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

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8

9 **ABSTRACT**

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

24

25 **KEY WORDS**

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

27

28 **Introduction**

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

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

44 *Camelina sativa* (L.) Crtz. also known as the false flax, or the gold-of-pleasure, is a Brassicaceae which was an
45 important oil crop in Europe during the Bronze and Iron Ages [11]. It was cultivated until the 19th century in
46 France and to a lesser extent in Holland, Belgium and Russia [12]. In the early twentieth century, 5000 hectares
47 of false flax were still cultivated in northern France [13]. Camelina is recognized for its rusticity because it can
48 tolerate a wide range of pedoclimatic conditions [13] and requires low agronomic inputs [14]. The plant has
49 lower nitrogen requirements and a shorter growing season than rapeseed [15–17]. Moreover, camelina is
50 reported to be tolerant to drought and heat [18], resistant to cold [19] and to different pathogens and insects [20,
51 21] thanks to various anti-nutritional compounds produced (e.g., Matthaüs and Zubr [22]). This plant can be used
52 in mixed cropping systems with legumes, not only for water and nitrogen management [23, 24], but also for
53 weed control [25]. Camelina oil offers good opportunities as a biofuel crop and functional food as it contains
54 exceptionally high levels of omega-3 fatty acids, and over 50% of its fatty acids are polyunsaturated [26, 27].

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

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

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

70

71 **Materials and Methods**

72 **Insects and Plants**

73 For each species, colonies were initiated from a single apterous parthenogenetic female and were separately
74 maintained in ventilated Plexiglas[®] cages (360 x 240 x 110 mm) in growth chambers under controlled conditions
75 ($20 \pm 2^\circ\text{C}$, $60 \pm 5\%$ relative humidity (RH), and 16L:8D photoperiod at 4.7 klux) to induce parthenogenesis.
76 Aphid clones were used to minimize intraspecific variability and to ensure a certain uniformity of response.

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

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

87 **Early steps of the camelina plantlets colonization process**

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

98 **Electrical penetration graph studies**

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

112 **Aphid performance on their host plants and on camelina**

113 The aim of this test was to study, for each species of aphids, their performance on camelina plantlets compared
114 to those on their host plant. First instar nymphs (< 24h old) of aphids were obtained from parthenogenetic adult
115 females placed on an artificial diet 24 h before the experiment. The artificial diet was prepared according to
116 Febvay *et al.* [41] and modified by Down *et al.* [42]. For each aphid species, groups of five nymphs were
117 transferred onto the abaxial face of leaves in the middle of the canopy and enclosed in clip-cages. In each clip-
118 cage, the date of appearance of the first offspring was used to define the end of the pre-reproductive period. At
119 the end of this period, one single apterous adult female was kept in a clip-cage. Fecundity was assessed every
120 two days for a duration equivalent to twice the pre-reproductive period as described in Le Roux *et al.* [43]. Pre-
121 reproductive period duration, daily fecundity, intrinsic rate of natural increase (r_m) and the population's doubling
122 time ($DT = \ln 2 / r_m$) were calculated using the DEMP 1.5.2 Software [44] on replicates ranging from 31 to 40
123 individuals. The intrinsic rate of natural increase (r_m) was calculated as $\sum e^{-r_m x} l_x m_x = 1$, where x is the age,
124 l_x the age-specific survival, and m_x the age-specific fecundity [45]. This parameter was selected to compare the
125 ability of the different aphid species to establish a population on camelina and on their host plant.

126 **Statistical analysis**

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

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

137

138 **Results**

139 **Early steps of camelina plantlets colonization process**

140 At the end of the 24-h choice bioassay the four aphid species exhibited the same ability to leave the platform
141 (GLM using a binomial distribution, $\chi^2 = 0.894$; $P > 0.05$) or to land on camelina (GLM using a binomial
142 distribution, $\chi^2 = 0.885$; $P > 0.05$) (Fig. 2). The percentage of taking off ranged from 35 % (*R. padi*) to 60 %
143 (*M. persicae* and *B. brassicae*). The percentage of aphids landing on camelina ranged from 20 % (*R. padi*) to
144 35 % (*M. persicae*).

145 **Electrical penetration graph studies**

146 There was a significant effect of the aphid species for the following parameters (Table 1) : total duration of
147 probing ($H = 28.98$; $P < 0.001$), number of probes ($H = 17.43$; $P < 0.001$), number of pathway phases
148 ($H = 14.61$; $P < 0.01$), time of 1st probe to 1st E and E2 ($H = 17.32$ & $H = 17.91$; $P < 0.001$), mean phloem
149 salivation phase (E1) duration ($H = 16.45$; $P < 0.001$) and mean phloem sap ingestion (E2) duration ($H = 25.49$;
150 $P < 0.001$).

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

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

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

162 **Aphid performance on their host plants and on camelina**

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

165 Kruskal-Wallis statistical analysis showed an aphid species effect on all parameters on camelina presented in
166 Table 2 : pre-reproductive period ($H = 95.6$; $P < 0.05$), longevity ($H = 106.1$; $P < 0.05$), daily fecundity
167 ($H = 60.1$; $P < 0.05$), intrinsic rate of natural increase (r_m) ($H = 28.1$; $P < 0.05$) and doubling time ($H = 28.1$;
168 $P < 0.05$). Inter-specific pairwise comparisons showed that the pre-reproductive period was significantly higher
169 for *B. brassicae* and shorter for *R. padi* compared to all other species of aphid on camelina ($P < 0.05$). Daily
170 fecundity was significantly lower for *R. padi*, and conversely, more than twice as high for *A. fabae* ($P < 0.05$).
171 Adult longevity was nearly as long for *M. persicae* and *B. brassicae* than for *A. fabae* and *R. padi* ($P < 0.05$).
172 The intrinsic rate of natural increase and doubling time of *A. fabae* were significantly higher compared to
173 *B. brassicae* and *R. padi* ($P < 0.05$). The r_m and doubling time of *M. persicae* and *R. padi* were significantly
174 lower compared to *B. brassicae* ($P < 0.05$).

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

180

181 **Discussion**

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

186 **Camelina colonization ability**

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

200 Once initial contact and plant surface assessment has been made, aphids probe the epidermis and then display
201 stylet pathway activity in the mesophyll before ingesting sap within phloem tissues, defining the final acceptance
202 of the plant [51]. In the present EPG study, the suitability of camelina for all the aphid species is supported by
203 the absence of any stress indicator such as high xylem sap consumption, longer salivation phase (E1) or many
204 phases of stylet derailment [57–59]. In our study, although the total duration of phloem ingestion was reduced in
205 *B. brassicae* compared to the two generalist aphids, other parameters such as the time to the first phloem
206 ingestion stylet derailment and pathway phase periods were similar for all three species. These results are not
207 consistent with previous studies which showed that specialist insects make faster decisions than generalist ones
208 [60]. However they confirm that the lower acceptability of camelina by *B. brassicae* was not due to features of
209 the peripheral tissue layers of the leaves but to phloem-located cues. One hypothesis is that aphids encountered

210 deterrents compounds which could explain the high number of probes and pathway phases observed in
211 *B. brassicae* and *R. padi*, although the total duration of the pathway phase remained equivalent for all aphids
212 species. Indeed, the number of probes is higher in the less suitable host [61]. A first candidate could be the
213 camalexine which is a phytoalexin found specifically in *C. sativa* and not in rapeseed [62,63]. Onyilagha *et al.*
214 [64] studied other compounds involved in the response of a Brassicaceae specialist insect, the crucifer flea beetle
215 (*Phyllotreta cruciferae*) (Coleoptera: Chrysomelidae) to camelina. They showed that camelina tissues present a
216 large concentration of feeding deterrent components, such as flavone and quercetin glycosides, contrary to
217 Brassica species such as *B. napus*, which contains large amounts of kaempferol identified as a phagostimulant.
218 *B. brassicae* exhibited the same difficulties as the crucifer flea beetle on camelina, suggesting that *C. sativa*
219 bears original deterrent compounds that specifically affect Brassicaceae specialists. The possibility that
220 *M. persicae* and *A. fabae* may have prevented the coagulation of phloem proteins and the formation of callose
221 after entering phloem vessels cannot be excluded [65].

222 Concerning aphid performance on plants, survival and above all daily fecundity on camelina were also
223 contrasted between the aphid species tested, confirming the results obtained from the EPG study. *A. fabae* and
224 *M. persicae* exhibited both the highest r_m and phloem sap consumption. It is noteworthy that the short longevity
225 of *A. fabae* was compensated by a very high daily fecundity, corresponding to a trade-off relative to plant quality
226 [66]. As expected, on camelina, the cereal specialist *R. padi* ingested very little phloem sap and its performances
227 were very weak compared to the other aphid species. This indicates a type of antixenosis in which the strong
228 feeding behavior alteration on the plant leads to the alteration of insects' physiological parameters [67].
229 Although, it was expected that the Brassicaceae specialist performed better on camelina than the generalist
230 aphids [68], the generalists species seemed to be more efficient. Those results clearly indicate that *Camelina*
231 *sativa* could become a potential host for these species mainly for the generalist ones which developed as well or
232 even better than on their rearing host.

233 **Epidemiologic and agronomic implications**

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

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

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

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

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

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

262

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272 **References cited**

- 273 1. Food and Agriculture Organization of the United Nations (2014) Food and Agriculture Organization of the
274 United Nations. <http://www.fao.org/home/en/>. Accessed 15 March 2014.
- 275 2. Valentine J, Clifton-Brown J, Hastings A, et al. (2012) Food vs. fuel: the use of land for lignocellulosic “next
276 generation” energy crops that minimize competition with primary food production. *GCB Bioenergy* 4:1–
277 19. doi: 10.1111/j.1757-1707.2011.01111.x
- 278 3. Durrett TP, Benning C, Ohlrogge J (2008) Plant triacylglycerols as feedstocks for the production of biofuels.
279 *Plant J* 54:593–607. doi: 10.1111/j.1365-313X.2008.03442.x
- 280 4. Cermak SC, Biresaw G, Isbell TA, et al. (2013) New crop oils—Properties as potential lubricants. *Ind Crops*
281 *Prod* 44:232–239. doi: 10.1016/j.indcrop.2012.10.035
- 282 5. Zanetti F, Monti A, Berti MT (2013) Challenges and opportunities for new industrial oilseed crops in EU-27:
283 A review. *Ind Crops Prod* 50:580–595. doi: 10.1016/j.indcrop.2013.08.030
- 284 6. Cardone M, Mazzoncini M, Menini S, et al. (2003) *Brassica carinata* as an alternative oil crop for the
285 production of biodiesel in Italy: agronomic evaluation, fuel production by transesterification and
286 characterization. *Biomass and Bioenergy* 25:623–636. doi: 10.1016/S0961-9534(03)00058-8
- 287 7. Alford DV, Nilsson C, Ulber B (2003) Insect pests of oilseedrape. *Biocontrol Oilseed Rape Pests*. Blackwell
288 Science Ltd, pp 9–42
- 289 8. Kovács G, Kaasik R, Metspalu L, et al. (2013) Could *Brassica rapa*, *Brassica juncea* and *Sinapis alba*
290 facilitate the control of the cabbage seed weevil in oilseed rape crops? *Biol Control* 65:124–129. doi:
291 10.1016/j.biocontrol.2013.01.011
- 292 9. Zehnder G, Gurr GM, Kühne S, et al. (2007) Arthropod pest management in organic crops. *Annu Rev*
293 *Entomol* 52:57–80. doi: 10.1146/annurev.ento.52.110405.091337
- 294 10. Pavlista AD, Isbell TA, Baltensperger DD, Hergert GW (2011) Planting date and development of spring-
295 seeded irrigated canola, brown mustard and camelina. *Ind Crops Prod* 33:451–456. doi:
296 10.1016/j.indcrop.2010.10.029

- 297 11. Kroll H (1994) Ein archaologischer Rapsfund des 16. Jahrhunderts, entdeckt in Heide in Holstein,
298 Norddeutschland. *J Agron Crop Sci* 173:17–21. doi: 10.1111/j.1439-037X.1994.tb00569.x
- 299 12. Fröhlich A, Rice B (2005) Evaluation of *Camelina sativa* oil as a feedstock for biodiesel production. *Ind*
300 *Crops Prod* 21:25–31. doi: 10.1016/j.indcrop.2003.12.004
- 301 13. Bonjean A, Le Goffic F (1999) *Camelina sativa* (L.) Crantz : une opportunité pour l’agriculture et l’industrie
302 européennes. *Oilseeds fats, Crop Lipids* 6:28–34.
- 303 14. Naranjo SE, Stefanek MA (2012) Feeding behavior of a potential insect pest, *Lygus hesperus*, on four new
304 industrial crops for the arid southwestern USA. *Ind Crops Prod* 37:358–361. doi:
305 10.1016/j.indcrop.2011.12.020
- 306 15. Solis A, Vidal I, Paulino L, et al. (2013) *Camelina* seed yield response to nitrogen, sulfur, and phosphorus
307 fertilizer in South Central Chile. *Ind Crops Prod* 44:132–138. doi: 10.1016/j.indcrop.2012.11.005
- 308 16. Johnson JMF, Gesch RW (2013) *Calendula* and *camelina* response to nitrogen fertility. *Ind Crops Prod*
309 43:684–691. doi: 10.1016/j.indcrop.2012.07.056
- 310 17. Putnam DH, Budin JT, Field LA, Breene WM (1993) *Camelina*: A promising low-input oilseed. In: Janick J,
311 Simon JE (eds) *New Crop*. Wiley, New York, pp 314–322
- 312 18. French AN, Hunsaker D, Thorp K, Clarke T (2009) Evapotranspiration over a *camelina* crop at Maricopa,
313 Arizona. *Ind Crops Prod* 29:289–300. doi: 10.1016/j.indcrop.2008.06.001
- 314 19. Schillinger WF, Wysocki DJ, Chastain TG, et al. (2012) *Camelina*: Planting date and method effects on stand
315 establishment and seed yield. *F Crop Res* 130:138–144. doi: 10.1016/j.fcr.2012.02.019
- 316 20. Sharma G, Kumar VD, Haque A, et al. (2002) *Brassica* coenospecies : a rich reservoir for genetic resistance
317 to leaf spot caused by *Alternaria brassicae*. *Euphytica* 125:411–417. doi: 10.1023/A:1016050631673
- 318 21. Henderson AE, Hallett RH, Soroka JJ (2004) Prefeeding Behavior of the Crucifer Flea Beetle, *Phyllotreta*
319 *cruciferae*, on Host and Nonhost Crucifers. *J Insect Behav* 17:17–39. doi:
320 10.1023/B:JOIR.0000025130.20327.1a
- 321 22. Matthaüs B, Zubr J (2000) Variability of specific components in *Camelina sativa* oilseed cakes. *Ind Crops*
322 *Prod* 12:9–18. doi: 10.1016/S0926-6690(99)00040-0
- 323 23. Paulsen HM (2007) Mischfruchtanbausysteme mit Ölpflanzen im ökologischen Landbau 1. Ertragsstruktur
324 des Mischfruchtanbaus von Leguminosen oder Sommerweizen mit Leindotter (*Camelina sativa* L. Crantz).
325 *Landbauforsch Völkenrode* 1:107–117.
- 326 24. Groeneveld JH, Klein A-M (2013) Pollination of two oil-producing plant species: *Camelina* (*Camelina*
327 *sativa* L. Crantz) and pennycress (*Thlaspi arvense* L.) double-cropping in Germany. *GCB Bioenergy* 1–10.
328 doi: 10.1111/gcbb.12122
- 329 25. Saucke H, Ackermann K (2006) Weed suppression in mixed cropped grain peas and false flax (*Camelina*
330 *sativa*). *Weed Res* 46:453–461. doi: 10.1111/j.1365-3180.2006.00530.x
- 331 26. Abramovič H, Butinar B, Nikolič V (2007) Changes occurring in phenolic content, tocopherol composition
332 and oxidative stability of *Camelina sativa* oil during storage. *Food Chem* 104:903–909. doi:
333 10.1016/j.foodchem.2006.12.044
- 334 27. Berhow MA, Polat U, Glinski JA, et al. (2013) Optimized analysis and quantification of glucosinolates from

- 335 *Camelina sativa* seeds by reverse-phase liquid chromatography. *Ind Crop Prod* 43:119–125. doi:
336 10.1016/j.indcrop.2012.07.018
- 337 28. Gardiner MA, Tuell JK, Isaacs R, et al. (2010) Implications of Three Biofuel Crops for Beneficial
338 Arthropods in Agricultural Landscapes. *BioEnergy Res* 3:6–19. doi: 10.1007/s12155-009-9065-7
- 339 29. Bourke D, Stanley D, O'Rourke E, et al. (2013) Response of farmland biodiversity to the introduction of
340 bioenergy crops: effects of local factors and surrounding landscape context. *GCB Bioenergy* 1–15. doi:
341 10.1111/gcbb.12089
- 342 30. Kelly DW, Paterson RA, Townsend CR, et al. (2009) Parasite spillback: a neglected concept in invasion
343 ecology? *Ecology* 90:2047–56. PMID: 19739367
- 344 31. Broadbent L, Heathcote GD (1958) Properties and host range of Turnip crinkle, rosette and yellow mosaic
345 viruses. *Ann Appl Biol* 46:585–592. doi: 10.1111/j.1744-7348.1958.tb02242.x
- 346 32. Toba HH (1962) Studies on the host range of watermelon mosaic virus in Hawaii. *Plant Dis* 46:409–410.
- 347 33. Hill DS (1983) *Myzus persicae* (Sulz). *Agric. insect pests Trop. their Control*. Cambridge University Press, p
348 746
- 349 34. Markham PG, Pinner MS, Raccach B, Hull R (1987) The acquisition of a caulimovirus by different aphid
350 species: comparison with a potyvirus. *Ann Appl Biol* 111:571–587. doi: 10.1111/j.1744-
351 7348.1987.tb02015.x
- 352 35. Gols R, Veenemans C, Potting RPJ, et al. (2012) Variation in the specificity of plant volatiles and their use
353 by a specialist and a generalist parasitoid. *Anim Behav* 83:1231–1242. doi: 10.1016/j.anbehav.2012.02.015
- 354 36. Boquel S, Delayen C, Couty A, et al. (2012) Modulation of Aphid Vector Activity by Potato virus Y on In
355 Vitro Potato Plants. *Am Phytopathol Soc* 96:82–86. doi: 10.1094/PDIS-06-11-0499
- 356 37. Brunissen L, Cherqui A, Pelletier Y, et al. (2009) Host-plant mediated interactions between two aphid
357 species. *Entomol Exp Appl* 132:30–38. doi: 10.1111/j.1570-7458.2009.00862.x
- 358 38. Tjallingii WF (1988) Electrical recording of stylet penetration activities. In: Elsevier (ed) *Aphids Their Biol.*
359 *Nat. Enemies Control. World Crop Pests*. Amsterdam, The Netherlands, pp 95–108
- 360 39. Giordanengo P (2014) EPG-Calc: a PHP-based script to calculate electrical penetration graph (EPG)
361 parameters. *Arthropod Plant Interact* 8:163–169. doi: 10.1007/s11829-014-9298-z
- 362 40. Tjallingii WF, Hogen Esch T (1993) Fine structure of aphid stylet routes in plant tissues in correlation with
363 EPG signals. *Physiol Entomol* 18:317–328. doi: 10.1111/j.1365-3032.1993.tb00604.x
- 364 41. Febvay G, Delobel B, Rahbé Y (1988) Influence of the amino acid balance on the improvement of an
365 artificial diet for a biotype of *Acyrtosiphon pisum* (Homoptera: Aphididae). *Can J Zool* 66:2449–2453.
366 doi: 10.1139/z88-362
- 367 42. Down RE, Gatehouse AMR, Hamilton WDO, Gatehouse JA (1996) Snowdrop lectin inhibits development
368 and decreases fecundity of the Glasshouse Potato Aphid (*Aulacorthum solani*) when administered in vitro
369 and via transgenic plants both in laboratory and glasshouse trials. *J Insect Physiol* 42:1035–1045. doi:
370 10.1016/S0022-1910(96)00065-0
- 371 43. Le Roux V, Saguez J, Vincent C, Giordanengo P (2004) Rapid Method to Screen Resistance of Potato Plants
372 Against *Myzus persicae* (Homoptera: Aphididae) in the Laboratory. *J Econ Entomol* 97:2079–2082. doi:

373 10.1603/0022-0493-97.6.2079

374 44. Giordanengo P (2012) DEMP 1.5.2, programme php pour calculer les paramètres démographiques (tables de
375 survie).

376 45. Birch LC (1948) The intrinsic rate of natural increase of an insect population. *J Anim Ecol* 17:15–26.

377 46. R Core Team (2013) R: A Language and Environment for Statistical Computing. R Foundation for Statistical
378 Computing, Vienna, Austria. <http://www.R-project.org/>.

379 47. Siegel S, Castellan JN (1988) Nonparametric statistics for the behavioral sciences. *Nonparametric Stat.*
380 *Behav. Sci.* McGraw-Hill, New York, p 399

381 48. Dunn J (1964) Multiple comparisons using rank sums. *Technometrics* 6:241–252.

382 49. Georgin P, Gouet M (2000) Statistiques avec Excel 2000. 338.

383 50. Niemeyer HM (1990) Secondary plant chemicals in aphid-host interactions. RK Campbell RD Eikenbary
384 Aphid-plant genotype *Interact* 101–111.

385 51. Powell G, Tosh CR, Hardie J (2006) Host plant selection by aphids: behavioral, evolutionary, and applied
386 perspectives. *Annu Rev Entomol* 51:309–30. doi: 10.1146/annurev.ento.51.110104.151107

387 52. Chapman RF, Bernays EA, Simpson SJ (1981) Attraction and repulsion of the aphid, *Cavariella aegopodii*,
388 by plant odors. *J Chem Ecol* 7:881–888. doi: 10.1007/BF00992385

389 53. Nottingham SF, Hardie J, Dawson GW, et al. (1991) Behavioral and electrophysiological responses of
390 Aphids to host and nonhost plant volatiles. *J Chem Ecol* 17:1231–42. doi: 10.1007/BF01402946

391 54. Pickett JA, Wadhams LJ, Woodcock CM, Hardie J (1992) The chemical ecology of aphids. *Annu Rev*
392 *Entomol* 37:21–40. doi: 10.1146/annurev.en.37.010192

393 55. Hardie J (1989) Spectral specificity for targeted flight in the Black bean Aphid, *Aphis fabae*. *J Insect Physiol*
394 35:619–626. doi: 10.1111/j.1365-3032.1993.tb00612.x

395 56. Hori M (1998) Repellency of Rosemary oil against *Myzus persicae* in a laboratory and in a screenhouse. *J*
396 *Chem Ecol* 24:1425–1432. doi: 10.1023/A:1020947414051

397 57. Sauvion N (1995) Effets et modes d'action de deux lectines à mannose sur le puceron du pois, *Acyrtosiphon*
398 *pisum* (Harris). PhD thesis. INSA Lyon. 257.

399 58. Prado E, Tjallingii WF (1997) Effects of previous plant infestation on sieve element acceptance by two
400 aphids. *Entomol Exp Appl* 82:189–200. doi: 10.1046/j.1570-7458.1997.00130.x

401 59. Sauge M-H, Lacroze J, Poëssel J, et al. (2002) Induced resistance by *Myzus persicae* in the peach cultivar
402 “Rubira.” *Entomol Exp Appl* 102:29–37. doi: 10.1046/j.1570-7458.2002.00922.x

403 60. Bernays EA, Funk DJ (1999) Specialists make faster decisions than generalists: experiments with aphids.
404 *Proc R Soc B* 266:151–156. doi: 10.1098/rspb.1999.0615

405 61. Cole RA (1997) Comparison of feeding behaviour of two Brassica pests *Brevicoryne brassicae* and *Myzus*
406 *persicae* on wild and cultivated brassica species. *Entomol Exp Appl* 85:135–143. doi: 10.1046/j.1570-
407 7458.1997.00243.x

408 62. Browne LM, Conn KL, Ayert WA, Tewariy JP (1991) The camalexins: New phytoalexins produced in the
409 leaves of *Camelina sativa* (Cruciferae). *Tetrahedron* 41:3909–3914. doi: 10.1016/S0040-4020(01)86431-0

410 63. Kuśnierczyk A, Winge P, Jørstad TS, et al. (2008) Towards global understanding of plant defence against

- 411 aphids - timing and dynamics of early *Arabidopsis* defence responses to cabbage aphid (*Brevicoryne*
412 *brassicae*) attack. *Plant Cell Environ* 31:1097–1115. doi: 10.1111/j.1365-3040.2008.01823.x
- 413 64. Onyilagha JC, Gruber MY, Hallett RH, et al. (2012) Constitutive flavonoids deter flea beetle insect feeding
414 in *Camelina sativa* L. *Biochem Syst Ecol* 42:128–133. doi: 10.1016/j.bse.2011.12.021
- 415 65. Will T, Bel AJE Van (2006) Physical and chemical interactions between aphids and plants. *J Exp Bot*
416 57:729–737. doi: 10.1093/jxb/erj089
- 417 66. Stadler B (1995) Adaptive allocation of resources and life-history trade-offs in aphids relative to plant
418 quality. *Oecologia* 102:246–254. doi: 10.1007/BF00333257
- 419 67. Le Roux V, Dugravot S, Campan E, et al. (2008) Wild *Solanum* resistance to aphids: antixenosis or
420 antibiosis? *J Econ Entomol* 101:584–91. doi: 10.1603/0022-0493(2008)101[584:WSRTAA]2.0.CO;2
- 421 68. Gols R, Bukovinszky T, van Dam NM, et al. (2008) Performance of generalist and specialist herbivores and
422 their endoparasitoids differs on cultivated and wild *Brassica* populations. *J Chem Ecol* 34:132–43. doi:
423 10.1007/s10886-008-9429-z
- 424 69. Le Guigo P, Maingeneau A, Le Corff J (2012) Performance of an aphid *Myzus persicae* and its parasitoid
425 *Diaeretiella rapae* on wild and cultivated Brassicaceae. *J Plant Interact* 7:326–332. doi:
426 10.1080/17429145.2011.628417
- 427 70. Fereres A, Moreno A (2009) Behavioural aspects influencing plant virus transmission by homopteran
428 insects. *Virus Res* 141:158–168. doi: 10.1016/j.virusres.2008.10.020
- 429 71. Irwin M, Kampmeier GE, Weisser WW (2007) Aphids movement : process and consequences. In: H.F.Van
430 Emden and R. Harrington (ed) *Aphids as Crop pests*. CABI Publishing, Oxon, UK, pp 153–186
- 431 72. Séguin-Swartz G, Eynck C, Gugel RK, et al. (2009) Diseases of *Camelina sativa* (false flax). *Can J plant*
432 *Pathol* 31:375–386. doi: 10.1080/07060660909507612
- 433 73. Martín B, Collar JL, Tjallingii WF, Fereres A (1997) Intracellular ingestion and salivation by aphids may
434 cause the acquisition and inoculation of non-persistently transmitted plant viruses. *J Gen Virol* 78:2701–
435 2705. doi: 10.1099/vir.0.80632-0
- 436 74. Hooks CRR, Fereres A (2006) Protecting crops from non-persistently aphid-transmitted viruses: a review on
437 the use of barrier plants as a management tool. *Virus Res* 120:1–16. doi: 10.1016/j.virusres.2006.02.006
- 438 75. Lithourgidis AS, Dordas CA, Damalas CA, Vlachostergios DN (2011) Review article Annual intercrops : an
439 alternative pathway for sustainable agriculture. *Aust J Crop Sci* 5:396–410. ISSN: 1835-2693

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

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

449

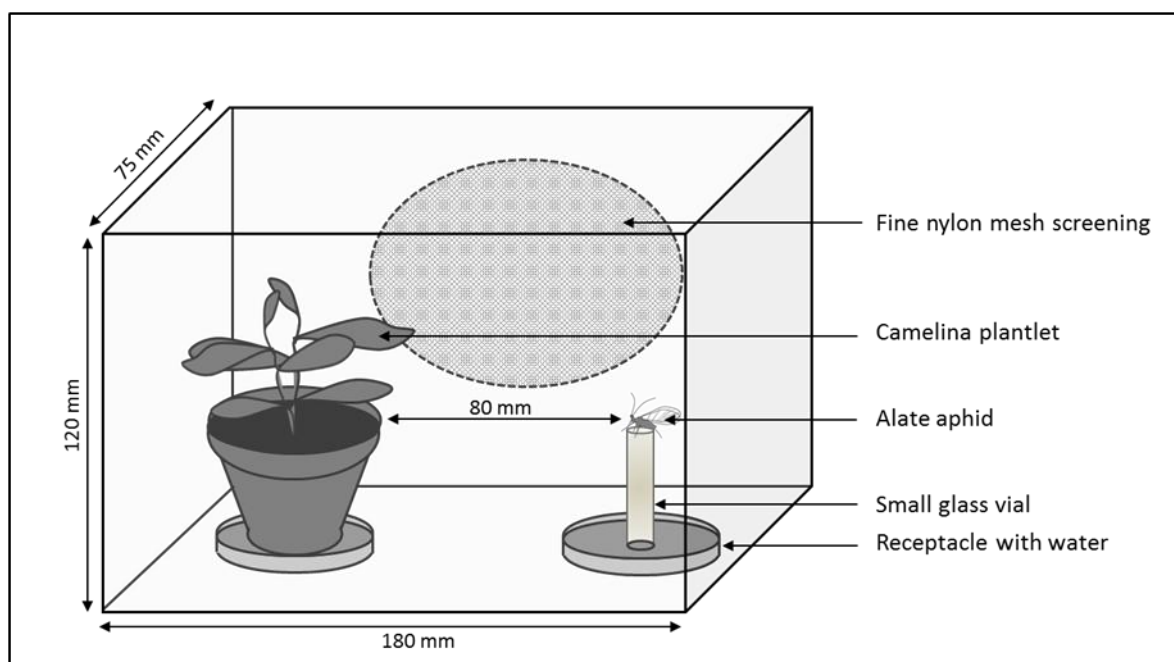
	Kruskal-Wallis test	<i>A. fabae</i>			<i>B. brassicae</i>			<i>M. persicae</i>			<i>R. padi</i>		
	H(P)	n = 34			n = 38			n = 40			n = 31		
Pre-reproductive period (days)	95.6 (***)	7.00	\pm 0.17	bc	9.79	\pm 0.10	a	7.95	\pm 0.18	b	6.26	\pm 0.12	c
Longevity (days)	106.1 (***)	14.59	\pm 0.52	b	24.90	\pm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

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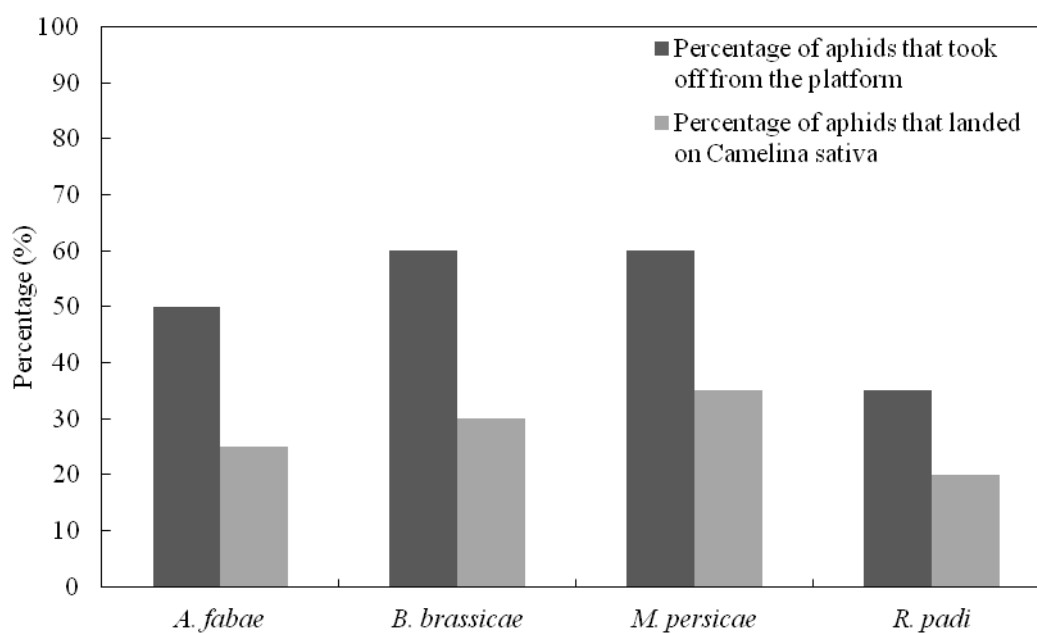
451 Asterisks indicate a significant difference: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ associated with H (Kruskal-Wallis test); the letters within a row indicate significant

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.



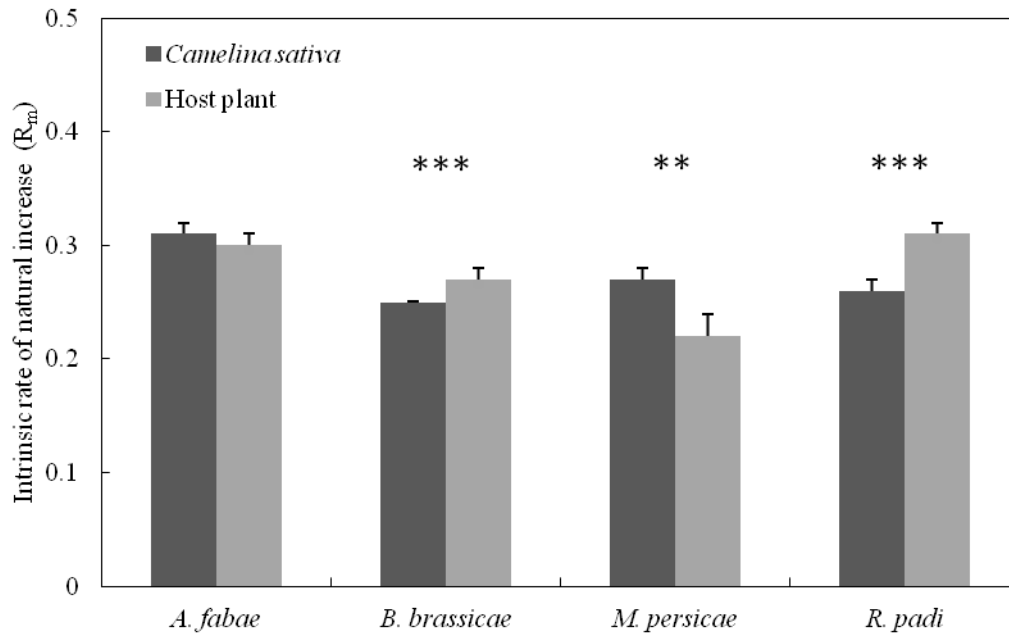
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460 **Fig. 3** Intrinsic rate of natural increase (r_m) (\pm SEM), of different aphid species reared on *Camelina sativa* and on
461 their respective host plants, i.e., *Vicia fabae*, *Brassica napus*, *Solanum tuberosum*, *Hordeum vulgare*. For each
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



465