Harnessing the aphid life cycle to reduce insecticide reliance in apple and peach orchards. A review

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Abstract Apple and peach orchards are chemical-intensive systems, and aphids are one of their major pests. Aphids alter fruiting and shoot development, and they can spread viruses. Decades of insecticide use have developed aphid resistance, which calls on research to provide alternatives to chemicals for pest management. Here, we review the literature to identify, for each stage of the aphid life cycle, existing alternatives based on either top-down (i.e. aphid predation or parasitism) or bottom up (i.e. increase of host plant resistance) processes. Firstly, it was found that most studies focus on top-down processes, namely on conservation biological control aiming to preserve existing populations of natural enemies: predators, parasitoids and nematodes. This is achieved by (i) providing shelters (i.e. planting hedges, weed or flower strips) or alternative preys in periods of aphid scarcity or (ii) choosing chemicals with the lowest disruptive effects. Those methods prove more efficient when used early in the season, i.e. before the exponential increase of aphid populations. Fostering the complex of natural enemies is also preferable than just supporting one single enemy. Secondly, other techniques, like (i) releasing biological control agents (entomopathogenic fungi, nematodes) or (ii) using pheromone lures to prevent autumnal sexual reproduction, are currently adapted

for their use in orchard conditions. Thirdly, bottom-up regulation has to be devised as a long-term strategy, which could start by choosing a cultivar enabling genetic avoidance or developing genetic resistance. Then, aphid development can be reduced by the control of shoot growth or nitrogen accumulation in response to pruning or moderate water and nutrient inputs. At last, autumnal return of aphids could be disrupted by techniques such as kaolin applications that impair aphid host plant location. It is concluded that these alternative methods have to be adapted to local conditions and combined in long-term strategies in order to decrease the infestation risks throughout the orchard lifespan.

Keywords Pest management · Apple tree · Peach tree · Aphids · Alternative methods

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1 Introduction

Apple and peach are the major fruit crops worldwide. In 2013, according to the FAO (Food and Agricultural Organization) data on world deciduous fruit tree production, apple ranked 1st with a yearly production of more than 80.10^6 tons, while peach and nectarine ranked 4th with more than 21.10^6 tons, behind grapes and pear (FAO 2016).

Aphids are considered as major peach and apple pests under temperate and Mediterranean climates. First, they can harm fruit production by their detrimental effects on fruit quality, including reduction of fruit size (Filajdić et al. 1995), deformation of fruit shape (Hullé et al. 2006) or premature fruit fall (Van Emden et al. 1969). Second, they reduce overall tree vigour due to phloem sap intake, organ deformation (leaf rolling, shoot twisting), chlorosis, sooty mould development on honeydew and leaf fall (Dedryver et al. 2010). These effects can result in a decrease in C reserves and so alter long-term growth (Zvereva et al. 2010). Third, aphids can be vectors of virus transmission, including the plum pox virus, which leads to tree death (Rimbaud et al. 2015). The action threshold levels for insecticide application are low, with 1–2% of infested shoots for *Dysaphis plantaginea* (Passerini) and 8–10% for *Aphis pomi* (De Geer) (Barbagallo et al. 2007). Sometimes a single leaf deformation is enough to trigger insecticide application, due to fear of virus transmission (Penvern et al. 2010). However, data on yield loss attributable to aphids in fruit trees are scarce relative to data available for annual crops (e.g. wheat, sugar beet, potatoes (Dedryver et al. 2010)). Nevertheless, direct evaluation in an organic apple orchard attributes 21.4% of unmarketable apple fruits to *D. plantaginea* damage (Simon et al. 2011a). A modelling approach suggested a strong negative impact (more than 5% reduction in fruit growth) of *D. plantaginea* on apple fruit growth even at low aphid density (De Berardinis et al. 1994). The small number of dedicated studies may be explained by a seemingly low impact of aphids on current year fruit yield. Indeed, several studies have shown that aphid density has almost no effect on the current year yield (Filajdić et al. 1995; Grechi et al.

2008) but possibly on that of future years due to the reduction of tree vigour. Thus, multi-year experiments are needed to quantify aphid impact on yield, as suggested by a modelling approach in which aphid impact was only detected in a multi-year perspective (Bevacqua et al. 2016).

Nowadays, chemical insecticides are still widely used to control aphid populations in peach and apple orchards (Simon et al. 2011a), but due to high environmental costs and implementation of restrictive guidelines, alternatives to chemicals are needed. Moreover, pest populations resistant to chemicals have developed. A single clone of *D. plantaginea* can accumulate several resistance mechanisms conferring resistance to diverse insecticides (Delorme et al. 1999). Seven different mechanisms of resistance to insecticides have been identified in *Myzus persicae* (Sulzer), enabling this species to withstand many chemicals (Bass et al. 2014). Moreover, for a single mechanism, such as target site resistance to pyrethroids in *M. persicae*, the resistance can depend on several loci and different alleles which can coexist in a single individual (Panini et al. 2015). Another detriment of pesticide use is the perturbation of natural enemies. Laboratory studies showed for instance that some insecticides are lethal to ladybeetles and lacewings (Garzón et al. 2015) and reduced the predation activity of earwigs having been exposed to pesticides (Malagnoux et al. 2015a). In apple orchards, earwig occurrence decreased with the increase of insecticide treatments (Malagnoux et al. 2015b). The spider community was also negatively affected by the use of insecticides in organic apple orchards (Marliac et al. 2016). The side effects of pesticides could possibly be reduced by changing the mode of application, using for instance, trunk injection (VanWoerkom et al. 2014), or applying less toxic substances such as insecticidal soap (Karagounis et al. 2006). Another solution is to seek alternative methods to chemicals (Fig. 1).

In an ecosystem, herbivorous insect abundance is controlled by both top-down and bottom-up processes (Hunter and Price 1992), i.e. by the abundance and voracity of their natural enemies and by the quality and suitability of their host plant. Both control levels could be exploited for a more sustainable pest management. This review presents the alternative methods to chemicals for aphid management in apple and peach orchards adapted to each stage of the aphid life cycle. We start therefore with a quick overview of the diverse life cycles of aphid species infesting apple and peach trees. Then, the possible alternatives mobilising both bottom-up and top-down processes are presented for each aphid life cycle stage. Their side effects on other orchard pests and pathogens, and on fruit yield are finally evaluated.

Fig. 1 *Left photograph*, aphid colony on apple tree. *Right photograph*, ladybeetle larva and pupa on apple tree

2 Aphid species infesting apple and peach orchards

Numerous aphid species—with different life cycles (Fig. 2)—are able to colonise and damage peach and apple trees (examples in Table 1). Some species are monoecious (M in Table 1), i.e. they stay on their woody host species all year round, others are dioecious (D in Table 1), i.e. they alternate during the year between a primary host, on which aphids overwinter (the woody host plant), and a secondary host (usually an herbaceous plant), on which aphids spend the summer season. Aphid life cycles are characterized by multiple generations of parthenogenetic reproduction, with females asexually giving birth to female instars. If the parthenogenetic generations are interrupted by one generation of sexual reproduction in autumn, the cycle is called holocyclic (H in Table 1). In that case, sexual females lay cold resistant eggs after mating. In dioecious species, the gynoparae performs the migration between the two host plants and then mate. In monoecious species, the sexual female is called the sexuparae. Then, in spring, eggs hatch, giving birth to the fundatrices (wingless stem mothers). If the parthenogenesis is continuous, the cycle is qualified as anholocyclic (A in Table 1). To face adverse conditions, such as crowding or poor host quality, as well as to enable migration between host plants for dioecious species, aphids can produce winged morphs (Moran 1992; Hardy et al. 2015).

3 Bottom-up and top-down control methods at different aphid life cycle phases

Modification of host plant suitability through genetic resistance or modification of the abiotic environment, which exert bottom-up regulation on aphid populations (Fig. 3), embraces several aspects: (i) nutritional quality of phloem sap, which is mainly defined by the amino acid profile (Ryan et al. 2015) and the absence of defensive compounds (Czerniewicz et al. 2011), (ii) phloem sap accessibility, which is related to physical properties like viscosity or turgor pressure (Smith and

Chuang 2014), (iii) settlement site availability, which corresponds for most orchard aphid species to the number of growing apices, (iv) plant architecture, branching complexity and connectivity of the plant entities (Costes et al. 2012) and (v) canopy microenvironment (Pangga et al. 2012).

In addition to bottom-up regulation, diverse organisms can exert a top-down regulation of aphid populations through predation or parasitism (Fig. 3) and can so be considered as bio-control agents: natural enemies, i.e. predators and parasitoids, entomopathogenic fungi and nematodes. Generally, three main approaches of biological control are distinguished: (i) conservation biological control, which is based on enhancement of biocontrol agents naturally occurring in the field, (ii) biological control by augmentation, which consists in the release of biocontrol agents and (iii) introduction biological control (not treated in this review), which aims at managing exotic pests through the introduction of their natural enemies (Hopper 2003).

3.1 Egg hatching

3.1.1 Bottom-up: genetic avoidance

The synchronisation of host plant phenology and aphid life cycle is of prime importance for the success of fruit tree infestation by aphids in spring. Cultivar choice, or more specifically, the precocity of the chosen cultivar, can impair spring aphid settlement through phenological avoidance. Indeed, fundatrices are not well-armed to face unfavourable conditions (Moran 1992). So, if aphid eggs hatch while bud burst of the host plant has not yet started, the fundatrices will not be able to find new leaves to feed upon and so their survival might be strongly compromised (Dapena and Miñarro 2001). As a possible consequence of asynchrony between aphid hatching and bud burst, late bud bursting apple cultivars are less infested and damaged by *D. plantaginea* than early bud bursting cultivars (Miñarro and Dapena 2007). Indeed, developmental processes of both aphids (Pruess 1983; Satar et al. 2008; Nematollahi et al. 2016) and host plants (Kervella

Fig. 2 Variants of fruit tree aphid life cycle. In spring, aphids undergo asexual reproduction on their woody host. In summer, monoecious species stay on the woody host while dioecious species fly to their secondary host. In autumn, dioecious species fly back to their woody

host. Holocyclic species undergo sexual reproduction and oviparae lay overwintering eggs whereas anholocyclic species overwinter as wingless females

et al. 1995; Carisse and Jobin 2006) are temperature dependant, i.e. rely on degree-day accumulation above a threshold below which development stops. So, genetic avoidance usually means that a higher threshold delays the plants' development with respect to the insects' requirements.

3.1.2 Top-down

The top-down processes acting at the egg hatching stage are the same as the ones detailed in the section below. However, it should be emphasised that the efficiency of top-down control

Table 1 Life cycle characteristics and host use of the main aphid species of apple and peach trees in European orchards

	Life cycle	Host	Sources
Apple tree, <i>Malus domestica</i> Borkh.			
<i>Aphis pomi</i> De Geer	H	M	Hullé et al. 2006
<i>Aphis spiraecola</i> Patch	A	M	Hullé et al. 2006
<i>Dysaphis plantaginea</i> (Passerini)	H	D	Hullé et al. 2006
<i>Dysaphis devecta</i> (Walker)	H	M	Ryan et al. 2015
<i>Eriosoma lanigerum</i> (Hausmann)	A	M	Hullé et al. 2006
<i>Rhopalosiphum insertum</i> (Walker)	H	D	Hullé et al. 2006
Peach tree, <i>Prunus persica</i> (L.) Batsch			
<i>Brachycaudus persicae</i> Passerini	H	D	Hullé et al. 2006; Penvern et al. 2010
<i>Brachycaudus prunicola</i> (Kaltenbach)	H	M	Penvern et al. 2010
<i>Brachycaudus schwartzi</i> (Börner)	H	M	Hullé et al. 2006; Penvern et al. 2010
<i>Hyalopterus pruni</i> (Geoffroy)	H	D	Hullé et al. 2006
<i>Myzus persicae</i> Sulzer	H	D	Hullé et al. 2006; Penvern et al. 2010
<i>Myzus varians</i> Davidson	H	D	Hullé et al. 2006; Penvern et al. 2010

Life cycle: A anholocyclic, H holocyclic. Host: D dioecious, M monoecious

Fig. 3 Possible methods to control aphid populations in apple and peach orchards by mobilizing bottom-up and top-down processes

depends on the precocity of the action, due to the exponential increase of aphid populations. So, natural enemies that are active early in the season are of crucial importance (Wyss 1995; Stewart-Jones et al. 2008; Nagy et al. 2013).

3.2 Parthenogenetic reproduction

3.2.1 Bottom-up

Genetic resistance Genetic resistance can be separated into two categories: antixenosis resistance, which prevents plant colonisation, and antibiosis resistance, which alters pest development and/or reproduction (Sauge et al. 2006; Sauge et al. 2011). Genotypes can also be tolerant to aphids, meaning that they can bear abundant aphid populations without a strong negative impact on production or growth (Angeli and Simoni 2006).

In peach, cultivars resistant to *M. persicae* have been identified (Verdugo et al. 2016). ‘Weeping Flower Peach’ (Sauge et al. 2011) and ‘Rubira’ (Sauge et al. 1998, 2002, 2006; Pascal et al. 2002; Lambert and Pascal 2011) possess single dominant resistance genes, Rm1 and Rm2, respectively, conferring antixenosis resistance. The peach cultivars ‘Malo konare’ and ‘Summergrand’ and the related wild *Prunus davidiana* ((Carrière) Franch.) show antibiosis resistance. The resistance of *P. davidiana* is polygenic, i.e. located on seven QTLs (Sauge et al. 2011), and strongly reduces aphid fecundity (Sauge et al. 1998, 2011). ‘Malo konare’ and

‘Summergrand’ resistances increase aphid pre-reproductive development time (Sauge et al. 1998).

In apple, Stoeckli et al. (2008b) identified two QTLs for resistance to *D. plantaginea* and *Dysaphis devecta* (Walker, F.), respectively, and Bus et al. (2007) identified three major genes for resistance to *Eriosoma lanigeru* (Hausmann): *Er1* from ‘Northern Spy’, *Er2* from ‘Robusta’ and *Er3* from *Malus sieboldii* ((Regel ex Dippel) Rehder) ‘Aotea 1’. As *E. lanigerum* also forms belowground colonies, it can also be relevant to use a resistant rootstock cultivar (Blommers 1994; Lordan et al. 2015). There are also three resistance genes to *D. devecta*: *Sd-1* from ‘Cox’s Orange Pippin’, *Sd-2* from ‘Northern Spy’ and *Sd-3* from *Malus robusta* ((Carrière) Rheder) and *Malus zumi* ((Matsum) Rheder) (Alston and Briggs 1977; Cevik and King 2002). The cultivar ‘Florina’ combines tolerance, antixenosis and antibiosis mechanisms of resistance to *D. plantaginea* (Qubbaj et al. 2005; Angeli and Simoni 2006), with a strong surface repellence and a resistance factor in phloem sieve elements (Marchetti et al. 2009). The cultivar ‘Golden Orange’ also shows resistance to *D. plantaginea* with a strong antixenotic effect on pre-adult instars (Angeli and Simoni 2006).

The introduction of genetic resistance to aphids into commercial cultivars can help to reduce aphid pressure in orchards. However, this option should be considered with caution as *E. lanigerum* (Bus et al. 2007; Smith and Chuang 2014) and *D. devecta* (Smith and Chuang 2014) developed populations that were virulent to apple genotypes expressing

monogenic resistance. Thus, to increase resistance durability, polygenic sources of resistance should be favoured over monogenic resistance (Lambert and Pascal 2011), even if it is more challenging to breed a cultivar with polygenic resistance (Smith and Chuang 2014) while maintaining interesting fruit quality characteristics.

Cultural practices to modify host plant suitability Host plant suitability for aphids encompasses several aspects, e.g. phloem sap nutritional quality and accessibility, and feeding site availability, which all can be manipulated by different cultural practices.

Phloem nutritional quality for aphids is mainly characterised by its provision of soluble amino acids and its C/N ratio. Indeed, low nitrogen availability is a major constraint of phloem feeding (Bonnemain 2010). Therefore, nutrient inputs such as nitrogen fertilisation that increase plant content in amino acids can positively impact aphid populations (Kyto et al. 1996; Sauge et al. 2010). Water supply as well can modify the amino acid pool, as demonstrated for alfalfa (Girousse et al. 1996).

In addition, water supply can modify the physical properties of the phloem, namely turgor pressure, osmotic potential and sap viscosity (Ryan and Asao 2014; Sevanto 2014). Aphid performance on *Dactylis glomerata* (L.) has been shown to be negatively impacted by water soluble carbohydrate content (Alkhedir et al. 2013). As a moderate water restriction reduces plant growth but has no impact on photosynthesis (Mitchell et al. 2013), an increased sap viscosity resulting from increased carbohydrate contents and consequently a decreased phloem accessibility to aphids can be expected. The hypothesis of reduced phloem accessibility has been suggested to explain reduced aphid performance on water stressed apple and peach trees: *A. pomi*—apple tree (Mody et al. 2009) and *M. persicae*—peach tree (Rousselin et al. 2016).

For most aphid species, feeding site availability is related to the number and spatial organisation (i.e. connections) of the growing shoots, which are partly determined by the training system. In apple trees, for instance, the success of colony dispersal within the canopy is reduced by the complexity of tree branching for *D. plantaginea* (Simon et al. 2011b). *M. persicae* (Grechi et al. 2008) and *A. pomi* (Stoeckli et al. 2008a) performances were furthermore positively correlated to individual shoot growth, which could be modulated by pruning intensity, water and nutrient inputs. The negative effect of nitrogen restriction on the performance of *M. persicae* on peach has thus been shown to be mediated namely by a restriction of vegetative growth (Rousselin et al. 2016). Moreover, low pruning intensity reduces individual shoot elongation rate, as plant vigour is distributed across a higher number of shoots, which results in limited *M. persicae* infestation (Grechi et al. 2008).

Canopy microenvironment such as foliar leaf temperature is of prime importance for insect fitness. This environmental condition can be strongly impacted due to water stress or restriction, leading to stomatal closure (Pangga et al. 2012).

The combination and intensities of the cultural practices commonly used in commercial orchards affect the plant physiological status. Their final outcome on plant suitability is hardly predictable as favourable and unfavourable plant traits were simultaneously affected. Nonetheless, there is a consensus that the control of vegetative growth or nitrogen accumulation in growing shoots by pruning, adapted fruit load (Mediene et al. 2002; Bussi et al. 2010; Lauri et al. 2014), and by moderate water and nutrient inputs reduce the development of aphid colonies.

3.2.2 Top-down

Conservation biological control To foster natural enemy populations, different measures of habitat management have been implemented to provide shelter, substitution prey in periods of aphid scarcity on crop trees, and pollen and nectar (Dedryver et al. 2010; Simon et al. 2010; Markó and Keresztes 2014). Shelters can increase survival of natural enemies, which was shown, for example, for provision of hay mulch around tree trunks, which significantly increased the overwintering survival rate of *Aphelinus mali* (Haldeman), a parasitoid of *E. lanigerum* (Zhou et al. 2014). Other studies considered the possible effects of groundcover on the abundance of aphid natural enemies and aphids themselves. The results are contrasting, varying in relation to arthropod species actually occurring in orchard ecosystems, the initial aphid infestation severity, the cover plant species and the synchronicity between tree phenology and cover plant flowering. On the one hand, it has been shown that even if flowering alleys increase spider abundance in apple orchards compared to bare ground, there might be no effect on *A. pomi* aphid abundance (Markó and Keresztes 2014). In addition, extrafloral nectar sources decreased predation of *Aphis spiraeicola* (Patch) by a Coccinellidae: *Harmonia axyridis* (Pallas) by providing alternative food resources (i.e. nectar) to the predator (Spellman et al. 2006). On the other hand, weed strips in apple orchards increase aphidophagous predator abundance (e.g. Araneae, Cecidomyiidae, Chrysopidae, Heteroptera) and reduce *D. plantaginea* aphid abundance (Wyss et al. 1995). Consistently, the addition of sweet alyssum (*Lobularia maritima* (L.)) caused a decrease in *E. lanigerum* abundance due to increased abundance of natural enemies (e.g. spiders and Anthocoridae) that switch between the flowers and the tree canopy (Gontijo et al. 2013). In the context of conservation biological control, it seems noteworthy that fostering the whole complex of natural enemies is more promising to reach sustainable biological control than just supporting single natural enemy species. For example, the coaction of different

predator and parasitoid species was shown to provide complementary control of *E. lanigerum* in an apple orchard (Gontijo et al. 2015). Another study showed temporal complementarity between earwigs, acting in spring, and *A. mali*, acting in summer and fall for control of *E. lanigerum* (Lordan et al. 2015). Although not yet shown for aphids, different enemy species may provide complementary pest control on different fruit tree cultivars in the same orchard (Mody et al. 2017).

The limitation of insecticide use (Brown 2008; Dedryver et al. 2010) and the choice of selective molecules less harmful to natural enemies (Gentz et al. 2010) can help to foster natural enemy populations, especially for species particularly sensitive to broad-spectrum insecticides such as parasitoids (Cross et al. 1999). A comparative study showed lower *D. plantaginea* abundance and higher natural enemy abundance in organic orchards than in conventional and integrated pest management (IPM) orchards. The authors suggest that the biocontrol of aphids has been disrupted in IPM and conventional orchards by chemical insecticides (Dib et al. 2016b).

To favour natural enemy populations and action, it can be relevant for control of some aphid species to disrupt aphid tending by ants. Ants may benefit from aphid honeydew and, in exchange, provide protection of aphids against natural enemies and increase colony hygiene (Stewart-Jones et al. 2008; Nagy et al. 2013). Preventing ants from climbing into the tree canopy by using sticky barriers reduced population size of *D. plantaginea* and also aphid-related damage to harvested fruits (Stewart-Jones et al. 2008). However, this method has many drawbacks, including the exclusion of crawling predators such as earwigs from the tree canopy and the need for labour-intensive regular application and control of sticky barriers. It also implies a strict management of row vegetation. It is therefore not applicable in large commercial orchards (Nagy et al. 2013). An alternative method consists in providing alternative carbohydrate sources to the ants, by the positioning of feeders with a sucrose solution on the trunk base. The set-up of such feeders in apple orchards proved to be as efficient as the traditional ant-exclusion technique for *D. plantaginea* control (Nagy et al. 2015).

Finally, the proliferation of biocontrol agents could be favoured: first, reconsidering the chemicals used for phytoprotection and second, adapting alternative methods, such as weed strips or ant feeding to the local biotic environment

Releases of biological control agents Entomopathogenic fungi can infest and kill individual aphids and so can cause colony collapse (Zhou and Feng 2010). The virulence of several species of fungi on *M. persicae* has been demonstrated in the laboratory: *Metarhizium* (Sorokin) strains (Shan and Feng 2010; Jandricic et al. 2014), *Purpureocillium lilacinum* (Jones and Samson) (Lee et al. 2015) and *Beauveria bassiana* ((Bals.-Criv) Vuill.) strains (Jandricic et al. 2014). The main

obstacle to overcome for an efficient use of fungi for aphid management in orchards is the adaptation of the fungus strains to the field conditions. A strong virulence is not sufficient for biocontrol purposes, the strains need also to be thermo- and UV-B-tolerant (Lee et al. 2015). The adequate formulation to preserve sporulation capacities has to be found (Zhou and Feng 2010). For aphids living in rolled leaves such as *D. plantaginea*, the efficient application of fungal spores for biocontrol can be arduous, so the use of *Lasius niger* (Linnaeus) ants as passive vector of the spores has been considered and resulted in infestation of aphid colonies (Bird et al. 2004). The use of entomopathogenic nematodes for aphid control has also been studied, but the results are not encouraging, with a low infectivity of the tested nematodes (Park et al. 2013; Berkvens et al. 2014).

Biological control by augmentation through releases of natural aphid enemies is not included in common orchard practices. The release of earwigs seems not to affect the abundance of *D. plantaginea* (Dib et al. 2016a). On the contrary, the release of larvae of *Adalia bipunctata* (Linnaeus) (i.e. a Coccinellidae) early in the season helps to achieve control of *D. plantaginea* populations. However, the effect has been obtained with a predator:prey ratio of 1:1 or 5:1 (Wyss et al. 1999), compromising the cost-efficiency of the method. So, further studies are needed, possibly exploiting codling moth exclusion nets, which are of extended use due to their side effects on fruit quality and orchard microclimate (Lloyd et al. 2005; Baïamonte et al. 2016), as a physical barrier to increase the efficiency of the releases (Dib et al. 2016a). Mummified aphids were found to be more efficient to release *Aphidius ervi* (Haliday) than adult parasitoids (Wei et al. 2005).

So, even if release methods are promising, they still face technical problems regarding their adaptation for aphid control in commercial orchards. Those technical issues need to be solved to allow large scale use of release methods.

3.3 Autumnal return (dioecious species)

3.3.1 Bottom-up: impairing host plant location and decreasing host plant suitability

Repeated autumn applications of kaolin have been shown to decrease the landing and larvae deposition of gynoparae of *D. plantaginea* on apple trees (Bürgel et al. 2005). The repeated treatments either suppress aphid populations in the following spring (Andreev et al. 2012) or reduce it, but not below economic threshold levels (Bürgel et al. 2005). The potential mechanisms underlying these effects are perturbation of visual and physical cues to recognise the host plant, and a limitation of aphid movement, feeding and oviposition on treated trees (Bürgel et al. 2005). Kaolin has also been tested in spring but yielded contradictory results. In an apple orchard, the aphid

abundances decreased after repeated spring application for *A. pomi* and increased for *D. plantaginea* and *E. lanigerum*. These results might be explained by a reduction of ant attendance on *A. pomi* and a lower efficiency of the natural enemies for the two other aphid species (Markó et al. 2008). Because of these contradictory results, kaolin should be used only in autumn to prevent aphid return.

Manual artificial defoliation in September or early October results in aphid absence in the following spring (Andreev et al. 2012). The possible mechanisms underlying this effect are that aphids fail to recognise their host plant in the absence of leaves or that autumnal aphids are unable to settle on leafless apple trees. This method seems promising; however, the effect of defoliation on tree reserves remains to be assessed, especially if this technique is to be repeated on a yearly basis.

Water restriction, suggested as a bottom-up method to reduce spring aphid populations, can postpone autumnal leaf senescence (Naschitz et al. 2014). Depending on the host plant and the aphid species considered, this delayed senescence can have contrasting effects. For the *Prunus padus* (L.)—*Rhopalosiphum padi* (Linnaeus) system, it has been found that aphid autumnal return is positively influenced by green leaves (Archetti and Leather 2005). On the contrary, early leaf senescence increases the number of overwintering eggs of *Euceraphis betulae* (Koch) on *Betula pendula* (Roth) in short autumn (Silfver et al. 2014).

Cultivar mixtures of apple trees with differential resistance to *D. plantaginea* has been shown to reduce aphid incidence on the susceptible cultivar compared to a pure stand of the susceptible cultivar. This positive effect of cultivar mixture has been attributed to a dilution effect of the resource, which is the susceptible cultivar (Parisi et al. 2013).

3.3.2 Direct action: use of sexual pheromone lures to impair mating partner location and reduction of aphid inoculum

During the sexual generation involving oviparae and winged males, oviparae release a sex pheromone to guide conspecific males. The two pheromone components (4aS,7S,7aR)-nepetalactone and (1R,4aS,7S,7aR)-nepetalactol are quite common among aphid species; however, it is the ratio between the two components which is species specific (Symmes et al. 2012). These sex pheromones could be used to monitor fall populations and also to disrupt mating (Boo et al. 2000; Symmes et al. 2012). A 1:1 ratio of the two components of the sex pheromone has been shown to be efficient to trap *Hyalopterus pruni* (Goeffroy) and *Brachycaudus helichrysi* (Kaltenbach) in prune orchards (*Prunus domestica* (L.)). However, the trap has also caught an important proportion of non-target aphid species, so the bait should be improved if it is to be used for monitoring purposes (Symmes et al. 2012). For *Tuberocephalus momonis* (Matsumura) in

peach orchards, the best performing blend of the pheromone components was 85:15 (Boo et al. 2000).

As dioecious aphid species spend the summer season on secondary hosts, the removal of those plants in the orchards and their vicinity might theoretically limit the autumnal return. However, this strategy is unrealistic for aphid species whose secondary hosts are too numerous (e.g. more than 400 for *M. persicae* (Bass et al. 2014)) or which are too mobile to be strongly affected by secondary host removal since their return flight likely covers long distances (e.g. *D. plantaginea* (Guillemaud et al. 2011)). For aphid species with a restricted secondary host plant range, such as *Hyalopterus pruni* (Goeffroy)—*Phragmites* (Adans) spp. or *Myzus varians* (Davidson)—*Clematis* (L.) spp., further investigations are needed before implementing host removal, as this practice may be rather time consuming and negatively related to other activities aiming at biodiversity conservation in the orchard vicinity.

3.3.3 Top-down: web-building spiders

Whereas some aphidophagous insects have been shown to be relatively inactive in autumn, web-building spiders have been observed in relevant quantity in an apple orchard (Wyss 1995). The finding that the number of spider webs in autumn is negatively correlated with aphid abundance in subsequent spring suggests that measures that increase spider abundance in orchards such as weed strips could help to reduce orchard infestation by winged aphids returning in autumn.

3.4 Overwintering forms

Studies focusing on alternatives to chemicals for control of overwintering aphid stages are scarce. *E. lanigerum* aphids overwinter as apterous females either on the roots or within the canopy of apple trees. Overwintering canopy colonies of *E. lanigerum* can be strongly reduced by earwigs, so any measure to favour earwig can have a positive effect on the control of this aphid (Lordan et al. 2015). Earwigs as natural enemies of aphids are considered in most studies to be beneficial for apple production (Dib et al. 2010b; Cross et al. 2015); however, as they can also damage fruits, they are sometimes considered as apple pest (Markó et al. 2008) and most of the time classified as peach pest (Saladini et al. 2016).

4 Side effects of alternative methods to chemicals for aphid control

4.1 Orchard pest community complexity

The implementation of alternative control methods for aphid management—such as modified host plant suitability or

environment—can have contrasting effects on other orchard pathogens or pests. These effects can be arduous to predict as the implementation of alternative methods can cause changes in both pest and natural enemy communities. Indeed, it has been observed in Southern France that a higher number of aphid species colonise peach trees in orchards that are less intensively treated with pesticides (Penvern et al. 2010).

For example, a tree cultivar selected to be resistant to a specific pest can be susceptible to another one. The peach cultivar ‘Rubira’ is resistant to *M. persicae* but susceptible to *Brachycaudus persicae* (Passerini) (Sauge et al. 1998; Sauge et al. 2002). Similarly, the apple cultivar ‘Florina’ is resistant to *D. plantaginea* and to scab (Miñarro and Dapena 2008), but susceptible to *E. lanigerum* (Abu-Romman and Ateyyat 2014). Deficit irrigation seems to reduce peach tree susceptibility to aphids and has also a positive effect on the control of brown rot. This effect of water restriction on brown rot might be due to a reduction of microcracks on the fruit surface, which limits the invasion of pathogens (Mercier et al. 2008). On the contrary, egg hatching of the buprestid *Capnodis tenebrionis* (Linnaeus) can be compromised by high soil humidity, so restrictive irrigation might have a positive effect on this stone orchard pest (Marannino and De Lillo 2007). The cultivar mixture of apple cultivars varying in their resistance to scab results in decreased scab and *D. plantaginea* infestations on the susceptible cultivar (Parisi et al. 2013). Ground cover management, which is suggested to positively influence biological control of aphids, may also increase vole (*Microtus savii* (De Selys-Longchamps)) populations (Bertolino et al. 2014). As the effects of the alternative methods implemented for aphid management can be either positive or negative depending on their effects on other pest species, they should be selected and combined according to locally important pest species to optimise the control of the orchard pest community. In this context, it is noteworthy that the implementation of alternative control methods for the management of other pests can also impact aphid dynamics. Indeed, codling moth exclusion nets closed in April during aphid development have been shown to decrease *D. plantaginea* abundance (Dib et al. 2010a).

4.2 Fruit production and quality

Innovative methods for aphid management can impact fruit yield and quality. Therefore, the implementation of alternatives to chemicals needs to consider also the production of marketable fruits, which is the farmer’s ultimate goal. That means taking into account all aspects of profitability, i.e. yield (fruit number and weight) and quality (fruit size, colour and sweetness).

Nitrogen restriction can impact yield, as demonstrated in apple orchards (Kühn et al. 2011). Water restriction has contrasting effects on fruit production and quality depending on

its time of application and intensity. It can either reduce yield (Naor et al. 1999, 2001; Girona et al. 2010) or have no effect (Mercier et al. 2008). However, economic losses related to lower yield may be compensated by higher fruit quality. Indeed, deficit irrigation may decrease peach fruit diameter (Mercier et al. 2008; Rahmati et al. 2015), but increase fruit softness (Mercier et al. 2008) and sugar content (Mercier et al. 2008; Rahmati et al. 2015). The economic valorisation could thus counterbalance the yield reduction as informed consumers are willing to pay more for fruits produced with less chemicals (Marette et al. 2012).

5 Conclusion

This study aims to identify the possible levers for the control of aphid populations in relation with plant phenology and insect life cycle (Fig. 3). This integrative approach is, to our knowledge, quite new and favours the design of long-term control strategies adapted to local scale taking into account climate, soil properties, tree physiological status, and the arthropod (pests and natural enemies) community. Indeed, most of the cultural practices, for example, training systems, regulated deficit irrigation and flower strips, that might be applied for controlling aphid abundance in peach and apple orchards, modify the overall tree functioning and the trees’ surroundings for a long period, and their effects could also be delayed and time-varying. They can thus not be used in response to an acute infestation event but have to be integrated in a long-term strategy. Bottom-up processes, which aim, for instance, to decrease plant suitability, need to be initiated before aphid outbreaks. Top-down control, on the other hand, can be limited in case of rapid and severe infestation (Wyss et al. 1995). Aphid outbreaks under favourable conditions can justify the use of chemicals as a last resort to solve inextricable situations. The choice of an adapted strategy is therefore a rather complex process, which has to take into account other main determinants of horticultural production, such as profitability, labour requests and maintenance of orchard productivity over time. It has also to be adapted to the local conditions.

The benefits of using alternative strategies could hardly be evaluated, and it is therefore difficult to determine relevant economic thresholds for the implementation of the alternative. Thus, the yield loss, the costs of the those methods compared to chemicals and the potentially increased value of the more environmentally friendly fruits were almost never considered. Indeed, most studies have focused on aphid abundance not on aphid damage. Moreover, as aphids impair vegetative growth, and therefore the number and the quality of buds that may develop the following spring, the repercussion of aphid abundance in 1 year should be assessed, not only on current-year yield but also on production potential of the following years.

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