114/4	80	114	19	18	1.09
<i>C. viridis</i>	L	90/3	82	237	22	22	0.23
	A	27/4	67	190	27	22	0.68
Typhlocybae							
<i>R. ulmi</i>	L	50/1	210	110	11	36	0.01
	A	370/3	89	123	14	52	0.10
<i>Aln. alneti</i>	L	140/1	150	92	8	35	0.13
	A	850/5	89	90	13	56	0.12

the essential Mn-dependent superoxide dismutase (Christophersen 1993, Tervahattu et al. 2001). In their ecological adaptation, cercopids must have found an optimal balance between toxic Cd and beneficial Mn. Rich supply of Mn seems to be so important for larvae that a high Cd is tolerated, whereas Cd is so dangerous for adults (= for the gametogenesis?) that Mn deficiency must be tolerated.

The exceptionally high Cd levels occurring in larvae of *Philaenus spumarius* and *Aphrophora alni* are rather unusual among insects. In fact, they are extremes for all Finnish insects in background areas (Nuorteva 1990, 1999, Nuorteva et al. 2001). The maxima were, of course, higher than the averages given in Table 3. Details for three samples with extremely high Cd levels are the following:

1. The highest Cd level, 38 ppm, was found in a sample consisting of 24 young adults of *Philaenus spumarius*, collected on 12 July 1996 from stems of *Tanacetum vulgare*, on a treeless rocky islet Stora Läggargrund, in Bromarv, on the Baltic. The levels of the other metals in the young adults were: Fe 1900 ppm, Zn 220 ppm, Mn 310 ppm and Cu 35 ppm.

2. The second highest Cd level, 35 ppm, was found in a sample of 50 larvae from the same population as the previous sample. The levels of the other metals in larvae were: Fe 200 ppm, Zn 300 ppm, Mn 420 ppm and Cu 28 ppm.
3. The third highest Cd level 30–31 ppm, was found in two samples of 20–22 larvae of *Aphrophora alni* collected from the underground base of *Populus tremula* saplings on 17 July 1996 on the small mainland promontory Vesterskatan, by Wätflaxvik in Bromarv, on the shore of the Baltic. The levels of the other metals in the larvae were: Fe 630–680 ppm, Zn 280–380 ppm, Mn 6,200–7,000 ppm and Cu 19–24 ppm.

Among other insects analysed in Finland, only one sample has reached a similar extreme level as that reported here for spittlebug larvae. This was a sample with a Cd level of 32 ppm consisting of last instar larvae of the phloem-feeding bark beetle *Hylurgops palliatus* (Gyll.) grown on a 13-m-high *Pinus sylvestris* felled on 29 March, 1986 in Espoo on the shore of the strongly acidified Lake Hauklampi (Nuorteva et al. 1986, Reijonen 1988).

The exceptionally high Cd level in spittlebug larvae may be dangerous for their predators. The only predator accessible to us in Bromarv study area was the sphecid wasp *Argyrotes (Gorytes) mystaceus* (L.) (*Hymenoptera, Crabronidae*). Its females collect spittlebug larvae as food for their own larvae. Because the species is rare in our study area, we were able to collect only two females from the flowers of *Angelica sylvestris* on 27 July, 1988 (when the season of spittle bug larvae is over). Its analysis revealed the following levels (ppm/dwt): Fe 280, Mn 270, Zn 180, Cu 24 and Cd 2.60. In comparison purposes we analysed two samples (5 specimens) of the sphecid wasp *Ammophila sabulosa* L., which collects lepidopterous caterpillars for its larvae. The analyses showed the following levels (ppm/dwt): Fe 390, Mn 39, Zn 135, Cu 20 and Cd 0.13. Thus, all metal levels (except Fe) were higher in *A. mystaceus*; Mn was 7 times and Cd 20 times higher. The high levels of Mn and Cd in spittlebug larvae is convincingly mirrored in the respective levels of an adult sphecid.

4.4. Localization of the extraordinarily high Cd level in spittlebug larvae

When one takes into consideration that xylem fluid is a watery fluid with extremely low nutritional value and minimal trace metal contents, it is paradoxical to note that spittlebug larvae feeding on xylem alone does accumulate record high levels of Cd. As described in the introduction, the spittle bugs receive enough of food by an extraordinary effective consumption of the dilute xylem fluid. The essential trace metals and toxic Cd may be caught and accumulated in a similar way. It raises, however, a question, how the spittle bugs does tolerate the extremely high levels of Cd in their body. A tentative hypothesis is (Nuorteva 1999) that Cd may exist in that voided and foamed fluid, which protects the spittlebug larvae against desiccation. It was believed that Cd possibly sediments onto the larval skin and remains there as harmless outer contamination when the foam evaporates. The studies of Lobacheva et al. (1994) supported this view, by showing that it is possible to effectively collect trace metals from water through flotation aided by surfactants.

To test the validity of this hypothesis, we analysed larval skins in three occasions:

First, we examined 25 larvae of *Aphrophora alni*, that had been artificially fed on *Sedum telephium*. When we analysed the larvae in total, we found 26 ppm of Cd, but when we collected and analysed their rejected skins we found only 9.6 ppm of Cd.

In the second instance, we reared 22 last instar larvae of *Aphrophora alni* on twigs of *Populus tremula*. When we analysed the larvae in total, we found 24 ppm of Cd but only 12 ppm of Cd in their rejected larval skins.

In the third instance, we reared 25 larvae of *Philaenus spumarius* on *Melampyrum silvaticum*. In analysing the larvae in total we found 22 ppm of Cd but only 3.9 ppm of Cd in their rejected skins.

These three analyses showed lower Cd levels in the rejected larval skins than in the overall levels. Thus, no confirmation for the skin surface contamination hypothesis was found.

The hypothesis was further tested by washing cercopid larvae in distilled water, in 70% ethanol and in 1% mixtures of ether and water. The washings failed to decrease the metal levels of the spittlebug larvae (Table 4).

For additional confirmation, *Aphrophora alni* foam was impregnated twice into filter papers. After drying, the filter papers and untreated controls were analysed for metals (Table 5). Only very weak signs of Fe, Zn and Cd elevation were noted.

Because none of the tests gave support for skin contamination with metals, a question arose: Which internal organ is capable of incorporating the Cd responsible for the high total level in spittlebug larvae and young adults?

A rough first orientation was performed by analysing the metal levels in various body parts of 26 *A. alni* larvae, collected from the base of Aspen saplings on 11–14 July 1999 in Wättlaxvik, Bromarv. The observed metal distribution is given in Table 6. Maximum Cd and Mn levels occurred in abdomens. The situation was the same as for Cd in *Graptopsaltria nigrofuscata* adults (Table 1).

To determine the site of Cd accumulation more exactly, various organs from larvae and adults of *Aphrophora alni* were dissected for analysis. Larvae were collected from the underground base of *Populus tremula* saplings on a small promontory at Wättlaxviken in Bromarv on 27 June 1999. The

Table 4. Effect of various kinds of washings on metal levels (ppm/dwt) of spittle bug larvae. n = number of larvae/length of larvae in millimeters.

Test animals	Quality of washing	Fe	Mn	Zn	Cu	Cd
<i>Aphrophora alni</i>						
n=16/6–7 mm	Distilled water	550	6,000	190	24	15
n=16/6–7 mm	No washing	440	4,600	210	18	13
n=20/8–9 mm	Distilled water	420	4,300	260	20	16
n=20/8–9 mm	No washing	430	4,200	250	17	14
n=27/8–10 mm	70% ethanol	1,400	4,100	260	18	26
n=27/8–10 mm	No washing	1,700	5,600	280	18	28
<i>Philaenus spumarius</i>						
n=46/2–4 mm	1% ether-water	3,700	220	470	21	31
n=97/2–4 mm	No washing	2,850	330	350	25	30

adults were reared from larvae collected in the same locality on 11 July 1999. Cd levels observed in the various organs are presented in Table 7.

The analyses showed that Cd does accumulate at very high levels in the intestine (130–180 ppm) and at considerable levels in the other organs (2–33 ppm). The high accumulation of Cd in the intestine is not surprising since inactivated toxic ele-

ment granulae have been observed in the intestinal walls of aphids and some other invertebrates (Ehrhardt 1965, Martoja et al. 1983, Prosi et al. 1983, Chapman 1985, Hopkin 1989, Esenin and Ma 2000). Cd obviously occurs there in the form of mineralized granules. Plentiful small whitish intestinal granulae were, in fact, already observed when the organs were separated by dissection un-

Table 5. Effect of twice replicated cercopid foam saturation of a filter paper on metal level (ppm/dwt).

Origin of foam	Fe	Mn	Zn	Cu	Cd
Control, untreated filter paper, n=2	19	7	8	5.0	0.02
<i>Aphrophora alni</i> foam on <i>Populus tremula</i> , n=2	26	9	20	6.0	0.05
<i>Philaenus spumarius</i> foam on <i>Tanacetum vulgare</i> , n=1	9	2	5	2.0	0.03
on <i>Chamaenerium angustifolium</i> , n=1	16	2	8	3.2	0.02

Table 6. Metal levels (ppm/dwt) in different body parts by *Aphrophora alni* larvae from a sample of 26 specimens collected from the base of Aspen saplings on 11–14.7.1999 in Wättlaxvik, Bromarv.

	Fe	Mn	Zn	Cu	Cd
Skin	530	1,400	150	30	12
Head	290	910	250	26	31
Legs	7,400	2,500	890	37	40
Thorax	1,300	6,500	250	29	47
Abdomen	940	8,700	570	?	58

Table 7. Cadmium levels (ppm/dwt) in various organs from larvae and adults of the spittlebug *Aphrophora alni*.

Organ	Larvae	Adults
Salivary glands (colorless)	3.9	1.7
Oesophagus(= foregut, red)	6.5	10.0
Intestine (yellowish-white)	130.0	180.0
Malpighian tubules (grey)	5.0	33.0
Mycetomes (with symbionts, red)	8.6	2.0

der the microscope. Inactivation of toxic Cd through formation of intestinal granulae allows cercopid larvae to tolerate a high Cd load. This ability is simultaneously a premise for sufficient intake of essential Mn.

The Cd levels observed in various organs of *A. alni* were not essentially higher in larvae than in adults, although the Cd levels measured for this species in total were clearly superior in the larvae (Table 3). This discrepancy is obviously an artefact resulting from the use of adults, which had just emerged in a rearing cage. The postemergence decrease of Cd had thus not yet been realized. The decrease may have been delayed by the lacking opportunity of the caged test animals to perform those instinctive host plant changes that occur in nature.

Host plant preferences shown by adults of *A. alni* have been experimentally evaluated already half a century ago (Nuorteva 1952). At that time, no knowledge existed about the metal levels in plant species used in the host plant preference tests for *A. alni*. Today such information is available. A host plant preference list, with recently noted Cd levels is given in Table 8. It is noteworthy that the three most preferred host plants (*Alnus glutinosa*, *A. incana* and *Betula pendula*) belong to the family *Betulaceae* and show the lowest Cd levels (mean 0.02–0.34 ppm), whereas the less preferred deciduous host plants (*Salix caprea*, *S. aurita* and *Populus tremula*) belong to the family *Salicaceae* and have higher Cd levels (0.63–0.72 ppm). Poplar, on which the larvae of *A. alni* develop, is the least favoured deciduous food plant of adults and has the highest Cd level.

As seen in Table 8, the instinctive mode of host plant selection by adults of *A. alni* may act as a mechanism supporting post-emergence Cd elimination. Such elimination may be necessary to pro-

Table 8. Some food plants of *Aphrophora alni* adults in order of preference as revealed by a series of host selection experiments (Nuorteva 1952), supplemented by Cd levels (ppm/dwt) in the Bromarv study area (*Alnus incana* from Tvärminne).

Plants in order of preference, number of analysed samples	Average of Cd	Absolute variation of Cd in analyses
<i>Betula pendula</i> n=9	0.34	0.19–0.67
<i>Alnus incana</i> n=2	0.06	0.005–0.006
<i>A. glutinosa</i> n=7	0.02	0.001–0.043
<i>Salix caprea</i> n=7	0.63	0.42–0.87
<i>S. phylicifolia</i> n=0		
<i>S. aurita</i> n=3	0.72	0.43–1.10
<i>Populus tremula</i> n=72	0.68	0.33–1.10
<i>Picea abies</i> (2nd-year) n=16	0.19	0.15–0.28

tect adult-stage gametogenesis, which is known to be sensitive to toxic metals.

In the host preference list for *A. alni* (Nuorteva 1952), the conifer *Picea abies* was more strongly avoided than any one of the deciduous food plants. For *A. alni* spruce is really an absolutely impossible host plant, not only in laboratory experiments but also in the field. In Northern America, several *Aphrophora* species (e.g. *A. canadensis* Walley) exist, by contrast, which are strictly bound to conifers (Kelson 1964, Furniss and Carolin 1980). We have analysed two samples of larvae of *A. canadensis* (10 and 13 specimens) collected from *Pinus montana* in University of British Columbia gardens in Vancouver, on 9 July 1988. Their Cd level was low (2.7–4.3 ppm) and Mn level high (1,650–2,600 ppm). Low levels of both metals were observed in the needles of their host plant (0.09–0.11 ppm Cd and 100–155 ppm Mn). The conifer-adapted *Aphrophora* species seems to have a host metal adaptation system, which is essentially dissimilar to that of hardwood-adapted species.

In the Nagasawa garden in Japan, we noted another example where food plant selection helps auchenorrhynchous adults achieve low adult metal levels. We analysed metal levels in the roots of 11 trees and bushes and listed them in a series according to increasing level of Cd (Table 9). Three species of singing cicadas were present in the garden. According to information by Dr. Masami Hayashi, the main food plant for all three species is *Prunus*

Table 9. Metal levels in roots and wood of a selection of plant species in the Nagasawa garden in Shimizu, Japan. Data are listed according to increasing levels of Cd. *Prunus persica* Batsch. is the main food plant (***) for the cicadas *Graptopsaltria nigrofuscata*, *Cryptotympana facialis* and *Meimuna opalifera*. For *C. facialis*, *Camellia japonica* (*) is another food source.

Plant species	Al	Fe	Zn	Cu	Cd	Pb
Roots						
<i>Prunus persica</i> Batsch. ***	520	160	18	7	0.05	3.7
<i>Thea sinensis</i> L.	860	720	32	7	0.09	5.6
<i>Ardisia crispa</i> A.DC.	1,300	920	29	6	0.10	2.0
<i>Camellia japonica</i> L. *	8,700	1100	62	14	0.15	3.1
<i>Cinnamomum camphora</i> Sieb.	870	660	10	11	0.15	2.7
<i>Camellia sasanqua</i> Thunb.	1,300	890	20	13	0.39	2.5
<i>Benzoin umbellatum</i> Rehd.	1,100	1,400	87	19	0.45	3.9
<i>Xanthoxylum piperitum</i> DC.	2,300	1,200	50	11	0.49	6.6
<i>Fatsia japonica</i> Decne & Pl.	1,500	100	28	15	0.60	5.9
<i>Eriobotrya japonica</i> Lindl.	3,500	2,300	69	62	0.96	6.3
<i>Aucuba japonica</i> Thunb.	1,900	1,900	760	15	3.20	7.2
Wood						
<i>Prunus persica</i> Batsch. ***	32	14	24	3	0.00	0.2
<i>Ardisia crispa</i> A.DC.	15	12	6	2	0.05	0.0

persica Batsch, and for *Cryptotympana facialis*, in addition *Camellia japonica* L. Again it is noteworthy that the most favoured food plant has the lowest Cd level as well as a low level of all other metals (Table 9). The situation is similar to that of *Aphrophora alni*, which upon reaching adulthood, also prefers food plants with very low Cd levels.

4.5. Influence of food on metal levels of *Philaenus spumarius*

The spittlebug *Philaenus spumarius* was the only polyphagous species available for the examination of the influence of food plant metal levels on the metal levels in auchenorrhynchous *Homoptera*.

Table 10. Food plant influence on the metal levels (ppm/dwt) of larvae (L) and young adults (YA) of *Philaenus spumarius*. Plant levels were analysed from the leaves. n = number of plant samples analysed or, in animals, the number of specimens/number of samples.

Species	n	Fe	Zn	Mn	Cu	Cd
Poaceae (Graminaceae)	29	76	265	30	5	0.05
<i>Philaenus spumarius</i> L	20/1	5,300	280	1,300	26	3.5
<i>Chamaenerium angustifolium</i>	7	108	78	110	10	0.1
<i>Philaenus spumarius</i> L	120/3	3,367	407	197	20	10.9
<i>Philaenus spumarius</i> YA	11/1	2,500	220	210	27	17.0
<i>Filipendula ulmaria</i>	21	101	91	305	8	0.5
<i>Philaenus spumarius</i> L	110/4	1,900	343	1,003	26	15.0
<i>Philaenus spumarius</i> YA	24/1	2,200	210	640	34	21.0
<i>Tanacetum vulgare</i>	7	54	94	85	7	1.0
<i>Philaenus spumarius</i> L	97/2	2,850	350	340	25	30.0
<i>Philaenus spumarius</i> YA	24/1	1,900	220	310	35	38.0
<i>Melampyrum</i> spp.	8	150	509	1330	26	1.20
<i>Philaenus spumarius</i> L	80/2	825	405	4,400	35	26.0
<i>Philaenus spumarius</i> YA	28/2	1,050	250	2,800	37	25.5

Collecting foam-embedded larvae and young adults separately from various species of food plants was relatively easy. Adults, in contrast, jumped and flew so actively in the vegetation that it was impossible to identify their food plants.

When Cd and some other metals were analysed in larvae and young adults collected from five dissimilar host plants, the levels of all metals in spittlebugs were found to be higher than in their host plants (only exception: Zn in *Melampyrum*) (Table 10). In practically all cases, the metal levels in larvae were higher than in young adults. Inordinately high Mn levels were observed in *Melampyrum* spp. as well as in spittlebugs living on it. The plant levels of Cd clearly mirrored the levels in spittlebugs. No such relationship was evident in other metals.

Philaenus spumarius is an exceedingly polyphagous species, having in Finland 158 documented host plants, practically all dicotyledonous (Halkka et al. 1967). The assumption has been supposed that it tolerates such a wide variety of hosts because its larvae feed on xylem sap, which is an unusual food source and is relatively free from the chemical defences common in phloem sap (Owen 1988, Thomson 1999). Our observation about the exceedingly rich occurrence of the severely toxic Cd in the larvae of this species strongly challenges this view.

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