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

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REVIEW ARTICLE

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

6 **Aurélie Rousselin<sup>1</sup> · Daniele Bevacqua<sup>1</sup> · Marie-Hélène Sauge<sup>1</sup> · Françoise Lescourret<sup>1</sup> ·**  
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 8

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11 **Abstract** Apple and peach orchards are chemical-intensive  
 12 systems, and aphids are one of their major pests. Aphids alter  
 13 fruiting and shoot development, and they can spread viruses.  
 14 Decades of insecticide use have developed aphid resistance,  
 15 which calls on research to provide alternatives to chemicals  
 16 for pest management. Here, we review the literature to identi-  
 17 fy, for each stage of the aphid life cycle, existing alternatives  
 18 based on either top-down (i.e. aphid predation or parasitism)  
 19 or bottom up (i.e. increase of host plant resistance) processes.  
 20 Firstly, it was found that most studies focus on top-down pro-  
 21 cesses, namely on conservation biological control aiming to  
 22 preserve existing populations of natural enemies: predators,  
 23 parasitoids and nematodes. This is achieved by (i) providing  
 24 shelters (i.e. planting hedges, weed or flower strips) or alter-  
 25 native preys in periods of aphid scarcity or (ii) choosing  
 26 chemicals with the lowest disruptive effects. Those methods  
 27 prove more efficient when used early in the season, i.e. before  
 28 the exponential increase of aphid populations. Fostering the  
 29 complex of natural enemies is also preferable than just  
 30 supporting one single enemy. Secondly, other techniques, like  
 31 (i) releasing biological control agents (entomopathogenic fun-  
 32 gi, nematodes) or (ii) using pheromone lures to prevent au-  
 33 tumnal sexual reproduction, are currently adapted for their use  
 34 in orchard conditions. Thirdly, bottom-up regulation has to be  
 35 devised as a long-term strategy, which could start by choosing

a cultivar enabling genetic avoidance or developing genetic 36  
 resistance. Then, aphid development can be reduced by the 37  
 control of shoot growth or nitrogen accumulation in response 38  
 to pruning or moderate water and nutrient inputs. At last, 39  
 autumnal return of aphids could be disrupted by techniques 40  
 such as kaolin applications that impair aphid host plant loca- 41  
 tion. It is concluded that these alternative methods have to be 42  
 adapted to local conditions and combined in long-term strate- 43  
 gies in order to decrease the infestation risks throughout the 44  
 orchard lifespan. 45

**Keywords** Pest management · Apple tree · Peach tree · 46  
 Aphids · Alternative methods 47

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67	3.3.2 Direct action: use of sexual pheromone lures to
68	impair mating partner location and reduction of
69	aphid inoculum
70	3.3.3 Top down: web-building spiders
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## 80 1 Introduction

Q2 81 Apple and peach are the major fruit crops worldwide. In 2013,  
82 according to the FAO (Food and Agricultural Organization)  
83 data on world deciduous fruit tree production, apple ranked  
84 1st with a yearly production of more than 80.10<sup>6</sup> tons, while  
85 peach and nectarine ranked 4th with more than 21.10<sup>6</sup> tons,  
86 behind grapes and pear (FAO 2016).

87 Aphids are considered as major peach and apple  
88 pests under temperate and Mediterranean climates.  
89 First, they can harm fruit production by their detrimental  
90 effects on fruit quality, including reduction of fruit  
91 size (Filajdić et al. 1995), deformation of fruit shape  
92 (Hullé et al. 2006) or premature fruit fall (Van Emden  
93 et al. 1969). Second, they reduce overall tree vigour due  
94 to phloem sap intake, organ deformation (leaf rolling,  
95 shoot twisting), chlorosis, sooty mould development on  
96 honeydew and leaf fall (Dedryver et al. 2010). These  
97 effects can result in a decrease in C reserves and so  
98 alter long-term growth (Zvereva et al. 2010). Third,  
99 aphids can be vectors of virus transmission, including  
100 the plum pox virus, which leads to tree death (Rimbaud  
101 et al. 2015). The action threshold levels for insecticide  
102 application are low, with 1–2% of infested shoots for  
103 *Dysaphis plantaginea* (Passerini) and 8–10% for *Aphis*  
104 *pomi* (De Geer) (Barbagallo et al. 2007). Sometimes a  
105 single leaf deformation is enough to trigger insecticide  
106 application, due to fear of virus transmission (Penvern  
107 et al. 2010). However, data on yield loss attributable to  
108 aphids in fruit trees are scarce relative to data available  
109 for annual crops (e.g. wheat, sugar beet, potatoes  
110 (Dedryver et al. 2010)). Nevertheless, direct evaluation  
111 in an organic apple orchard attributes 21.4% of unmar-  
112 ketable apple fruits to *D. plantaginea* damage (Simon  
113 et al. 2011a). A modelling approach suggested a strong  
114 negative impact (more than 5% reduction in fruit  
115 growth) of *D. plantaginea* on apple fruit growth even  
116 at low aphid density (De Berardinis et al. 1994). The

small number of dedicated studies may be explained by 117  
a seemingly low impact of aphids on current year fruit 118  
yield. Indeed, several studies have shown that aphid 119  
density has almost no effect on the current year yield 120  
(Filajdić et al. 1995; Grechi et al. 2008) but possibly on 121  
that of future years due to the reduction of tree vigour. 122  
Thus, multi-year experiments are needed to quantify 123  
aphid impact on yield, as suggested by a modelling 124  
approach in which aphid impact was only detected in 125  
a multi-year perspective (Bevacqua et al. 2016). 126

Nowadays, chemical insecticides are still widely used to 127Q3  
control aphid populations in peach and apple orchards 128  
(Simon et al. 2011a), but due to high environmental costs 129  
and implementation of restrictive guidelines, alternatives 130  
to chemicals are needed. Moreover, pest populations 131  
resistant to chemicals have developed. A single clone of 132  
*D. plantaginea* can accumulate several resistance mechanisms 133  
conferring resistance to diverse insecticides (Delorme et al. 134  
1999). Seven different mechanisms of resistance to insecti- 135  
cides have been identified in *Myzus persicae* (Sulzer), en- 136  
abling this species to withstand many chemicals (Bass et al. 137  
2014). Moreover, for a single mechanism, such as target site 138  
resistance to pyrethroids in *M. persicae*, the resistance can 139  
depend on several loci and different alleles which can coexist 140  
in a single individual (Panini et al. 2015). Another detriment 141  
of pesticide use is the perturbation of natural enemies. 142  
Laboratory studies showed for instance that some insecticides 143  
are lethal to ladybeetles and lacewings (Garzón et al. 2015) 144  
and reduced the predation activity of earwigs having been 145  
exposed to pesticides (Malagnoux et al. 2015a). In apple or- 146  
chards, earwig occurrence decreased with the increase of in- 147  
secticide treatments (Malagnoux et al. 2015b). The spider 148  
community was also negatively affected by the use of insec- 149  
ticides in organic apple orchards (Marliac et al. 2016). The 150  
side effects of pesticides could possibly be reduced by chang- 151  
ing the mode of application, using for instance, trunk injection 152  
(VanWoerkom et al. 2014), or applying less toxic substances 153  
such as insecticidal soap (Karagounis et al. 2006). Another 154  
solution is to seek alternative methods to chemicals (Fig. 1). 155

In an ecosystem, herbivorous insect abundance is controlled 156  
by both top-down and bottom-up processes (Hunter 157  
and Price 1992), i.e. by the abundance and voracity of their 158  
natural enemies and by the quality and suitability of their host 159  
plant. Both control levels could be exploited for a more sus- 160  
tainable pest management. This review presents the alterna- 161  
tive methods to chemicals for aphid management in apple and 162  
peach orchards adapted to each stage of the aphid life cycle. 163  
We start therefore with a quick overview of the diverse life 164  
cycles of aphid species infesting apple and peach trees. Then, 165  
the possible alternatives mobilising both bottom-up and top- 166  
down processes are presented for each aphid life cycle stage. 167  
Their side effects on other orchard pests and pathogens, and 168  
on fruit yield are finally evaluated. 169

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



170 **2 Aphid species infesting apple and peach orchards**

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

195 **3 Bottom-up and top-down control methods**  
 196 **at different aphid life cycle phases**

197 Modification of host plant suitability through genetic resis-  
 198 tance or modification of the abiotic environment, which exert  
 199 bottom-up regulation on aphid populations (Fig. 3), embraces  
 200 several aspects: (i) nutritional quality of phloem sap, which is  
 201 mainly defined by the amino acid profile (Ryan et al. 2015)  
 202 and the absence of defensive compounds (Czerniewicz et al.  
 203 2011)), (ii) phloem sap accessibility, which is related to phys-  
 204 ical properties like viscosity or turgor pressure (Smith and

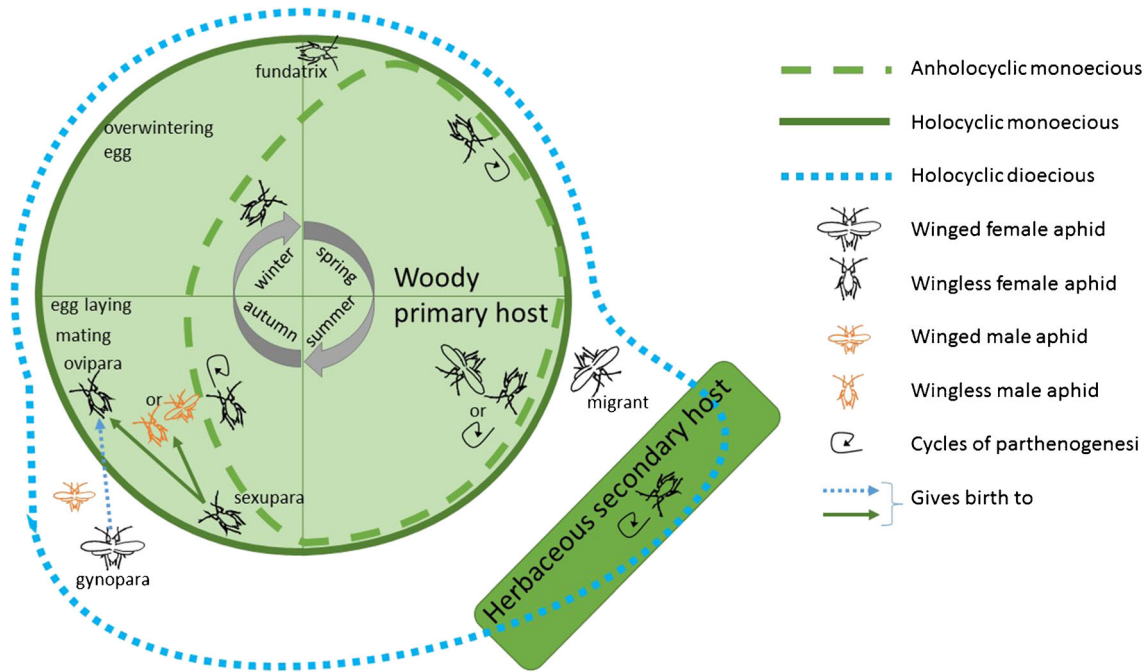
Chuang 2014), (iii) settlement site availability, which corre-  
 sponds for most orchard aphid species to the number of grow-  
 ing apices, (iv) plant architecture, branching complexity and  
 connectivity of the plant entities (Costes et al. 2012) and (v)  
 canopy microenvironment (Pangga et al.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

In addition to bottom-up regulation, diverse organisms can  
 exert a top-down regulation of aphid populations through pre-  
 dation 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 enhance-  
 ment of biocontrol agents naturally occurring in the field,  
 (ii) biological control by augmentation, which consists in  
 the release of biocontrol agents and (iii) introduction bio-  
 logical control (not treated in this review), which aims at man-  
 aging 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 infes-  
 tation by aphids in spring. Cultivar choice, or more specific-  
 ally, 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 asyn-  
 chrony 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

241 et al. 1995; Carisse and Jobin 2006) are temperature dependant, i.e. rely on degree-day accumulation above a threshold  
 242 below which development stops. So, genetic avoidance usually means that a higher threshold delays the plants' develop-  
 243 ment with respect to the insects' requirements.  
 244  
 245

3.1.2 Top-down

246

The top-down processes acting at the egg hatching stage are  
 247 the same as the ones detailed in the section below. However, it  
 248 should be emphasised that the efficiency of top-down control  
 249

t1.1 **Table 1** Life cycle characteristics  
 t1.2 and host use of the main aphid  
 t1.3 species of apple and peach trees in  
 t1.4 European orchards

		Life cycle	Host	Sources
t1.4	Apple tree, <i>Malus domestica</i> Borkh.			
t1.5	<i>Aphis pomi</i> De Geer	H	M	Power et al. 1992; Hullé et al. 2006
t1.6	<i>Aphis spiraecola</i> Patch	A	M	Hullé et al. 2006
t1.7	<i>Dysaphis plantaginea</i> (Passerini)	H	D	Hullé et al. 2006
t1.8	<i>Dysaphis devector</i> (Walker)	H	M	Ryan et al. 2015
t1.9	<i>Eriosoma lanigerum</i> (Hausmann)	A	M	Hullé et al. 2006
t1.10	<i>Rhopalosiphum insertum</i> (Walker)	H	D	Hullé et al. 2006
t1.11	Peach tree, <i>Prunus persica</i> (L.) Batsch			
t1.12	<i>Brachycaudus persicae</i> Passerini	H	D	Hullé et al. 2006; Penvern et al. 2010
t1.13	<i>Brachycaudus prunicola</i> (Kaltenbach)	H	M	Penvern et al. 2010
t1.14	<i>Brachycaudus schwartzi</i> (Börner)	H	M	Hullé et al. 2006; Penvern et al. 2010
t1.15	<i>Hyalopterus pruni</i> (Geoffroy)	H	D	Hullé et al. 2006
t1.16	<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

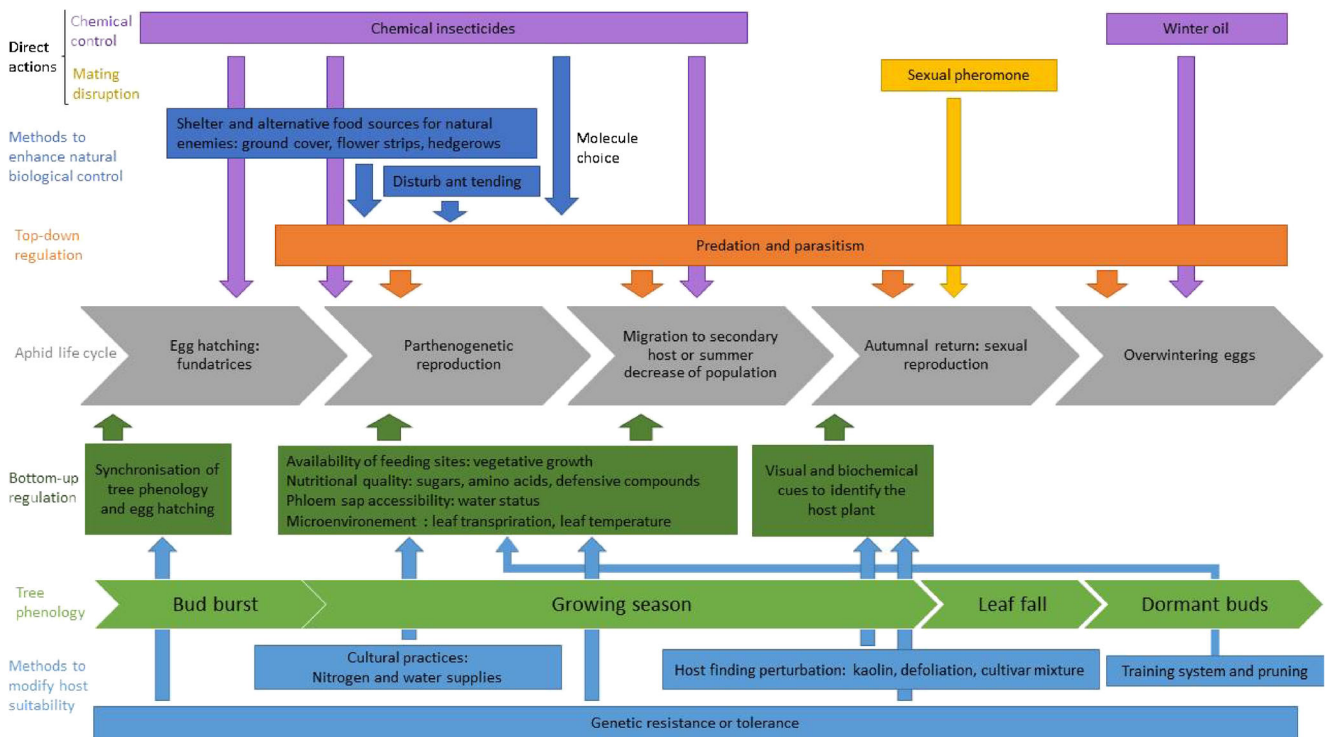


Fig. 3 Possible methods to control aphid populations in apple and peach orchards by mobilizing bottom-up and top-down processes

250 depends on the precocity of the action, due to the exponential  
 251 increase of aphid populations. So, natural enemies that are  
 252 active early in the season are of crucial importance (Wyss  
 253 1995; Stewart-Jones et al. 2008; Nagy et al. 2013).

254 **3.2 Parthenogenetic reproduction**

255 **3.2.1 Bottom-up**

256 **Genetic resistance** Genetic resistance can be separated into  
 257 two categories: antixenosis resistance, which prevents plant  
 258 colonisation, and antibiosis resistance, which alters pest de-  
 259 velopment and/or reproduction (Sauge et al. 2006; Sauge et al.  
 260 2011). Genotypes can also be tolerant to aphids, meaning that  
 261 they can bear abundant aphid populations without a strong  
 262 negative impact on production or growth (Angeli and  
 263 Simoni 2006).

264 In peach, cultivars resistant to *M. persicae* have been iden-  
 265 tified (Verdugo et al. 2016). ‘Weeping Flower Peach’ (Sauge  
 266 et al. 2011) and ‘Rubira’ (Sauge et al. 1998, 2002, 2006;  
 267 Pascal et al. 2002; Lambert and Pascal 2011) possess single  
 268 dominant resistance genes, Rm1 and Rm2, respectively, con-  
 269 ferring antixenosis resistance. The peach cultivars ‘Malo  
 270 konare’ and ‘Summergrand’ and the related wild *Prunus*  
 271  *davidiana* ((Carrière) Franch.) show antibiosis resistance.  
 272 The resistance of *P. davidiana* is polygenic, i.e. located on  
 273 seven QTLs (Sauge et al. 2011), and strongly reduces aphid  
 274 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 devectora*  
 (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. devectora*: *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 com-  
 mercial cultivars can help to reduce aphid pressure in or-  
 chards. However, this option should be considered with cau-  
 tion as *E. lanigerum* (Bus et al. 2007; Smith and Chuang  
 2014) and *D. devectora* (Smith and Chuang 2014) developed  
 populations that were virulent to apple genotypes expressing

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

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

314 Phloem nutritional quality for aphids is mainly characterised  
315 by its provision of soluble amino acids and its C/N ratio.  
316 Indeed, low nitrogen availability is a major constraint of phlo-  
317 em feeding (Bonnemain 2010). Therefore, nutrient inputs such  
318 as nitrogen fertilisation that increase plant content in amino  
319 acids can positively impact aphid populations (Kyto et al.  
320 1996; Sauge et al. 2010). Water supply as well can modify  
321 the amino acid pool, as demonstrated for alfalfa (Girousse  
322 et al. 1996).

323 In addition, water supply can modify the physical proper-  
324 ties of the phloem, namely turgor pressure, osmotic potential  
325 and sap viscosity (Ryan and Asao 2014; Sevanto 2014).  
326 Aphid performance on *Dactylis glomerata* (L.) has been  
327 shown to be negatively impacted by water soluble carbohy-  
328 drate content (Alkhedir et al. 2013). As a moderate water  
329 restriction reduces plant growth but has no impact on photo-  
330 synthesis (Mitchell et al. 2013), an increased sap viscosity  
331 resulting from increased carbohydrate contents and conse-  
332 quently a decreased phloem accessibility to aphids can be  
333 expected. The hypothesis of reduced phloem accessibility  
334 has been suggested to explain reduced aphid performance on  
335 water stressed apple and peach trees: *A. pomi*—apple tree  
336 (Mody et al. 2009) and *M. persicae*—peach tree (Rousselin  
337 et al. 2016).

338 For most aphid species, feeding site availability is related to  
339 the number and spatial organisation (i.e. connections) of the  
340 growing shoots, which are partly determined by the training  
341 system. In apple trees, for instance, the success of colony  
342 dispersal within the canopy is reduced by the complexity of  
343 tree branching for *D. plantaginea* (Simon et al. 2011b).  
344 *M. persicae* (Grechi et al. 2008) and *A. pomi* (Stoekli et al.  
345 2008a) performances were furthermore positively correlated  
346 to individual shoot growth, which could be modulated by  
347 pruning intensity, water and nutrient inputs. The negative ef-  
348 fect of nitrogen restriction on the performance of *M. persicae*  
349 on peach has thus been shown to be mediated namely by a  
350 restriction of vegetative growth (Rousselin et al. 2016).  
351 Moreover, low pruning intensity reduces individual shoot  
352 elongation rate, as plant vigour is distributed across a higher  
353 number of shoots, which results in limited *M. persicae* infes-  
354 tation (Grechi et al. 2008).

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

359 The combination and intensities of the cultural practices  
360 commonly used in commercial orchards affect the plant phys-  
361 iological status. Their final outcome on plant suitability is  
362 hardly predictable as favourable and unfavourable plant traits  
363 were simultaneously affected. Nonetheless, there is a consen-  
364 sus that the control of vegetative growth or nitrogen accumu-  
365 lation in growing shoots by pruning, adapted fruit load  
366 (Mediene et al. 2002; Bussi et al. 2010; Lauri et al. 2014),  
367 and by moderate water and nutrient inputs reduce the devel-  
368 opment of aphid colonies.

### 3.2.2 Top-down 369

370 **Conservation biological control** To foster natural enemy  
371 populations, different measures of habitat management have  
372 been implemented to provide shelter, substitution prey in pe-  
373 riods of aphid scarcity on crop trees, and pollen and nectar  
374 (Dedryver et al. 2010; Simon et al. 2010; Markó and Keresztes  
375 2014). Shelters can increase survival of natural enemies,  
376 which was shown, for example, for provision of hay mulch  
377 around tree trunks, which significantly increased the  
378 overwintering survival rate of *Aphelinus mali* (Haldeman), a  
379 parasitoid of *E. lanigerum* (Zhou et al. 2014). Other studies  
380 considered the possible effects of groundcover on the abun-  
381 dance of aphid natural enemies and aphids themselves. The  
382 results are contrasting, varying in relation to arthropod species  
383 actually occurring in orchard ecosystems, the initial aphid  
384 infestation severity, the cover plant species and the synchro-  
385 nicity between tree phenology and cover plant flowering. On  
386 the one hand, it has been shown that even if flowering alleys  
387 increase spider abundance in apple orchards compared to bare  
388 ground, there might be no effect on *A. pomi* aphid abundance  
389 (Markó and Keresztes 2014). In addition, extrafloral nectar  
390 sources decreased predation of *Aphis spiraeicola* (Patch) by a  
391 Coccinellidae: *Harmonia axyridis* (Pallas) by providing alter-  
392 native food resources (i.e. nectar) to the predator (Spellman  
393 et al. 2006). On the other hand, weed strips in apple orchards  
394 increase aphidophagous predator abundance (e.g. Araneae,  
395 Cecidomyiidae, Chrysopidae, Heteroptera) and reduce  
396 *D. plantaginea* aphid abundance (Wyss et al. 1995).  
397 Consistently, the addition of sweet alyssum (*Lobularia*  
398 *maritima* (L.)) caused a decrease in *E. lanigerum* abundance  
399 due to increased abundance of natural enemies (e.g. spiders  
400 and Anthocoridae) that switch between the flowers and the  
401 tree canopy (Gontijo et al. 2013). In the context of conserva-  
402 tion biological control, it seems noteworthy that fostering the  
403 whole complex of natural enemies is more promising to reach  
404 sustainable biological control than just supporting single nat-  
405 ural enemy species. For example, the coaction of different

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

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

426 To favour natural enemy populations and action, it can be  
 427 relevant for control of some aphid species to disrupt aphid  
 428 tending by ants. Ants may benefit from aphid honeydew  
 429 and, in exchange, provide protection of aphids against natural  
 430 enemies and increase colony hygiene (Stewart-Jones et al.  
 431 2008; Nagy et al. 2013). Preventing ants from climbing into  
 432 the tree canopy by using sticky barriers reduced population  
 433 size of *D. plantaginea* and also aphid-related damage to harvested  
 434 fruits (Stewart-Jones et al. 2008). However, this method  
 435 has many drawbacks, including the exclusion of crawling  
 436 predators such as earwigs from the tree canopy and the need  
 437 for labour-intensive regular application and control of sticky  
 438 barriers. It also implies a strict management of row vegetation.  
 439 It is therefore not applicable in large commercial orchards  
 440 (Nagy et al. 2013). An alternative method consists in providing  
 441 alternative carbohydrate sources to the ants, by the positioning  
 442 of feeders with a sucrose solution on the trunk base.  
 443 The set-up of such feeders in apple orchards proved to be as  
 444 efficient as the traditional ant-exclusion technique for  
 445 *D. plantaginea* control (Nagy et al. 2015).

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

450 **Releases of biological control agents** Entomopathogenic  
 451 fungi can infest and kill individual aphids and so can cause  
 452 colony collapse (Zhou and Feng 2010). The virulence of several  
 453 species of fungi on *M. persicae* has been demonstrated in  
 454 the laboratory: *Metarhizum* (Sorokin) strains (Shan and Feng  
 455 2010; Jandricic et al. 2014), *Purpureocillium lilacinum* (Jones  
 456 and Samson) (Lee et al. 2015) and *Beauveria bassiana*  
 457 ((Bals.-Criv) Vuill.) strains (Jandricic et al. 2014). The main

458 obstacle to overcome for an efficient use of fungi for aphid  
 459 management in orchards is the adaptation of the fungus strains  
 460 to the field conditions. A strong virulence is not sufficient for  
 461 biocontrol purposes, the strains need also to be thermo- and  
 462 UV-B-tolerant (Lee et al. 2015). The adequate formulation to  
 463 preserve sporulation capacities has to be found (Zhou and  
 464 Feng 2010). For aphids living in rolled leaves such as  
 465 *D. plantaginea*, the efficient application of fungal spores for  
 466 biocontrol can be arduous, so the use of *Lasius niger*  
 467 (Linnaeus) ants as passive vector of the spores has been considered  
 468 and resulted in infestation of aphid colonies (Bird et al.  
 469 2004). The use of entomopathogenic nematodes for aphid  
 470 control has also been studied, but the results are not encouraging,  
 471 with a low infectivity of the tested nematodes (Park  
 472 et al. 2013; Berkvens et al. 2014).

473 Biological control by augmentation through releases of  
 474 natural aphid enemies is not included in common orchard  
 475 practices. The release of earwigs seems not to affect the abundance  
 476 of *D. plantaginea* (Dib et al. 2016a). On the contrary, the  
 477 release of larvae of *Adalia bipunctata* (Linnaeus) (i.e. a  
 478 Coccinellidae) early in the season helps to achieve control of  
 479 *D. plantaginea* populations. However, the effect has been obtained  
 480 with a predator:prey ratio of 1:1 or 5:1 (Wyss et al. 1999),  
 481 compromising the cost-efficiency of the method. So, further  
 482 studies are needed, possibly exploiting codling moth exclusion  
 483 nets, which are of extended use due to their side effects on  
 484 fruit quality and orchard microclimate (Lloyd et al. 2005;  
 485 Baiamonte et al. 2016), as a physical barrier to increase the  
 486 efficiency of the releases (Dib et al. 2016a). Mummified  
 487 aphids were found to be more efficient to release *Aphidius ervi*  
 488 (Haliday) than adult parasitoids (Wei et al. 2005).  
 489

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

494 **3.3 Autumnal return (dioecious species)**

495 *3.3.1 Bottom-up: impairing host plant location and decreasing host plant suitability*

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



508	abundances decreased after repeated spring application for	peach orchards, the best performing blend of the pheromone	558
509	<i>A. pomi</i> and increased for <i>D. plantaginea</i> and <i>E. lanigerum</i> .	components was 85:15 (Boo et al. 2000).	559
510	These results might be explained by a reduction of ant atten-	As dioecious aphid species spend the summer season on	560
511	dance on <i>A. pomi</i> and a lower efficiency of the natural enemies	secondary hosts, the removal of those plants in the orchards	561
512	for the two other aphid species (Markó et al. 2008). Because of	and their vicinity might theoretically limit the autumnal return.	562
513	these contradictory results, kaolin should be used only in au-	However, this strategy is unrealistic for aphid species whose	563
514	umn to prevent aphid return.	secondary hosts are too numerous (e.g. more than 400 for	564
515	Manual artificial defoliation in September or early October	<i>M. persicae</i> (Bass et al. 2014)) or which are too mobile to	565
516	results in aphid absence in the following spring (Andreev et al.	be strongly affected by secondary host removal since their	566
517	2012). The possible mechanisms underlying this effect are	return flight likely covers long distances (e.g. <i>D. plantaginea</i>	567
518	that aphids fail to recognise their host plant in the absence of	(Guillemaud et al. 2011)). For aphid species with a restricted	568
519	leaves or that autumnal aphids are unable to settle on leafless	secondary host plant range, such as <i>Hyalopterus pruni</i>	569
520	apple trees. This method seems promising; however, the effect	(Geoffroy)— <i>Phragmites</i> (Adans) spp. or <i>Myzus varians</i>	570
521	of defoliation on tree reserves remains to be assessed, espe-	(Davidson)— <i>Clematis</i> (L.) spp., further investigations are	571
522	cially if this technique is to be repeated on a yearly basis.	needed before implementing host removal, as this practice	572
523	Water restriction, suggested as a bottom-up method to re-	duce spring aphid populations, can postpone autumnal leaf	573
524	senescence (Naschitz et al. 2014). Depending on the host	may be rather time consuming and negatively related	574
525	plant and the aphid species considered, this delayed senes-	to other activities aiming at biodiversity conservation in the	575
526	cence can have contrasting effects. For the <i>Prunus padus</i>	orchard vicinity.	
527	(L.)— <i>Rhopalosiphum padi</i> (Linnaeus) system, it has been		
528	found that aphid autumnal return is positively influenced by	3.3.3 Top-down: web-building spiders	576
529	green leaves (Archetti and Leather 2005). On the contrary,	Whereas some aphidophagous insects have been shown to be	577
530	early leaf senescence increases the number of overwintering	relatively inactive in autumn, web-building spiders have been	578
531	eggs of <i>Euceraphis betulae</i> (Koch) on <i>Betula pendula</i> (Roth)	observed in relevant quantity in an apple orchard (Wyss	579
532	in short autumn (Silfver et al. 2014).	1995). The finding that the number of spider webs in autumn	580
533	Cultivar mixtures of apple trees with differential resistance	is negatively correlated with aphid abundance in subsequent	581
534	to <i>D. plantaginea</i> has been shown to reduce aphid incidence	spring suggests that measures that increase spider abundance	582
535	on the susceptible cultivar compared to a pure stand of the	in orchards such as weed strips could help to reduce orchard	583
536	susceptible cultivar. This positive effect of cultivar mixture	infestation by winged aphids returning in autumn.	584
537	has been attributed to a dilution effect of the resource, which		
538	is the susceptible cultivar (Parisi et al. 2013).	3.4 Overwintering forms	585
539		Studies focusing on alternatives to chemicals for control of	586
		overwintering aphid stages are scarce. <i>E. lanigerum</i> aphids	587
540	3.3.2 Direct action: use of sexual pheromone lures to impair	overwinter as apterous females either on the roots or within	588
541	mating partner location and reduction of aphid inoculum	the canopy of apple trees. Overwintering canopy colonies of	589
		<i>E. lanigerum</i> can be strongly reduced by earwigs, so any	590
542	During the sexual generation involving oviparae and winged	measure to favour earwig can have a positive effect on the	591
543	males, oviparae release a sex pheromone to guide conspecific	control of this aphid (Lordan et al. 2015). Earwigs as natural	592
544	males. The two pheromone components (4aS,7S,7aR)-	enemies of aphids are considered in most studies to be bene-	593
545	nepetalactone and (1R,4aS,7S,7aR)-nepetalactol are quite	ficial for apple production (Dib et al. 2010b; Cross et al.	594
546	common among aphid species; however, it is the ratio be-	2015); however, as they can also damage fruits, they are some-	595
547	tween the two components which is species specific	times considered as apple pest (Markó et al. 2008) and most of	596
548	(Symmes et al. 2012). These sex pheromones could be used	the time classified as peach pest (Saladini et al. 2016).	597
549	to monitor fall populations and also to disrupt mating (Boo		
550	et al. 2000; Symmes et al. 2012). A 1:1 ratio of the two com-	4 Side effects of alternative methods to chemicals	598
551	ponents of the sex pheromone has been shown to be efficient	for aphid control	599
552	to trap <i>Hyalopterus pruni</i> (Geoffroy) and <i>Brachycaudus</i>		
553	<i>helichrysi</i> (Kaltenbach) in prune orchards ( <i>Prunus domestica</i>	4.1 Orchard pest community complexity	600
554	(L.)). However, the trap has also caught an important propor-	The implementation of alternative control methods for aphid	601
555	tion of non-target aphid species, so the bait should be im-	management—such as modified host plant suitability or	602
556	proved if it is to be used for monitoring purposes (Symmes		
557	et al. 2012). For <i>Tuberocephalus momonis</i> (Matsumara) in		

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

610 For example, a tree cultivar selected to be resistant to a  
 611 specific pest can be susceptible to another one. The peach  
 612 cultivar ‘Rubira’ is resistant to *M. persicae* but susceptible to  
 613 *Brachycaudus persicae* (Passerini) (Sauge et al. 1998; Sauge  
 614 et al. 2002). Similarly, the apple cultivar ‘Florina’ is resistant  
 615 to *D. plantaginea* and to scab (Miñarro and Dapena 2008), but  
 616 susceptible to *E. lanigerum* (Abu-Romman and Ateyyat  
 617 2014). Deficit irrigation seems to reduce peach tree suscepti-  
 618 bility to aphids and has also a positive effect on the control of  
 619 brown rot. This effect of water restriction on brown rot might  
 620 be due to a reduction of microcracks on the fruit surface,  
 621 which limits the invasion of pathogens (Mercier et al. 2008).  
 622 On the contrary, egg hatching of the buprestid *Capnodis*  
 623 *tenebrionis* (Linnaeus) can be compromised by high soil hu-  
 624 midity, so restrictive irrigation might have a positive effect on  
 625 this stone orchard pest (Marannino and De Lillo 2007). The  
 626 cultivar mixture of apple cultivars varying in their resistance  
 627 to scab results in decreased scab and *D. plantaginea* infesta-  
 628 tions on the susceptible cultivar (Parisi et al. 2013). Ground  
 629 cover management, which is suggested to positively influence  
 630 biological control of aphids, may also increase vole (*Microtus*  
 631 *savii* (De Selys-Longchamps)) populations (Bertolino et al.  
 632 2014). As the effects of the alternative methods implemented  
 633 for aphid management can be either positive or negative de-  
 634 pending on their effects on other pest species, they should  
 635 be selected and combined according to locally important pest  
 636 species to optimise the control of the orchard pest community.  
 637 In this context, it is noteworthy that the implementation  
 638 of alternative control methods for the management of  
 639 other pests can also impact aphid dynamics. Indeed, codling  
 640 moth exclusion nets closed in April during aphid development  
 641 have been shown to decrease *D. plantaginea* abundance (Dib  
 642 et al. 2010a).

643 **4.2 Fruit production and quality**

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

651 Nitrogen restriction can impact yield, as demonstrated in  
 652 apple orchards (Kühn et al. 2011). Water restriction has con-  
 653 trasting effects on fruit production and quality depending on

its time of application and intensity. It can either reduce yield 654  
 (Naor et al. 1999, 2001; Girona et al. 2010) or have no effect 655  
 (Mercier et al. 2008). However, economic losses related to 656  
 lower yield may be compensated by higher fruit quality. 657  
 Indeed, deficit irrigation may decrease peach fruit diameter 658  
 (Mercier et al. 2008; Rahmati et al. 2015), but increase fruit 659  
 softness (Mercier et al. 2008) and sugar content (Mercier et al. 660  
 2008; Rahmati et al. 2015). The economic valorisation could 661  
 thus counterbalance the yield reduction as informed con- 662  
 sumers are willing to pay more for fruits produced with less 663  
 chemicals (Marette et al. 2012). 664

665 **5 Conclusion**

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

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

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