Chapter 3
Psyllid Vectors

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Abstract '*Candidatus* Phytoplasma' species are mostly transmitted from plant to plant by phloem feeding hemipterans, primarily leafhoppers (Cicadellidae) and planthoppers (Fulgoroidea) (Hemiptera, Auchenorrhyncha). However, there is one group of phytoplasmas, the 16SrX or apple proliferation group, whose members are transmitted by psyllid vectors of the superfamily Psylloidea (Hemiptera, Sternorrhyncha). These psyllid-transmitted phytoplasmas are genetically closely related and are associated with economically important diseases of fruit trees such as pear decline, apple proliferation and European stone fruit yellows. The psyllid vector species of these phytoplasmas are also closely related and all belong to the genus *Cacopsylla*. Both, phytoplasmas and psyllid vectors, are geographically limited to the Palaearctic region, mainly Europe. Only pear decline and peach yellow leaf roll phytoplasmas have probably been introduced to America along with their vectors. As phytoplasma-infected trees cannot be cured and resistant plant material is not available to the growers, preventive control measures such as vector control are of paramount importance to limit the spread of these diseases. Thus, detailed

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knowledge about the biology and ecology of the vector species, their host plants as well as knowledge about the transmission parameters is crucial.

Keywords Phytoplasmas · Psyllid vectors · Epidemiology · Pear decline · Apple proliferation · European stone fruit yellows

3.1 Introduction

The jumping plant-lice or psyllids form the well-defined superfamily Psylloidea which belongs to the suborder Sternorrhyncha of the order Hemiptera. About 4.000 species of this superfamily are described worldwide including about 400 species in Europe (Burckhardt 1994; Burckhardt and Ouvrard 2012). All recognised phytoplasma vectors are found in the genus *Cacopsylla* which is part of the subfamily Psyllinae within the family Psyllidae (Weintraub and Beanland 2006; Burckhardt and Ouvrard 2012). An electronic determination key for the most important *Cacopsylla* species found on Rosaceae in Europe is available at the internet by www.psyllidkey.eu (Burckhardt et al. 2008). Table 3.1 gives an introductive overview of the most important phytoplasma diseases and their agents which are

Table 3.1 Phytoplasma diseases of fruit crops, their associated agents, psyllid vectors and vector's host plant

Psyllid species	Phytoplasma	Disease	Host plant
Cacopsylla picta	'*Candidatus* Phytoplasma mali'	Apple proliferation	*Malus* x *domestica*
Cacopsylla melanoneura	'*Candidatus* Phytoplasma mali'	Apple proliferation	*Crataegus* spp., *Malus* x *domestica*
Cacopsylla pruni A and B[a]	'*Candidatus* Phytoplasma prunorum'	European stone fruit yellows	*Prunus* spp.
Cacopsylla pyri	'*Candidatus* Phytoplasma pyri'	Pear decline	*Pyrus* spp.
Cacopsylla pyricola	'*Candidatus* Phytoplasma pyri'	Pear decline	*Pyrus* spp.
Cacopsylla pyricola	'*Candidatus* Phytoplasma pyri'	Peach yellow leaf roll (USA)	*Prunus persica*
Cacopsylla pyrisuga[b]	'*Candidatus* Phytoplasma pyri'	Pear decline	*Pyrus* spp.
Cacopsylla chinensis	'*Candidatus* Phytoplasma pyri' strain PD-TW	Pear decline-Taiwan	*Pyrus* spp.
Cacopsylla qianli[b]	'*Candidatus* Phytoplasma pyri' strain PD-TW	Pear decline-Taiwan	*Pyrus* spp.

[a]Complex of two cryptic species A and B
[b]Presumed vectors

transmitted by psyllid vectors. So far, all important fruit crop diseases associated with the presence of phytoplasmas of the group 16SrX are vectored by psyllids.

The basic geographical distribution of the most important psyllid vectors in Europe and neighbouring regions has been assessed during the COST action FA0807 and is available online (Costphytoplasma 2013).

Psyllids are phloem feeders and both nymphs and adults feed on plant sap. Depending on the species, the eggs are laid on the new buds, in crevices of the bark or on leaves where they can produce pit-like deformations on the leaf blade (Hodkinson 2009). The nymph development passes through five instars which are more or less strongly flattened dorso-ventrally (Burckhardt 1994). Phytoplasma vector species on apple and stone fruits are – like other North temperate psyllids – univoltine whereas pear psyllids with the exception of *Cacopsylla pyrisuga* (Foerster 1848) are mostly polyvoltine with overlapping generations. Polyvoltine vector species usually overwinter as adults on or near to their host plants. Univoltine vector species have an obligate emergence as imagines (= emigrants) to their overwintering plants, such as conifers, and return to their respective reproduction host plants in spring (= remigrants) (Mayer et al. 2011; Burckhardt 1994). This applies for *Cacopsylla pruni*, *C. melanoneura* and *C. picta* (Thébaud et al. 2009; Mayer and Gross 2007; Cermák and Lauterer 2008; Tedeschi et al. 2002; Jarausch et al. 2013; Jarausch and Jarausch 2014, 2016). In these cases overwintering was observed only on conifers at higher altitudes (Mayer and Gross 2007; Thébaud et al. 2009; Pizzinat et al. 2011; Ulubaş Serçe et al. 2011). Migration to the respective reproduction or overwintering plant seems to be direct and may take place even over long distances. Plant volatiles are exploited by the psyllids to find their reproduction host plants or overwintering plants during migration (Gross 2016; Mayer and Gross 2007; Mayer et al. 2011).

As phytoplasmas are phloem-limited, only phloem-feeding insects can potentially acquire and transmit the pathogen (Weintraub and Beanland 2006). The insects acquire the phytoplasma during feeding in the phloem of infected plants. The following process of phytoplasma passage and multiplication in the insect body comprises the latent or incubation phase and the infectivity period where the insect can transmit the pathogen. Detailed descriptions of the cellular processes of transport and multiplication in the insect body have been reported for leafhoppers (Weintraub and Beanland 2006; Hogenhout et al. 2008). So far, these mechanisms of phytoplasma transmission remain to be demonstrated for psyllid vectors as well. Several publications show that psyllids transmit the pathogen in a persistent propagative manner (Carraro et al. 2001a, b; Thébaud et al. 2009). The length of time needed for an individual to become infectious seems to differ among the psyllid vectors. However, it is of paramount importance for the disease spread by univoltine vectors: vectors with a long latent phase predominantly transmit the phytoplasma after overwintering when remigrating into the orchards (monocyclic disease spread on regional scale). In contrast, vectors with a short latent phase transmit the phytoplasma already before migration as well as after overwintering (polycyclic disease spread on local and regional scale) (Jarausch et al. 2013).

3.2 *Cacopsylla picta*

Cacopsylla picta (Foerster 1848) (Figs. 3.1 and 3.2) is distributed only in Europe and is monophagous on *Malus* spp. (Jarausch and Jarausch 2010; Ouvrard 2017). The insect completes one generation per year and overwinters as adult on conifers. At the end of winter (March/April), *C. picta* remigrants move from the overwintering sites to apple trees for oviposition (Jarausch and Jarausch 2014). The insects of the new generation (emigrants) feed on their reproduction host until the beginning of July when they leave the apple trees as adults (Mattedi et al. 2008; Jarausch et al. 2011). Findings of phytoplasma-infected individuals of *C. picta* have been reported from many different countries: Italy, Germany, Bosnia-Herzegovina, France, Switzerland, Finland, Czech Republic, Bulgaria, Spain and Croatia (Frisinghelli et al. 2000; Jarausch et al. 2003, 2011; Carraro et al. 2008; Delić et al. 2008; Lemmetty et al. 2011; Ludvikova et al. 2011; Etropolska et al. 2015; Miñarro et al. 2016; Križanac et al. 2017). In north-east Italy, the natural infection rate of *C. picta* was found between 9% and 13%, respectively for overwintering and offspring adults (Carraro et al. 2008). In the main apple growing regions of Italy, Trentino and Alto Adige (South Tyrol) (Italy), mean infection rates of 6% (Mattedi et al. 2008), 11% (Baric et al. 2010) and 20% (Fischnaller et al. 2017) for remigrants were reported. In Germany, about 10% of overwintered *C. picta* were found naturally

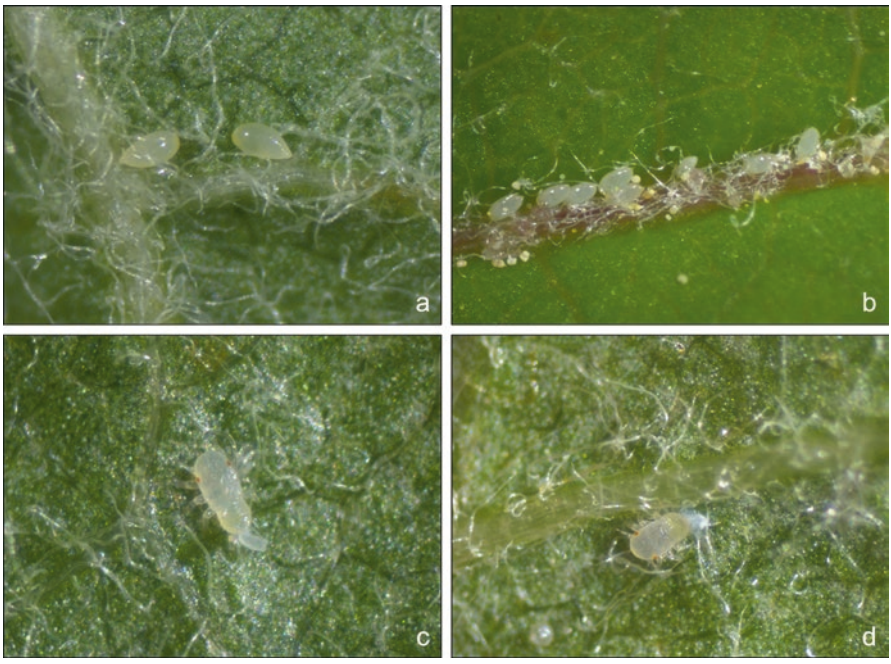

Fig. 3.1 *Cacopsylla picta* pre-imaginal stages: (**a** and **b**) eggs, (**c** and **d**) nymphs (Courtesy by L. Görg)

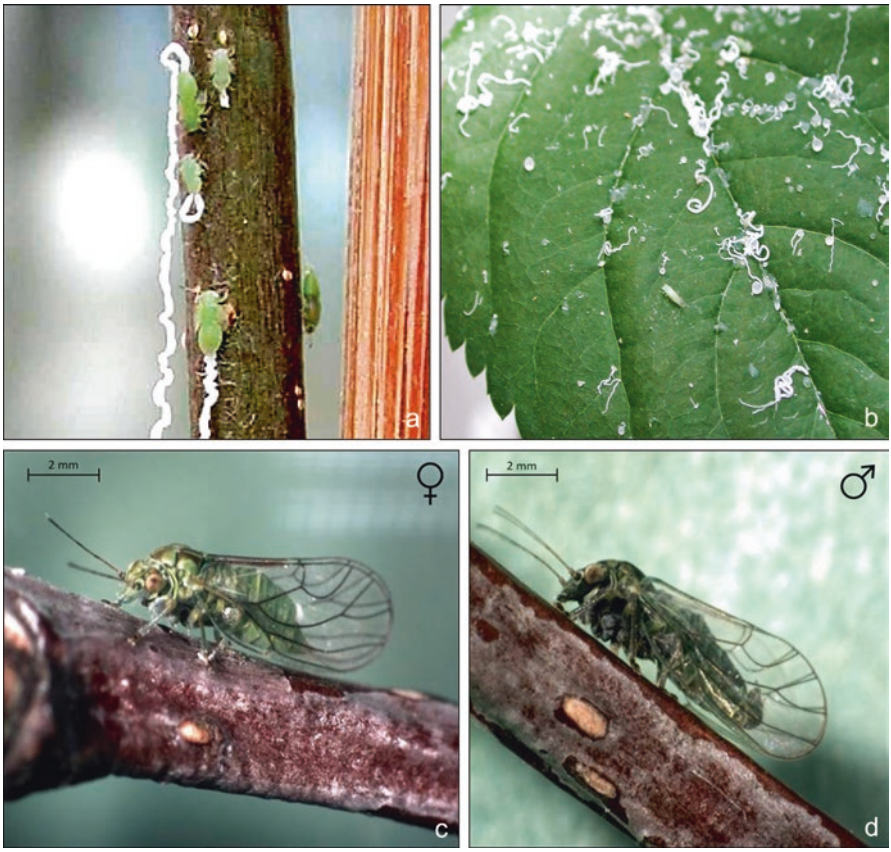

Fig. 3.2 *Cacopsylla picta*: (**a**) 5th stage nymph with waxy secretions, (**b**) newly emerged adult, (**c**) overwintered female and (**d**) overwintered male

infected with the pathogen every year (Jarausch et al. 2004, 2007a, 2011). Data for Northern Switzerland (10%) (Jarausch et al. 2011), Western France (Alsace: 14%) (Jarausch et al. 2011), Finland (11%) (Lemmetty et al. 2011) and Spain (13%) (Miñarro et al. 2016) were in a similar range. A lower infection rate of roughly 3% was reported from Bulgaria (Etropolska et al. 2015). Jarausch et al. (2011) found no significant relationship between the infection status of the orchard and the infection rate of *C. picta* remigrants captured within these orchards, although a tendency of higher infection rates in abandoned orchards was observed.

These data can be explained by a regional dispersal of remigrant individuals and by a certain percentage of transovarial transmission of the phytoplasma as detected by Mittelberger et al. (2017). During experimental transmission trials in different laboratories in Germany and Italy it was confirmed that both emigrants and remigrants of *C. picta* can transmit the agent efficiently (Jarausch et al. 2004, 2007a, 2011; Carraro et al. 2008; Mattedi et al. 2008). However, the transmission efficiency

was usually higher with remigrants (range of 8–45% with groups of 5 individuals) than with emigrants (range of 2–20% with groups of up to 20 individuals) (Jarausch et al. 2011). Both, males and females, can transmit the phytoplasma and are naturally infected to a similar percentage. As males and females are present in the orchards at a ratio of 1:1.4 (Jarausch et al. 2011), both genders can contribute to the spread of apple proliferation phytoplasma (‘*Ca*. P. mali’).

The phytoplasma concentration in the infected individuals of *C. picta* was extremely high and ranged between 10^6 and 10^8 as measured by quantitative PCR (Jarausch et al. 2011; Mayer et al. 2009). Phytoplasma-infected and infective psyllids appeared among the first remigrants of *C. picta* in apple orchards in early spring, indicating winter-retention of the pathogen (Jarausch et al. 2011; Mattedi et al. 2008). Furthermore, phytoplasma concentrations in the remigrants were constantly high and did not differ significantly during the first 7 weeks after arrival in the orchard (Jarausch et al. 2011). Thus, remigrants are considered to be infective during their whole life span on apple after overwintering. Although remigrants readily transmitted the phytoplasma under experimental conditions, this could not be verified by bait plant trails in the orchard: natural transmission in the orchards in Trentino was found to be situated during the migration period of the new generation of *C. picta* (Mattedi et al. 2008). Transmission by emigrants before leaving the orchard is not also supported by experimental transmission trials, but also by quantitative PCR data which indicate that ‘*Ca.* P. mali’ multiplies very quickly to high concentrations after experimental acquisition (Pedrazzoli et al. 2007). Individuals born on infected plants acquired the phytoplasma to nearly 100% while new adults emerged on healthy plants and fed thereafter on infected plants had only an acquisition rate of about 10% (Jarausch et al. 2010).

In conclusion, *C. picta* is able to transmit ‘*Ca*. P. mali’ during the entire period when they are present on apple trees. As remigrants as well as emigrants are able to transmit, a polycyclic disease spread is supposed in which remigrants disperse the pathogen on a regional as well as local scale and emigrants on a local scale (Jarausch et al. 2011). Although the population density of *C. picta* in the orchards is usually low (Jarausch et al. 2009, 2011), this species is considered to be the main vector of apple proliferation wherever it is present.

In Germany, *C. picta* transmits all three ‘*Ca.* P. mali’ subtypes AT-1, AT-2 and AP as defined by Jarausch et al. (2000) (W. Jarausch, unpublished data) while in Alto Adige (South Tyrol) (Italy) the spread of apple proliferation seems to be predominantly linked to the transmission of subtype AT-2 by *C. picta* (Baric et al. 2011). All three subtypes were also identified in *C. picta* of North East Italy (Martini et al. 2008). *C. picta* individuals captured in Finland were infected with subtypes AT-2 and AP (Lemmetty et al. 2011). Jarausch et al. (2010) also reported differences in acquisition, multiplication and transmission efficiencies among different strains of ‘*Ca.* P. mali’. Interestingly, strains which multiplied best in the insect exhibited the lowest titers in apple plantlets.

3.3 *Cacopsylla melanoneura*

Cacopsylla melanoneura (Fig. 3.3) has a holo-Palaearctic distribution and is oligophagous on Rosaceae plants such as *Crataegus* spp., *Malus domestica*, *Mespilus germanica* and *Pyrus communis* (Ouvrard 2017). This species was originally described as hawthorn psyllid (Lal 1934; Ossiannilsson 1992; Lauterer 1999), while successively it has become an economically injurious pest of apple trees in particular in relation to the spreading of the apple proliferation disease (Alma et al. 2000;

Fig. 3.3 *Cacopsylla melanoneura* life stages: (**a**) eggs, (**b**) 1st and 2nd stage nymphs, (**c**) 5th stage nymph, (**d**) newly emerged female, (**e**) overwintered female, (**f**) overwintered male (DISAFA, Entomology unit, University of Torino, Italy)

Tomasi et al. 2000; Tedeschi et al. 2002). In most of the areas where the presence of the disease has been recorded, *C. melanoneura* and *C. picta* occur sympatrically (Jarausch et al. 2003; Delić et al. 2005; Mattedi et al. 2008; Miñarro et al. 2016), in some others (Northwestern Italy and Norway) only *C. melanoneura* has been reported (Tedeschi et al. 2002; Brede 2017).

Several studies on natural infection rate and vector ability of this species revealed a diversified scenario. Generally in apple growing regions where *C. melanoneura* and *C. picta* coexist, the latter has a major vector role (Frisinghelli et al. 2000; Mattedi et al. 2008; Jarausch et al. 2003, 2004, 2007a), while *C. melanoneura* has been considered ineffective in transmitting '*Ca.* P. mali' (Mayer et al. 2009). On the contrary in the areas where *C. picta* does not occur, in particular in Northwestern Italy, *C. melanoneura* has an important role in the spreading of the disease (Tedeschi et al. 2002, 2003; Tedeschi and Alma 2004). Indeed, natural infection rates in apple orchards is very low, less than 1% in Germany, Northern Switzerland, Eastern France (Mayer et al. 2009); but ranging from 4.2% (0,6% in average) in South Tyrol (Northeastern Italy) (Baric et al. 2010; Fischnaller et al. 2017) to 5–6.2% in Trentino region (Northeastern Italy) where the role of this insect as vector of '*Ca.* P. mali' has been recently reviewed (Malagnini et al. 2010; Tedeschi et al. 2012), and reaching around 4% and up to 45% in a 100% infected orchard in Northwestern Italy (Tedeschi et al. 2003). Moreover, against a non-transmission reported in Germany, 0.36% of infected plants were obtained after transmission trials with *C. melanoneura* from Trentino (Northeastern Italy) (Mattedi et al. 2008), while in Northwestern Italy 29.4% of plants inoculated with naturally infected overwintered adults (88.9% in the case of insects collected in a 85% infected orchard) tested positive to '*Ca.* P. mali' (Tedeschi and Alma 2004). Due to the fact that these transmission trials were carried out using batches of around 20 specimens/test plant, a range of 1.4–8.4% of probability of transmission by a single *C. melanoneura* was estimated in Northwestern Italy (Tedeschi and Alma 2006). In particular it was highlighted the crucial role of overwintered individuals in comparison to newly emerged adults due to a higher percentage of '*Ca.* P. mali'-positive individuals (3.6% vs. 0.8%) and a longer period spent in apple orchards (14.6 vs. 6 weeks) (Tedeschi et al. 2002, 2003). These differences in relation to vector attitude of *C. melanoneura* are confirmed also by the phytoplasma titre in the insect. In Germany, the maximum phytoplasma concentration never exceeded 40,000 copies/individual in field collected insects, far below the minimum titre threshold found for an effective transmission by *C. picta* (10^6–10^8 phytoplasma DNA copies) (Jarausch et al. 2007a, 2011; Mayer et al. 2009). However, in Northwestern Italy '*Ca.* P. mali' reached a concentration of 10^4–10^6 copies/individual *C. melanoneura* (Monti et al. 2013). The life cycle is similar to that of *C. picta*, but the overwintering adults appear earlier in the year on *Crataegus* spp. or apple trees (Mayer et al. 2011). This migration is dependent on a temperature threshold, recorded in the orchards, which in Northeastern Italy has been found to be around 9.5°C (Tedeschi et al. 2012). Likewise the new generation abandons the host plant earlier (end May–June) than *C. picta* to migrate to the aestivation and overwintering plants (Mattedi et al. 2008; Tedeschi et al. 2002). The overwintering plants are reached, thanks to warm ascending currents, at different

altitudes depending on the geographical area, 462–535 m a.s.l. in South Moravia, mainly 1350–1650 m a.s.l. in Northwestern Italy (Cermák and Lauterer 2008; Pizzinat et al. 2011). Different conifer species were recorded as overwintering plants and by caging on them newly emerged adults from hawthorn or apple plants it was possible to follow the whole life cycle of the psyllid throughout the year (Pizzinat et al. 2011). No correlation between immigration dynamics and apple phenology could be demonstrated; however, oviposition occurs at bud burst while egg peak and hatchings are always before the first flowering. This confirmed a good degree of synchrony between *C. melanoneura* and host-plant growth, being linked with temperatures as stated for psyllids in general by Hodkinson (2009).

In order to apply well-timed control strategies, Tedeschi et al. (2012) defined an immigration index based on the maximum temperatures of the 7 days registered in the apple orchard, to predict the arrival of the overwintered adults. In practice, in the Valsugana valley (Northeastern Italy) where this study was carried out, psyllids start to reach the apple orchards when this threshold is 9.5°C. In other areas this threshold should be adjusted either according to historical collection data or by programming periodical field collections. Moreover, other geographical factors associated with the winter sites location (e.g., the regional orography, the main air streams and distance from apple orchards) may differently affect the psyllid migration process and influence its presence or absence, both in terms of time and quantity, in a given apple orchard (Tedeschi et al. 2012).

Concerning host plants, so the plants on which *C. melanoneura* feed, copulate, lay eggs and completes its immature to adult life cycle, several studies attributed diverse roles to hawthorn or apple, depending on different geographical areas. In Northwestern Italy, *C. melanoneura* is equally common in both apple orchards and on *Crataegus monogyna* plants; moreover hawthorn plants have been found infected with '*Ca.* P. mali' entailing a possible role of this plant as a phytoplasma source of inoculum (Tedeschi et al. 2009). On the contrary in Germany this psyllid preferred hawthorn as host plant which, however, was not found infected with the phytoplasma (Mayer et al. 2009).

All the different roles assigned to *C. melanoneura* (i.e. efficiency in acquiring and transmitting '*Ca.* P. mali') by the studies conducted to date suggest the existence of different populations at both geographical and host plant scale (Malagnini et al. 2010, 2013; J. Gross and R. Tedeschi, unpublished results), but also of different combinations of psyllid populations and phytoplasma strains (Baric et al. 2011). In particular there is a strict co-occurrence of AT-1-associated subtypes of '*Ca.* P. mali' and *C. melanoneura* in several regions of Northwestern Italy, where *C. melanoneura* is considered to be the most important vector of apple proliferation (Casati et al. 2010), while in other regions where *C. picta* is the principal vector there is the dominance of '*Ca.* P. mali' subtypes AT-2 (Cainelli et al. 2004; Jarausch et al. 2000; Baric et al. 2011) or AP (Jarausch et al. 2000, 2004; Martini et al. 2008).

3.4 *Cacopsylla pruni*

Cacopsylla pruni (Scopoli 1763) (Fig. 3.4) is widespread in its native Western Palearctic area (Ossiannilsson 1992; Steffek et al. 2012; Ouvrard 2017). This psyllid species is strictly oligophagous on *Prunus* spp., completes one generation per year and overwinters as an adult on conifers. At the end of winter – early spring, according to the climatic conditions and the geographic zones, adult remigrants move from the overwintering plants back to *Prunus* spp. for oviposition. They prefer wild, uncultivated *Prunus* spp. as host plants such as *P. spinosa* (blackthorn) or *P. cerasifera* (myrobolan) (Labonne and Lichou 2004; Jarausch et al. 2008) but they

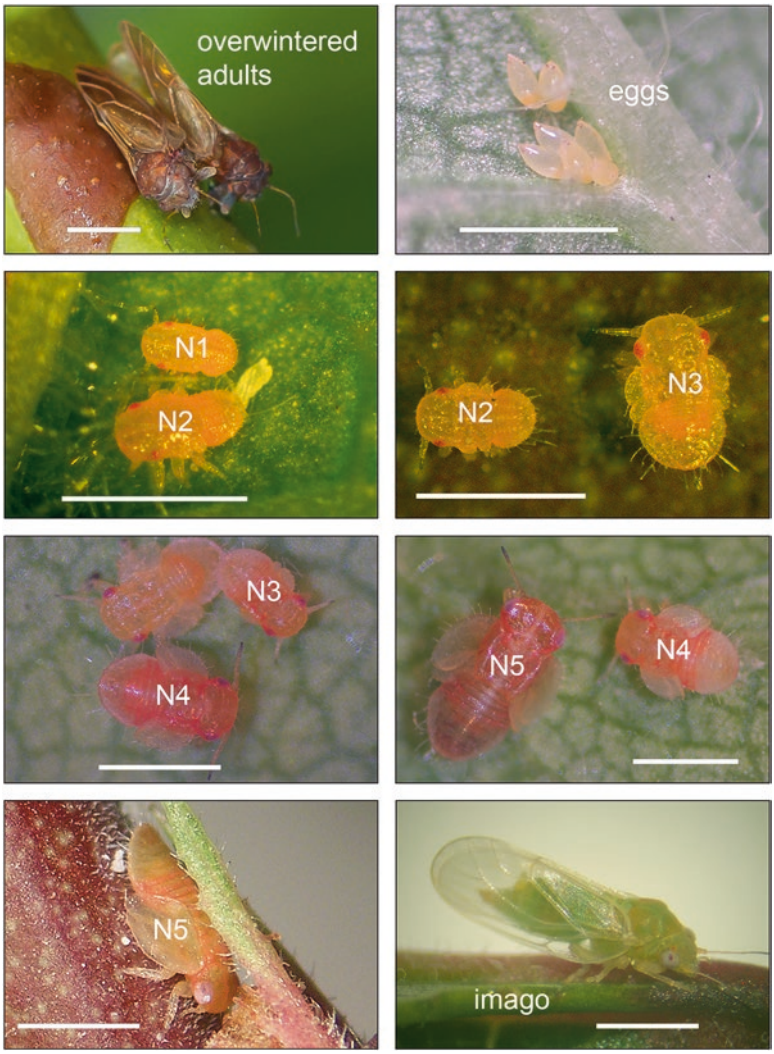

Fig. 3.4 *Cacopsylla pruni* life stages Bar = 1 mm

can also reproduce on cultivated *Prunus* e.g. apricot, peach or European and Japanese plum. Interestingly, remigrants were highly attracted by rootstock suckers of apricot trees where high oviposition rates could be observed and population densities of newly emerged adults were high (Labonne and Lichou 2004). The adults of the new generation feed on their reproduction hosts until the beginning of July, when they leave the *Prunus* plants to move to their overwintering plants (Carraro et al. 2001b, 2004; Thébaud et al. 2009). So far, *C. pruni* is the only psyllid species described as vector of '*Ca*. P. prunorum' (Carraro et al. 1998; Jarausch et al. 2001, 2007b, 2008; Thébaud et al. 2009; Marcone et al. 2010). A comprehensive overview of the distribution of '*Ca.* P. prunorum' and its vector *C. pruni* in European fruit-growing areas was reviewed by Steffek et al. (2012). Recently, Peccoud et al. (2013) proposed that *C. pruni* is a complex of two cryptic species, provisionally named *C. pruni* "A" and *C. pruni* "B". Population genetics analysis with microsatellite markers (Sauvion et al. 2007) showed that the two species overlap over a large geographical area around the Mediterranean (N. Sauvion, unpublished data) and there are indications that both cryptic species are potential vectors of '*Ca*. P. prunorum'.

Naturally infected individuals of *C. pruni* were found in several European countries like Italy (Carraro et al. 1998), France (Yvon et al. 2004), Spain (Laviña et al. 2004), Czech Republic (Fialová et al. 2004), Switzerland (Ramel and Gugerli 2004), Germany (Jarausch et al. 2007b), Bosnia-Herzogovina (Delić et al. 2008), Turkey (Ulubaş Serçe et al. 2011), Austria (Lethmayer et al. 2011) and Bulgaria (Etropolska et al. 2016). Interestingly, the natural infection rate of *C. pruni* highly varies among different geographical zones and in most of the described cases very few individuals were carrying the phytoplasma in the field. In Germany, Jarausch et al. (2007b, 2008) found 2–3% of the field collected overwintered adults naturally infected by '*Ca*. P. prunorum'. Similar low infection rates of only 0.6% were confirmed in France by Jarausch et al. (2001) and Thébaud et al. (2008). In contrast, Ermacora et al. (2011) reported infection rates in the first remigrants in apricot orchards in Northeastern Italy of 56.4% reaching a plateau slightly exceeding 80% in the last two captures. Ulubaş Serçe et al. (2011) found a mean percentage of 23% infected individuals of *C. pruni* collected on *P. spinosa* or wild plum. In a recent study, Maier et al. (2013) ascertained the phytoplasma in 0–11.5% of the remigrants and in 0–3.44% of the springtime generation insects in lower Austria.

The transmission of '*Ca*. P. prunorum' by different developmental stages of *C. pruni* was studied in detail under controlled conditions (Carraro et al. 1998, 2001b, 2004). The overwintered adults (remigrants) as well as the adults of the new generation (emigrants) of *C. pruni* were able to transmit the agent to healthy test plants. The remigrants were often already infected and infectious when they reached their *Prunus* hosts in early spring. The authors concluded that *C. pruni* transmits the winter-retained phytoplasma that had been acquired the previous year. The overwintered psyllids continued to transmit the pathogen in a persistent manner until their death. During transmission trials under controlled conditions conducted in Germany by Jarausch et al. (2007b, 2008), the vector capacity of overwintered and new generation adults of *C. pruni* was consistently lower than that described by Carraro et al. (2001b, 2004). Similar low infectivity and transmission rates of only 0.6%

were confirmed in France by Jarausch et al. (2001) and Thébaud et al. (2008). Thébaud et al. (2009) demonstrated that the population of *C. pruni* has an extremely long "effective latency" period which lasts the overwintering period. During this time the phytoplasma concentration within the insects continuously rises reaching a maximum of 10^7 phytoplasmas per insect at remigration. They concluded that only overwintered adults can efficiently transmit the agent and, thus, the disease spread is monocyclic. The vertical (transovarial) transmission of '*Ca.* P. prunorum' was not observed by Carraro et al. (1998) and Thébaud et al. (2009) whilst Tedeschi et al. (2006) proved the existence of this passage in *C. pruni*. Many studies showed that wild *Prunus* spp. play an essential role in the epidemiology of the disease, not only as a reservoir of the psyllid vectors but also of the phytoplasma, in particular blackthorn (*P. spinosa*) and myrobalan plum (*P. cerasifera*) (Jarausch et al. 2001, 2008; Carraro et al. 2002; Fialová et al. 2004, 2007; Labonne and Lichou 2004; Laviña et al. 2004; Poggi Pollini et al. 2004; Yvon et al. 2004; Ramel and Gugerli 2004; Delić et al. 2008; Maier et al. 2013). Recently, Sabaté et al. (2016) pointed out the role of *P. mahaleb* as potential reservoir of '*Ca*. P. prunorum' and its vector *C. pruni* in Spain. Whereas low populations of *C. pruni* were found on cultivated *Prunus spp.* such as *P. armeniaca, P. persica, P. amygdalus* and *P. domestica,* much higher vector densities were reported from different wild *Prunus* spp. such as *P. spinosa, P. cerasifera, P. domestica* and *P. salicina*. Interestingly, the wild *P. spinosa* and *P. cerasifera,* which represented reservoirs for the pathogen and the vector, rarely showed typical symptoms (Carraro et al. 2002; Jarausch et al. 2008). In conclusion, many wild *Prunus* spp. play an important role in the epidemiology of ESFY disease as the cycle of '*Ca*. P. prunorum' as well as of its vector *C. pruni* can be completed independently from the presence of infected cultivated stone fruit trees. In order to determine the distance that psyllids could spread the pathogen by natural means, Maier et al. (2013) tracked the dispersal of *C. pruni* in a model apricot orchard in lower Austria during a mark, release and recapture experiment. The study proved a fast and frequent tree-to-tree movement of *C. pruni* adults. Insects easily covered distances from row to row or even farther (ca. 13 m) within 24 hours after release and were present in a large part of the model orchard after 8 days (up to 24 m from the release point).

3.5 Pear Psyllids

In Europe, three recognized or presumed vectors of pear decline disease (PD) live on pear: *Cacopsylla pyri* (Linné 1758) (Fig. 3.5), *C. pyricola* (Foerster 1848), and *C. pyrisuga* (Foerster 1848). *C. pyri* is reported from Europe, the Caucasus, Central Asia, the Russian Far East and China; *C. pyricola* naturally occurs in the Western Palaearctic and has been introduced into the USA and Canada in the early nineteenth century (Ossiannilsson 1992; Ouvrard 2017). The two species are oligophagous on *Pyrus* species such as *P. communis*, *P. eleagrifolia*, *P. pyraster*, *P. amygdaliformis* and *P. salicifolia* (Burckhardt 1994). The biology of *C. pyri* and *C.*

Fig. 3.5 *Cacopsylla pyri* life stages: (**a**) eggs, (**b**) nymphs, (**c**) adults, (**d**) female (DISAFA, Entomology unit, University of Torino, Italy)

pyricola is similar since both are polyvoltine (Burckhardt and Hodkinson 1986). Thus, *C. pyri* can complete 4–5 generations in Central Europe and up to 8 generations in Southern France. Two morphologically distinct forms can be distinguished: a darkish winter form (*C. pyri* f. *pyri*) and a light summer form (*C. pyri* f. *pyrarboris*). *C. pyricola* has 4–5 generations in France and 3–4 in the USA with the darker winter form (*C. pyricola* f. *simulans*) appearing as one and the lighter summer form (*C. pyricola* f. *pyricola*) as 3–4 generations per year, respectively. The first oviposition of the winter form coincides with raising temperatures in early spring on leave buds and midribs of the leaves (Burckhardt 1994). In contrast, *C. pyrisuga* is univoltine; the adults overwinter on conifers and remigrate to *Pyrus* spp. by middle March to April. Egg deposition takes place in two different steps at the beginning of April and second in the middle of May followed by a 6 week lasting nymph development and the emergence of new adults in June. All three pear psyllids can cause direct damage on pear trees: the nymphs affect plant growth by sucking phloem-sap, while the secreted honeydew burns plant tissue and favours the growth of sooty mold.

First reports of pear psyllids as vectors of phytoplasmas came from the Pacific coast of North America. Jensen et al. (1964) identified *C. pyricola* as the vector of '*Ca.* P. pyri' at a time when the disease was thought to be virus-borne. Since then no

further vector has been described for the USA. However, the distribution of the putative vectors of '*Ca.* P. pyri' in Europe and the whole Palearctic region is diverse: while for Great Britain only *C. pyricola* has been described as vector (Davies et al. 1992), *C. pyri* was identified as main vector in France (Lemoine 1984), Italy (Carraro et al. 1998) and Spain (Garcia-Chapa et al. 2005). In Czech Republic (Kucerova et al. 2007; Ludvikova et al. 2011) and in lower Austria (Lethmayer et al. 2011) all three pear psyllid species were found naturally infected with '*Ca*. P. pyri', while in Turkey only *C. pyri* carried the phytoplasma albeit all the three species were present in the investigated regions (Kaya et al. 2016). In contrast to *C. pyri* and *C. pyricola*, the vector capability of *C. pyrisuga* is so far not yet confirmed (Jarausch and Jarausch 2010). Recently, a fourth pear psyllid, the polyvoltine species *Cacopsylla bidens* (Šulc 1907) has been found infected with '*Ca.* P. pyri' in Bulgaria (Etropolska et al. 2015). Also for this species its vector capability still needs to be proven.

After the identification of *C. pyricola* as vector for '*Ca*. P. pyri' in California (Jensen et al. 1964), many investigations in the USA and Europe followed in order to determine the infection rate of the psyllids and to analyse the transmission parameters. In United Kindgdom transmission trials carried out with field-collected *C. pyricola* yielded transmission rates between 3–61% depending on the collection site of the psyllids (Davies et al. 1992). Acquisition of '*Ca*. P. pyri' by *C. pyricola* from experimentally infected pear seedlings was best in August and lowest in winter. In California, Blomquist and Kirkpatrick (2002a) detected the pathogen in both winter and summer forms of *C. pyricola*, but without a clear seasonal trend. The number of phytoplasmas per psyllid was estimated to range from 1×10^6 to 8.2×10^7 with higher titre in the winter form. They concluded that psyllid-mediated spring infections could happen well before '*Ca*. P. pyri' would normally recolonize the upper part of the tree from the roots. In Italy, Carraro et al. (1998, 2001a) detected '*Ca*. P. pyri' in 55% of groups of *C. pyri* collected from March to October in the orchards and 30% of the inoculated test plants became infected. They could furthermore show that *C. pyri* retained the phytoplasma during winter, but could not transmit PD to dormant plants. Raddadi et al. (2011) tested *C. pyri* collected in Italian pear orchards detecting '*Ca.* P. pyri' in 26% of the specimens (in 27% of males, and in 25% of females) with nested-PCR and in 51% of the individuals through quantitative PCR with a number of '*Ca.* P. pyri' cells ranging from 1.43×10^1 to 8.50×10^5 per *C. pyri* individual. Moreover, fluorescent *in situ* hybridization (FISH) allowed to detect '*Ca.* P. pyri' in Malpighian tubules and salivary glands of *C. pyri*. Garcia-Chapa et al. (2005) found that the percentage of infected individuals in Spain is similar from June to August but reaching a rate of almost 100% in September coinciding with the maximum phytoplasma titre in the aerial plant parts. The highest transmission rate to an artificial sucrose medium was obtained in August and also in October. Although the percentage of infected psyllids was similar for both genders, '*Ca*. P. pyri' transmission by females was significantly higher than by males. During transmission trials under controlled conditions Caglayan et al. (2010) showed the capability of *C. pyri* to transmit PD from infected pears to healthy periwinkles and confirmed it as vector of '*Ca*. P. pyri' in Turkey.

PD has also been found in Taiwan (PD-TW) where the European species *C. pyri* and *C. pyricola* are not present. Liu et al. (2007) found two other *Cacopsylla* species, *C. qianli* and *C. chinensis*, infected with the PD-TW phytoplasma. Their role in transmission of PD-TW phytoplasma in Taiwan remains to be clarified. But recently Liu et al. (2011) proved the transmission capacity of *C. chinensis* during transmission trials in Taiwan. Based on PCR detection and symptom development they showed that pear trees were either infected by PD-TW or PD-TWII phytoplasma strains, or co-infected by both, when exposed to *C. chinensis* specimens.

Insect vectors for peach yellow leaf roll (PYLR) phytoplasma have been searched intensively in California in the 1980s and 1990s. As two similar diseases, western X and PYLR, associated with two genetically distinct phytoplasmas exist in the same region, only the application of molecular methods enabled to proof that a psyllid is the main vector of PYLR phytoplasma. Experimental transmission of PYLR phytoplasma to peach seedlings was achieved with field collected *C. pyricola* from naturally infected peach trees (Guerra 1997). In field surveys for leafhoppers and psyllids in diseased peach orchards only *C. pyricola* proved to be infected with PYLR phytoplasma as confirmed by molecular means (Blomquist and Kirkpatrick 2002b). Ten to 25% of groups of 10 individuals were positive indicating a high infection rate. Infected psyllids were captured from peach as well as from pear grown in the neighbourhood. The population dynamics of *C. pyricola* was similar in peach and pear with low densities in summer and an increase in autumn. Thus, the spread of PYLR is dependent on adjacent pear orchards where presumably the vector reproduces (Purcell et al. 1981).

3.6 Genetics

Morphological differentiation is problematic due to extensive resemblance of some psyllid species especially among females and is error-prone for nymphs (Oettl and Schlink 2015). DNA-based techniques for the identification of insect species have recently become of particular interest either to support or even to replace traditional morphological discrimination (Jenkins et al. 2012). Molecular methods offer in particular advantages for the identification of immature stages where distinct morphological characters are lacking or are not sufficient for discrimination at the species level. Furthermore, molecular methods can help to identify insects which are damaged by removal from sticky traps. One approach is PCR-RFLP based on the cytochrome c oxidase subunit I (COI) region. This gene is widely used as barcoding marker for species determination and provides therefore a valuable tool also for the identification of invasive insect species and quarantine pests. This method has been successfully applied for the molecular discrimination of *C. melanoneura* and *C. picta* from other *Cacopsylla* species which are difficult to distinguish by morphological means (Oettl and Schlink 2015). This rapid and cost-effective approach allowed also a reliable identification of nymphal stages.

Tedeschi and Nardi (2010) developed a molecular tool based on the mitochondrial control region (CR) to distinguish psyllid species living together on hawthorn:

C. melanoneura and *C. affinis*. This PCR assay allowed the species identification by using specific primers and different sizes of the PCR products. By testing individuals of *C. melanoneura* from different regions in Italy, two genetic variants were detected by this method. The variants differed by the presence (WI, with indel) or the absence (WOI, without indel) of a 56 bp indel. Whereas the WOI type was dominant in all tested regions the WI type was consistently found at low percentages ranging from 5% to 31%. Recently, WI and WOI variants of *C. melanoneura* were also detected by this approach in Bulgaria (Etropolska et al. 2016). A distinction of different populations of *C. melanoneura* was enabled by the development of microsatellite markers for this species (Malagnini et al. 2007). With these SSR markers populations from apple could be differentiated form those of hawthorn indicating that two different host races of *C. melanoneura* may exist (Malagnini et al. 2013). Whether these genetic differences are linked to the observed differences in phytoplasma vectoring ability is not known.

Microsatellite genotyping was also applied to analyse the population structure of *C. pruni* (Sauvion et al. 2007, 2009). Based on the analysis of nine microsatellite *loci* two distinct populations of *C. pruni* – named A and B – were identified. Peccoud et al. (2013) demonstrated that both groups can be phylogenetically separated on their ITS2 sequences. These authors developed specific PCR primers for each group enabling an easy molecular typing of *C. pruni* A and B. It is important to note that both groups cannot be distinguished morphologically. As far as known, both populations occur sympatrically in Southern France while type B is predominant in most of the other European regions. Etropolska et al. (2016) found only *C. pruni* type B in different regions of Bulgaria.

3.7 Rearing

Although all Psylloidea pass through 5 instars, the period for complete nymph development under natural conditions can be highly influenced by variations of ambient temperature, humidity and voltinism status (Hodkinson 2009). This inconvenience can be eliminated by the establishment of rearings under controlled and standardised conditions. Breeding of polyvoltine species without host alternation such as *C. pyri* can be started from field collections on *Pyrus* cv. all around the year. However, also multivoltine species such as *C. pyricola* or *C. pyri* undergo a reproductive diapause in the autumn generation (Hodkinson 2009). Compared with polyvoltine psyllid species, the austere life cycle and obligate host change of univoltine species makes collection and rearing difficult. However, efforts undertaken during the last years identified the key factors for the establishment of permanent rearings of the univoltine species *C. picta* and *C. pruni*.

The most common way to establish psyllid colonies usually starts from pairs or groups of field collected adults which are caged on specific host plants for copula-

tion and oviposition. In order to obtain healthy psyllid populations for diverse laboratory use, standardised plant material from tissue culture or from seedlings was used, e.g. from *Malus* cultivars Golden Delicious or Royal Gala for *C. picta* and *C. melanoneura* colonies (Jarausch et al. 2004; Mayer et al. 2009; Tedeschi et al. 2003) or from *Prunus* cultivars *P. marianna*, *P. salicina or P. cerasifera* for *C. pruni* (Carraro et al. 2001b, 2004; Jarausch et al. 2008; Thébaud et al. 2009), respectively. Since transovarial transmission of the phytoplasma has been demonstrated for *C. picta* (Mittelberger et al. 2017) and *C. pruni* (Tedeschi et al. 2006), PCR testing of individuals has to be done to ensure a phytoplasma-free psyllid population. For subsequent acquisition trials, rearings were directly installed on phytoplasma-infected *Malus* or *Prunus* cultivars under similar rearing conditions.

Breedings of the most important univoltine *Cacopsylla* vector species *C. picta, C. melanoneura* and *C. pruni* were installed in cages, bugdorms or glass vessels infested with mature females and males collected from their natural host plants from February until April (Carraro et al. 2002; Jarausch et al. 2004, 2008; Mayer et al. 2008a; Tedeschi et al. 2003). The preimaginal development under recommended rearing conditions for these northern temperate species (20–25°C day and around 15°C night, relative humidity between 50–80% and natural day light conditions of light:dark, 16:8 hours) (Jarausch and Weintraub 2014) takes about 5 weeks until emergence of new adults. Thus, psyllid colonies could be maintained on the reproduction host plant under experimental conditions for several months, at least until autumn of the same year. However, as univoltine vector species have an obligate alternation of plants for reproduction and overwintering, a permanent rearing was not possible. For a long time it was believed that conifers are used by migrating *Cacopsylla* species just for shelter during winter time (Burckhardt 1994; Burckhardt et al. 2014). It remained unclear whether overwintering psyllids actually fed on conifers (Hodkinson 2009). Recent studies confirmed that these species have a feeding activity on overwintering plants (Gallinger and Gross 2018), and die when isolated on a deciduous conifers plant such as *Larix decidua* (Pizzinat et al. 2011). Thus, Jarausch and Jarausch (2014) succeeded for the first time to maintain a hibernating continuous colony of *C. picta* until the next year and hence they could establish a permanent rearing of this vector species. Based on empiric data from field observations in combination with results obtained during laboratory experiments they elaborated the following parameters and key factors for a successful overwintering of *C. picta* and the establishment of a continuous rearing: (i) smooth host plant switch, (ii) moderate summer temperatures and sufficient humidity, (iii) natural winter climate conditions with cold and frost and (iv) suitable conifer species, in this case spruce or pine. The model suggests a direct migration of emigrants from the reproduction host apple to conifers as aestivation and overwintering plants in summer and vice versa to apple orchards for remigrants in early spring. However, the host plant switch does not occur abrupt, but is characterized by a smooth adaptation phase from its host for reproduction to its overwintering plants as experimentally demonstrated. Despite some species-specific particularities, the same approach was adopted for rearing the vector of '*Ca*. P. prunorum', *C. pruni* (Jarausch and

Jarausch 2016). These studies confirmed that both psyllid species are univoltine and cannot reproduce on conifers.

A further rearing approach for *C. pruni* was applied by Thébaud et al. (2008) using sleeve cages on healthy or infected *Prunus* plants. Thébaud et al. (2009) found *C. pruni* on *Picea abies* at an altitude of 1260 m a.s.l. and were able to overwinter them in sleeve cages on these conifers but survival rates ranged only between 1.2 and 8.9%. Using a similar approach, Pizzinat et al. (2011) could hibernate *C. melanoneura* in branch cages on different coniferous species at an altitude between 1442 and 1636 m a.s.l. in Northwestern Italy.

3.8 Multitrophic Interaction

The secret language of the earth's ecosystem involves a multitude of players that populate the playing field and occupy different rungs on the food chain (Wartenberg 2016; Gross 2016; Sauvion et al. 2017). The actors include plants, plant feeding insects, insect feeding insects, plant parasites, insect parasites, pathogenic and beneficial microorganisms, vectoring organisms, pollinators, and more (Gross 2016; Corcket et al. 2017; Kaiser et al. 2017; Giron et al. 2017). Thus, fundamental research on the biology and ecology including chemically mediated multitrophic interactions of vectoring psyllids is needed for understanding vector epidemiology, plant pathogen transmission and for developing appropriate and sustainable control measures of vectors and pathogens (Gross 2016).

The natural enemies of phloem-feeding insects (predators, parasitoids, or entomopathogens) may have large effects on speciation, community composition and ecosystem processes (Elzinga et al. 2007). Hence, these plant-pathogen–vector systems are of particular interest, in which a transmitted pathogen infects both, its host plant and vector insect, because pathogens and their differing hosts (plant and insect) must develop co-adapted strategies to avoid deleterious effects of each other (Gross 2016). In general, the pattern of volatile organic compounds (VOCs) released from plant modules (leaves and flowers) can change both quantitatively and qualitatively with abiotic (e.g. warming, drought) and biotic stressors (e.g. herbivore feeding, pathogen infection).

The role of allelochemicals for psyllid behavior and the influence of phytoplasma infections on volatile production of psyllid host plants were studied during the last 12 years (Gross 2016). For identifying their particular host plants for feeding and reproduction, volatile signals are used in many species during migration (Gross and Mekonen 2005; Mayer et al. 2008a, 2008b, 2009; Soroker et al. 2004; Weintraub and Gross 2013). Also non-volatile phloem/xylem components influence host choice and maybe oviposition behaviour (Mayer et al. 2011). By analysing the VOCs emitted by the leaves of apple trees, it was shown that '*Ca*. P. mali' changed the odour of infected trees compared to healthy ones (Mayer et al. 2008a). In pear trees infected with '*Ca*. P. pyri', the expression of ethylbenzoate differed significantly between infected and healthy trees. The virulence of different strains of '*Ca*. P.

mali' was proven to influence the pattern of produced volatiles in the model plant tobacco as well as in apple trees both quantitatively and qualitatively (Rid et al. 2016). The influence of volatiles on the interactions between the pathogen '*Ca*. P. mali', the host plants for reproduction (apple trees) and overwintering (conifers) of its vector *C. picta* and the proposed epidemiology of '*Ca*. P. mali' is the most studied so far: *C. picta* reproduces on apple and new adults emerge at phenology stages 69–71 (late blossom, early fruit development) of the apple plant. These emigrants are attracted by β-caryophyllene (Mayer et al. 2008b), which is mainly produced by infected apples during this time (Mayer et al. 2008a), and both males and females are lured to infected plants (J. Gross, unpublished data), increasing the number of psyllids, which are able to acquire the phytoplasma. Witches' broom produced exclusively by infected plants increase their leaf surface and may support the emission of volatile β-caryophyllene (Mayer et al. 2011). Shortly after feeding on apple, the adults emigrate to conifers where they stay until spring (Mayer and Gross 2007). After overwintering, the psyllids return to apple trees (remigrants), but now prefer to lay their eggs on uninfected plants, which increases the opportunity to transmit the phytoplasma (Mayer et al. 2011). Which signals may regulate this egg-laying behaviour still remains unknown and are the focus of ongoing research. By developing on apple plants infected by '*Ca*. P. mali', the nymphs of *C. picta* suffered higher mortality and remained smaller compared to the ontogenetic development on uninfected plants (Mayer et al. 2011). In contrast, infection by '*Ca*. P. mali' was tolerated by adults and seems to have no detrimental effect. Thus, females of *C. picta* evolved mechanisms to minimize harmful effects for their offspring emanated by the phytoplasma by avoiding oviposition on infected plants. In this context it seems possible that non-volatile signals from phloem sap could be involved in the psyllids' final decision (J. Gross, unpublished data). This behavior ensures the development of a new, vital vector generation, which is important for the spread of the phytoplasma. In conclusion, the complex multitrophic interactions between phytoplasma, plant and vector may result in both higher numbers of transmitting vector insects and a very effective transmission of the phytoplasma within the insect population.

The outcome of the research on multitrophic interactions is the key for developing innovative and sustainable applications in phytomedicine. Besides intraspecific active pheromones, also interspecific active allelochemicals such as β-caryophyllene or ethylbenzoate can be used as lures in traps. Different classes of infochemicals (attractants, arrestants, and repellents) can be combined to attract-and-kill strategies, push-and-pull or push-pull-kill strategies (Gross and Gündermann 2016). By using allelochemicals instead of pheromones, the emission rates of the attractive compounds, often plant produced kairomones, has to be multiple times higher than by using pheromones, requiring new types of dispensers or microencapsulated infochemicals (Gross 2017). Signals triggering interactions between psyllids, phytoplasma and plants and within psyllid species are not restricted to volatile and non-volatile infochemicals, as the existence of acoustic communication in courtship behaviour of *C. pyri* has been shown recently (Eben et al. 2014). This may enable innovative attempts for the control of *C. pyri* by extending push-and-pull strategies to acoustic signals and including the use of both attractive chemical and acoustic

signals in combination with repellent signals (also acoustic or chemical) (Gross 2017). Based on the results on multitrophic interactions the development of chemically lured traps for monitoring and mass trapping has recently started (Eben and Gross 2013; Gross and Gündermann 2016).

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