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1 **Discrepancy in laboratory and field attraction of apple fruit moth**
2 ***Argyresthia conjugella* to host plant volatiles**

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14 **Abstract** – Apple fruit moth *Argyresthia conjugella* is a specialist seed predator of rowan
15 *Sorbus aucuparia*. Large-scale synchronous fluctuation of seed production in rowan,
16 named masting, drives apple fruit moth to seek alternative host plants such as apple,
17 during years when rowan berries are not available for oviposition. The role of plant
18 volatile compounds in attraction of gravid apple fruit moth females has been studied in a
19 laboratory wind tunnel. Volatiles from rowan branches with green berries stimulate female
20 moths to fly upwind and to land at the odour source. In contrast, females are not
21 attracted to rowan branches without green berries, and they are not attracted to apple,
22 showing that the chemical stimulus from rowan berries is required for attraction.
23 Attraction to synthetic compounds identified from rowan, anethole and 2-phenyl ethanol,
24 confirms the role of plant volatiles in host finding. These two compounds show, however,
25 a discrepant behavioural effect in wind tunnel and field tests. Field traps baited with 2-
26 phenyl ethanol capture female moths, but anethole does not produce significant captures.
27 Wind tunnel tests produce opposite results: moths fly upwind towards the anethole lure,
28 while 2-phenyl ethanol is not attractive at all. Wind tunnel attraction to 2-phenyl ethanol
29 is achieved by adding odour from a rowan branch without berries, which is not attractive
30 on its own. This finding demonstrates that interaction with the background odour
31 contributes to the behavioural effect of plant volatile stimuli in the field.

32 **Key Words** – Host plant attraction, volatile organic compounds, background odour,
33 anethole, 2-phenyl ethanol, rowan

34 Introduction

35 The principal mode of insect-plant communication is chemical. Deciphering the volatile
36 signatures which guide insects to food sources and oviposition sites is a current urgent
37 research challenge (Pichersky & Gershenzon, 2002; Bruce *et al.*, 2005; Owen & Penuelas,
38 2005). These signals are sufficiently precise to let insects distinguish between host and
39 non-host plants, and to choose plants in a suitable phenological or physiological state.
40 Plant signals comprise substantial variation, on the other hand, since volatile emissions
41 change continuously through phenological development, and in response to environmental
42 and biotic challenges. And the message of any individual plant is blurred and diffused as it
43 blends into the background odour released from surrounding vegetation.

44 Apple fruit moth *Argyresthia conjugella* (Lepidoptera, Argyresthiidae) is particularly
45 suitable for studying the odour space that encodes recognition and attraction to different
46 plant hosts. Apple fruit moth is, despite its common name, a specialist seed predator of
47 rowan *Sorbus aucuparia*. Seed production in rowan shows large-scale yearly fluctuations,
48 named masting, a reproductive strategy in shrubs and trees to minimize seed loss
49 (Silvertown, 1980). Apple fruit moth females lay eggs on apple *Malus domestica* only
50 during rowan intermasting years, when rowan berries are not available. Apple is,
51 however, not suitable for larval development (Ahlberg, 1927; Kobro *et al.*, 2003).

52 Co-occurrence of volatile compounds in rowan and apple, which are both rosaceous
53 plants, may account for fatal attraction of *A. conjugella* females to apple for oviposition. A
54 blend of 2-phenyl ethanol and anethole has been identified as an attractant for apple fruit
55 moth, according to comparative chemical analysis and antennography of rowan and apple
56 headspace. Traps baited with 2-phenyl ethanol and anethole captured a large number of
57 females, but these field trapping tests do not answer the question whether the females
58 were attracted over a distance, or whether they merely arrived from branches in close
59 proximity to the traps (Bengtsson *et al.*, 2006).

60 Wind tunnel bioassays have played an important role in the identification of sex
61 pheromones, and are an essential tool also for the investigation of kairomones since they
62 enable direct observation of the upwind attraction response under controlled stimulus and
63 environmental conditions (Rojas, 1999; Pettersson *et al.*, 2001; Tasin *et al.*, 2006, 2007).
64 However, unlike with sex pheromones, attraction to plant compounds in the laboratory
65 does not always translate into attraction in the field and vice versa (Coracini *et al.* 2004;
66 Mumm & Hilker, 2005; Yang *et al.*, 2005). We here show the results of a first wind tunnel
67 study of apple fruit moth *A. conjugella* attraction to their preferred host plant rowan and
68 the substitute host apple. Attraction to single synthetic volatiles anethole and 2-phenyl
69 ethanol is reversed in the laboratory and in the field. Stimulus interaction with
70 background volatiles is proposed as an explanation for this discrepant behavioural effect.

71 **Materials and methods**

72 *Insects*

73 Rowan berries infested with last-instar larvae of apple fruit moth *A. conjugella* were
74 collected in several localities in Southern Norway. Apple fruit moth *A. conjugella* is a
75 specialized seed predator of rowan, undergoing obligatory diapause, and cannot be reared
76 in the laboratory. Diapausing pupae were overwintered outdoors. In spring, pupae were
77 kept at 4°C until they were transferred to Plexiglass cages for eclosion under a LD 18:6 h
78 photocycle, 20-24°C and 55-70% rH. Newly eclosed insects were collected daily, males
79 and females were kept in the same cages for mating. Insects were available for
80 experimentation during 10 weeks.

81 *Wind Tunnel Tests*

82 The wind tunnel (Witzgall *et al.*, 2001) has a flight section of 63 x 90 x 200 cm and
83 was lit diffusely from above and from one side at 6 lux. Wind speed was 30 cm/s, and the
84 temperature ranged from 19 to 22°C. Tests with plant material were done during
85 seasonal flight period of *A. conjugella*. Newly cut branches with and without clusters of
86 small green rowan berries and branches with green apples (cv. Aroma, Ø up to 5 cm) at
87 the developmental stage suitable for apple fruit moth oviposition, were enclosed in 2-l
88 glass jars. The apple cv. Aroma is most susceptible for attack by apple fruit moth
89 (Bengtsson *et al.*, 2006). Clean air from a tank passed over the plant material and left the
90 jar at 30 cm/s, through a glass tube (4 mm ID x 20 mm). The glass jar was hidden
91 behind a perforated metal grid (pore size 5 mm), and the outlet of the jar was fit into one
92 enlarged pore of this metal grid, 30 cm from the ground, in the centre of the wind tunnel.
93 The tip of the glass tube, protruding c. 2 cm into the tunnel, was covered by a glass
94 cylinder (12.5 x 10 cm), which was mounted to the perforated metal grid, and which was
95 covered with a metal mesh (2 x 2 mm mesh size). The rubber septa formulated with plant
96 compounds (see below) were suspended in the centre of this cylinder. The odour source
97 did thus not provide a visual cue for upwind orientation.

98 Synthetic plant compounds in hexane solution were formulated at 1 mg on red rubber
99 septa (VWR International, Stockholm, Sweden). Treatments included 2-phenyl ethanol,
100 anethole (93.8% and 96.2% chemical purity by GC, respectively; Shin-Etsu Chemical Co.,
101 Tokyo), and a 1:1-blend of both compounds. Synthetic pheromone (*Z*)-11-hexadecenyl
102 acetate (*Z*11-16Ac) (Jaastad *et al.*, 2002) was formulated on red rubber septa at 100 µg
103 (99.7% isomeric purity, Pherobank, Wageningen, The Netherlands). A rubber septum
104 impregnated with 100 µl hexane served as control treatment.

105 Wind tunnel tests were undertaken 3 to 6 h into the scotophase, which corresponds to
106 the peak female and male activity period (Jaastad *et al.*, 2005). Three- to four-day-old

107 male and female moths were put singly into labeled glass tubes (2.5 x 15 cm) stoppered
108 with gauze on both ends, 10 min before tests. Individual insects were introduced into the
109 tunnel by positioning the glass tube onto a holder, 180 cm downwind from the source and
110 30 cm from the ground. They were given 3 min to respond and the following types of
111 behaviour were recorded: take-off, flying upwind over 40 cm towards the source, and
112 source contact after 180 cm of upwind-oriented flight in the centre of the wind tunnel.
113 The time before take-off was also recorded. Insects were tested in batches of up to 25,
114 the last moth was tested at the earliest 72 min after the first. After the wind tunnel
115 session, all insects were sexed. Each odour source was tested with at least 40 females, on
116 3 to 6 different days, according to availability of insects eclosing from diapause. Six
117 sources were also tested with least 40 males. Two treatments, in random order, were
118 tested each day. Insects were used only once.

119 *Field trapping tests*

120 Synthetic 2-phenyl ethanol and anethole diluted in hexane were formulated on red
121 rubber septa (VWR International). Treatments were 2-phenyl ethanol, anethole, and a 1:1
122 blend of both compounds. Treatments were tested in two concentrations 100 µg and 10
123 mg, adding to 200 µg and 20 mg in the blend, respectively. Tetra traps were hung at c. 2
124 m on rowan branches in forests ($n = 10$). Traps within one block were c. 5 m apart, and
125 they were placed at random. All treatments were replicated once in each location
126 (randomized complete block). Distance between blocks was at least 50 m. Traps were
127 checked regularly during 2 weeks. The development of the flight period was followed
128 according to the day-degree model for apple fruit moth (Kobro, 1988).

129 *Statistical analysis*

130 The number of moths recorded for each behavioural step in the wind tunnel was
131 subjected to a 2x2 Fisher's exact test. The results are presented as percentages to
132 simplify comparison between treatments. In the field experiment, the number of female
133 moths captured was subjected to an analysis of deviance for poisson-distributed data.
134 Significance level of a post-hoc Tukey test was set to 0.05.

135 **Results**

136 *Wind tunnel tests*

137 In the wind tunnel, 38% of the test females flew upwind over 40 cm and 19% reached
138 the source outlet of air, which had passed through a glass jar containing a freshly cut
139 rowan branch with berries. The number of females landing was significantly different from
140 blank ($P = 0.0028$). Few females started to fly towards air passing over a rowan branch

141 without berries or an apple branch, the number of females responding was not different
142 from blank (Fig. 1).

143 Tests with synthetic compounds showed that anethole stimulated females to fly upwind
144 and 15% of the test females landed at the source (significantly different from blank; $P =$
145 0.0119). In contrast, 2-phenyl ethanol did not attract any females to the source (Fig. 1).

146 The combination of odour from a rowan branch without berries, and synthetic 2-phenyl
147 ethanol, released as a blend from the same glass jar, produced a synergistic effect on
148 female attraction and landing at source ($P = 0.0196$). In comparison, landings at a blend
149 of synthetic anethole plus rowan leaf odour ($P = 0.116$), or to a blend of anethole plus 2-
150 phenyl ethanol were not different from blank ($P = 0.2412$) (Fig. 1).

151 Wind tunnel sessions on one day comprised batches of up to 25 females, which were
152 tested within up to 120 min (3 min response time plus handling). There was no
153 correlation between mean take off time and time before the moths were introduced into
154 the tunnel ($r = 0.06$; $P = 0.12$).

155 Male moths were tested with six sources. Most males responded to the blend of
156 anethole and 2-phenyl ethanol, but the but the number of males landing was not different
157 from blank ($F = xz$, $P = 0.2429$). For comparison, 65% of males ($n = 52$) landed at a
158 source of sex pheromone containing 100 μg (*Z*)-11-hexadecenyl acetate.

159 *Field trapping tests*

160 Field traps in rowan trees, baited with 2-phenyl ethanol or a 1:1 blend of 2-phenyl
161 ethanol and anethole captured significantly more females than blank traps, which
162 remained empty. Trap capture with anethole was not significant (Fig. 1). The poisson
163 model showed highly significant variation between treatments ($F = 47.2$, $df = 5$, $P <$
164 0.001). Trap captures with 2-phenyl ethanol and anethole, at a 100-fold lower dose, were
165 not significantly different from blank traps (data not shown).

166 The comparison of field and laboratory attraction of apple fruit moth to synthetic
167 compounds 2-phenyl ethanol and anethole shows opposite results. As single compound,
168 2-phenyl ethanol was attractive in the field, while anethole was attractive in the wind
169 tunnel. The combination of 2-phenyl ethanol and odour from a rowan branch without
170 berries, both of which did not produce significant attraction by themselves, attracted a
171 significant number of females in the wind tunnel (Fig. 1).

172 **Discussion**173 *Rowan volatiles attract mated apple fruit moth females*

174 Attraction of apple fruit moth *A. conjugella* females to air passing over rowan branches
 175 with berries demonstrates the importance of odour cues for host finding in apple fruit
 176 moth. The number of females flying upwind over 180 cm to an odour source not providing
 177 visual cues for orientation, during a test period of only 3 min, is significant. A rate of 19%
 178 landings in response to odour from rowan branches with berries compares with the host
 179 plant attraction obtained with other lepidopteran species in wind tunnels (Landolt, 1989;
 180 Cossé *et al.*, 1994; Phelan *et al.*, 1991; Rojas, 1999; Olsson *et al.*, 2005; Tasin *et al.*,
 181 2005, 2006, 2007).

182 Lack of attraction to apple branches, on the other hand, correlates well with the
 183 observation that apple is only an ersatz host of apple fruit moth (Ahlberg, 1927; Kobro *et*
 184 *al.*, 2003). The wind tunnel test shows that females are not attracted to apple over a
 185 distance. Gravid females may become more responsive to apple volatiles with age, when
 186 deprived of suitable oviposition substrate during intermasting years (Mayhew, 1997).

187 *Background odour effects female attraction to rowan volatiles*

188 Attraction to synthetic rowan volatiles, 2-phenyl ethanol and anethole (Bengtsson *et*
 189 *al.*, 2006), further corroborates that plant volatiles mediate attraction of mated apple fruit
 190 moth females. Interestingly, tests with these two compounds show opposite results in the
 191 laboratory wind tunnel and in the field.

192 Traps baited with 2-phenyl ethanol placed in rowan branches captured apple fruit
 193 moths, while 2-phenyl ethanol did not elicit a behavioural response in the wind tunnel.
 194 Contrasting field and laboratory results are most likely due to interaction of the test
 195 stimulus with the background odour: a combination of 2-phenyl ethanol and volatiles
 196 emanating from a rowan branch had a clear synergistic effect in charcoal-filtered wind
 197 tunnel air. On the other hand, lack of field attraction to anethole indicates that more
 198 active or more abundant rowan volatiles mask or interfere with anethole. This is
 199 corroborated by wind tunnel tests, showing that rowan volatiles did not enhance
 200 attraction to anethole.

201 Background odour has been shown to affect attraction of several other insects to plant
 202 volatiles, although the difference is not as striking as shown here with apple fruit moth.
 203 Pear ester is used to monitor codling moth *Cydia pomonella* populations in orchards, but
 204 does not attract codling moths in the wind tunnel (Light *et al.*, 2001; Knight & Light,
 205 2005a,b; Yang *et al.*, 2005). Likewise, (*E*)- β -farnesene attracts codling moth males in
 206 apple orchards, but not in charcoal-filtered wind tunnel air. The main volatile compound of
 207 apple headspace, (*E,E*)- α -farnesene, has a synergist effect on attraction to (*E*)- β -

208 farnesene in the wind tunnel, but not in the field (Coracini *et al.*, 2004). An olfactometer
209 bioassay of the parasitoid *Chrysonotomyia ruforum* in response to Scots pine with host
210 eggs of the sawfly *Diprion pini* provides another example (Mumm & Hilker, 2005): (*E*)- β -
211 farnesene was attractive only when embedded in pine odour.

212 Discrepancies in insect behaviour in the field and laboratory may result from visual and
213 olfactory stimulus interaction (Schoonhoven *et al.*, 2005). Visual cues, however, cannot
214 explain the mismatch of apple fruit moth laboratory and field attraction to anethole and 2-
215 phenyl ethanol. Furthermore, the amount of compound used in field and laboratory
216 cannot account for these differences. Field tests with different amounts on rubber septa
217 show that 10 mg of 2-phenyl ethanol on rubber septa is suitable for field attraction. A
218 tenfold lower dose was used in the wind tunnel, which produces attraction similar to a
219 rowan branch.

220 A contrasting behavioural effect of single plant volatiles in the laboratory and field re-
221 emphasizes that it is crucial to study plant-insect communication in ecologically realistic
222 settings. Plant volatiles are, for one, not perceived as single compounds, since plants
223 release hundreds of compounds. The use of point sources in wind tunnel and field
224 trapping tests may produce another artefact. It is conceivable that rowan trees produce
225 large and diffuse odour clouds of varying composition: leaves and fruit clusters release
226 different volatile blends (Bengtsson *et al.*, 2006), and these plumes would, through
227 turbulences created by leaves and branches, intermingle and fuse with plumes from
228 adjacent plant organs and from surrounding plants. The temporal structure of sex
229 pheromone plumes is a principal factor for male moth upwind orientation to pheromone-
230 releasing females. Males respond to fluctuating and intermittent plumes, while
231 continuous, uniform pheromone clouds are not sufficient to elicit orientation flights
232 (Kennedy *et al.*, 1981; Baker *et al.*, 1985; Murlis *et al.*, 1992).

233 *Towards the identification of apple fruit moth kairomone*

234 Anethole, which is a major component of anise and fennel aroma, has been reported
235 from only four plant genera, including apple (Knudsen *et al.*, 1993, 2006; Bengtsson *et*
236 *al.*, 2001). It has been shown to attract scarabid beetles (Tóth *et al.*, 2004) and bibionid
237 flies (Cherry, 1998). In comparison, 2-phenyl ethanol is widespread throughout the plant
238 kingdom. It occurs in 34 of 174 genera listed by Knudsen *et al.* (1993, 2006), and is
239 frequently found in insect-pollinated plants (Andersson *et al.*, 2002). Accordingly, 2-
240 phenyl ethanol is known to attract a wide range of species from different taxa, including
241 Lepidoptera (Haynes *et al.*, 1991; Honda *et al.*, 1998; Imai *et al.*, 1998; Zilkowski *et al.*,
242 1999).

243 A synergistic effect of 2-phenyl ethanol and rowan leaf volatiles demonstrates that
244 rowan headspace contains yet unidentified behaviourally active compounds. The role of

245 anethole as host signal for apple fruit moth is still unclear, since it does not show a
246 synergistic interaction with leaf volatiles or 2-phenyl ethanol.

247 Females become attracted to rowan branches with fruit clusters both in the laboratory
248 and in natural habitats, suggesting that a more complete signal facilitates perception
249 against a noisy background. Such a more complete kairomone blend is expected to
250 produce an even stronger behavioural effect in an apple orchard, where the females
251 migrate in search of oviposition sites during rowan intermasting years. The identification
252 of further attractant volatiles and the behavioural mechanisms of host orientation in apple
253 fruit moth is subject of an ongoing study.

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259 References

- 260 Ahlberg, O. (1927) Rönnbärsmalen, *Argyresthia conjugella* Zell. En redogörelse för
261 undersökningar åren 1921-1926 (in Swedish with English summary). – Meddel. Nr.
262 324 från Centralanstalten för försöksväsendet på jordbruksområdet,
263 Lantbruksentomologiska avdelningen, Stockholm.
- 264 Andersson, S., Nilsson, L.A., Groth, I. & Bergström, G. (2002) Floral scents in butterfly-
265 pollinated plants: possible convergence in chemical composition. *Botanical Journal of*
266 *the Linnean Society*, **140**, 129-153.
- 267 Baker, T.C., Willis, M.A., Haynes, K.F. & Phelan, P.L. (1985) A pulsed cloud of sex
268 pheromone elicits upwind flight in male moths. *Physiological Entomology*, **10**, 257-
269 265.
- 270 Bengtsson, M., Bäckman, A.-C., Liblikas, I., Ramirez, M.I., Borg-Karlson, A.-K., Ansebo,
271 L., Anderson, P., Löfqvist, J. & Witzgall, P. (2001) Plant odor analysis of apple:
272 antennal response of codling moth females to apple volatiles during phenological
273 development. *Journal of Agricultural and Food Chemistry*, **49**, 3736-3741.
- 274 Bengtsson, M., Jaastad, G., Knudsen, G., Kobro, S., Bäckman, A.-C., Pettersson, E. &
275 Witzgall, P. (2006) Plant volatiles mediate attraction to host and non-host plant in
276 apple fruit moth, *Argyresthia conjugella*. *Entomologia Experimentalis et Applicata*,
277 **118**, 77–85.
- 278 Bruce, T.J.A., Wadhams, L.J. & Woodcock, C.M. (2005) Insect host location: a volatile
279 situation. *Trends in Plant Science*, **10**, 269-274.
- 280 Cherry, R. (1998) Attraction of the lovebug, *Plecia nearctica* (Diptera: Bibionidae) to
281 anethole. *Florida Entomologist*, **81**, 559-562.
- 282 Coracini, M., Bengtsson, M., Liblikas, I. & Witzgall, P. (2004) Attraction of codling moth
283 males to apple volatiles. *Entomologia Experimentalis et Applicata*, **110**, 1-10.

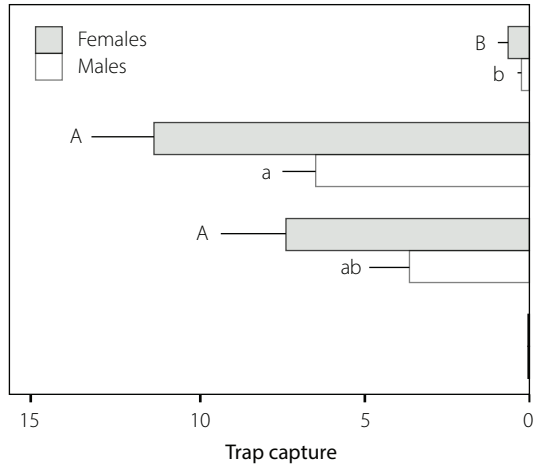
- 284 Cossé, A.A., Endris, J.J., Millar, J.G. & Baker, T.C. (1994) Identification of volatile
285 compounds from fungus-infected date fruit that stimulate upwind flight in female
286 *Ectomyelois ceratoniae*. *Entomologia Experimentalis et Applicata*, **72**, 233-238.
- 287 Haynes, K.F., Zhao, J.Z. & Latif, A. (1991) Identification of floral compounds from *Abelia*
288 *grandiflora* that stimulate upwind flight in cabbage looper moths. *Journal of*
289 *Chemical Ecology*, **17**, 637-646.
- 290 Honda, K., Omura, H. & Hayashi, N. (1998) Identification of floral volatiles from
291 *Ligustrum japonicum* that stimulate flower-visiting by cabbage butterfly, *Pieris*
292 *rapae*. *Journal of Chemical Ecology*, **24**, 2167-2180.
- 293 Imai, T., Maekawa, M., Tsuchiya, S. & Fujimori, T. (1998) Field attraction of *Hoplia*
294 *communis* to 2-phenylethanol, a major volatile component from host flowers, *Rosa*
295 spp. *Journal of Chemical Ecology*, **24**, 1491-1497.
- 296 Jaastad, G., Anderson, P., Bengtsson, M., Kobro, S., Knudsen, G. & Witzgall, P. (2002)
297 Sex pheromone of apple fruit moth *Argyresthia conjugella* (Lepidoptera,
298 *Argyresthiidae*). *Agricultural and Forest Entomology*, **4**, 1-4.
- 299 Jaastad, G., Knudsen, G., Kobro, S. & Witzgall, P. (2005) When does the apple fruit moth
300 *Argyresthia conjugella* fly and oviposit? *Entomologia Experimentalis et Applicata*,
301 **115**, 351-353.
- 302 Kennedy, J.S., Ludlow, A.R. & Sanders, C.J. (1981) Guidance of flying male moths by
303 wind-borne sex pheromone. *Physiological Entomology*, **6**, 395-412.
- 304 Knight, A.L. & Light, D.M. (2005a) Dose-response of codling moth (Lepidoptera:
305 Tortricidae) to ethyl (*E,Z*)-2,4-decadienoate in apple orchards treated with sex
306 pheromone dispensers. *Environmental Entomology*, **34**, 604-609.
- 307 Knight, A.L. & Light, D.M. (2005b) Factors affecting the differential capture of male and
308 female codling moth (Lepidoptera: Tortricidae) in traps baited with ethyl (*E,Z*)-2,4-
309 decadienoate. *Environmental Entomology*, **34**, 1161-1169.
- 310 Knudsen, J.T., Tollsten, L. & Bergström, G.L. (1993) Floral scents - a checklist of volatile
311 compounds isolated by head-space techniques. *Phytochemistry*, **33**, 253-280.
- 312 Knudsen, J.T., Eriksson, R., Gershenzon, J. & Ståhl, B. (2006) Diversity and distribution of
313 floral scent. *Botanical Review*, **72**, 1-120.
- 314 Kobro, S. (1988) Temperaturavhengighet hos rognebærmøll. (In norwegian)
315 *Væstskyddsrapporter, Jordbruk*, **53**, 115-121.
- 316 Kobro, S., Søreide, L., Djønn, E., Rafoss, T., Jaastad, G. & Witzgall, P. (2003) Masting of
317 rowan *Sorbus aucuparia* L. and consequences for the apple fruit moth, *Argyresthia*
318 *conjugella* Zeller. *Population Ecology*, **45**, 25-30.
- 319 Landolt, P.J. (1989) Attraction of the cabbage looper to host plants and host plant odor in
320 the laboratory. *Entomologia Experimentalis et Applicata*, **53**, 117-124.
- 321 Light, D.M., Knight, A.L., Henrick, C.A., Rajapaska, D., Lingren, B., Dickens, J.C.,
322 Reynolds, K.M., Buttery, R.G., Merrill, G., Roitman, J. & Campbell, B.C. (2001) A
323 pear-derived kairomone with pheromonal potency that attracts male and female
324 codling moth, *Cydia pomonella* (L.). *Naturwissenschaften*, **88**, 333-338.
- 325 Mayhew, P.J. (1997) Adaptive patterns of host-plant selection by phytophagous insects.
326 *Oikos*, **79**, 417-428.
- 327 Mumm, R. & Hilker, M. (2005) The significance of background odour for an egg parasitoid
328 to detect plants with host eggs. *Chemical Senses*, **30**, 337-343.

- 329 Murlis, J., Elkington, J.S. & Cardé, R.T. (1992) Odor plumes and how insects use them.
330 *Annual Review of Entomology* **37**, 505-532.
- 331 Olsson, P.-O.C., Anderbrant, O. & Löfstedt, C. (2005) Flight and oviposition behaviour of
332 *Ephestia cautella* and *Plodia interpunctella* in response to odours of different
333 chocolate products. *Journal of Insect Behavior*, **18**, 363–380.
- 334 Owen, S.M. & Penuelas, J. (2005) Opportunistic emissions of volatile isoprenoids. *Trends*
335 *in Plant Science*, **10**, 420-426
- 336 Pettersson, E.M., Birgersson, G. & Witzgall, P. (2001) Synthetic attractants for the bark
337 beetle parasitoid *Coeloides bostrichorum* Giraud (Hymenoptera: Braconidae)
338 *Naturwissenschaften*, **88**, 88-91.
- 339 Phelan, P.L., Roelofs, C.J., Youngman, R.R. & Baker, T.C. (1991) Characterization of
340 chemicals mediating ovipositional host-plant finding by *Amyelois transitella* females.
341 *Journal of Chemical Ecology*, **17**, 599-613.
- 342 Pichersky, E. & Gershenzon, J. (2002) The formation and function of plant volatiles:
343 perfumes for pollinator attraction and defense. *Current Opinion in Plant Biology*, **5**,
344 237–243
- 345 Rojas, J.C. (1999) Electrophysiological and behavioural responses of the cabbage moth to
346 plant volatiles. *Journal of Chemical Ecology*, **25**, 1867-1883.
- 347 Schoonhoven, L.M., van Loon, J.J.A. & Dicke, M. (2005) *Insect-Plant Biology*. Oxford
348 University Press, Oxford.
- 349 Silvertown, J. W. (1980) The evolutionary ecology of mast seeding in trees. *Biological*
350 *Journal of the Linnean Society*, **14**, 235-250.
- 351 Tasin, M., Anfora, G., Ioriatti, C., Carlin, S., de Cristofaro, A., Schmidt, S., Bengtsson, M.,
352 Versini, G. & Witzgall, P. (2005) Antennal and behavioral responses of grapevine
353 moth *Lobesia botrana* females to volatiles from grapevine. *Journal of Chemical*
354 *Ecology*, **31**, 77-87
- 355 Tasin, M., Bäckman, A.-C., Bengtsson, M., Varela, N., Ioriatti, C. & Witzgall, P. (2006)
356 Wind tunnel attraction of grapevine moth females, *Lobesia botrana*, to natural and
357 artificial grape odour. *Chemoecology*, **16**, 87–92.
- 358 Tasin, M., Bäckman, A.-C., Coracini, M., Casado, D. & Witzgall, P. (2007) Synergism and
359 redundancy in a plant volatile blend attracting gravid grapevine moth females.
360 *Phytochemistry*, **68**, 203-209.
- 361 Tóth, M., Schmera, D. & Imrei, Z. (2004) Optimization of a chemical attractant for
362 *Epicometis (Tropinota) hirta* Poda. *Zeitschrift für Naturforschung*, **59**, 228-292.
- 363 Witzgall, P., Bengtsson, M., Rauscher, S., Liblikas, I., Bäckman, A.-C., Coracini, M.,
364 Anderson, P. & Löfqvist, J. (2001) Identification of further sex pheromone synergists
365 in the codling moth, *Cydia pomonella*. *Entomologia Experimentalis et Applicata*,
366 **101**, 131-141.
- 367 Yang, Z., Casado, D., Ioriatti, C., Bengtsson, M. & Witzgall, P. (2005) Pheromone pre-
368 exposure and mating modulate codling moth (Lepidoptera: Tortricidae) response to
369 host plant volatiles. *Agricultural and Forest Entomology*, **7**, 1-6.
- 370 Zilkowski, B.W., Bartelt, R.J., Blumberg, D., James, D.G. & Weaver, D.K. (1999)
371 Identification of host-related volatiles attractive to pineapple beetle *Carpophilus*
372 *humeralis*. *Journal of Chemical Ecology*, **25**, 229-252.
- 373

373 **Legend**

374 **Fig. 1.** Field and wind tunnel attraction of apple fruit moth *Argyresthia conjugella* to
375 synthetic rowan volatiles anethole and 2-phenyl ethanol, and natural volatiles from rowan
376 and apple twigs. Anethole and 2-phenyl ethanol were formulated on rubber septa, at 1
377 mg for wind tunnel, and at 10 mg for field tests. Field: Mean captures of female and male
378 moths in traps hung to rowan branches ($n = 10$). Treatments with different letters are
379 significantly different (Tukey test; $P < 0.05$). Wind tunnel: A rowan branch (*Sorbus*
380 *aucuparia*) with or without berries, a branch with green apples (*Malus domestica* cv.
381 *Aroma*), and rubber septa containing 1 mg of synthetic compound, were held in a 2-l
382 glass jar. An airstream passed through the glass jar and through a glass tube outlet into
383 the wind tunnel. Individual moths ($n = 40$ to 80) were scored for upwind orientation flight
384 over 40 cm and source contact, after 180 cm upwind flight. Numbers in bars show the
385 ratio between source contacts and upwind orientation flights over at least 40 cm. Three
386 treatments were tested with females only. For each bioassay, asterisks show significant
387 differences between each treatment and control (Fisher's exact test; * $P < 0.05$; ** $P <$
388 0.01).

Field trapping



Wind tunnel attraction

