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ORIGINAL PAPER

Cultivar-mediated effects on apple–*Dysaphis plantaginea* interaction

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Abstract

The question of whether food webs are resource or predation controlled is crucial for the development of sustainable IPM strategies in agriculture. Many IPM studies focus on top–down control, while little is known about bottom–up effects. Here, we unravelled the bottom–up interactions between rosy apple aphid (RAA) *Dysaphis plantaginea* and 13 apple cultivars in north-eastern Belgium. Population dynamics, apple leaf damage, preference and performance measurements were used to determine the interactions between RAA and apple cultivars. Seasonal abundances and RAA-infested shoots were significantly affected by the cultivar. The cultivars Fuji, Granny Smith, Jonagold and Cripps Pink harboured clearly higher numbers of aphids compared to other cultivars, especially Red Delicious. Regarding leaf damage degree, Fuji was significantly the most impacted, while the lowest damage was recorded on Red Delicious. The potential apparent competition among apple cultivars was evaluated using RAA overlap diagrams. By acting as a potential source of RAA, a particular cultivar can considerably affect other nearby cultivars. In host selection bioassays, significant differences in the choice behaviour of RAA were found in the laboratory for different apple cultivars. Other important findings from the reproduction–offspring performance bioassays revealed that while Fuji stimulated high production of nymphs, their development remained retarded on Fuji, compared to especially Boskoop on which significantly lower numbers of nymphs occurred. Our study provides a promising insight into the importance of studying apple–RAA interactions within an eco-friendly RAA management tactic.

Keyword Bottom–up effects · Rosy apple aphid · Apple cultivars · Indirect interaction · Preference · Performance

Key message

- Many IPM studies focus on top–down control, while little is known about bottom–up effects.
- The present study examines the effects of apple cultivar variation on apple–*Dysaphis plantaginea* interactions.
- Population dynamics, preferences and performances of *D. plantaginea* varied significantly among apple cultivars.
- *D. plantaginea*-mediated apparent competition between apple cultivars can have an important impact on *D. plantaginea* infestation levels.

Introduction

As a holocyclic and heteroecious species, the rosy apple aphid (RAA) *Dysaphis plantaginea* Passerini (Hemiptera: Aphididae) is a primary pest of apple in Belgium and Europe and responsible for severe yield losses, particularly in organic farming systems (Forrest and Dixon 1975; Blommers 1994; Bribosia et al. 2004; Bangels et al. 2008). Feeding by RAA on the phloem generates a diversity of economically important damage symptoms, in particular growth stunting, leaf curling and deformed fruits. Infested trees often produce apple fruits unsuitable for marketing (Tremblay 1988; Schepers 1989; Bribosia et al. 2004; Bangels et al. 2008). Apple leaf response to RAA feeding usually becomes visible in susceptible cultivars within 24 h (Forrest and Dixon 1975). Almost all apple cultivars are susceptible

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for RAA infestation, but the outcome of bottom–up effects (plant quality/suitability) related to this trophic interaction varied according to several abiotic and biotic factors including the cultivar ID (Arnaoudov and Kutinkova 2006; Angeli and Simoni 2006; Miñarro and Dapena 2007; Hellmann et al. 2008; Ballhorn et al. 2011). Many studies already well described the biology and behaviour of RAA (De Berardinis et al. 1994; Hemptinne et al. 1995), but there is lack of comparative information about behavioural and biological (reproduction and development time) parameters of RAA on different apple cultivars.

Currently, control of RAA by insecticide is common practice for achieving marketable yields in apple orchards. In the context of climate change, world population increases and the various side effects of pesticides, ecologists and many of other IPM researchers have been working to develop and promote efficient eco-friendly management programmes to reduce the dependency on synthetic pesticides (Altieri 1999; Lin 2011). To achieve this goal, scientific insights on the trophic interaction between host plants and pests need further elucidation.

Studies of plant–insect interactions are essential for understanding the dynamics of ecological communities including aphids (Sarmento et al. 2011). Identifying preference and performance of a given pest can help to predict infestation dynamics (Kalaitzaki et al. 2013; Macfadyen and Muller 2013) and to manipulate pest populations based on functional landscape engineering (Bianchi et al. 2010; Srinivasan et al. 2013). Based on the preference–performance hypothesis, a positive correlation of cultivar preference and RAA performance is assumed. This means that RAA adults are expected to migrate towards apple cultivars that maximize the fitness parameters of their nymphs. Several studies have already demonstrated positive preference–performance linkages in many insect systems (Price 1994; Mayhew 1997; Heisswolf et al. 2005; Staley et al. 2009), but not all (Mayhew 2001; Scheirs et al. 2004; Digweed 2006; Gripenberg et al. 2007; Alhmedi et al. 2018). Nutritional status of plant, offspring developmental circumstances (Scheirs et al. 2000), host chemistry (Züst and Agrawal 2016) and providing enemy-free space for offspring (Denno et al. 1990) are among the principal factors that can play an important role in the host selection process of females for feeding–reproduction.

Population dynamic changes are coupled to direct factors including weather, natural enemies, management regime, host quality or preference (Müller and Godfray 1997; Symondson et al. 2002; Tscharntke and Brandl 2004; Sarmento et al. 2011) as well as indirect factors including apparent competition (Montoya et al. 2009). These changes can directly impact insects and associated ecosystem services. However, the potential roles of herbivore-mediated apparent competition among plants have not yet received enough attention (Strauss 1991; Wootton 1994; Callaway 2007). Apparent competition is defined as an antagonistic interaction that occurs when the effects of one host plant species on the other are manifested through a common consumer such as an herbivore (Chaneton et al. 2010; Recart et al. 2013). Unfortunately, the lack in understanding of indirect interactions including apparent competition limit our ability to predict the consequences of changes in abundance of a given species, although they can significantly alter population dynamics, and associated ecosystem services, as strongly as direct interactions (Bonsall and Hassell 1997; Montoya et al. 2009; O’Connor et al. 2013; Sotomayor and Lortie 2015).

In this study, we investigated the effects of apple cultivar variation on apple–RAA interactions using field and laboratory experiments, by addressing the following questions: (i) Does RAA respond differently to various cultivars? (ii) Do cultivars respond differently to RAA feeding? and (iii) To which extent is the potential for RAA-mediated apparent competition likely to occur between cultivars? To answer these questions, we have assessed the seasonal population dynamics of RAA and related host leaf damage on different cultivars. In addition, we examined the preference–performance of RAA in response to the variation in apple cultivars in laboratory conditions.

Materials and Methods

Field experiments

The field study was conducted during 2018–2019 growing seasons in an insecticide-free apple orchard (location: Fruit Research Center (pcfruit), Sint-Truiden, Limburg, Belgium, 50.772554° N, 5.156127° E), centrally located in the main area of fruit tree production in Belgium. The orchard in which the experimental design was established was for more than 20 years treated homogeneously in soil management and fertilizer gifts and does not have an inclination.

Apple cultivars and experimental design

Thirteen apple (*Malus domestica* L.) cultivars were planted in repeated plot pattern with eight identical blocks containing a strict order of 13 single-tree cultivars with 18 rows in a 1-ha orchard. All the trees were planted in spring 2000. The order of cultivars in each plot was Braeburn, Elstar, Golden Delicious, Granny Smith, Jonagold, Jonagored, Red Delicious*, Gala, Boskoop, Cox, Bramley’s Seedling*, Fuji and Cripps Pink*, all grafted on rootstock M9. The varieties with an asterisk are not commercially planted in Belgium and used as international references in those plots. For completeness, we mention that Jonagored is a mutant of Jonagold, but since it is being mentioned separately in the WAPA yearly apple harvest predictions (WAPA 2020), we also here refer to it as two distinct cultivars. Two blocks were selected for conducting the field monitoring. The distance between trees was 1.5 m, while the distance between each two rows was 3.5 m. A schematic set-up of the study field is illustrated in Fig. 1.

Population dynamics of RAA

The aphid population dynamic on different apple cultivars was assessed in 2018 and 2019 to evaluate the RAA response to host variation. Two parameters were measured to evaluate the seasonal population dynamics of RAA on apple cultivars: infestation within tree and population abundance. At each monitoring time, ten trees per cultivar were randomly selected for conducting the assessments (using Microsoft Excel number randomization). Activities of natural enemies were not considered in the present study.

RAA infestation level within tree

This parameter was evaluated by calculating the proportion of tree shoots infested by aphids each year. Ten trees per cultivar and three lowest branches per tree were selected for conducting the infestation assessments. All healthy and RAA-infested shoots growing on each branch were counted in order to calculate the proportion of infested shoots per branch. The assessments were conducted at one time interval in 2018 when RAA reached its first peak on apple trees on 21 May and at five time intervals in 2019.

RAA population size

This parameter, representing the RAA abundance, was evaluated by counting the total number of size-based RAA colonies on the ten apical leaves per shoot. Three terminal shoots representing the three lowest branches were selected for assessing RAA abundance. For each scanned shoot, the counted colonies were classified based on their sizes by considering the diameter and related shape (roundish, oval, etc.) of each colony. The varied shapes of colonies present a challenge for measuring and adopting the own diameter and related abundance category, where the colonies are not always roundish. The shape was estimated based on the distribution of main aphid population of each colony, and this means that the scattered individuals surrounding the colony were not considered when adopting the colony shape. The area of each non-roundish colony was calculated and then converted to roundish shape for adopting the diameter and then the related abundance category. We used six diameter-based categories for classifying RAA colonies infesting the ten apical leaves per shoot (Dib et al 2016; Alhmedi et al 2018). $A=0$, no aphids; $B=20$, colony diameter ≤ 1 cm or scattered individuals; $C=50$, colony diameter >1–2 cm; $D=100$, colony diameter >2–3 cm; $E=200$, colony diameter >3–4 cm; $F=500$, colony diameter >4 cm. The abundance of aphids per each selected shoot was assessed by summing the colonies found on that shoot. On ten trees per cultivar, the population abundance assessments were conducted at five time intervals in 2019.

Leaf damage

This parameter was quantified by assessing curled leaves which are typically formed as a response of apple cultivars to RAA feeding. More specifically, the proportion of tree shoots associated with curled leaves, on which only the ten apical leaves per shoot were considered in the damage evaluation, was calculated. All shoots growing on the three lowest branches per tree were considered in the damage assessments. Leaf damage levels were assessed on ten trees per cultivar at one date, end of May, in 2018, and at two dates, mid-May and mid-June, in 2019.

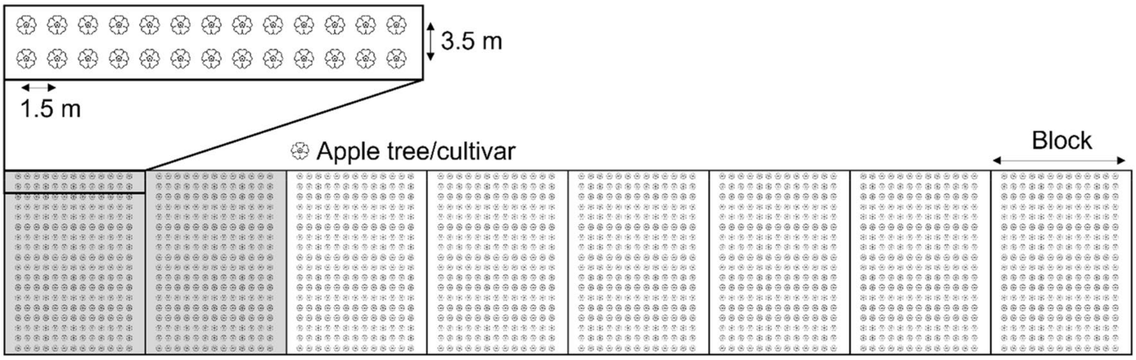

Fig. 1 A schematic set-up of the study site

Laboratory experiments

Aphid mass rearing

The RAA population was originated from an aphid colony collected from an apple orchard (cultivar Topaz), which is located at 1 km from the experimental field. Based on the plant material availability, the laboratory RAA population was maintained on young apple plants originated from Golden Delicious seeds at 20 °C, 16:8-h LD cycle, 65 ± 5% relative humidity with 16:8-h LD photoperiod for rearing and experiments in a climate-controlled room.

Choice test

The experiments were carried out on ten healthy RAA-free shoots per cultivar (± 15 cm), which originated from the 13 apple cultivars included in the field study. Each shoot was separately kept in a small water-filled cylindrical container (5 cm in diameter and 10 cm height) in order to maintain the freshness as long as possible. Foam stoppers were used on the top of containers to avoid the aphids to fall in the container. Then, sets of 13 twigs representing the study cultivars were placed in transparent cages. (Internal dimensions are 45 × 45 × 45 cm, front and back are of transparent plastic for observing RAA activity, while other sides are of polyester mesh netting for ventilation.) In each cage, twig-containing containers were placed in the inner lateral zone with circle-shaped distribution and a set of 20 apterous aphid adults were introduced in the cage centre using 90-mm wet filter paper-prepared Petri dishes which were left open in the middle of the circle of containers. The cages were placed in two plant growth chambers with identical conditions as those of the mass-rearing population. The choice test was replicated ten times, and the number of adults that did choose after 24 h was recorded.

Reproduction rate and development time

Laboratory experiments were carried out to determine the performance of RAA on the 13 apple cultivars included in the field study. Reproduction rate and development time of nymphs to reach the adult stage were considered for measuring the RAA performance. The bioassays were conducted using 35-mm Petri dishes with leaf discs on agar. More than 1000 old nymphs were allowed to feed and develop on healthy apple plants originated from Golden Delicious seeds, and then, the reproductive females were selected for testing. Three RAA females (3 days old) were carefully introduced onto each Petri dish using a micro paint brush. The Petri dishes were then transferred to a climate chamber to allow the reproduction of aphids under the conditions of 20 °C, 65 ± 5% RH and 16L/8D photoperiod. The females were removed after 24 h, and the nymphs produced during this period were counted. These nymphs were kept in Petri dishes with leaf agar discs until the adult stage, and new Petri dishes with fresh apple leaf discs were used every 2–3 days until development of adults. Ten replicates were performed for each cultivar.

Data analysis

Using Minitab 18 software (Minitab Inc. 2017), a Tukey test, for separating the means at $p \leq 0.05$, after a generalized linear model (GLM), was applied to determine the significance of differences between apple cultivars ($p \leq 0.05$) in RAA population abundances, RAA infestation within tree and leaf damage level measured during the field study. Differences between numbers of RAA adults that did choose between apple cultivars, reproduction rate and development time of RAA were also evaluated using the Tukey test after GLM analysis. Aphids that were scored as no choice were excluded from the statistical analysis. All data were subjected to variance homogeneity analysis (Levene's test), and if $p \leq 0.05$, a data transformation procedure was applied. Moreover, all laboratory data were checked for normality (Ryan–Joiner test) to assess whether they followed a normal distribution. The skewness of the data was compensated by either log10 $(n + 1)$ transformation of aphid densities or arcsine transformation of percentage data. While choice and reproduction data were normally distributed and then subjected for GLM and the Tukey test, development time data were not normally distributed and hence a nonparametric Kruskal–Wallis test was applied. Principal component analysis (PCA) was also performed using the statistical software XLSTAT 2016 on the field (2019) and laboratory data collected from 13 apple cultivars. This allowed us to explore variation patterns among apple cultivars in the different interaction parameters with RAA investigated in both the field (RAA abundances, infestation within tree and leaf damage) and the laboratory (host choice for feeding, reproduction rate and development time) and thus allowed us to assess how the cultivars were correlated based on these interaction parameters.

Quantitative RAA overlap diagrams were constructed to generate predictions about the extent of potential RAA-mediated apparent competition between apple cultivars and to contribute to our understanding of the potential intraspecific interactions between host plants and their ecological consequences. For constructing the quantitative overlap diagrams, we used data on RAA abundances and associated leaf damage levels recorded on the study cultivars in 2019. For that purpose, we adapted a tool developed by Müller et al. (1999) as a means to assess the potential for apparent competition "indirect interactions via RAA population" between apple cultivars and to compare its importance at lower trophic levels. Different apple cultivars are linked using the quantitative measure d_{ij}. Here, the probability that a fraction of RAA population attacking cultivar i are likely to have developed on cultivar j is calculated as

$$d_{ij} = \sum_k \left[\frac{a_{ik}}{\sum_l a_{il}} \frac{a_{jk}}{\sum_m a_{mk}} \right]$$

where a_{ik} is the fraction of aphids k found on cultivar i and a_{jk} is the fraction of aphids k found on cultivar j. The sums of k and l include all RAA individuals, and that of m includes the percentages of leaf damage on all cultivars. Hence, the index $d_{ij}=0$ when cultivars i and j do not share any RAA individuals at all, and $d_{ij}=1$, when all aphids attacking cultivar i have developed on cultivar j, or vice versa in case of d_{ji}. All quantitative overlap diagrams were constructed in the Mathematica 5.0 (Wolfram Research 2003).

Results

Field experiments

RAA infestation within tree

RAA infestation was expressed by the percentage of RAA-infested leaf clusters per tree. The statistical analysis applied on all data collected from the two-year field survey revealed significant differences between apple cultivars in the RAA infestation levels, both in 2018 ($F_{12,377}=24.71$; $p<0.001$, Fig. 2) and in 2019 ($F_{12,377}=58.64$; $p<0.001$, Fig. 3). Overall, similar patterns of RAA infestation were detected on apple cultivars in both study years 2018–2019. In both study years, the lowest percentage of infestation recorded in May was found on Red Delicious, Braeburn, Cox and Elstar. Temporally different patterns of RAA infestation within the tree on the different cultivars recorded in 2019 are shown in Table 1 and Fig. 3. In early May 2019, the highest percentage of infestation was registered on Fuji, Cripps Pink, Bramley's Seedling and Gala ($F_{12,377}=61.52$; $p<0.001$). However, Granny Smith, Jonagold and Cripps Pink, followed by Bramley's Seedling, Fuji and Golden Delicious, showed the highest percentage of infestation by the end of May 2019 ($F_{12,377}=27.20$; $p<0.001$) compared to other apple cultivars (Table 1). While the RAA infestation in apple trees clearly declined towards mid-June 2019, Cripps Pink (20.3%) and Fuji (21%) showed considerable infestation.

RAA abundance

Main activities of RAA population were recorded in 2019 on all apple cultivars from May to June; however, late activities were observed in August only on the cultivars Golden Delicious, Granny Smith and Gala (Table 1, Fig. 3). The results of statistical analysis (GLM, Table 1) revealed a highly significant effect of cultivars on RAA abundances during the season (in 15 May: $F_{12,377}=44.52$; $p<0.001$, in 31 May: $F_{12,377}=62.44$; $p<0.001$, in 14 June: $F_{12,377}=15.47$; $p<0.001$, in 1 August: $F_{12,377}=20.84$; $p<0.001$, in 15 August: $F_{12,377}=12.50$; $p<0.001$). However, the differences were most obvious in some of the cultivars examined (Tukey test, Table 1). In early May, Fuji hosted the highest number of RAA, while the lowest was observed on Braeburn compared to other cultivars. In late May, high numbers of RAA were remarkably found on Granny Smith, Jonagold and Fuji. While the RAA population declined rapidly towards 14 June, higher numbers of aphids were found on the cultivars Fuji and Cripps Pink compared to other study cultivars. All results are presented in Table 1 and Fig. 3.

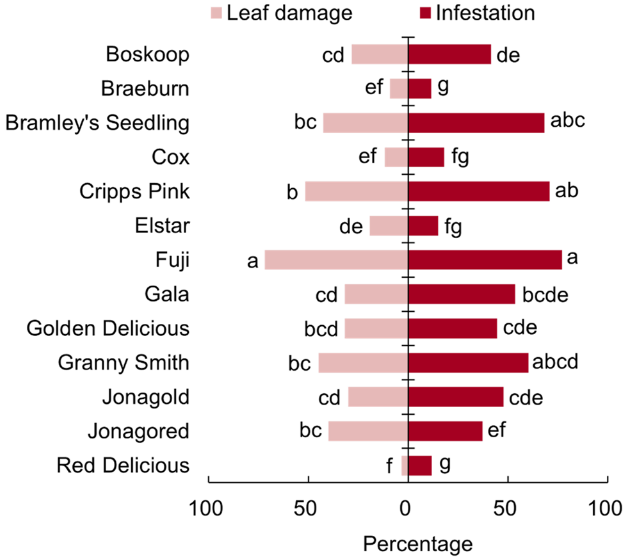

Fig. 2 Percentage of infestation and RAA-induced leaf damage recorded on 13 apple cultivars in 2018 (21 May). Left bars represent leaf damage, while right bars represent the infestation. Different letters within each observation parameter indicate significant differences (GLM and Tukey test, $p \leq 0.05$; data were previously arcsine transformed)

Leaf damage

RAA-infested trees exhibited different responses, illustrated by clusters of curled leaves, to aphid feeding on the cultivars investigated in 2018–2019 (Figs. 2, 4, respectively). Statistically, RAA generated significantly varying degrees of leaf damage in both study years (May 2018: $F_{12,377}=24.58$; $p<0.001$, May 2019: $F_{12,377}=22.06$; $p<0.001$, June 2019: $F_{12,377}=14.32$; $p<0.001$). The data collected in May of both years indicated that the leaves of cultivar Fuji were the most damaged by RAA feeding, while the leaves of Red Delicious, followed by Braeburn

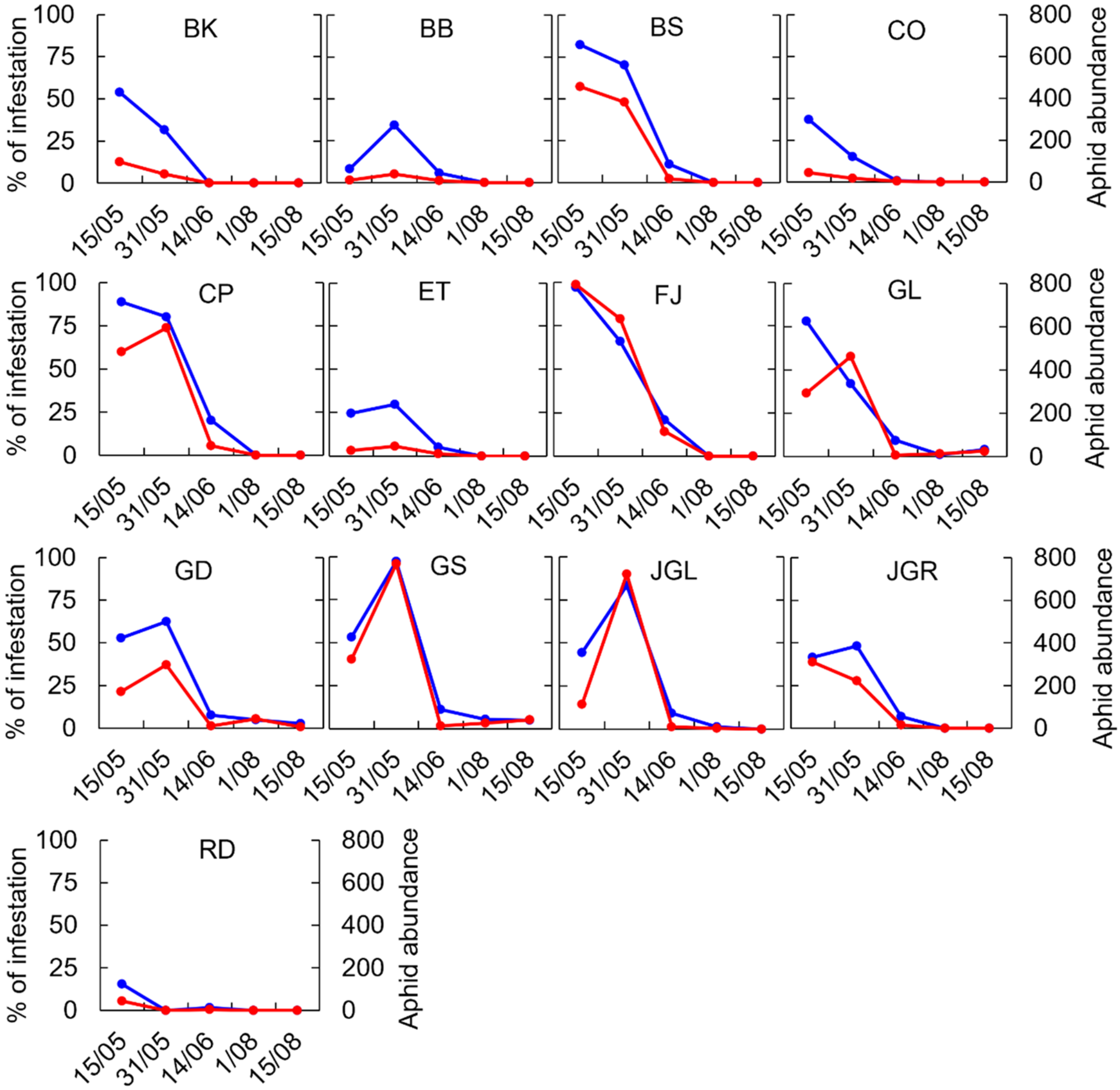

Fig. 3 Abundances of RAA (mean numbers per shoot, red lines) and infestation within tree (mean percentages, blue lines) recorded on 13 apple cultivars from May to August in 2019. BK = Boskoop, BB = Braeburn, BS = Bramley's Seedling, CO = Cox, CP = Cripps Pink, ET = Elstar, FJ = Fuji, GL = Gala, GD = Golden Delicious, GS = Granny Smith, JGL = Jonagold, JGR = Jonagored, RD = Red Delicious

and Cox, were remarkably less impacted by aphid feeding compared to other cultivars examined in the present study. In May 2018–2019, the leaf damage levels ranged from 3.3% and 2.5% in the Red Delicious cultivar to 71.7% and 88.3% in the Fuji cultivar, respectively. In June 2019, a significantly higher leaf damage (63.3%) was recorded on Fuji, while the lowest leaf-damaged cultivar was Red Delicious with 6.7% (Fig. 4).

The principal component analysis applied on the whole field dataset clearly showed the variation patterns in RAA abundance , infestation within tree and RAA-induced leaf damage among apple cultivars in 2019 (Fig. 5A).

RAA-mediated indirect interactions

The potential indirect effects (apparent competition) between apple cultivars are shown with links connecting two cultivars that shared RAA individuals in the quantitative RAA overlap diagrams (Fig. 6), which seasonally varied in the strength of apparent competition. These diagrams consist of a set of sequentially vertices, each representing a cultivar. Circles of varying diameters at each vertex represent the potential apparent competition. The extent a cultivar circle is coloured white represents d_{ii} and coloured black represents d_{ij}. If two cultivars i and j are connected, then the width of the

Table 1 Mean number of RAA (per shoot) and percentage of infestation per apple tree in 2019

Cultivar	15 May	31 May	14 June	1 August	15 August
RAA abundance					
Boskoop	100.3def	43.7fg	0.0e	0.0b	0.0c
Braeburn	10.7g	39.7fg	9.7cde	0.0b	0.0c
Bramley's Seedling	457.3b	384.7cd	17.3bc	0.0b	0.0c
Cox	45.0efg	16.3fg	2.7de	0.0b	0.0c
Cripps Pink	480.0b	589.7bc	45.3ab	0.0b	0.0c
Elstar	24.7fg	44.3f	9.3cde	0.0b	0.0c
Fuji	789.3a	631.3ab	114.0a	0.0b	0.0c
Gala	293.7bc	463.7bcd	7.3cde	13.7b	25.7ab
Golden Delicious	172.3cd	296.7de	10.7cde	44.3a	7.3bc
Granny Smith	322.7bc	767.3a	13.0cde	26.7a	41.3a
Jonagold	116.0de	719.0a	11.3cde	3.3b	0.0c
Jonagored	311.0cd	223.7e	16.7cd	0.0b	0.0c
Red Delicious	42.7efg	0.0g	2.7de	0.0b	0.0c
F	44.52	62.44	15.47	20.84	12.50
df	12,377	12,377	12,377	12,377	12,377
p-value	<0.001	<0.001	<0.001	<0.001	<0.001
Percentage of infestation					
Boskoop	53.9d	31.6efg	0.0e	0.0b	0.0b
Braeburn	8.2g	34.4efg	5.7bcde	0.0b	0.0b
Bramley's Seedling	82.5bc	70.2bc	11.0b	0.0b	0.0b
Cox	37.2de	14.9gh	0.7de	0.0b	0.0b
Cripps Pink	88.7ab	80.1ab	20.3a	0.0b	0.0b
Elstar	24.5ef	29.7fg	5.0bcde	0.0b	0.0b
Fuji	97.0a	65.9bcd	21.0a	0.0b	0.0b
Gala	78.1c	42.1def	9.4b	1.3b	4.2a
Golden Delicious	52.8d	62.4bcde	7.8bcd	4.9a	2.8a
Granny Smith	53.3d	97.0a	11.2b	5.4a	4.9a
Jonagold	44.4d	83.3ab	9.2bc	1.4b	0.0b
Jonagored	41.7de	48.3cdef	6.8bcd	0.0b	0.0b
Red Delicious	15.5fg	0.0h	1.5cde	0.0b	0.0b
F	61.52	27.20	14.18	21.95	12.46
df	12,377	12,377	12,377	12,377	12,377
p-value	<0.001	<0.001	<0.001	<0.001	<0.001

GLM and the Tukey test on previously log10 $(n+1)$-transformed data were applied, $p \leq 0.05$. Different letters in the same date indicate a significant difference between cultivars, and (a) represents the highest abundance and infestation

polygon at i represents d_{ij} and at j represents d_{ji}. In the quantitative RAA overlap diagram for early season (15 May), the majority of RAA population attacking apple cultivars likely tended to have developed on Fuji and less on Cripps Pink, Granny Smith and Bramley's Seedling cultivars and then moved to other cultivars (Fig. 6). According to the overlap diagram for the subsequent month (June), the cultivars Fuji and Cripps Pink were probably the predominant sources of RAA attacking other cultivars. In other words, a proportion of leaf damage on other cultivars is probably caused by RAA individuals that have potentially moved from Fuji and Cripps Pink towards those cultivars.

Laboratory experiments

Choice test

The results of statistical analysis (GLM) revealed a highly significant effect of cultivars on the choice of RAA adults ($F_{12,117}=9.88$; $p<0.001$; Fig. 7). In terms of preference significance, apple cultivars can be ranged in two groups. The first group represents the cultivars that have an elevated level of attraction (Bramley's Seedling, Cripps Pink, Jonagored, Fuji, Gala, Golden Delicious, Granny Smith, Jonagold), and the second group represents the cultivars that have a low level of attraction (Boskoop, Braeburn, Cox, Elstar, Red Delicious). The preference variation pattern of RAA adults between apple cultivars was also clearly highlighted in the PCA graphic (Fig. 5B).

Reproduction rate and development time

The mean number of nymphs produced by RAA females in the reproduction bioassays differed significantly between apple cultivars ($F_{12,117}=86.42$; $p<0.001$). Females produced the highest numbers of nymphs on Fuji, Cripps Pink, Gala and Golden Delicious, while the lowest numbers were recorded on Red Delicious, Cox and Boskoop (Fig. 8). However, the development time of RAA on Fuji was significantly ($H=97.52$; $p<0.001$) longer than on a potentially less preferred apple cultivar, Boskoop (Fig. 9). Nymphs completed their development on the cultivars Boskoop, Golden Delicious and Cripps Pink within 11–12 days, which is shorter than on the other cultivars (14–15 days). Nymphs developing on Golden Delicious spent in average 3.5 days less for reaching their adult stage when compared to those developing on Gala (Fig. 9). The variation pattern of RAA in reproduction rate and development time among apple cultivars was also obviously shown in the PCA graphic (Fig. 5B).

Discussion

Our study combines empirical data obtained from field and laboratory experiments to highlight RAA-mediated interaction strengths in the apple food web. The very low economic damage threshold and the strong mutualism level with farming ants are among the key factors that make RAA a serious pest in most apple orchards in Europe and North America (Forrest and Dixon 1975; Blommers 1994; Tremblay 1988;

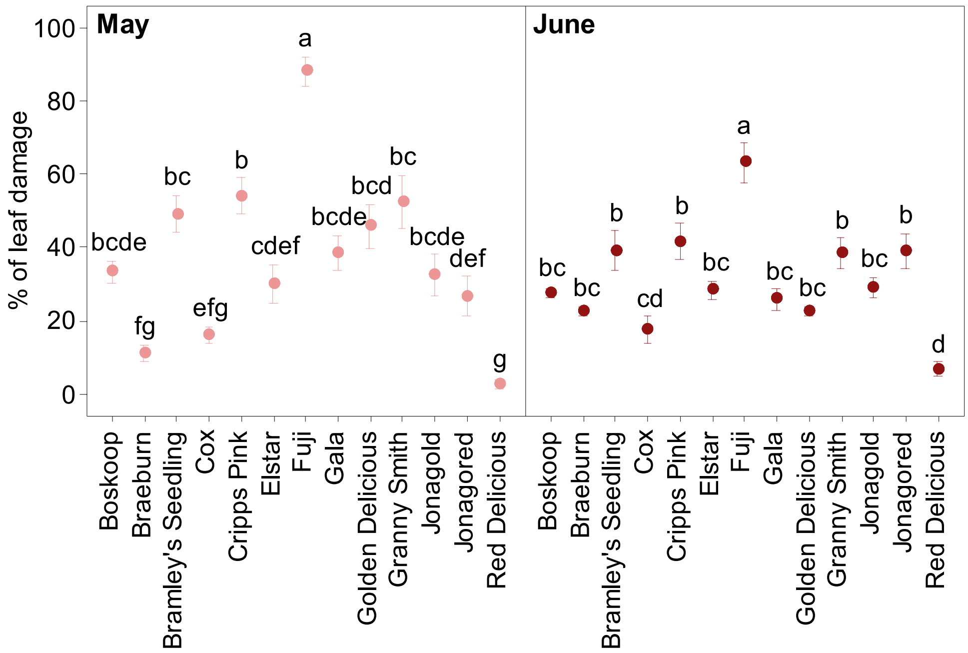

Fig. 4 Percentage of leaf damage (± SE) recorded during May and June in 2019 on studied apple cultivars (GLM and Tukey test, $p \leq 0.05$; data were previously arcsine transformed)

Schepers 1989; Bribosia et al. 2004). Usually, farmers do not take the cultivar into account to decide whether RAA has to be treated or not. Because RAA in intensively managed apple orchards are treated with pesticides from their first appearance (low economic threshold), the ecosystem functions where aphids simply represent the main food of many beneficial organisms are consequently impacted. Alternative strategies for managing aphids can be adopted to mitigate these impacts, including the implementation of eco-friendly tools like intercropping system and less susceptible cultivars (Martin-Guay et al. 2018).

The screening for seasonal interactions between aphids and hosts (apple cultivars) is vital for designing sustainable solutions for pest control (Tindo et al. 2009). We aimed in the current study to explore the intraspecific interactions between apple cultivars and RAA. Overall, the field population dynamic of RAA varied significantly among apple cultivars. Moreover, the seasonal changes in population dynamics of RAA and related leaf damages differed significantly between apple cultivars. Differential susceptibility of apple cultivars to RAA is evidently common (Angeli and Simoni 2006; Arnaoudov and Kutinkova 2006; Miñarro and Dapena 2007). Our results are consistent to a large extent with those reported by Arnaoudov and Kutinkova (2006) and Miñarro and Dapena (2007), but not with Anegli and Simoni (2006) who reported Red Delicious as a susceptible cultivar for RAA. This could be related to the fact that Red Delicious is not grown commercially in Belgium, and so, more local adaptation of RAA is needed under these circumstances. Natural enemies could represent another factor influencing the host choice and then the RAA population dynamic patterns observed in this study. Aphids like other herbivores were found to use chemical, visual and vibrational cues to detect natural enemies (Kunert et al. 2005; Gish 2021), which often elicits several defensive behaviours such as walking away and dropping off the plant that enable the aphids to avoid natural enemies and may induce changes in aphid life history traits (Ninkovic et al. 2013; Lagos 2017). Based on the preference–performance and enemy-free space hypotheses (Jaenike 1978; Price et al. 1980; Jeffries and Lawton 1984; Ninkovic et al. 2013), it is suggested that herbivores may prefer to feed on nutritionally poor hosts if they offer habitats better protected from natural enemies than nutritionally rich hosts (Thompson 1988). As an example from herbivores, Nomikou et al. (2003) found that adult whiteflies may avoid cucumber plants in the presence of predatory phytoseiid mites.

In the present study, RAA infestation patterns, preference behaviour, development time, reproduction rate and host cultivar variation formed a network of direct and indirect links that determined trophic interaction strengths between RAA and apple cultivars. Our laboratory bioassays confirmed to a large extent the population dynamic patterns of RAA on most cultivars observed in the field experiment, on which higher numbers of nymphs were produced on the attractant cultivars like Fuji and Cripps Pink, while less attractant cultivars (Red Delicious and Cox) induced lower number of nymphs. However, Jonagored showed different interaction pattern with RAA compared to the situation in field condition. RAA–apple interaction patterns observed in our work may be explained to some extent by the parental cultivar origin, especially for Cripps Pink (Lady Williams × Golden Delicious), Jonagold (Golden Delicious × Jonathan) and Gala (Kidd's Orange Red × Golden Delicious). There is lack

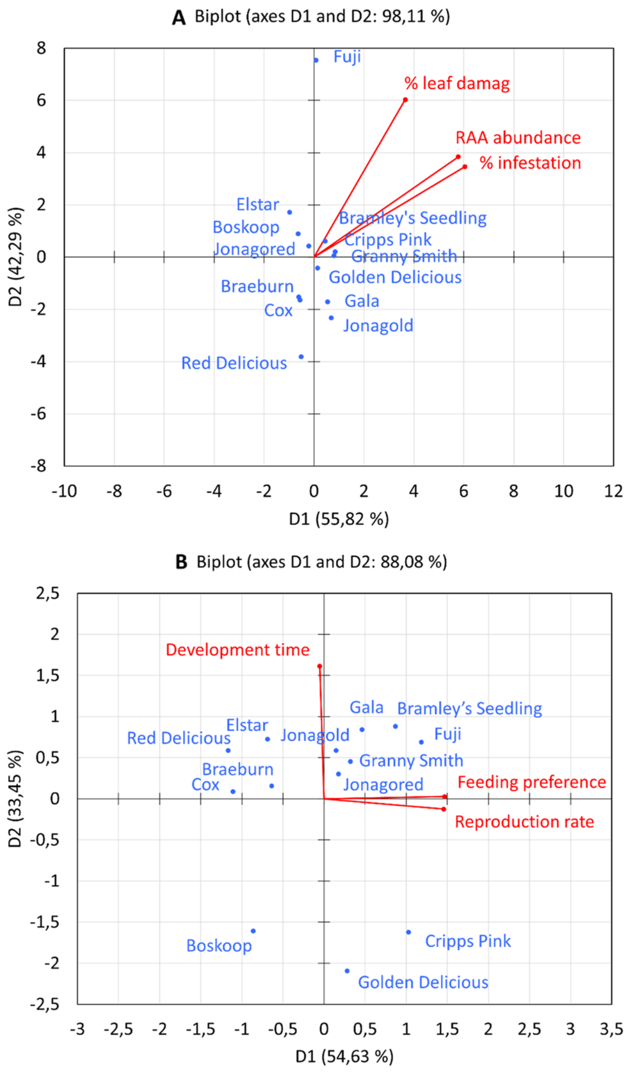

Fig. 5 Principal component analysis (PCA) based on the interaction of RAA population with 13 apple cultivars in field conditions A (RAA abundance, infestation within tree and leaf damage) and in laboratory conditions B (host choice, reproduction rate and development time). The PCA axes PC1 and PC2 are equivalent to Dim1 and Dim2, respectively

of information about the interaction of some apple parents with aphids. But as the resistance gene was reported to be highly heritable (Babura and Mustapha 2012), it is worth further investigation. Furthermore, our particular field data revealed that the most cultivated apple cultivars in Belgium (Jonagold with 41.1% of total area, followed by Jonagored with 15.5% and Golden Delicious with 10.1%) (Flemish government data 2020) showed susceptibility at intermediate level for RAA infestation compared to less planted cultivars investigated in this study.

Overall, our results provide a quantitative evidence that RAA adults are often, but not always, able to distinguish between cultivars and select the suitable host for the reproduction and development time of their nymphs, and this finding is consistent with the preference–performance hypothesis, in which the phytophagous adults select the host plant that maximizes offspring performance (Jaenike 1978, 1990; Gripenberg et al. 2010; Clark et al. 2011). However, RAA adults sometimes failed to select the most suitable host (development duration) for their nymphs, as illustrated in this study by the nymphs spending significantly more time on a highly preferred host (Fuji cultivar) for reaching the reproductive stage. Not only insects that have a wide host range (Fritz et al. 2000; Faria and Fernandes 2001; Friberg et al. 2015; Poyet et al. 2015; Alhmedi et al. 2019) often fail to provide a suitable host for their offspring. The insects with a narrow host range are also sometimes failing to find the most suitable host that offer the best performance for their offspring, as demonstrated in the present study. The development time data of nymphs to adults indicate that RAA adults are not always able to offer the optimal host for their offspring, and this result is consistent with those reported by Mayhew (1998), who found a similar trend when he tested the relationship between host–plant preference and different offspring fitness parameters of the oligophagous leafminer *Chromatomyia syngenesiae* Hardy (Diptera: Agromyzidae) under field and laboratory conditions.

Although RAA abundance has been shown to vary among apple cultivars and geographical zone (Angeli and Simoni 2006; Arnaoudov and Kutinkova 2006; Miñarro and Dapena 2007), we are not aware of studies that have reported the potential contribution of indirect effects between apple cultivars to variation in RAA abundance. The work reported here supports the hypothesis that indirect interactions mediated by shared organisms may be an important element in structuring ecological communities. The presence of 13 apple cultivars in a single and homogeneous orchard in terms of environmental conditions allowed us to present reliable data on the indirect interaction strength between apple cultivars mediated by shared RAA. Given the importance of a healthy food web to the survival of ecosystems on the planet, a major challenge of researchers is to understand the factors that mediate direct and indirect interactions between aphids and hosts. The results of apparent effects reported in this study reveal the RAA-mediated indirect interaction strength between apple cultivars and potentially related apple damage levels. This aspect of interaction measurements may be particularly important to less susceptible apple cultivars because RAA may prefer to move towards most susceptible cultivars. Potentially negative indirect effects were recorded from the intraspecific interaction analysis, on which population dynamics of RAA observed on the less susceptible cultivars were likely impacted by the presence of highly RAA-susceptible cultivars, especially Fuji and less for Cripps Pink. There are few studies focusing on the evaluation of

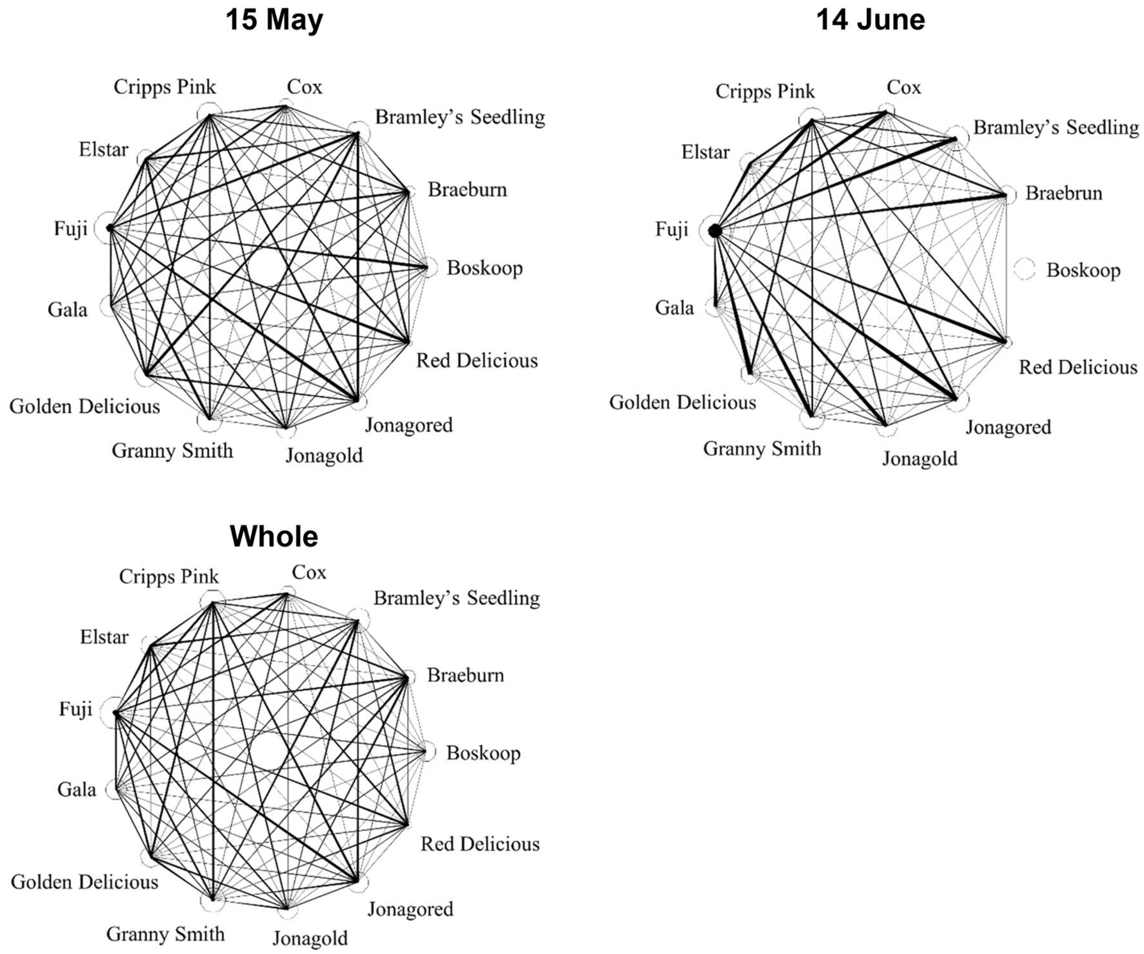

Fig. 6 RAA overlap diagrams constructed for 13 tested apple cultivars. The diameter of each white circle indicates the contribution of a cultivar as a responsible of its own leaf damage via RAA developed on same cultivar, while the black circle sizes represent the contribution of a cultivar as a source of RAA that caused leaf damage on other cultivars. Links between apple cultivars denote RAA density-mediated indirect interaction strength, where the link width to each species represents the potential RAA-mediated effect derived from another apple cultivar as a source of RAA

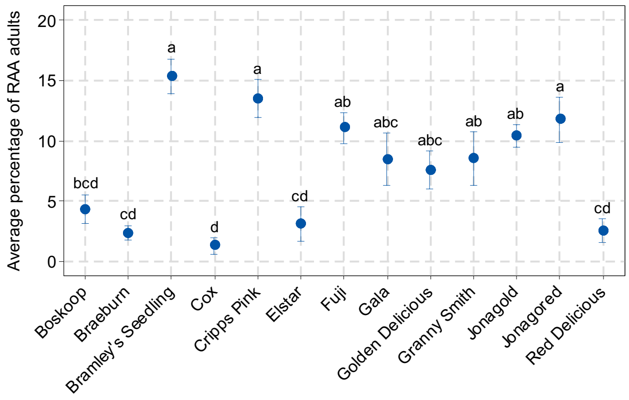

Fig. 7 Average percentage (± SE) of RAA adults ($N = 20$) recorded on the shoots of 13 studied apple cultivars. Spots with same letters are not significantly different (GLM and Tukey test on previously arcsine-transformed data were applied, $p \leq 0.05$)

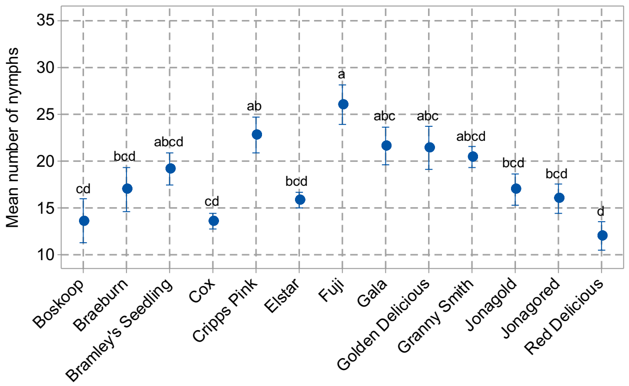

Fig. 8 Mean number (± SE) of nymphs produced by three RAA females ($N = 30$ per cultivar) on 13 apple cultivars using Petri dishes with leaf discs during 24 h in no-choice assays. Spots with same letters are not significantly different (GLM and Tukey test on previously log10 $(n + 1)$-transformed data were applied, $p \leq 0.05$)

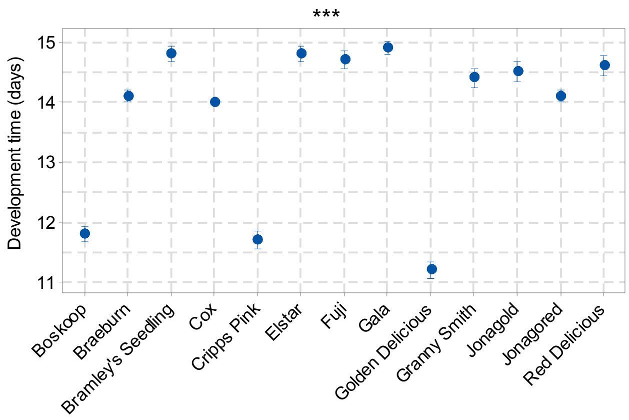

Fig. 9 Development time (days, mean numbers ± SD) of RAA from nymph to adult on the 13 apple cultivars. The asterisks illustrate a cultivar-dependent significant difference for the duration of aphid development from nymph to adult (Kruskal–Wallis test, $p \leq 0.05$; based on the equal variances' test, no data transformation was needed)

indirect interaction strength between host plants mediated by herbivores (Karban et al. 2000). Harrison and Karban (1986) demonstrated in their study investigating interspecific interactions that the early occurrence of tiger moth *Arctia caja* (Lepidoptera: Arctiidae) negatively affected the suitability of the host plant to Lymantriidae moths that occur late in the season. Similar evidence of negative indirect interaction was found by Redman and Scriber (2000) in their field and laboratory experiments.

Quantitative aphid overlap diagrams offer promise for future studies. Because the interactions between RAA and apple cultivars are dynamic, particularly in time (what occurs in one year may not occur at same strength at another year), the next step should be to confirm the seasonal indirect interactions under controlled biotic conditions. This will further improve our knowledge of apparent relations between apple cultivars mediated by RAA. Subsequent studies to explore the impact of host variation on the interactions between RAA and other associated insects, like natural enemies and ants, are highly recommended, as well as the assessment of the link between the leaf damage level and fruit damage in response to cultivar variation. The knowledge provided from our study could help in designing eco-friendly management strategies and reduce the over-adoption of chemicals for managing pests in less susceptible cultivars.

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Author contributions All authors conceived and designed the experiments. AA conducted the experiments. AA analysed the data and wrote the manuscript. All authors read, edited and approved the manuscript.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights This article does not contain any studies with human or vertebrate animal subjects performed by any of the authors.

Informed consent Informed consent was obtained from all individual participants included in the study.

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