



Bottom-up effects of apple cultivars on parasitoids via aphid hosts

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Abstract

Variability of intraspecific host plant quality for phytophagous insects may have consequences on the structure and functioning of associated food webs. The quality of host plants can affect aphids fitness, influencing their life history traits and altering the nutritional resources available to higher trophic levels, potentially affecting the development of solitary parasitoids. Here, we assessed the potential bottom-up effects of intraspecific variability among three cultivars (Gala, Ariane, and Greensleeves) of the domesticated apple tree (*Malus domestica*) with putative resistance towards the rosy apple aphid (*Dysaphis plantaginea*) on the aphid's performance, and its cascading effects on the parasitoid *Ephedrus cerasicola*. We measured aphids pre-reproductive period, lipid, and water contents, and recorded their feeding behavior using the electropenetrography technique. Parasitoid developmental duration, sex ratio, hind tibia size, and female egg load were measured and used to evaluate *E. cerasicola* performance according to the cultivar on which their aphid hosts had been reared. Only the development time of parasitoids was found to be longer on Ariane and Green Sleeves cultivars than on the Gala cultivar. Aphid-feeding behavior variables related to phloem consumption were negatively impacted on apple tree cultivars on which the development time of parasitoids had been reduced. We discuss ways in which cultivar quality can be an important component of tritrophic interactions: the resistant Ariane and Green Sleeves cultivars negatively impacted the aphids but appeared to have limited bottom-up effects on the parasitoids.

Keywords Bottom-up effects · Trophic interactions · Intraspecific diversity · *Dysaphis plantaginea* · Parasitoid · Apple orchard

Introduction

Intraspecific variability in the quality of plants as hosts for phytophagous insects may have complex consequences for the structure and dynamics of associated food webs (Wimp et al. 2005; Underwood 2009; Barbour et al. 2016).

Differences in quality between plant individuals could modulate the distribution, abundance, and performance of both the phytophagous insects and their natural enemies (Moon et al. 2000; Ode 2006; Kaiser et al. 2017), as well as plant pathogens (Laine et al. 2011). In a context of crop domestication, the process of artificially selecting plants to increase their productivity has usually been accompanied by an increase of their vulnerability to biotic and abiotic stresses compared to their wild ancestors (Macfadyen and Bohan 2010). A given cultivated plant species, through a range of cultivars, can, therefore, present intraspecific variability in its morphological traits, nutrient contents, and the concentration of secondary compounds (O'Reilly-Wapstra et al. 2007; War et al. 2012; López-Goldar et al. 2018).

Host-plant quality can influence trophic interactions directly, as exemplified by life history traits of herbivorous insects, and indirectly, by influencing the quantity and quality of resources available to upper trophic levels (Kaplan et al. 2016). Phytophagous insects represent a food source

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for both predators and parasitoids. However, unlike predators that can feed on several individual preys, solitary endoparasitoids have only one host and obtain all their resources from it during their embryonic and larval development (Rivero and West 2005; Harvey and Gols 2018). Apart from the direct impacts of plant attributes such as morphology, semiochemicals, and texture on natural enemies, plants can indirectly affect these natural enemies through various multitrophic interactions. These include processes mediated by the sequestration of plant allelochemicals by herbivores, the influence of plant nutrition and resistance on herbivore quality, and interactions involving microbial symbionts (Agrawal 2000; Karimzadeh and Wright 2008). Alhmedi et al. (2022) recently conducted an assessment of bottom-up interactions between the rosy apple aphid (*Dysaphis plantaginea*) and 13 different apple cultivars, yielding valuable insights. At the cultivar level, they observed that adult *D. plantaginea* individuals were most of the time able to discriminate between these cultivars and select the appropriate hosts for their reproduction and the development of their progeny. Miñarro and Dapena (2007) revealed that cultivar phenology plays a role in its resistance towards *D. plantaginea*. Major resistance factors seem to be located in the phloem sieve elements (Marchetti et al. 2009), but molecules responsible for the resistance traits have not been identified yet. Intraspecific variation among apple cultivars is known to lead to divergent performance of the apple blossom weevil *Anthonomus pomorum* parasitoids and may trigger enhanced pest control through different parasitoid species (Mody et al. 2017). However, to our knowledge, so far no study has explored this bottom-up effect of apple cultivars on *D. plantaginea* parasitoids.

Aphids acquire sugars directly from the phloem sap as well as some lipids such as sterols and may synthesize phospholipids from sugars obtained in the phloem. They acquire amino acids from two sources, the diet of phloem sap and their endosymbiotic bacteria, and can compensate for water stress by ingesting xylem sap (Emden and Harrington 2007). It is, therefore, expected that in aphid–parasitoid interactions, the quality of the aphid host for its parasitoid mostly depends on the ability of the aphid host to feed from the plant phloem tissue and on overall plant quality (Stadler and Mackauer 1996; Monticelli et al. 2020). However, to our knowledge, no study has investigated how the bottom-up effect of apple cultivar resistance may affect parasitoid life history traits via a modification of the life history traits, resources, and feeding behavior of their aphid hosts.

We assessed the cultivar-mediated bottom-up effects of different cultivars of the domesticated apple (*Malus domestica*) on the performance of *Ephedrus cerasicola*, a commercially available parasitoid of the rosy apple aphid (*D. plantaginea*), one of *M. domestica* major pests (Blackman and Eastop 2000). Our study addressed the following

questions: (1) Can intraspecific plant variability, through a range of cultivars, affect the aphid life history traits and resources for the parasitoid? (2) If so, can the qualitative and quantitative differences observed in the aphid host explain the observed morphological and physiological differences in the parasitoid? (3) Can differences in aphid performance and feeding behavior explain the differences observed at the third trophic level?

To answer these questions, we selected three apple cultivars putatively exhibiting different degrees of resistance towards *D. plantaginea*. The performance of the *E. cerasicola* parasitoids was investigated through the measure of their size, development time, and the egg load of females according to the cultivar on which their aphid host had been reared. The sex ratio of emerging parasitoids was also recorded. In order to provide explanatory elements, the development time, the size (estimated through their fresh mass), and the resources (lipid and water contents) contained in *D. plantaginea* nymphs and adults were studied as well as their feeding behavior using the electropenetrography technique.

Materials and methods

Plants and insects

Three cultivars of the domesticated apple tree *Malus domestica* were used for the experiments. They were selected based on their sensitivity or resistance to pests and pathogens. Gala is a cultivar considered as sensitive to aphids (Miñarro and Dapena 2007) and pathogens such as the apple scab *Venturia inaequalis* (Bastiaanse et al. 2015) or the powdery mildew *Podosphaera leucotricha* (Lahlali et al. 2020), whereas Ariane and Green Sleeves are resistant to the apple scab and the fire blight *Erwinia amylovora*, respectively (Chevreau et al. 1998; Laurens et al. 2005). The three cultivars used were supplied as vitroplants by Végépolys Valley (Angers, France). Upon reception, their height was around 4 cm, and they had 6 ± 2 leaves. All cultivars were then grown in plastic pots ($60 \times 60 \times 70$ cm) with commercial sterilized potting soil (Botanic, reference: 386,895, 86.50 g per pot) and maintained in a growth chamber under controlled conditions (temperature 20 ± 1 °C, 16:8 h L:D photoperiod, $60 \pm 5\%$ relative humidity (RH), and 35 PPFD). For all the experiments, plants were used at a comparable phenological stage with six to nine fully developed leaves per plant and a height of 6 to 8 cm (13 ± 2 weeks after potting) (following Marolleau et al. 2017 and Denoirjean et al. 2022).

The rosy apple aphids were provided by INRAE and originated from a colony captured in spring 2018 in an orchard of Agrocampus ouest in Angers (France) (Philippe Robert, personal communication). The aphid population

was mass reared on the Jonagold cultivar and maintained in a climate-controlled room (same conditions as above) to maintain parthenogenesis reproduction. The Jonagold cultivar was supplied by CRA-W (Gembloux, Belgium) and obtained by in vitro multiplication (Druat 1997). Synchronized aphid nymphs were obtained by isolating adult females on a leaf on the host plant for 24 h in an aerated plastic box (36 × 24 × 14 cm). The adults were then removed from the host plant and the nymphs left to develop until they were used in the experiments.

For this study, we used the generalist endoparasitoid wasp *Ephedrus cerasicola*, a commercially available parasitoid of the rosy apple aphid. Individuals were obtained as mummies from Viridaxis (Charleroi, Belgium). Upon reception, mummies were placed individually in plastic tubes (75 × 13 mm) closed with a cotton plug in a climate chamber at 20 ± 1 °C and 16:8 h L:D photoperiod pending their emergence and use for the experiments.

Aphid life history traits and resources

Pre-reproductive period, mass, lipid, and water contents were measured on aphids which had been reared, on the different cultivars, enclosed in a clip-cage system composed of a plier supporting an acrylic transparent cylinder (Ø 1.5 cm, 0.8 cm long) closed by a nylon gauze while the airtightness on the leaf was ensured using felt.

To determine aphid pre-reproductive period (duration in days from the day they were larviposited to the day they first laid a nymph), three to four synchronized neonate aphids were isolated in a clip-cage placed on the abaxial part of a leaf of the plant on which they had been larviposited. Four to five clip cages were placed per plant on the most expanded leaves (one cage per leaf). Plants were then individually placed in an aerated plastic box (36 × 24 × 14 cm). Observations were done every 24 h until the day of their first larviposition as adults. The numbers of aphids and plants used to evaluate the pre-reproductive period were 19 aphids on 7 Gala cultivar plants, 20 aphids on 7 Ariane cultivar plants, and 27 aphids on 11 Green Sleeves cultivar plants.

Aphids were freeze dried at -20 °C in 0.5 ml Eppendorf vials. They were then weighed individually to the nearest 0.01 mg to obtain their fresh mass using a Mettler-electrobalance Me22, Mettler-Toledo (Zaventem, Belgium). Then, they were dried for 3 days at 60 °C to obtain their individual dry mass. The individual water content (%) was calculated as the water mass (fresh mass – dry mass) divided by the fresh mass. Aphid individual water content and weight were respectively obtained from 59 to 60 nymphs on 6 Gala cultivar plants, 60 nymphs on 8 Ariane cultivar plants, and 58 to 60 nymphs on 5 Green Sleeves cultivar plants. For adults, the results were obtained from 59 to 60

adults on 6 Gala cultivar plants, 60 adults on 7 Ariane cultivar plants, and 60 adults on 7 Green Sleeves cultivar plants.

Quantification of the lipid content of four-day-old nymphs and 10-day-old young adult aphids was performed as described by Pirotte et al. (2018). For lipid extraction, each dried aphid was individually placed into an Eppendorf tube containing 1 mL of chloroform/methanol (2:1 v:v) solution to dissolve fats and placed in a mechanical agitator for 2 weeks. After that, aphids were dried at 60 °C for 12 h to let the remains of the chloroform/methanol solution evaporate. Aphids were weighed again in order to measure the individual fat mass (µg) which was expressed as the difference in mass before and after lipid extraction. The individual fat content (%) was calculated as the fat mass divided by the dry mass. We quantified both the fat mass and the fat content as the fat content is a widely used metric to compare individuals among each other (Gwynn et al. 2005; Albittar et al. 2019), but the fat mass represents what will actually be consumed by the parasitoid larva (i.e., the available resource). For the fat mass and the fat content, the number of replicates for nymphs was 49 nymphs on 6 Gala cultivar plants, 50 nymphs on 8 Ariane cultivar plants, and 41 nymphs on 5 Green Sleeves cultivar plants. For adults, the results were obtained from 59 adults on 6 Gala cultivar plants, 56 adults on 7 Ariane cultivar plants, and 59 adults on 7 Green Sleeves cultivar plants.

Feeding behavior of aphids and EPG recording

We used the electropenetrography (EPG) technique (Tjallingii 1988) to compare the feeding behavior of aphids placed on plants of the three apple cultivars.

Recordings were carried out on 10-day-old aphids, each one being connected to an electrode consisting of a 20-µm diameter, 2-cm-long gold wire glued to a 2-cm-long copper wire soldered to the head of a 2.2-mm diameter brass nail used to track the electrical signals of the aphid stylets in the apple leaf. Aphids were connected by the dorsal part of their abdomen to the gold wire of the electrode via a drop of conductive water-based silver glue (EPG systems, Wageningen, the Netherlands). Eight aphids were individually placed to feed on the abaxial part of a fully expanded leaf of eight individual plants. Their feeding behavior was recorded for 8 h during the photophase by the Giga-8 DC-EPG amplifier inside a Faraday cage in a room under controlled conditions (20 ± 1 °C, $60 \pm 5\%$ RH, 35 PPFD and a 16:8 h L:D photoperiod).

Acquisition and analysis of the EPG waveforms were carried out using the EPG Style+ software (EPG Systems, <http://www.epgsystems.eu>). Different EPG parameters were determined from the waveforms of the EPG data, and they were calculated using the EPG-Calc 6.1.7 software (Giordanengo 2014). The "Pr" waveform corresponded to

the probing behavior in the plant tissue (parameters studied: number of probings (n_{Pr}), number of brief probings (< 3 min, N_{bPr}), total duration of probing (s_{Pr}), and time before the first probe ($t > 1Pr$)). Waveform “C” corresponded to stylet pathways in intracellular apoplastic plant tissues (parameters studied: number of pathway phases (n_C), total duration of pathway phase (s_C)). Waveform “E1” represented salivation within phloem vessels (parameter studied: number of salivation phases (s_{E1}) and total duration of salivation (s_{E1})). Waveform “E2” represented passive phloem sap ingestion (parameters studied: number of phloem sap ingestion events (n_{E2}) and total duration of phloem sap ingestion (s_{E2})). Waveform “G” corresponded to active xylem sap ingestion (parameters studied: number of xylem sap ingestion events (n_G), total duration of xylem sap ingestion (s_G)). Lastly, waveform “F” corresponded to derailment of the stylets (parameters studied: number of stylets derailment (n_F), total duration of stylets derailment (s_F)). The numbers of aphids and plants used to evaluate the probing behavior were 27 aphids on 13 Gala cultivar plants, 26 aphids on 14 Ariane cultivar plants, and 31 aphids on 15 Green Sleeves cultivar plants.

Parasitoid life history traits

The life history traits measured for parasitoids after their development in aphids on the three cultivars were the developmental time, the sex ratio of emerging individuals, the length of their hind leg tibia, and the egg load of females. These parameters were used as proxies to evaluate their fitness.

Upon emergence, parasitoids were sexed and mating was allowed for 48 h by grouping three females and two males in a 15 mL plastic tube (120 × 35 mm) with a drop of 1:3 water:honey solution under the cap to feed and hydrate them. Two- to three-day-old parasitoids (three females and two males) were released into an insect-proof Nylon mesh box (30 × 30 × 30 cm) containing one apple host plant on which 25 to 40 four-day-old aphid nymphs had been placed. Nylon mesh boxes were then placed in a controlled room (20 ± 1 °C, $60 \pm 5\%$ RH, 35 PPFD, and a 16:8 h L:D photoperiod) for the duration of the experiment. A cotton soaked in diluted honey was placed inside the box to provide food for the adult parasitoids. After 36 h, the parasitoids were removed from the box to avoid any superparasitism (i.e., multiple parasitism on single hosts). When parasitized aphids had formed sufficiently developed mummies (dark brown color and rigid cuticle), they were carefully removed from the host plant and individually placed in a plastic tube (75 × 13 mm) in the same controlled room until parasitoid emergence. The development time (in days) was determined as the time between the day parasitoid parents were introduced into the cage and the day their offspring emerged.

Emergences were checked every day at the same time. Parasitoids were sexed at emergence. In total, 9 Gala, 9 Ariane, and 9 Green Sleeves cultivar plants were used to rear parasitoid individuals (males and females) of which several life history traits were measured. To calculate the mean development time, 182 parasitoids developed in aphids reared on the Gala cultivar were used, 114 for the Ariane cultivar and 123 for the Green Sleeves cultivar. Sex ratio was calculated on a total of 189 adult parasitoids for Gala cultivars, 120 for Ariane cultivars, and 124 for Green Sleeves cultivars.

On the day of emergence, male parasitoids were individually stored in a freezer at -80 °C. Emerged females were placed individually in a plastic tube (75 × 13 mm) for 48 h in the controlled room at 20 °C with a cotton ball soaked in the water/honey mixture to feed them, in order to let them develop their egg stock before they were placed individually in a freezer at -80 °C. Tibias of male and female individuals were photographed under a Leica M205C stereo-microscope and measured using a software Leica application suite (Tougeron et al. 2020). The size of the tibia was measured on 42 parasitoid individuals reared in aphids on the Gala cultivar, 37 on the Ariane cultivar, and 50 on the Green Sleeves cultivar. Female egg load was determined under the same stereo-microscope. Females were placed in a drop of Phosphate-Buffered Saline (0.1%), their ovaries dissected, and the number of mature eggs recorded (Le Lann et al. 2012). The egg load was determined on 21 parasitoid individuals reared on the Gala cultivar, 17 on the Ariane cultivar, and 29 on the Green Sleeves cultivar.

Statistical analysis

All data analysis was performed using the R studio software version 4.1.2 (R, Core Team, 2022). For some parameters, we have specified the mean and the standard error of the mean in the results section.

To study the effect of apple cultivar on aphid nymphs and adult life history traits (fresh mass, fat mass, fat content, water content), a Generalized Linear Mixed Model (GLMM) using a Gaussian distribution was performed. The apple cultivar was included as the main factor and the identity of each apple tree was used in the model as a random effect. The effect of the aphid cultivar on aphid pre-reproductive period was carried out using the Cox proportional hazards (CPH) regression model, which is suitable to treat time-dependent parameters. The assumption of validity of proportional hazards was tested using the function “coxph” (survival package v3.1.8) (Therneau and Grambsch 2000).

Data analysis on EPG parameters describing the number of occurrences of a particular phase (e.g., “ n_{E2} ”) was carried out using a Generalized Linear Model (GLM) with a Poisson distribution (link = “log”), suited for count data. EPG data on feeding phase durations (e.g., duration

of phloem sap ingestion “s_E2”) were tested using a GLM with Gamma (link=“inverse”) distribution, best suited for duration analyses. Data analysis on EPG parameters describing time before the first probe (“t.1Pr”) and before the first phloem sap ingestion (“t.1E2”) was carried out using the Cox proportional hazards (CPH) regression model. The absence of an EPG reading was treated as a missing value. The proportion of aphids performing each EPG parameter was tested using a Chi-square test of homogeneity.

To test the bottom-up effect of the cultivar on the parasitoids, GLMMs were performed. The measurement of individuals that had developed in aphids reared on the same individual plant led us to use the identity of each apple plant as a random effect. The size of the parasitoid tibiae was normally distributed; therefore, a GLMM using a Gaussian distribution was used. For data of female parasitoids egg load, a GLMM using a Poisson distribution was used. Parasitoid sex ratio was analyzed by a GLMM using a binomial distribution and analysis of parasitoid development time was carried out using the Cox proportional hazards (CPH) regression model.

Likelihood ratio and Chi-square post hoc comparison tests were carried out by pairwise comparisons using

estimated marginal means (EMM) (emmeans package) (Lenth et al. 2022).

Results

Aphid life history traits

There was a significant effect of the apple cultivar on the mean individual fresh mass of aphid nymphs (GLMM: $\chi^2 = 26.68$, Df=2, $P < 0.001$). The mean individual fresh mass of aphid nymphs was significantly lower when they were reared on Green Sleeves plants (EMM comparison; Gala vs Ariane, $P = 0.061$; Gala vs Green Sleeves, $P < 0.001$; Ariane vs Green Sleeves, $P = 0.006$) compared to nymphs reared on Gala or Ariane cultivars (Fig. 1, FrM_ny). The mean individual fresh mass was significantly reduced for nymphs reared on the Green Sleeves cultivar ($51.65 \pm 3.88 \mu\text{g}$) when compared to the susceptible cultivar Gala ($116.42 \pm 6.18 \mu\text{g}$). The mean individual fresh mass of nymphs reared on Ariane ($90.83 \pm 5.95 \mu\text{g}$) did not differ significantly from that of nymphs reared on Gala. However, for adults, there was no

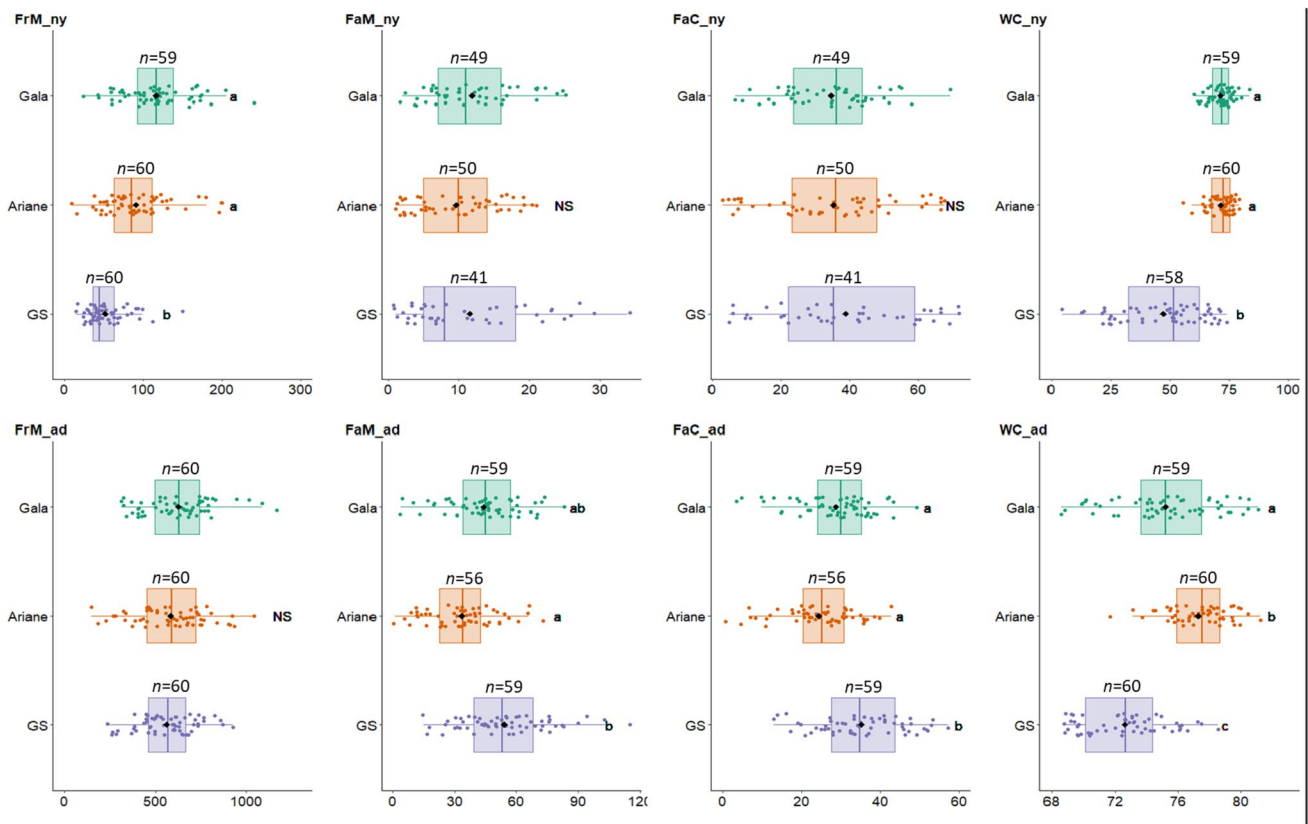


Fig. 1 Mean individual fresh mass (μg, nymphs: FrM_ny and adults: FrM_ad), fat mass (μg, nymphs: FaM_ny and adults: FaM_ad), fat content (% nymphs: FaC_ny and adults: FaC_ad), and water content (% nymphs: WC_ny and adults: WC_ad) of *Dysaphis plantaginis*

reared on each apple tree cultivar (GS: Green Sleeves). Aphid nymphs were four-day-old and adults were 10-day-old. Box plots show mean (black dot). Different letters indicate significant differences at the 5% threshold (post hoc EMM pairwise comparisons)

significant effect of the apple cultivar on the mean individual fresh mass (GLMM: $\chi^2 = 1.26$, Df=2, $P = 0.533$) (Fig. 1, FrM_ad).

There was no significant effect of the apple cultivar on the mean individual fat mass of nymph aphids (GLMM: $\chi^2 = 1.26$, Df=2, $P = 0.531$), whereas the mean individual fat mass of aphid adults was significantly influenced by apple cultivar (GLMM: $\chi^2 = 12.76$, Df=2, $P = 0.001$) (Fig. 1, FaM_ny). For adults, the mean individual fat mass of aphids reared on Green Sleeves was significantly greater than that of aphids reared on Ariane but was not significantly different from that of aphids reared on Gala (EMM comparison; Gala vs Ariane, $P = 0.196$; Gala vs Green Sleeves, $P = 0.178$, Ariane vs Green Sleeves, $P = 0.001$). The mean individual fat mass of adults was $44.19 \pm 2.27 \mu\text{g}$ for aphids reared on Gala, $33.54 \pm 2.17 \mu\text{g}$ for those reared on Ariane, and $54.25 \pm 2.78 \mu\text{g}$ for those reared on Green Sleeves (Fig. 1, FaM_ad).

The mean individual fat content was statistically similar for aphid nymphs (GLMM: $\chi^2 = 1.01$, Df=2, $P = 0.605$) (Fig. 1, FaC_ny). However, the mean individual fat content was significantly different for aphid adults depending on the cultivar on which they had been reared (GLMM: $\chi^2 = 25.99$, Df=2, $P < 0.001$). Mean individual fat contents were significantly lower for aphids reared on Gala ($28.73 \pm 1.26\%$) and Ariane ($24.33 \pm 1.24\%$) compared to the mean individual fat content of aphids on Green Sleeves ($32.24 \pm 1.40\%$) (EMM comparison; Gala vs Ariane, $P = 0.124$, Gala vs Green Sleeves, $P = 0.006$, Ariane vs Green Sleeves, $P < 0.001$) (Fig. 1, FaC_ad).

There was a significant effect of the apple cultivar on the mean water content values of both aphid nymphs and adults (Nymphs, GLMM: $\chi^2 = 69.35$, Df=2, $P < 0.001$. Adults, GLMM: $\chi^2 = 39.72$, Df=2, $P < 0.001$). The water content of aphid nymphs was significantly lower when they were reared on Green Sleeves ($47.17 \pm 2.35\%$) compared to that of nymphs reared on Gala or Ariane ($71.37 \pm 0.67\%$ for Gala and $71.44 \pm 0.68\%$ for Ariane) (EMM comparison; Gala vs Ariane, $P = 0.986$; Gala vs Green Sleeves, $P < 0.001$; Ariane vs Green Sleeves, $P < 0.001$) (Fig. 1, WC_ny). The water content levels of aphid adults were influenced by apple cultivar. It was smaller for aphids reared on Green Sleeves ($72.29 \pm 0.37\%$), intermediate for those reared on Gala ($75.08 \pm 0.43\%$), and greater for those reared on Ariane ($77.31 \pm 0.26\%$) (EMM comparison; Gala vs Ariane, $P = 0.028$; Gala vs Green Sleeves, $P = 0.001$, Ariane vs Green Sleeves, $P < 0.001$) (Fig. 1, WC_ad).

There was no significant effect of the apple cultivar on the pre-reproductive period of aphids (CPH model: $\chi^2 = 0.51$, Df=2, $P = 0.78$). The average pre-reproductive period on the Gala cultivar was 11.05 ± 0.26 days, for aphids on Ariane, it was 10.95 ± 0.36 days, and for aphids on Green Sleeves, it was 11.26 ± 0.34 days (EMM comparison, Gala vs Ariane,

$P = 0.962$; Gala vs Green Sleeves, $P = 0.998$; Ariane vs Green Sleeves, $P = 0.933$) (Fig. 2).

Aphid-feeding behavior

The total duration of phloem sap ingestion by aphids was significantly different depending on the cultivar (GLM: $\chi^2 = 32.44$, Df=2, $P < 0.001$) (Fig. 3) as it was the case for the proportion of aphids performing sustained phloem sap ingestion (> 10 min) (χ^2 test of homogeneity, $\chi^2 = 21.98$, Df=2, $P < 0.001$) (Fig. 4). The duration of phloem sap ingestion was significantly shorter for aphids feeding on the Ariane cultivar (7.29 ± 1.55 min) compared to that of aphids on the Gala or Green Sleeves cultivars (58.29 ± 11.61 min and 59.03 ± 19.20 min, respectively) (EMM comparison; Gala vs Ariane, $P = 0.004$; Gala vs Green Sleeves, $P = 0.999$; Ariane vs Green Sleeves, $P = 0.004$) (Fig. 3).

The proportion of aphids performing sustained phloem sap ingestion (> 10 min) was significantly smaller on the two resistant cultivars (chi-square test: $\chi^2 = 21.98$, Df=2, $P > 0.001$): 66.67% of aphids feeding on Gala performed sustained phloem ingestion, whereas only 7.70% did on Ariane and 25.80% on Green Sleeves (post hoc chi-square test; Gala vs Ariane, $P > 0.001$; Gala vs Green Sleeves, $P = 0.004$, Ariane vs Green Sleeves, $P = 0.150$) (Fig. 4).

The number of probings (n_Pr) and the total duration of probing (s_Pr) were significantly different for aphids depending on the cultivar on which they fed (for n_Pr, GLM: $\chi^2 = 14.31$, Df=2, $P < 0.001$. For s_Pr, GLM: $\chi^2 = 8.01$, Df=2, $P < 0.018$) (Supplementary Table S1). n_Pr and s_Pr were significantly smaller for aphids on the Gala cultivar compared to those of aphids on Ariane or Green Sleeves cultivars. The number of brief probings (n_bPr) was significantly smaller for aphids on Gala compared to aphids on Green Sleeves, whereas the number of brief probings (n_bPr) performed by aphids on Ariane was not significantly different from those of aphids on the two other cultivars (GLM: $\chi^2 = 1.70$, Df=2, $P < 0.001$)

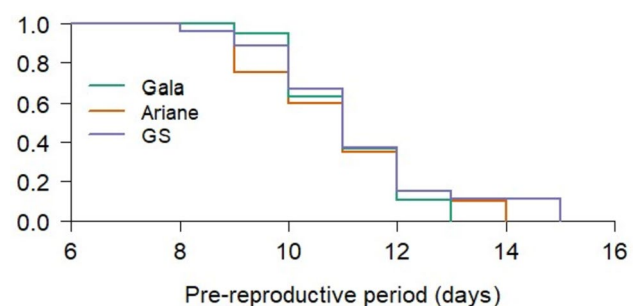


Fig. 2 Pre-reproductive period (days) of *Dysaphis plantaginea* reared on each apple tree cultivar (GS: Green Sleeves). Gala $n = 19$; Ariane $n = 20$; Green Sleeves $n = 27$

Fig. 3 Total duration of phloem sap ingestion (min) by *Dysaphis plantaginea* on each apple tree cultivar tested (GS: Green Sleeves). Box plots show the means (black diamond) and medians (vertical bar). Different letters indicate significant differences at the 5% threshold (post hoc EMM pairwise comparisons). Gala $n=27$; Ariane $n=26$; Green Sleeves $n=31$

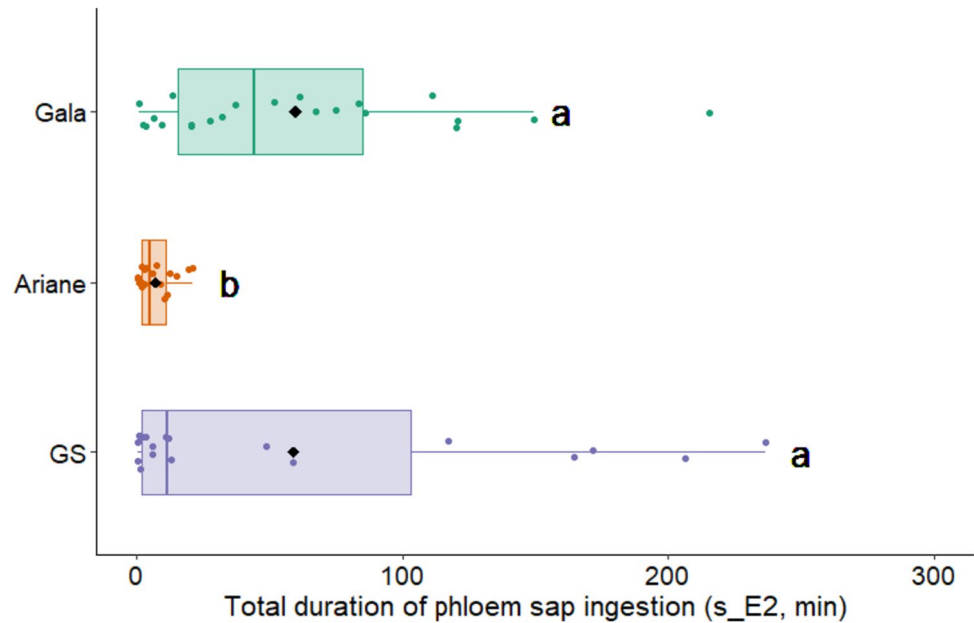
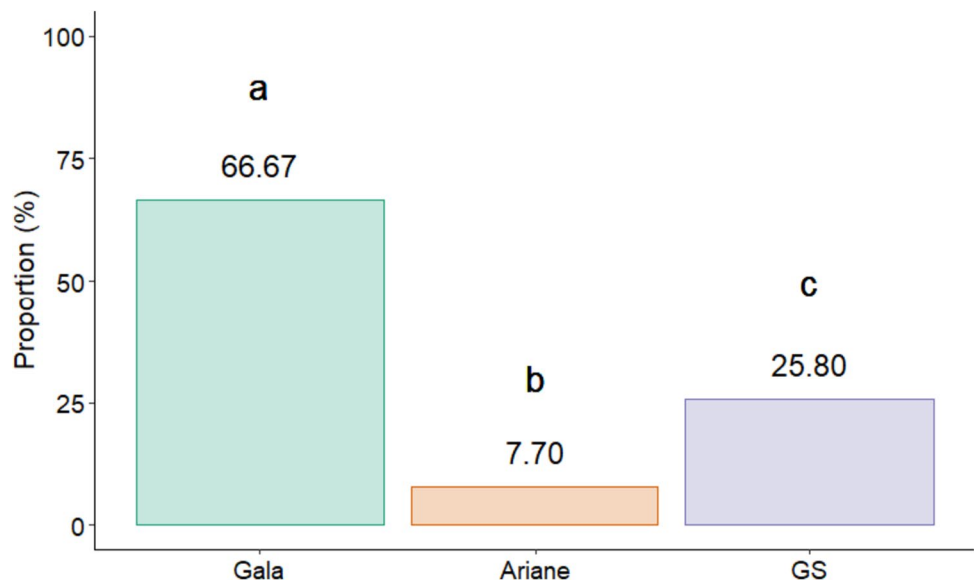


Fig. 4 Proportion (%) of *Dysaphis plantaginea* performing sustainable phloem sap ingestion on each apple tree cultivar tested (GS: Green Sleeves). Different letters indicate significant at the 5% threshold (post hoc using chi-square tests). Gala $n=27$; Ariane $n=26$; Green Sleeves $n=31$

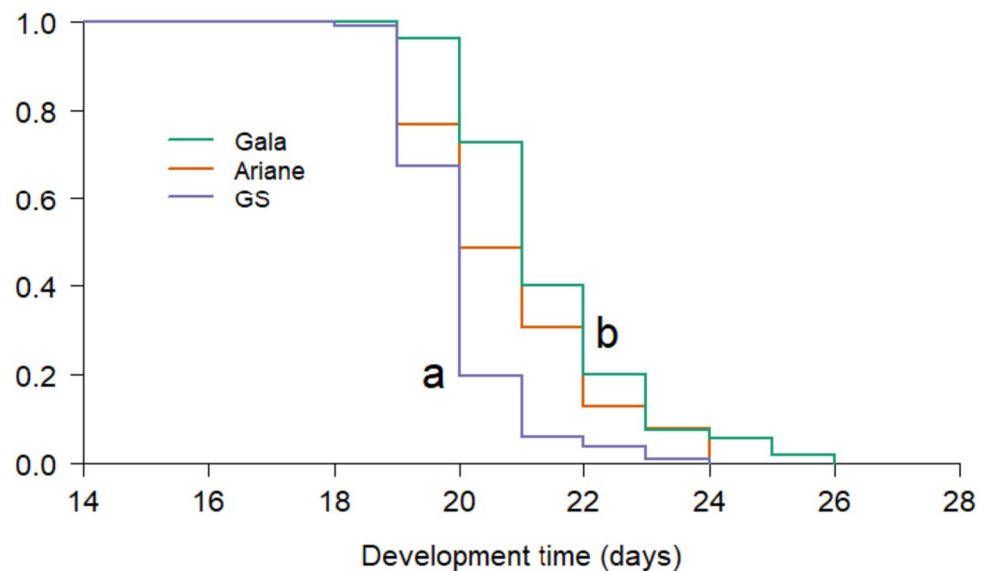


(Supplementary Table S1). The total duration of xylem sap ingestion (s_G) was not significantly different depending on the apple cultivar at the 5% threshold ($\chi^2 = 5.59$, $df = 2$, $P = 0.061$) (Supplementary Table S1). However, it can be noted that the total duration of xylem sap ingestion (s_G) was the shortest for aphids on the Gala cultivar and the longest for those on the Ariane cultivar. None of the other EPG data linked to the pathway phase, the salivation phase or the derailed stylets phase showed any significant difference in aphid stylets activity according to the apple cultivar (Supplementary Table S1).

Parasitoid life history traits

The average development time varied significantly by apple cultivar (CPH: $\chi^2 = 6.47$, $Df = 2$, $P = 0.039$). It was longer for parasitoids developing in aphids reared on Ariane (22.08 ± 0.23 days) or Green Sleeves (21.86 ± 0.19 days) compared to those reared on the sensitive cultivar Gala (20.45 ± 0.14 days) (Fig. 5) (EMM comparison; Gala vs Ariane, $P = 0.082$; Gala vs Green Sleeves, $P = 0.06$, Ariane vs Green Sleeves, $P = 0.927$). There was also a significant effect of the sex of the parasitoids on their development

Fig. 5 Development time (days) of *Ephedrus cerasicola* in aphids reared on different apple tree cultivars, with males and females taken altogether for each cultivar. Gala $n=138$; Ariane $n=55$; Green Sleeves $n=39$



time: males developed faster than females, regardless of the apple cultivar (CPH: $\chi^2 = 12.11$, Df = 1, $P < 0.001$).

The parasitoid sex ratio was not significantly different depending on the cultivar on which the aphid hosts had been reared (GLMM: $\chi^2 = 0.57$, Df = 2, $P = 0.752$). There were 47.1% of female parasitoids emerging from aphids reared on the Gala cultivar, 45.0% of female parasitoids emerging from aphids reared on Ariane, and 46.8% of female parasitoids emerging from aphids reared on Green Sleeves.

The mean egg load of emerged females was not significantly different depending on the cultivar on which their aphids host had been reared (GLMM: $\chi^2 = 2.31$, Df = 2, $P = 0.315$). The mean egg load of parasitoids was 272.85 ± 18.96 eggs for those developing in aphids reared on Gala, 287.82 ± 17.04 eggs for those developing in aphids reared on the Ariane cultivar, and 308.48 ± 15.77 eggs for those developing in aphids reared on the Green Sleeves cultivar.

There was no significant effect of the apple cultivar on the tibia length of female or male parasitoids (GLMM: $\chi^2 = 4.12$, Df = 2, $P = 0.128$). The tibia length of female parasitoids developing on aphids reared on Gala cultivar was 0.555 ± 0.011 mm, for female parasitoids on Ariane, it was 0.543 ± 0.012 mm, and for those reared in aphids on Green Sleeves, it was 0.585 ± 0.006 mm. The tibia length of male parasitoids developing in aphids reared on Gala cultivar was 0.494 ± 0.013 mm; for male parasitoids in aphids on Ariane, it was 0.473 ± 0.013 mm, and for those reared in aphids on Green Sleeves, it was 0.507 ± 0.008 mm. There was, however, a significant difference between the tibia size of females and males (GLMM: $\chi^2 = 99.85$, Df = 1, $P < 0.001$) (EMM comparison: females on Gala vs males on Gala, $P < 0.001$; females on Ariane vs males on Ariane,

$P = 0.001$; females on Green Sleeves vs males on Green Sleeves, $P < 0.001$).

Discussion

Our experiments showed that the intraspecific variability represented by apple cultivar did exert contrasting effects on aphids (both nymphs and adults), potentially inducing variability in the nutritional resources they embody for parasitoids. The change in aphid life history traits can be partly explained by the modification of the feeding behavior, especially during the phloem-related phases. These changes recorded at the aphid level did affect the developmental duration of parasitoids but not their other traits measured in this study (*e.g.*, sex ratio, tibia size, and female egg load).

Resistance genes to various pathogens, including bacteria, fungi, nematodes, and viruses benefited from an earlier research effort compared to resistance genes against aphids (Dogimont et al. 2010). Our hypothesis that the cultivars known for their resistance towards pathogens could also be resistant to aphids was confirmed by our results. The quality of aphids as hosts for parasitoids was influenced by the intraspecific variability of the apple tree host plants. Indeed, we observed a significant reduction in the fresh mass of aphid nymphs reared on the Green Sleeves cultivar, which was consistent with other studies on the effect of plant resistance on aphid mass (Martin and Johnson 2011; Kersch-Becker and Thaler 2015). However, we did not observe differences in the fresh mass of the adults depending on the cultivar on which they were reared. This is in contradiction with the study of Kouamé and Mackauer (1992) which showed that daily starvation of young aphids led to a lower adult fresh mass highlighting that aphids were

unable to compensate completely for water and nutrient loss resulting from starvation. Adult aphids reared on the resistant Ariane apple cultivar had lower lipid masses and lipid contents than those reared on Green Sleeves, the other resistant cultivar. These results are consistent with other studies that have shown a reduction in the lipid content of aphids and other insects, such as the lesser grain borer, when reared on low-quality plants (Perez-Mendoza et al. 1999; Tabadkani et al. 2013). These differences in host quality could be explained by the physiological variability of *Malus sp.* at the intraspecific scale. For instance, Massonnet et al. (2007) showed that photosynthetic activity and stomatal activity of apple trees could differ due to differences in primary compounds between cultivars. The water content was lower for the aphids reared on the Green Sleeves cultivar compared to the aphids reared on the two other cultivars. Few studies have investigated the effect of plant resistance on insect water content, although it may play an important role in the plant–insect interaction. Indeed, both fat and water contents contribute to insect survival toward plant secondary metabolites, and in this context, water content may play a more important role than fat content (Reid and Ahn 2020). The lower water content observed in aphids reared on the Green Sleeves-resistant cultivar may have been linked to the detoxification of secondary metabolites (Reid et al. 2017).

It is known that the quantity and quality of food consumed by aphids can impact their quality as resources for parasitoids (Souissi and Rü 1998). Studying the feeding behavior of aphids in relation to the cultivar on which they fed allowed us to explore whether possible changes in aphid feeding behavior could impact the life history traits of parasitoids. Phloem-related variables in *D. plantaginea* feeding on the resistant Ariane and Green Sleeves cultivars generally exhibited lower numbers and shorter durations compared to the phloem sap ingestion variables of aphids on the susceptible Gala cultivar. This is consistent with the work of Marchetti et al. (2009) on the feeding behavior of *D. plantaginea* on the resistant apple cultivar Florina. In their study, the altered feeding behavior of phloem-related variables was attributed to the presence of resistance factors in the phloem sap tubes, and more specifically to the presence of phenolic compounds that would have prevented the aphids from feeding correctly, and therefore, reduced the number of ingestion phases, the total ingestion time, and the proportion of aphids that performed an ingestion phase of phloem sap longer than 10 min. In our study, the lower phloem sap feeding of aphids on the Ariane cultivar could explain their lower mass of lipids, because the sugars assimilated by aphids are partly allocated to their lipid synthesis (Douglas 2003). Other studies have also observed a reduction in lipid mass in aphids and other insects, such as the African fruit beetle or the lesser grain borer, in response to reduced phloem sap feeding (Perez-Mendoza et al. 1999;

Auerswald and Gäde 2000; Tabadkani et al. 2013). However, in the study of Marchetti et al. (2009), the resistance of the Florina cultivar also impacted other variables of aphid feeding behavior (e.g., duration before the first probing phase) that were not significantly different depending on the aphid host plant cultivar in our study. This would indicate that in our case, the cultivars did not present repulsive factors on their surface contrary to what had been proposed for the Florina cultivar. Our results also showed that the duration of xylem sap ingestion by aphids was numerically yet not significantly longer on the Ariane cultivar. We suggest that this result may be due to the difficulty of aphids to feed on phloem sap as well as to a possible difference in the water balance between the apple cultivars, as stomatal conductance is known to be cultivar dependent (Massonnet et al. 2007). This may also explain why the water content of aphids was greater on the Ariane cultivar because the ingestion of xylem sap allows to regulate the water balance of aphids (Spiller et al. 1990; Pompon et al. 2010).

Therefore, the amount of resources available (fresh mass) and the quality of these resources (lipid and water content) seem to have been significantly affected depending on the apple cultivar on which the aphid host had been reared. Further studies on this model would allow a better understanding and evaluation of the quality of resources contained in aphid hosts for their parasitoids.

The development time of the parasitoids was found to be longer when their aphid hosts were reared on the aphid-resistant Ariane or Green Sleeves cultivars. As no difference in aphid development duration was observed, this was more likely due to the difference in resources that aphids represented for parasitoids. The amount of lipids contained in their host is important for aphid parasitoids as to our knowledge they are not able to perform lipogenesis (Visser and Ellers 2008; Ruther et al. 2021). However, this is not the only resource on which they depend during their development. Other resources such as amino acids or carbohydrates are also necessary for parasitoids development. For example, Coskun & Emre (2015) demonstrated that a reduced amino acid diet for parasitoids had an impact on their development and could decrease the proportion of individuals reaching emergence. An increase in the development time of *Aphidius colemani* was also observed when it developed in *M. persicae* feeding on resistant common cabbage plants (Kalule and Wright 2005). Parasitoids size at emergence is usually related to the resources available in their hosts during their development (Kaplan et al. 2016; Pirotte et al. 2018). Since we observed a lower fresh mass in aphid nymphs reared on the Green Sleeves cultivar, we expected to observe a significant difference in parasitoids tibia size depending on the cultivar of their hosts as demonstrated in other studies (Harvey et al. 1995; Cohen et al. 2005). Lipids are known to be

directly involved in egg production for parasitoids (Ellers and Van Alphen 1997; Zhao and Zera 2002). Therefore, we expected female parasitoids that developed in aphids reared on the Green Sleeves cultivar to have greater egg loads, as the aphids had a greater lipid mass than those reared on the two other cultivars. However, this proxy was not significantly different, which could be explained by the fact that in parasitoids, egg load is usually positively correlated with size (King 1988; Visser 1994). Size being unchanged in our study, the egg load was not modified. This result also supports a possible trade-off between size and development duration.

To conclude, our results demonstrated that cultivar quality can be an important factor in tritrophic interactions: the resistant Ariane and Green Sleeves cultivars negatively impacted the aphids but appeared to have limited bottom-up effects on parasitoids. We postulate that the minor effects of both resistant cultivars on parasitoids compared to their higher negative effects on aphid life history traits and feeding behavior could be due to a buffer effect on the aphid trophic level, thus, reducing the negative effects of plant resistance as proposed by Chesnais et al. (2016). In a field application context, our results suggest that the search for new resistant cultivars may not hinder the performance of parasitoids and their ability to regulate aphid populations. With regard to the pathogen resistance known for the two aphid-resistant cultivars studied here, our results appear encouraging in the context of integrated crop protection including biological control, which aims to free itself from phytosanitary products.

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Data availability The datasets analyzed during the current study are available at the following url: <https://doi.org/10.5281/zenodo.8387112>

Declarations

Conflict of interest The authors declare that they have no competing interests.

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