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

Aurélie Rousselin, Daniele Bevacqua, Marie-Helene Sauge, Françoise Lescourret, Mody Karsten, Marie Odile Jordan

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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 Rousselin¹ · Daniele Bevacqua¹ · Marie-Hélène Sauge¹ · Françoise Lescourret¹ ·**
 7 **Karsten Mody² · Marie-Odile Jordan¹**
 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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✉ Marie-Odile Jordan
 marie-odile.jordan@inra.fr

Q1 ¹ INRA, UR1115 Plantes et Systèmes de culture Horticoles (PSH),
 Domaine St Paul, Site Agroparc, 84914 Avignon Cedex
 09 Avignon, France

² Ecological Networks, Biology, Technische Universität Darmstadt,
 Schnittspahnstr. 3, 64287 Darmstadt, Germany

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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 80.10⁶ tons, while 85 peach and nectarine ranked 4th with more than 21.10⁶ 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

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

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

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

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 comprom-
 ised (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

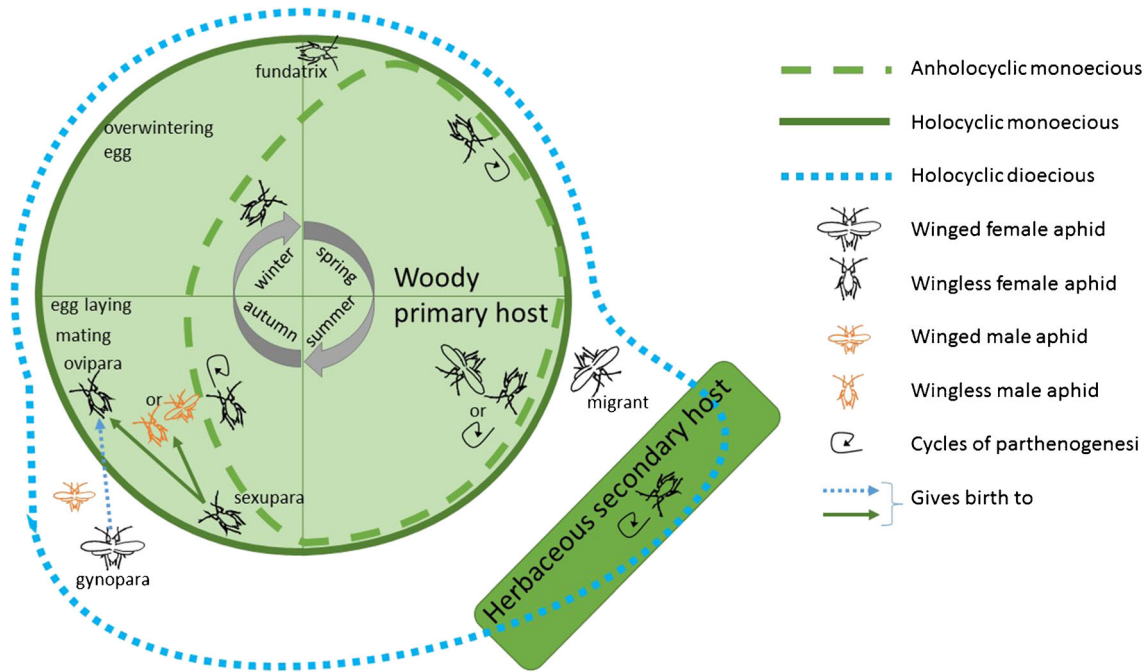


Fig. 2 Variants of fruit tree aphid life cycle. In spring, aphids undergo asexual reproduction on their woody host. In summer, monoecious species stay on the woody host while dioecious species fly to their secondary host. In autumn, dioecious species fly back to their woody host. Holocyclic species undergo sexual reproduction and oviparae lay overwintering eggs whereas anholocyclic species overwinter as wingless females

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 spiraeicola</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

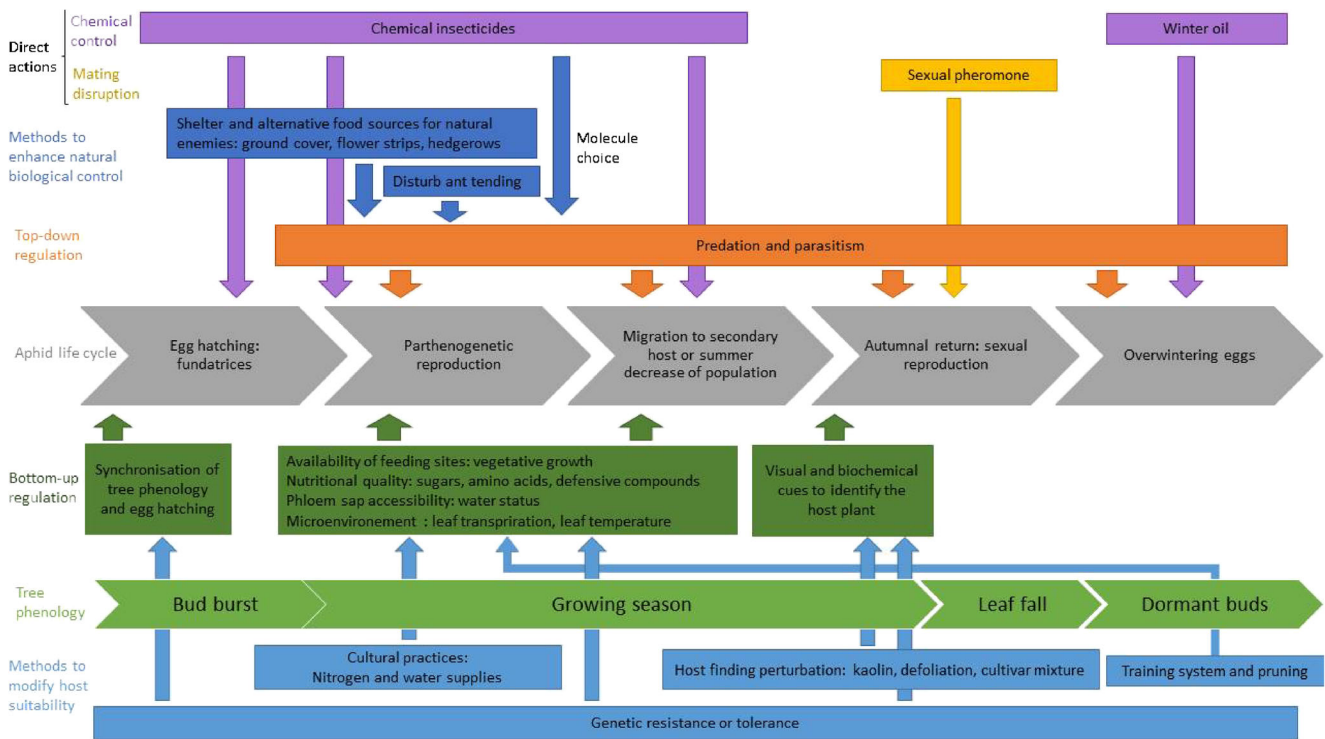


Fig. 3 Possible methods to control aphid populations in apple and peach orchards by mobilizing bottom-up and top-down processes

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 abun-
 422 dance 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 conven-
 425 tional 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 har-
 434 vested fruits (Stewart-Jones et al. 2008). However, this meth-
 435 od 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 provid-
 441 ing alternative carbohydrate sources to the ants, by the posi-
 442 tioning 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 sev-
 453 eral 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 con-
 468 sidered 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 encour-
 471 aging, 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 abun-
 476 dance of *D. plantaginea* (Dib et al. 2016a). On the contrary,
 477 the 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 ob-
 480 tained with a predator:prey ratio of 1:1 or 5:1 (Wyss et al.
 481 1999), compromising the cost-efficiency of the method. So,
 482 further studies are needed, possibly exploiting codling moth
 483 exclusion nets, which are of extended use due to their side
 484 effects on fruit quality and orchard microclimate (Lloyd
 485 et al. 2005; Baiamonte et al. 2016), as a physical barrier
 486 to increase the efficiency of the releases (Dib et al. 2016a).
 487 Mummified aphids were found to be more efficient to
 488 release *Aphidius ervi* (Haliday) than adult parasitoids (Wei
 489 et al. 2005).

490 So, even if release methods are promising, they still face
 491 technical problems regarding their adaptation for aphid con-
 492 trol 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*
 496 *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 repeat-
 500 ed treatments either suppress aphid populations in the follow-
 501 ing 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	3.3.3 Top-down: web-building spiders	576
528	found that aphid autumnal return is positively influenced by	Whereas some aphidophagous insects have been shown to be	577
529	green leaves (Archetti and Leather 2005). On the contrary,	relatively inactive in autumn, web-building spiders have been	578
530	early leaf senescence increases the number of overwintering	observed in relevant quantity in an apple orchard (Wyss	579
531	eggs of <i>Euceraphis betulae</i> (Koch) on <i>Betula pendula</i> (Roth)	1995). The finding that the number of spider webs in autumn	580
532	in short autumn (Silfver et al. 2014).	is negatively correlated with aphid abundance in subsequent	581
533	Cultivar mixtures of apple trees with differential resistance	spring suggests that measures that increase spider abundance	582
534	to <i>D. plantaginea</i> has been shown to reduce aphid incidence	in orchards such as weed strips could help to reduce orchard	583
535	on the susceptible cultivar compared to a pure stand of the	infestation by winged aphids returning in autumn.	584
536	susceptible cultivar. This positive effect of cultivar mixture	3.4 Overwintering forms	585
537	has been attributed to a dilution effect of the resource, which	Studies focusing on alternatives to chemicals for control of	586
538	is the susceptible cultivar (Parisi et al. 2013).	overwintering aphid stages are scarce. <i>E. lanigerum</i> aphids	587
539		overwinter as apterous females either on the roots or within	588
540	3.3.2 Direct action: use of sexual pheromone lures to impair	the canopy of apple trees. Overwintering canopy colonies of	589
541	mating partner location and reduction of aphid inoculum	<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	4 Side effects of alternative methods to chemicals	598
550	et al. 2000; Symmes et al. 2012). A 1:1 ratio of the two com-	for aphid control	599
551	ponents of the sex pheromone has been shown to be efficient	4.1 Orchard pest community complexity	600
552	to trap <i>Hyalopterus pruni</i> (Geoffroy) and <i>Brachycaudus</i>	The implementation of alternative control methods for aphid	601
553	<i>helichrysi</i> (Kaltenbach) in prune orchards (<i>Prunus domestica</i>	management—such as modified host plant suitability or	602
554	(L.)). However, the trap has also caught an important propor-		
555	tion of non-target aphid species, so the bait should be im-		
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**

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

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

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