Is the Oil Seed Crop Camelina sativa a Potential Host for Aphid Pests?

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Is the oil-seed crop *Camelina sativa* a potential host for aphid pests?

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ABSTRACT

Camelina sativa is a Brassicaceae that was commonly cultivated in Europe until the 19th century. Recently, it has received much interest as an alternative oil-seed crop because of its particular oil composition and low requirements in terms of agronomic inputs and its resistance to some Brassicaceae chewing insects. However, little is known about the consequences of its reintroduction on piercing-sucking insects pests that are not Brassicaceae specialists but that are likely to transmit phytoviruses. In this context, laboratory experiments were conducted to investigate the potential colonization of camelina by four major aphid species of northern France. Orientation tests, feeding behavior assessed by Electrical Penetration Graph and demographic bioassays showed that the polyphagous species, *Aphis fabae* (Scop) and *Myzus persicae* (Sulzer), were able to land, feed, and reproduce on the plant. They even fed and performed better on camelina than the Brassicaceae specialist *Brevicoryne brassicae* (L.). Surprisingly, to a lesser extent, *Camelina sativa* could also be a suitable host for the cereal specialist *Rhopalosiphum padi* (L.). The colonization ability of camelina by the different aphids is discussed in terms of the degree of specialization and physico-chemical characteristics of the plant. Camelina may therefore constitute a reservoir for aphid species issued from surrounding crops and their associated pathogens.

KEY WORDS

False flax, host plant suitability, Aphididae, EPG, demographic parameters, phytoviruses, bioenergy crop.

Introduction

The consumption of vegetable oils in the world is expected to increase by 2% per year [1]. Although some concerns have been raised relating to potential competition with food crops [2], vegetable oils used for biofuels and biodiesel present many advantages (e.g. natural viscosity, toxicity, biodegradability) which make them attractive sustainable alternatives to the non-renewable petroleum derivatives [3–5]. These oils can be extracted from major conventional oil crops [6], including soybean (*Glycine* max), rapeseed/canola (*Brassica napus*), palm (*Elaeis guineensis*), sunflower (*Helianthus annuus*), cottonseed (*Gossypium hirsutum*), flax (*Linum usitatissimum*) and peanut (*Arachis hypogaea*). In northern Europe, rapeseed is the dominant oilseed crop used for biofuel and some pests and diseases present throughout the plant lifecycle are key constraints to its production [7]. Control of oilseed rape pests relies on heavy use of insecticides that are costly and negatively impact biodiversity [8].

It has been shown that an increase in the plant species diversity may facilitate natural pest control in annual cropping systems [9]. In order to reduce Europe's dependence on non-renewable feedstocks, long-term breeding programs and agronomic studies are necessary to increase diversity of oil crops. New promising oilseed crops such as camelina (*Camelina sativa*) or brown mustard (*Brassica juncea*), which present special chemical composition and agronomic properties can provide alternative to current production systems [5, 10].

Camelina sativa (L.) Crtz. also known as the false flax, or the gold-of-pleasure, is a Brassicaceae which was an important oil crop in Europe during the Bronze and Iron Ages [11]. It was cultivated until the 19th century in France and to a lesser extent in Holland, Belgium and Russia [12]. In the early twentieth century, 5000 hectares of false flax were still cultivated in northern France [13]. Camelina is recognized for its rusticity because it can tolerate a wide range of pedoclimatic conditions [13] and requires low agronomic inputs [14]. The plant has lower nitrogen requirements and a shorter growing season than rapeseed [15–17]. Moreover, camelina is reported to be tolerant to drought and heat [18], resistant to cold [19] and to different pathogens and insects [20, 21] thanks to various anti-nutritional compounds produced (e.g., Matthaüs and Zubr [22]). This plant can be used in mixed cropping systems with legumes, not only for water and nitrogen management [23, 24], but also for weed control [25]. Camelina oil offers good opportunities as a biofuel crop and functional food as it contains exceptionally high levels of omega-3 fatty acids, and over 50% of its fatty acids are polyunsaturated [26, 27].

The reintroduction of camelina in Europe could bring major agronomic and economic benefits, but may also modify local ecosystems balance [28, 29]. One major risk is that Camelina may act as a reservoir of pests or a

reservoir of vector of viruses. According to theoretical models, the introduction of a new host plant into an established host-parasite system can sometimes reduce ("dilute") or increase ("spill-back") the transmission of pathogens to native host species [30]. The suitability of camelina could depend on the degree of herbivore specialization of the aphid pests, which are the major vectors of phytoviruses on Brassicaceae. However, the interaction between aphids and camelina has not been studied so far. A systemic approach is essential to assess the risk of the introduction of *C. sativa* on a wide range of potential insects usually associated or not with the crop. Thus, we investigated the colonization process of four major aphid pests (Hemiptera: *Aphididae*) which are all vectors of Brassicaceae phytoviruses [31–35]. *Aphis fabae* (black bean aphid) and *Myzus persicae* (green peach aphid) are two polyphagous species, while *Brevicoryne brassicae* (cabbage aphid) feeds exclusively on plants of the *Brassicaceae* family, and *Rhopalosiphum padi* (bird cherry aphid) is a specialist of monocots.

In laboratory experiments we investigated if the four aphid species could successfully land on, feed and reproduce on *Camelina sativa*, relatively to their degree of specialization towards Brassicaceae. We then discuss the agronomical and epidemiological implications of our findings.

Materials and Methods

Insects and Plants

For each species, colonies were initiated from a single apterous parthenogenetic female and were separately maintained in ventilated Plexiglas® cages (360 x 240 x 110 mm) in growth chambers under controlled conditions (20 ± 2°C, 60 ± 5% relative humidity (RH), and 16L:8D photoperiod at 4.7 klux) to induce parthenogenesis. Aphid clones were used to minimize intraspecific variability and to ensure a certain uniformity of response.

The *M. persicae* colony was established from one parthenogenetic female collected in 1999 in a potato field near Loos-en-Gohelle (France) and was reared on potato plants (*Solanum tuberosum* cv.*"*Desirée*"*). The colonies of *R. padi* and *B. brassicae*, provided in 2008 by INRA-Le Rheu (Rennes, France), were reared on barley (*Hordeum vulgare* cv.*"*Cervoise*"*) and on rapeseed (*Brassica napus cv. "*Stego*"*) respectively. The colony of *A. fabae*, provided in 2012 by Gembloux Agro-Bio-Tech (Belgium) was reared on broad beans (*Vicia faba* cv.*"*Maya*"*).

Plantlets used for the experiments were obtained from tubers for potato and from seeds for the other plants. They were grown for 4 weeks in 60 mm plastic pots with commercial sterilized potting soil under the controlled conditions described above. *Camelina sativa* (cv. *"*Calena*"*) seeds were provided by the University of Natural Resources and Life Sciences, Vienna (Austria).

Early steps of the camelina plantlets colonization process

The aim of this test was to observe the abilities of the four different aphids species to fly towards and land on camelina. The experimental set up used was modified from Boquel *et al*. [36] and consisted of 10 ventilated Plexiglas® chambers (180 x 120 x 75 mm) used simultaneously inside which a single camelina plant was set (Fig. 1). At 80 mm from the plant, a single alate aphid was positioned with a small paintbrush at the top of a small tower (50 mm high), which was placed in a Petri dish lid containing water to avoid aphid plant colonization by walking. Twenty-four hours after its introduction, aphid location (on the plant, inner walls or ground of the experimental chamber) was recorded. This bioassay was conducted with alate aphids synchronized in their flight phase according to Brunissen *et al*. [37]. For each experimental set up, 10 aphids were tested taking care to use the 4 aphid species, with at least 2 individuals per species. For each aphid species, a total of 20 individuals were individually tested.

Electrical penetration graph studies

The DC-electrical penetration graph (DC-EPG) technique [38] was used to investigate the aphid feeding behaviour on *Camelina sativa*. A thin gold wire (20 µm in diameter and 2 cm in length) was tethered on the insect's dorsum by conductive water-based silver glue. Eight aphids were then connected to the Giga-8 DC-EPG amplifier and placed on a plantlet leaf of eight different plants and a second electrode was inserted into the soil of the potted plants to complete the electrical circuit. The recordings were performed continuously for 8 h during the day, with one aphid per plant. Alate aphids were synchronized in their flight phase prior to the EPG testing. The whole aphid-plant system was placed inside a Faraday cage at 20 ± 1° C. Acquisition and analysis of the EPG waveforms were carried out with PROBE 3.5 software (EPG Systems, www.epgsystems.eu). Parameters from the recorded EPG waveforms were calculated with EPG-Calc 6.1 software [39]. These parameters were based on six different EPG waveforms described by Tjallingii and Esch [40] corresponding to : (C) stylet pathways in plant tissues except phloem and xylem; (pd) to potential drops (intracellular stylet punctures); (E1) to salivation in phloem elements; (E2) to passive phloem sap ingestion; (G) to active xylem sap ingestion; and (F) to derailed stylet mechanics. For each aphid species, 20-21 individuals were tested.

Aphid performance on their host plants and on camelina

The aim of this test was to study, for each species of aphids, their performance on camelina plantlets compared to those on their host plant. First instar nymphs (< 24h old) of aphids were obtained from parthenogenetic adult females placed on an artificial diet 24 h before the experiment. The artificial diet was prepared according to Febvay *et al.* [41] and modified by Down *et al.* [42]. For each aphid species, groups of five nymphs were transferred onto the abaxial face of leaves in the middle of the canopy and enclosed in clip-cages. In each clip-cage, the date of appearance of the first offspring was used to define the end of the pre-reproductive period. At the end of this period, one single apterous adult female was kept in a clip-cage. Fecundity was assessed every two days for a duration equivalent to twice the pre-reproductive period as described in Le Roux *et al.* [43]. Pre-reproductive period duration, daily fecundity, intrinsic rate of natural increase (r_m) and the population's doubling time (DT = ln2/r_m) were calculated using the DEMP 1.5.2 Software [44] on replicates ranging from 31 to 40 individuals. The intrinsic rate of natural increase (r_m) was calculated as $\Sigma e^{-r_m x} l_x m_x = 1$, where x is the age, l_x the age-specific survival, and m_x the age-specific fecundity [45]. This parameter was selected to compare the ability of the different aphid species to establish a population on camelina and on their host plant.

Statistical analysis

Mean values are given with their standard error of the mean (SEM). A generalized linear model, using a binomial distribution (R 3.0.0 - R Development Core Team 2013 [46]), was applied to compare the aphid abilities to leave the platform and to land on camelina.

EPG parameters were compared between aphid species by using a Kruskal-Wallis one-way analysis of variance (H value), followed by nonparametric pairwise comparisons using the Siegel and Castellan solution [47] with a Dunn's correction [48] of the alpha threshold. The Intrinsic rate of natural increase (r_m) of each aphid species was compared on camelina and on their respective host plant by a Mann-Whitney U test using the Siegel and Castellan solution [47]. Because homocedasticity of all distributions were not confirmed, EPG and r_m analysis were performed with the Kruskal & Wallis's utility and Mann & Whitney 's utility, carried out by Georgin and Gouet [49] (http://Anastats.fr).

Results

Early steps of camelina plantlets colonization process

At the end of the 24-h choice bioassay the four aphid species exhibited the same ability to leave the platform (GLM using a binomial distribution, $\chi^2 = 0.894$; $P > 0.05$) or to land on camelina (GLM using a binomial distribution, $\chi^2 = 0.885$; $P > 0.05$) (Fig. 2**)**. The percentage of taking off ranged from 35 % (*R. padi*) to 60 % (*M. persicae* and *B. brassicae)*. The percentage of aphids landing on camelina ranged from 20 % (*R. padi*) to 35 % (*M. persicae*).

Electrical penetration graph studies

There was a significant effect of the aphid species for the following parameters (Table 1) : total duration of probing (H = 28.98; $P < 0.001$), number of probes (H = 17.43; $P < 0.001$), number of pathway phases (H = 14.61; $P < 0.01$), time of 1st probe to 1st E and E2 (H = 17.32 & H = 17.91; $P < 0.001$), mean phloem salivation phase (E1) duration (H = 16.45; $P < 0.001$) and mean phloem sap ingestion (E2) duration (H = 25.49; $P < 0.001$).

Total duration of probing was significantly longer for the two polyphagous species *A. fabae* and *M. persicae* than for the two oligophagous species *B. brassicae* and *R. padi (*$P < 0.05$*)*. The number of probes was significantly higher for *B. brassicae* and *R. padi* ($P < 0.05$).

Regarding pathway phase parameters, the total duration of this phase and the mean number of potential drops were not significantly different between aphid species (H = 2.97 & H = 6.71; $P > 0.05$).

For the phloem phase parameters, *R. padi* exhibited at least a two times greater shorter salivation phase (E1) than the other aphid species (H = 15.28; $P < 0.01$). Concerning the mean phloem sap ingestion (E2), *R. padi* ingested almost no phloem and *B. brassicae* fed for a duration of four to five times less than *A. fabae* and *M. persicae*. However, mean duration of the xylem sap ingestion (G) phase was not significantly different between aphid species (H = 4.18; $P > 0.05$). Finally, the total duration of stylet derailment phase in the mesophyll (F) was inconsequential for all species (H = 6.43; $P > 0.05$).

Aphid performance on their host plants and on camelina

Biological and demographic parameters of adult aphids were measured for each species of aphid on camelina and its respective host-plant, but only the r_m data are presented when aphids were tested on their host plant.

Kruskal-Wallis statistical analysis showed an aphid species effect on all parameters on camelina presented in Table 2 : pre-reproductive period ($H = 95.6$; $P < 0.05$), longevity ($H = 106.1$; $P < 0.05$), daily fecundity ($H = 60.1$; $P < 0.05$), intrinsic rate of natural increase (r_m) ($H = 28.1$; $P < 0.05$) and doubling time ($H = 28.1$; $P < 0.05$). Inter-specific pairwise comparisons showed that the pre-reproductive period was significantly higher for *B. brassicae* and shorter for *R. padi* compared to all other species of aphid on camelina ($P < 0.05$). Daily fecundity was significantly lower for *R. padi*, and conversely, more than twice as high for *A. fabae* ($P < 0.05$). Adult longevity was nearly as long for *M. persicae* and *B. brassicae* than for *A. fabae* and *R. padi* ($P < 0.05$). The intrinsic rate of natural increase and doubling time of *A. fabae* were significantly higher compared to *B. brassicae* and *R. padi* ($P < 0.05$). The r_m and doubling time of *M. persicae* and *R. padi* were significantly lower compared to *B. brassicae* ($P < 0.05$).

The Intrinsic rate of natural increase (r_m) of each aphid species was compared on camelina and on its respective host plant (Fig. 3). The oligophagous species *B. brassicae* and *R. padi* had a significantly higher r_m on their respective host plants *B. napus* and *H. vulgare* ($U = 296$ and $U = 325$, respectively; $P < 0.001$). Conversely, for *M. persicae*, the r_m was significantly lower on its rearing plant ($U = 247$; $P < 0.01$). Finally, for *A. fabae*, this parameter was not significantly different between the two plants ($U = 521$; $P > 0.05$).

Discussion

This study clearly showed that the four aphid species are likely to successfully colonize *Camelina sativa* as they all produced progeny on this plant. However, the two polyphagous species *A. fabae* and *M. persicae* and the two specialist species *B. brassicae* (cabbage specialist) and *R. padi* (cereal specialist) performed differently.

Camelina colonization ability

Host plant colonization by alate aphids is regulated by a sequence of steps [50, 51]: first, the host location and landing, followed by plant exploration and evaluation by brief testing probes. In the 24-h no-choice test, all four aphid species showed the same ability to leave the platform, to fly toward *C. sativa* and to land on it. In our experimental set up, flight orientation was probably triggered not only by volatile organic compounds emitted by the plant [52–54] but also by visual stimuli [55]. Furthermore, the time to the first probe was not different among the four aphid species. This suggests that *C. sativa* potential cues located on the plant's surface (e.g., wax or toughness of the leaf surface or volatiles) did not modulate orientation (attractive vs. repellent) nor probing (phagostimulant vs. deterrent) by aphids. These observations may seem surprising, as one would expect that the two generalist aphid species would be less attracted than the Brassicaceae specialist, *B. brassicae* and the cereal specialist not at all. Indeed, generalist aphids are usually indifferent or repelled by isothiocyanates emitted by Brassicaceae [53, 56], while specialist aphids are stimulated by secondary compounds [50]. However, Matthaüs and Zubr [22] indicated that camelina emitted mainly non-volatile isothiocyanates, certainly limiting attractant and repellent effects.

Once initial contact and plant surface assessment has been made, aphids probe the epidermis and then display stylet pathway activity in the mesophyll before ingesting sap within phloem tissues, defining the final acceptance of the plant [51]. In the present EPG study, the suitability of camelina for all the aphid species is supported by the absence of any stress indicator such as high xylem sap consumption, longer salivation phase (E1) or many phases of stylet derailment [57–59]. In our study, although the total duration of phloem ingestion was reduced in *B. brassicae* compared to the two generalist aphids, other parameters such as the time to the first phloem ingestion stylet derailment and pathway phase periods were similar for all three species. These results are not consistent with previous studies which showed that specialist insects make faster decisions than generalist ones [60]. However they confirm that the lower acceptability of camelina by *B. brassicae* was not due to features of the peripheral tissue layers of the leaves but to phloem-located cues. One hypothesis is that aphids encountered

deterrents compounds which could explain the high number of probes and pathway phases observed in *B. brassicae* and *R. padi*, although the total duration of the pathway phase remained equivalent for all aphids species. Indeed, the number of probes is higher in the less suitable host [61]. A first candidate could be the camalexine which is a phytoalexin found specifically in *C. sativa* and not in rapeseed [62,63]. Onyilagha *et al.* [64] studied other compounds involved in the response of a Brassicaceae specialist insect, the crucifer flea beetle (*Phyllotreta cruciferae*) (Coleoptera: Chrysomelidae) to camelina. They showed that camelina tissues present a large concentration of feeding deterrent components, such as flavone and quercetin glycosides, contrary to Brassica species such as *B. napus*, which contains large amounts of kaempferol identified as a phagostimulant. *B. brassicae* exhibited the same difficulties as the crucifer flea beetle on camelina, suggesting that *C. sativa* bears original deterrent compounds that specifically affect Brassicaceae specialists. The possibility that *M. persicae* and *A. fabae* may have prevented the coagulation of phloem proteins and the formation of callose after entering phloem vessels cannot be excluded [65].

Concerning aphid performance on plants, survival and above all daily fecundity on camelina were also contrasted between the aphid species tested, confirming the results obtained from the EPG study. *A. fabae* and *M. persicae* exhibited both the highest r_m and phloem sap consumption. It is noteworthy that the short longevity of *A. fabae* was compensated by a very high daily fecundity, corresponding to a trade-off relative to plant quality [66]. As expected, on camelina, the cereal specialist *R. padi* ingested very little phloem sap and its performances were very weak compared to the other aphid species. This indicates a type of antixenosis in which the strong feeding behavior alteration on the plant leads to the alteration of insects' physiological parameters [67]. Although, it was expected that the Brassicaceae specialist performed better on camelina than the generalist aphids [68], the generalists species seemed to be more efficient. Those results clearly indicate that *Camelina sativa* could become a potential host for these species mainly for the generalist ones which developed as well or even better than on their rearing host.

Epidemiologic and agronomic implications

All four aphid species successfully developed and reproduced on camelina: *Myzus persicae* developed even better on *C. sativa* than on potatoes, which is consistent with the results of Le Guigo *et al*. [69] who showed that the polyphagous *M. persicae* performed better on Brassicaceae than Solanaceae. It was expected that *R. padi*, a cereal specialist, would be a "transient aphid"; i.e., occasionally landing, resting and hydrating on the plant [70] but surprisingly, camelina could also be a suitable host for this species, even if its performances were

lower than the other species. Therefore, *A. fabae*, *B. brassicae*, *M. persicae* and *R. padi* can be considered as camelina potential “colonizing aphids” [70, 71].

So far, very little is known about the phytoviruses that camelina may host. Séguin-Swartz *et al.* [72], state that camelina is likely to host three Brassicaceae viruses, the TCV (Turnip Crinkle Virus), the TRoV (Turnip Rosette Virus) and the TYMV (Turnip Yellow Mosaic Virus) and an Amaranthaceae virus, the BWYV (Beet Western Yellows Virus). In an epidemiological context, our feeding behavior analysis demonstrated that all four aphid species exhibited potential drops which is a suitable behavior for the vection of non-persistent plant viruses (requiring a landing and brief probes) [70, 73]. Their ability to form viable colonies also confirmed that the four aphid species are able to vector persistent virus (requiring a landing and a prolonged aphid phloem feeding) [70]. Therefore, virus propagation is an important risk factor to be considered carefully when planning the reintroduction of camelina in the agricultural landscape.

On the other hand, camelina could serve as "virus sink" as defined by Hooks and Fereres [74]. Indeed, camelina can host aphids that also feed on non-Brassicaceae conventional crops, such as potatoes, legumes and cereals. These aphids could then lose their virus charge on camelina (for instance the Barley Yellow Dwarf Virus for *R. padi* or the Potato Virus Y for *M. persicae*) and consequently become virus-free aphids.

The associations Brassicaceae - legume have often been used and promoted in organic but also conventional agriculture [23]. Intercropping usually minimizes environmental impacts by allowing lower inputs through reduced fertilizer and pesticide requirements [75]. For instance, mixed cropping peas with camelina had a great suppressive effect on weed coverage compared with sole pea [25]. The effect of mixed cropping with camelina on pest control has not been evaluated yet but is under investigation in our laboratory.

When evaluating the risks posed by the introduction a new plant in an agrosystem, it is essential to use a more systemic approach, including assessing its effect on a wide range of potential insect pests usually associated or not with the focal crop.

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442 **Table 1** Electrical penetration graph parameters (means ± SEM) calculated for four aphid species during an 8-h monitoring session on *Camelina sativa* plants.

	Kruskal-Wallis test	*A. fabae*		*B. brassicae*		*M. persicae*		*R. padi*	
EPG classes	H(*P*)	n = 21		n = 21		n = 20		n = 20	
General probing behaviour									
1. Time to first probe (min)	6.60 (NS)	10.02 ± 4.14		28.08 ± 15.31		20.59 ± 11.43		30.08 ± 9.86	
2. Total duration of probing (min)	28.98 (***)	383.86 ± 21.62	a	273.68 ± 18.91	b	375.52 ± 20.75	a	236.15 ± 17.61	b
3. Number of probes	17.43 (***)	9.01 ± 1.71	b	20.52 ± 2.49	a	10.05 ± 1.55	b	15.3 ± 2.13	a
Pathway phase									
4. Number of pathway phases	14.61 (**)	11.62 ± 1.76	b	23.81 ± 2.87	a	12.6 ± 1.73	b	17.15 ± 2.01	ab
5. Total duration of pathway phases (C) (min)	2.97 (NS)	219.71 ± 26.24		215.53 ± 18.44		174.25 ± 21.85		184.47 ± 17.93	
6. Mean number of potential drops (pd)	6.71 (NS)	62.48 ± 6.1		107.29 ± 12.52		76.7 ± 8.99		85.9 ± 12.65	
Phloem phase									
7. Time of 1st probe to 1st E (min)	17.32 (***)	239.59 ± 41.16	b	196.32 ± 39.89	b	181.95 ± 33.78	b	400.49 ± 29.09	a
8. Total duration phloem salivation phase (E1) (min)	15.287 (**)	15.92 ± 7.3	a	7.36 ± 2.65	a	8.12 ± 3.54	a	2.49 ± 1.62	b
9. Time of 1st probe to 1st E2 (min)	17.91 (***)	284.24 ± 41.97	ab	198.29 ± 39.73	b	204.14 ± 37.26	b	430.24 ± 21.12	a
10. Total duration phloem sap ingestion (E2) (min)	25.49 (***)	111.7 ± 34.21	a	28.76 ± 9.9	a	150.32 ± 35.58	a	0.1 ± 0.1	b
Other parameters									
11. Total duration of xylem ingestion (G) (min)	4.18 (NS)	36.54 ± 7.34		22.03 ± 5.81		33.72 ± 11.2		42.64 ± 9.11	
12. Total duration of stylet derailment (F) (min)	6.43 (NS)	0 ± 0		0 ± 0		1.19 ± 1.19		6.31 ± 5.11	

443

444 Asterisks indicate a significant difference*:* * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ associated with H (Kruskal-Wallis test); the letters within a row indicate significant

445 differences associated with following pairwise comparisons.

446

447

448 **Table 2** Mean (± SEM) population parameter values of four aphid species reared on *Camelina sativa*. H(*P*) Kruskal-Wallis test values with its probability within brackets.

449

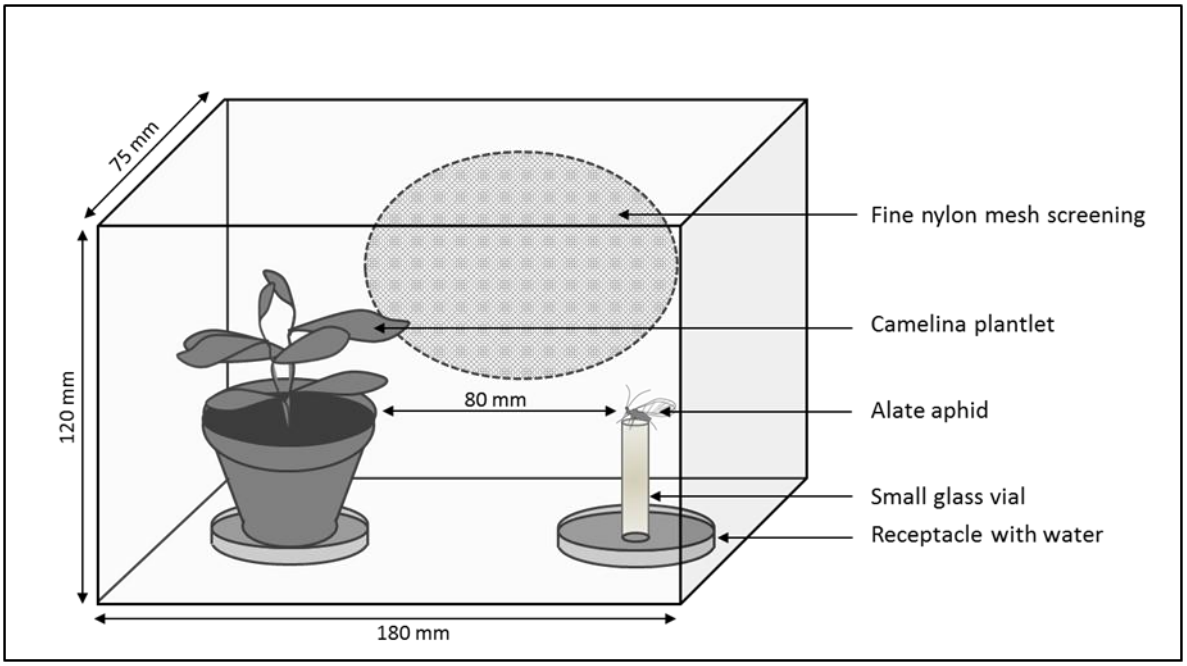
	Kruskal-Wallis test	*A. fabae*		*B. brassicae*		*M. persicae*		*R. padi*	
	H(*P*)	n = 34		n = 38		n = 40		n = 31	
Pre-reproductive period (days)	95.6 (***)	7.00 ± 0.17	bc	9.79 ± 0.10	a	7.95 ± 0.18	b	6.26 ± 0.12	c
Longevity (days)	106.1 (***)	14.59 ± 0.52	b	24.90 ± 0.058	a	22.75 ± 0.25	a	13.22 ± 0.32	b
Daily fecundity (nymphs per female)	60.1 (***)	3.50 ± 0.21	a	2.55 ± 0.11	b	2.89 ± 0.12	ab	1.41 ± 0.12	c
r_m (female per female per day)	28.1 (***)	0.31 ± 0.01	a	0.25 ± 0.00	b	0.27 ± 0.00	a	0.26 ± 0.01	ab
Doubling time (days)	28.1 (***)	2.30 ± 0.07	b	2.86 ± 0.05	a	2.60 ± 0.05	b	2.80 ± 0.14	ab

450

451 Asterisks indicate a significant difference*:* * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ associated with H (Kruskal-Wallis test); the letters within a row indicate significant

452 differences associated with following pairwise comparisons.

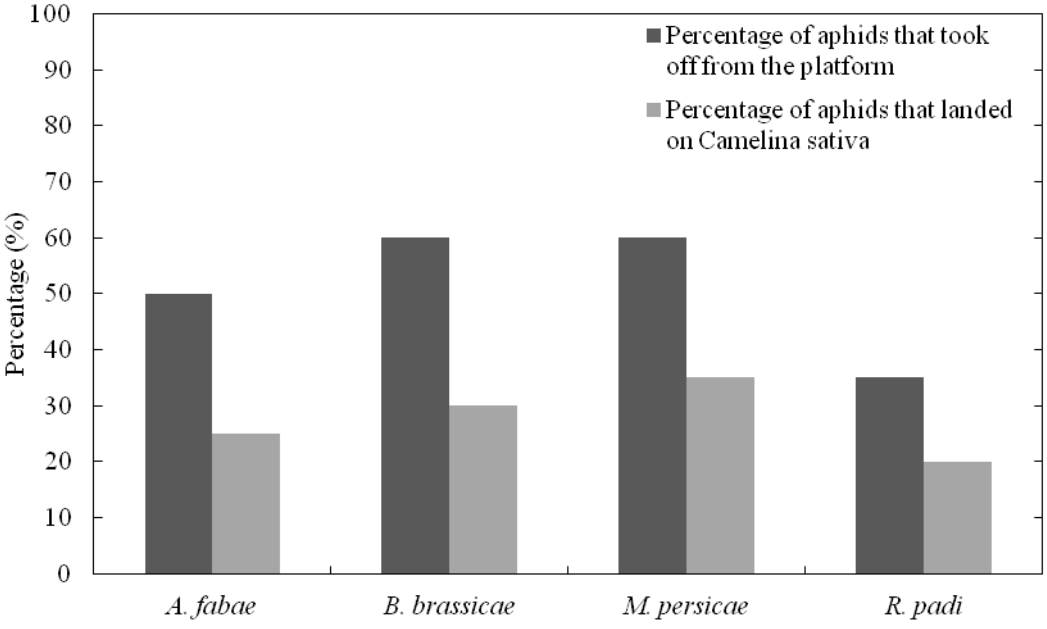
453 **Fig. 1** Experimental device used for the colonization experiment.



454

455 **Fig. 2** Percentage (n = 20) of aphids that took off from platform and the percentage of aphids that landed on

456 *Camelina sativa* at the end of a 24-h bioassay.



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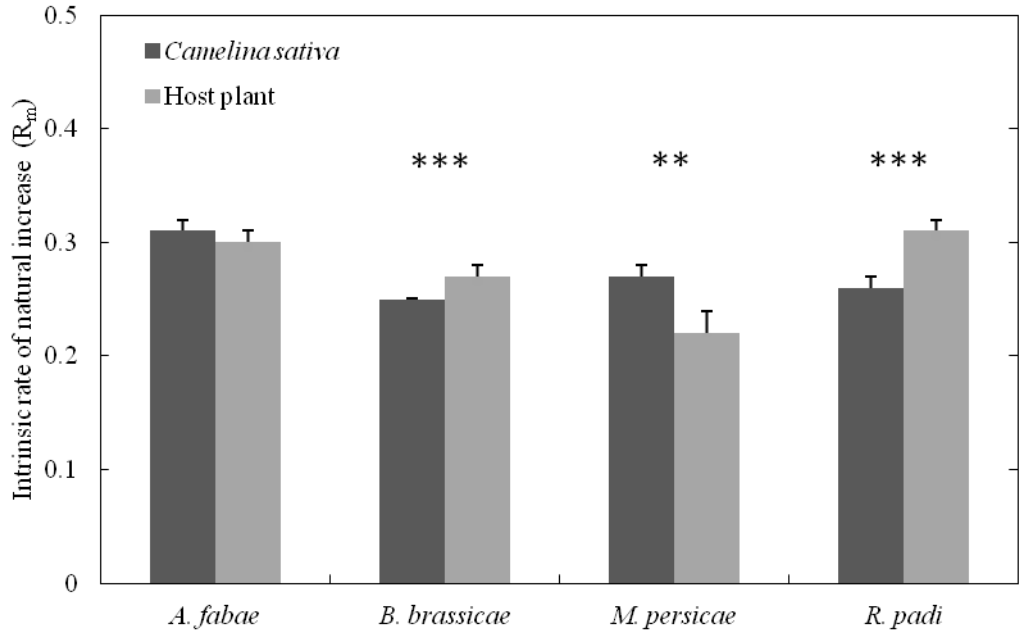
459

460 **Fig. 3** Intrinsic rate of natural increase (r_m) (± SEM), of different aphid species reared on *Camelina sativa* and on
461 their respective host plants, i.e., *Vicia fabae, Brassica napus, Solanum tuberosum, Hordeum vulgare*. For each
462 aphid species and each plant, 22 to 40 individuals were tested. Asterisks indicate a significant difference in a
463 choice test*:* * P <0.05, ** P <0.01, *** P <0.001 (Mann-Whitney U test).

464



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