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► To cite this version:

Arnaud Ameline, E. Kerdellant, A. Rombaut, Quentin Chesnais, F. Dubois, et al.. Status of the bioenergy crop miscanthus as a potential reservoir for aphid pests. *Industrial Crops and Products*, 2015, 74, pp.103-110. 10.1016/j.indcrop.2015.04.055 . hal-02631753

HAL Id: hal-02631753

<https://hal.inrae.fr/hal-02631753>

Submitted on 26 Oct 2023

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Status of the bioenergy crop miscanthus as a potential reservoir for aphid pests.

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16

17 **Abstract**

18

19 *Miscanthus* spp. (Poaceae) are large perennial C4-grasses that are receiving considerable
20 attention as bioenergy crops. Therefore, the introduction of miscanthus crops in Europe needs
21 continuous monitoring and risk assessment because they may serve as a refuge or a reservoir
22 for aphid pests and/or pathogens of conventional crops. Here we first report the results of two
23 field surveys conducted in northern France on the species composition of alate aphids flying
24 above *Miscanthus x giganteus* crops. Then, in a first laboratory experiment, we investigated
25 the colonization process on *M. x giganteus* of the four major aphid pests (Hemiptera:
26 *Aphididae*) trapped in the field study. Results showed that the performances of these species
27 in terms of feeding, survival and reproduction, on *M. x giganteus*, depended on their degree of
28 specialization towards Poaceae. The suitability of this plant was moderate for the Poaceae
29 specialist aphid *Rhopalosiphum padi* (L.), low for the polyphagous aphid species, *Aphis fabae*
30 (Scop) and *Myzus persicae* (Sulzer) and very low for the Brassicaceae specialist aphid
31 *Brevicoryne brassicae* (L.). Nevertheless, *M. x giganteus* cannot be considered as a reservoir
32 crop for these common aphid pests as their progenies did not reach the adult stage. In a
33 second laboratory experiment, the ability of the Poaceae specialist aphid *R. padi* to colonize
34 *M. x giganteus* and its putative parents, *M. sinensis* and *M. sacchariflorus* was assessed.
35 Results showed that *R. padi* was able to achieve its life cycle on *M. sacchariflorus* but not on
36 *M. sinensis*. The consequences of the introduction of miscanthus in the north of France are
37 discussed in terms of phytoviruses spreading and in terms of potential reservoir for aphid
38 pests from conventional neighboring crops.

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43 **Keywords:** *Miscanthus x giganteus*, Field survey, Host plant suitability, Aphididae, EPG,
44 Demographic parameters, Phytoviruses, Plant resistance

45

46 **1. Introduction**

47

48 The use of perennial herbaceous energy crops dedicated to the production of biofuels in order
49 to substitute fossil fuels is one way to reduce CO₂ emissions (Smith et al., 2000). In this
50 context, the countries of the European Union are committed to producing an increasing
51 proportion of their energy needs from renewable resources (Ericsson et al., 2009; Ferreira et
52 al., 2009; Lewandowski et al., 2006; Perry and Rosillo-Calle, 2008). Among all potential
53 plants, *Miscanthus x giganteus*, the sterile hybrid between *Miscanthus sinensis* and
54 *Miscanthus sacchariflorus*, has been extensively trialed as a biofuel in Europe since the early
55 1980s. Indeed, this promising candidate as a bioenergy crop is characterized by high biomass
56 yields, even in cool northern European conditions (Beale and Long, 1995), a C₄
57 photosynthetic pathway, a high tolerance to abiotic stresses, a perennial growth and a
58 sustainable production (Heaton et al., 2004). Therefore, as planting miscanthus for energy
59 production develops in Europe, an increased pathogen and pest pressure is likely to occur, and
60 the risk of severe damage must be carefully examined by continuous monitoring and risk
61 assessments. Miscanthus fields may indeed serve as a refuge or a reservoir for pests and/or
62 diseases of conventional crops (Jørgensen, 2011). For example, it has been shown that
63 *M. x giganteus* could be a suitable host for major maize pests such as the western corn
64 rootworm *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) and the fall armyworm

65 *Spodoptera frugiperda* (Lepidoptera: Noctuidae) (Gloyna et al., 2011; Prasifka et al., 2009;
66 Spencer and Raghu, 2009).

67 Among the agricultural pests, aphids are considered as the most serious ones, mainly because
68 of the indirect damage they cause through the spread of phytoviruses. Most of these
69 phytovirus vector species belong to the Aphidinae subfamily (Hemiptera: Aphididae), which
70 includes the genus *Aphis*, *Myzus* and *Macrosiphum* (Eastop, 1983). Phytoviruses are divided
71 into two main categories depending on their transmission mode. Non-persistent viruses are
72 spread by transient or non-colonizing alate aphids that make brief intracellular probes
73 (“potential drops”) when moving from plant to plant, whereas persistent viruses are
74 transmitted by colonizing aphids species and imply sustained feeding in the phloem (Hooks
75 and Fereres, 2006).

76 Some studies have shown that miscanthus may act as a perennial reservoir of phytoviruses
77 such as the barley yellow dwarf virus (BYDV) which can be transmitted in a persistent
78 manner by *Rhopalosiphum maidis* (Christian et al., 1994; Huggett et al., 1999), the
79 switchgrass mosaic virus (Agindotan et al., 2013) and the sorghum mosaic virus (Grisham et
80 al., 2012).

81 During a field sampling study in *M. x giganteus* crops in the UK, Semere and Slater (2007)
82 showed that Homoptera samples were dominated by Aphididae. However, in this broad scale
83 biodiversity study, identification was not carried out up to the species level. In an extensive
84 field survey set up in four different USA states, Bradshaw et al. (2010) recorded large
85 populations of the yellow sugarcane aphid, *Sipha flava* which is only present in America
86 (Blackman and Eastop, 2000) and the corn leaf aphid, *Rhopalosiphum maidis* which is
87 virtually cosmopolitan but absent in regions with severe winter conditions such as northern
88 Europe (Blackman and Eastop, 2000). The potential for the large-scale production of
89 miscanthus has also led to its evaluation as a host through laboratory experiments for *S. flava*

90 (Pallipparambil et al., 2014) and for *R. maidis* (Huggett et al., 1999). For instance, Coulette et
91 al. (2013) demonstrated that vitroplants of *Miscanthus sacchariflorus* were not suitable hosts
92 for the black bean aphid *Aphis fabae*, the green peach aphid *Myzus persicae*, and the bird
93 cherry aphid *Rhopalosiphum padi*. More recently, Pointeau et al. (2014) showed that
94 *Miscanthus sacchariflorus* and, to a lesser extent, *M. sinensis* were less suitable and
95 acceptable host plants for *R. maidis* than *M. x giganteus*.

96 In France, the first miscanthus crops were planted in 2006 and the surface area was essentially
97 localized in the northern part of the country. The introduction of such crops in an agricultural
98 landscape dominated by plants belonging to the Poaceae taxa (barley, wheat, maize) may
99 create new refuges or reservoirs not only for monocot specialist aphids but also for
100 polyphagous aphids associated with other main crops such as rapeseed, potato, legumes
101 (typically beans and peas), sugar beet, turnip, carrots and lettuce.

102 In the present study conducted in northern France, we first carried out a field survey of alate
103 aphids flying above *M. x giganteus* crops. We then made the following assumptions: (1) the
104 ability of the most abundant aphid pests trapped in the field to successfully feed and
105 reproduce on *M. x giganteus* would depend on their degree of specialization towards Poaceae
106 and (2) within the *Miscanthus* genus, there are different levels of resistance which can
107 modulate the performances of Poaceae aphid specialists. We tested these hypotheses through
108 laboratory bioassays. In a first one, we investigated the colonization process on
109 *M. x giganteus* of four major aphid pests (Hemiptera: *Aphididae*) trapped in the field study:
110 the two polyphagous species *Aphis fabae* (black bean aphid) and *Myzus persicae* (green peach
111 aphid), the Brassicaceae specialist *Brevicoryne brassicae* (cabbage aphid) and the Poaceae
112 specialist *Rhopalosiphum padi* (bird cherry aphid). In a second laboratory bioassay, we
113 investigated the colonization process of *R. padi* (i.e. the aphid species that performed the best

114 in the first laboratory experiment) on the three *Miscanthus* species studied in Europe for
115 biomass production, i.e., *M. x giganteus*, *M. sinensis* and *M. sacchariflorus*.

116

117

118 2. Materials and methods

119 2.1. Field studies

120 The experiments were conducted in *M. x giganteus* fields located on three different sites in
121 Picardy, northern France: two fields of 25 ha in Bougainville (49°51'18"N, 2°01'29"E and
122 49°51'21"N, 2°01'44"E) and one of 8 ha in Dreuil-les-Molliens (49°54'03"N, 2°02'23"E).
123 Fields in Bougainville were planted with *M. x giganteus* in 2008 and the one in Dreuil-les-
124 Molliens was planted in 2007. The aphid survey was conducted a first time in 2011 from May
125 2nd to July 29th and a second time in 2014 from May 7th to July 2nd. The field study started
126 immediately after crop harvesting and when it was stopped ca. two months later, the plants
127 had grown ca. 150 cm high. In each site, a yellow water trap used to catch different species of
128 alate aphids was placed on a pole just above the plant canopy and 50 meters away from the
129 border (Marame et al., 2010). Traps were checked every week and the insects caught were
130 kept in small plastic containers with 70 % ethanol until identification under a
131 stereomicroscope (Leica M165C).

132 All aphids trapped were identified at species level and only those considered as the main pests
133 in Picardy (FREDON PICARDIE Pest Monitoring Network) were taken into account for this
134 study. Eleven species were thus numbered: the green peach aphid *Myzus persicae* (Sulzer),
135 the black bean aphid *Aphis fabae* Scopoli, the cabbage aphid *Brevicoryne brassicae* (L.), the
136 willow-carrot aphid *Cavariella aegopodii* Scopoli, the pea aphid *Acyrtosiphon pisum*
137 (Harris), the birdcherry-oat aphid *Rhopalosiphum padi* (L.), the blackcurrant-sowthistle aphid
138 *Hyperomyzus lactucae* (L.), the grain aphid *Sitobion avenae* (F.), the potato aphid
139 *Macrosiphum euphorbiae* (Thomas), the lettuce aphid *Nasonovia ribisnigri* (Mosley) and the
140 willow-carrot aphid *Cavariella theobaldi* (Gillette & Bragg).

141

142 2.2. Insects and Plants for laboratory experiments

143 The *M. persicae* colony was established from one female collected in 1999 in a potato field
144 near Loos-en-Gohelle (France) and was reared on turnip plants (*Brassica rapa* cv. “purple top
145 white globe”). Both the colonies of *R. padi* and *B. brassicae* were provided in 2008 by INRA-
146 Le Rheu (Rennes, France) and they were reared on barley (*Hordeum vulgare* cv. “Cervoise”) and rapeseed (*Brassica napus* cv. “Stego”) respectively. The colony of *A. fabae*, provided in
147 2012 by Gembloux Agro-Bio-Tech (Belgium) was reared on broad beans (*Vicia faba* cv.
148 “Maya”).

150 For each aphid species, colonies were initiated from a single apterous parthenogenetic female
151 and maintained on their respective host plant in a ventilated Plexiglas[®] cage in different
152 growth chambers under $20 \pm 1^\circ\text{C}$, $60 \pm 5\%$ R.H., and 16:8 (L:D) photoperiod to induce
153 parthenogenesis.

154 Plantlets of the three *Miscanthus* species, i.e., *M. x giganteus* (cv. “GigB”, $2n = 3x = 57$),
155 *M. sacchariflorus* (cv. “Sac”, $2n = 2x = 38$) and *M. sinensis* (cv. “Goliath”, $2n = 4x = 76$)
156 (Zub et al., 2012) were obtained by *in vitro* multiplication as described by Rambaud et al.
157 (2013). Single rooted shoots coming from clusters, rooting in perlite, were potted in plastic
158 pots (firstly 9 x 9 x 10 cm, then 16 x 13 cm and 20 x 15 cm) containing potting soil in a
159 growth chamber under $20 \pm 2^\circ\text{C}$, $60 \pm 5\%$ R.H, and a 16:8 (L:D) photoperiod. Plants used in
160 the experiment were 8 to 12 weeks old (after potting) and 60 to 80 cm high.

161

162 2.3. Feeding behavior studies

163 The Electrical Penetration Graph DC-system described by Tjallingii (1978, 1988) was used to
164 investigate the feeding behaviour of alate aphids on *Miscanthus* spp. In a first bioassay, the
165 feeding behaviour of *M. persicae*, *R. padi*, *B. brassicae* and *A. fabae* was investigated on

166 *M. x giganteus* and in a second bioassay, the feeding behaviour of *R. padi* was investigated on
167 the three *Miscanthus* species.

168 To insert one aphid and one plant into an electrical circuit, a thin gold wire (20 µm diameter
169 and 2 cm long) was stuck on the insect's dorsum by conductive silver glue (EPG systems,
170 Wageningen, The Netherlands). Eight aphids were then connected to the Giga-8 DC-EPG
171 amplifier and each one was placed on a plantlet leaf of a different plant. A second electrode
172 was inserted into the soil of each of the potted plants to complete the electrical circuits. The
173 recordings were performed continuously for 8 hours during the day. Alate aphids in their
174 dispersal phase were collected on the inner wall of the rearing cages. Owing to their variable
175 propensity to fly or probe they were standardised in a Plexiglas[®] chamber (305 mm high,
176 152 mm diameter) as described by Brunissen et al. (2009). The whole aphid-plant system was
177 placed inside a Faraday cage at 20 ± 1°C. Acquisition and analysis of the EPG waveforms
178 were carried out with PROBE 3.5 software (EPG Systems, www.epgsystems.eu). Parameters
179 from the recorded EPG waveforms were calculated with EPG-Calc 6.1 software
180 (Giordanengo, 2014). These parameters were based on different EPG waveforms described by
181 Tjallingii and Hogen Esch (1993) corresponding to: (C) stylet pathways in plant tissues
182 except phloem and xylem; (pd) potential drops (intracellular stylet punctures); (E1) salivation
183 in phloem elements; (E2) passive phloem sap ingestion; (E1+E2) activity within phloem
184 vessels, (G) active xylem sap ingestion; and (F) derailed stylet mechanics. For the study
185 related to the feeding behavior of the four aphid species on *M. x giganteus*, 20 to 24
186 individuals were tested and for the study relating to the feeding behavior of *R. padi* on the
187 three *Miscanthus* species, 19 to 23 individuals were tested.

188

189 **2.4. Survival and reproductive traits bioassays**

190 In a first bioassay, the performances of *M. persicae*, *R. padi*, *B. brassicae* and *A. fabae* were
191 investigated on *M. x giganteus* and in a second bioassay the performances of *R. padi* were
192 investigated on the three *Miscanthus* species.

193 Pools of synchronized first instar nymphs (less than 24-hour old) of each aphid species were
194 obtained from parthenogenetic adult females placed on leaves of their host plant set in 1.5 %
195 agar in Petri dishes (90 mm diameter). To obtain synchronized young adults, first instar
196 nymphs were further kept in the same device for six to eight days, depending on the aphid
197 species.

198 For the nymph survival study, groups of five first instar nymphs were transferred onto the
199 plantlets to be tested. These groups of aphid nymphs were enclosed in clip cages on leaves at
200 mid-height of each plantlet and their survival was recorded every two days. For each of the
201 two bioassays, six to ten replicates were performed.

202 For the adult performance study, young adults were individually transferred onto the plantlets
203 to be tested. Survival and fecundity were assessed every day until the female died. For each of
204 the two bioassays, 25 to 40 replicates were performed.

205

206 **2.5. Statistical analysis**

207 Because the homoscedasticity of all distributions was not confirmed, non-parametric tests
208 were used. EPG parameters and demographic parameters were compared between aphid
209 species for the first bioassay and between plants for the second bioassay by using a Kruskal-
210 Wallis one-way analysis of variance (H value). Post-hoc multiple comparisons were carried
211 out with the non-parametric pairwise Mann-Whitney U test. The false discovery rate (FDR)

212 approach (Benjamini and Hochberg, 2009) was used to control the family-wise error rate. All
213 statistics were performed using R (R Development Core Team 2014).

214

215 **3. Results**

216 **3.1. Field study**

217

218 A total of 2436 alate aphids belonging to 50 different species were trapped in 2011 and 2014.
219 The 11 focal species represented 65 % of the identified individuals in the 2011 campaign and
220 80 % of the identified individuals in the 2014 campaign (Table 1). The two most abundant
221 species were the two polyphagous species *M. persicae* and *A. fabae* (54 % of the captures).
222 Conversely, the polyphagous species *M. euphorbiae* was hardly ever captured. *B. brassicae*
223 which feeds on a wide range of Brassicaceae plants was abundantly captured in 2011. The
224 Asteraceae specialists (*Hyperomyzus lactucae* and *Nasonovia ribisnigri*) represented less than
225 3 % of the captures. Finally, the Fabaceae specialist *Acyrtosiphum pisum*, the Apiaceae
226 specialist (*Cavariella* sp.), the Poaceae specialists (*Rhopalosiphum padi* and *Sitobion avenae*),
227 represented respectively less than 2 % of the captures.

228 These field results led us to evaluate through laboratory bioassay, the ability of miscanthus
229 colonization by the three main trapped aphid species (*Myzus persicae*, *Aphis fabae*,
230 *Brevicoryne brassicae*). Even if *R. padi* was not frequently trapped during these two field
231 surveys, it is probably the most important cereal pest and can be hosted by a large number
232 species belonging to more than 30 genera of Poaceae including maize, sorghum, barley
233 (Blackman and Eastop, 2000). Therefore, it was also chosen for subsequent laboratory
234 bioassays.

235

236 **3.2. Bioassay 1: feeding behavior and performance of the four aphid species on**

237 *M. x giganteus*

238 **3.2.1 Electrical penetration graph studies**

239 There was a significant effect of the aphid species for the following parameters (Table 2):
240 number of probes ($H = 16.06$; $P < 0.01$), total duration of probing ($H = 30.4$; $P < 0.001$),
241 number and total duration of pathway phases ($H = 15.92$; $P < 0.01$ & $H = 19.11$; $P < 0.001$),
242 number of potential drops ($H = 21.26$; $P < 0.001$), time of phloem phase ($H = 13.23$;
243 $P < 0.01$), total duration of phloem phase ($H = 20.41$; $P < 0.001$), total duration of xylem
244 ingestion ($H = 15.52$; $P < 0.05$).

245 The number of probes was significantly lower for *R. padi* compared to *A. fabae* and
246 *M. persicae* (Mann-Whitney *U* test, $P < 0.05$) but not compared to *B. brassicae*. The stylet
247 activities within plant tissues (over the 8-hour recording) ranged from 42 % for *B. brassicae*
248 to 74 % for *R. padi*. The Poaceae specialist *R. padi* exhibited the longest duration of probing
249 and *B. brassicae*, the shortest one, whereas the two polyphagous species exhibited
250 intermediate durations of total probing.

251 The number of pathway phases was significantly higher for *M. persicae* (Mann-Whitney *U*
252 test, $P < 0.05$). The total duration of this phase was significantly longer for the cereal aphid
253 *R. padi* than for *B. brassicae* and *M. persicae* (Mann-Whitney *U* test, $P < 0.05$). *R. padi*,
254 performed twice as many potential drops as *B. brassicae* (Mann-Whitney *U* test, $P < 0.05$)
255 and the other two aphid species presented intermediate values (Mann-Whitney *U* test,
256 $P < 0.05$).

257 As for the phloem phase parameters, *R. padi* and *M. persicae* took significantly less time to
258 access phloem vessels than *A. fabae* (Mann-Whitney *U* test, $P < 0.05$). The total duration of
259 the activity within phloem vessels (E1+E2) was weak for all aphids (less than 6 % of the 8-
260 hour recording). Nevertheless, this phase was significantly longer for *M. persicae* and *R. padi*
261 than for *B. brassicae* and *A. fabae* (Mann-Whitney *U* test, $P < 0.05$). All the species exhibited
262 phloem sap ingestion but the total duration of this phase, which was not significantly different
263 between species ($H = 3.71$; $P > 0.05$), was trivial and represented less than 4 % of the 8-hour
264 recording for all species.

265 Finally, the total duration of xylem sap ingestion (G) performed by *B. brassicae* was
266 significantly shorter than when it was performed by *A. fabae* and *R. padi* (Mann-Whitney *U*
267 test, $P < 0.05$), but not significantly so when it was performed by *M. Persicae*. The total
268 duration of stylet derailment phase (F) was not significantly different between aphid species
269 ($H = 7.40$; $P > 0.05$).

270

271 **3.2.2. Aphid performance on *M. x giganteus***

272 Kruskal-Wallis statistical analysis showed an aphid species effect on all parameters presented
273 in Table 3: adult survival ($H = 25.73$; $P < 0.05$), fecundity ($H = 71.75$; $P < 0.05$), nymph
274 survival ($H = 26.52$; $P < 0.05$). Inter-specific pairwise comparisons showed that the adult
275 survival was significantly shorter for *B. brassicae* (ca. 50 %) compared to all other species of
276 aphid (Mann-Whitney *U* test, $P < 0.05$). Fecundity was significantly higher in *R. padi* (Mann-
277 Whitney *U* test, $P < 0.05$) than in the other species. Concerning the nymph performance
278 study, none of the individuals reached the adult stage. In addition, the nymph survival was
279 longer for *R. padi* in comparison to *B. brassicae* and *M. persicae* (Mann-Whitney *U* test,
280 $P < 0.05$).

281

282 **3.3. Bioassay 2: feeding behavior and performance of *R. padi* on the three *Miscanthus***
283 **species**

284 **3.3.1 Electrical penetration graph studies**

285 There was a significant effect of the plant species on the total duration of probing ($H = 13.97$;
286 $P < 0.001$) and the total duration of phloem sap ingestion ($H = 8.58$; $P < 0.05$) (Fig 1). The
287 total duration of probing was significantly shorter on *M. sinensis* in comparison to the two
288 other plant species (Mann-Whitney U test, $P < 0.05$). Indeed, *R. padi* spent 60 % of the
289 recorded time in plant tissue (versus at least 69 % for the two other plant species). The total
290 duration of phloem sap ingestion was more than four times higher on *M. sacchariflorus*
291 (16.5 % of the time over the 8 h duration of recording) than on *M. x giganteus* (3.7 % of the
292 time over the 8 h recording) (Mann-Whitney U test, $P < 0.05$).

293 **3.3.2 *R. padi* performances on the three *Miscanthus* species**

294 Concerning the aphid performance study presented in Table 4, Kruskal-Wallis statistical
295 analysis showed a plant species effect on *R. padi* adult survival ($H = 41.20$; $P < 0.001$),
296 fecundity ($H = 20.11$; $P < 0.05$) and nymph survival ($H = 12.55$; $P < 0.01$). When aphids were
297 reared on *M. sacchariflorus*, nymphs survived twice longer than when they were reared on the
298 two other plant species (Mann-Whitney U test, $P < 0.05$), but only 3 nymphs out of the 31
299 individuals tested reached the adult stage. Similarly, adult survival was significantly longer on
300 *M. sacchariflorus*. The fecundity was negatively affected for aphids reared on *M. sinensis*
301 (Mann-Whitney U test, $P < 0.05$).

302

303 **4. Discussion**

304 Our study demonstrated that none of the four aphid species considered as the main crop pests
305 in Northern France (FREDON Picardie Pest Monitoring Network), which were also
306 abundantly trapped *M. x giganteus fields*, were able to achieve their life cycle on this plant
307 because their progeny did not reach the adult stage. Even if *M. x giganteus* did not represent a
308 reservoir for these common aphid pests of northern France, some differences in the suitability
309 of this plant appeared regarding to the aphid degree of specialization towards Poaceae. The
310 Poaceae specialist aphid *R. padi*, which performed better on *M. x giganteus* than the other
311 aphid species, was able to achieve its life cycle on *M. sacchariflorus*.

312

313 **4.1. *M. x giganteus* colonization ability by the four main aphid pest species**

314 Host plant selection by alate aphids is achieved through a sequence of several steps defined
315 by Niemeyer (1990) and Powell et al. (2006) : (1) pre-alighting behaviour, (2) landing, (3)
316 probing the epidermis, (4) stylet pathways activity in the mesophyll, (5) sieve element
317 puncture and salivation, (6) phloem acceptance and sustained sap ingestion and finally (7)
318 survival and reproduction. Our field study showed that the trapped aphid species were the
319 ones that are most frequently found in the main crops of the northern France and this,
320 regardless of their potential relationship with Poaceae. Indeed, aphids have little control over
321 the direction of their flight and the pre-alighting step appears to have negligible effect on the
322 host-plant selection (Dixon, 1998). Aphids do not exhibit clear discrimination between host
323 and non-host plants before they have landed and inserted their stylets (Kennedy and Booth,
324 1961; Kennedy et al., 1959a, 1959b). The two main trapped species were two polyphagous
325 species, *Myzus persicae* and *Aphis fabae*. These species are considered to be the main pests of
326 northern France crops as their host plant spectrum comprises a wide range of plant species
327 belonging to a large number of plant families including Poaceae (Blackman and Eastop,

328 2000). Surprisingly, the Brassicaceae specialist *Brevicoryne brassicae* was extensively
329 trapped in 2011 whereas the two cereal specialists *Rhopalosiphum padi* and *Sitobion avenae*
330 were much less frequently trapped.

331 The analysis of EPG parameters such as frequency, duration, and sequence of different
332 waveforms, are considered as valuable indicators for defining plant suitability or probing
333 interference by chemical and/or physical factors in plant tissues (Mayoral et al., 1996). In the
334 present EPG study, the total duration of pathway phases, the total duration of activity within
335 phloem vessels and more generally the total activity of the recorded time in plant tissues were
336 the highest for the Poaceae specialist *R. padi*, the lowest for the Brassicaceae specialist
337 *B. brassicae* and intermediate for the two polyphagous species. Aphids usually have a low
338 number of probes when feeding on suitable hosts (Cole, 1997). This was the case for *R. padi*
339 on *M. x giganteus* in our study. Moreover, the time to reach phloem vessels was the shortest
340 for *R. padi* and the longest for *B. brassicae*. Therefore, as expected, the suitability of
341 *M. x giganteus* varied according to the degree of specialization towards Poaceae of each aphid
342 species. And indeed, the Brassicaceae specialist cabbage aphid, *Brevicoryne brassicae*,
343 usually feeds on plants that accumulate glucosinolates, which stimulate its feeding and
344 oviposition (Ahuja et al., 2010; Wittstock et al., 2004). The lack of such secondary
345 metabolites in miscanthus plants could also explain its weak performances, i.e. feeding
346 behavior, survival and reproduction, of *B. brassicae* compared to the other aphid species.
347 Conversely, *R. padi* was the aphid species that performed the best on *M. x giganteus*,
348 although it performed less well than it did on barley, its conventional host plant (Chesnais et
349 al., 2014; Schliephake et al., 2013). The relatively weak performances of *R. padi* on
350 *M. x giganteus* could result from the different photosynthetic pathways occurring in its
351 common C3 host plant and in the C4 miscanthus. Indeed, Weibull (1990) demonstrated a
352 preference of *R. padi* for grasses with a C3-metabolic pathway. He hypothesized that *R. padi*,

353 having evolved in the Palaearctic region, has not had yet the adequate opportunity to adapt to
354 C4-grasses that grow mainly in warmer regions. The polyphagous species *Aphis fabae* and
355 *Myzus persicae* exhibited intermediate performances in comparison to the two specialist aphid
356 species. This is in accordance with Tosh et al. (2003) who found that, during the host plant
357 selection phases 4, 5 and 6 (see above, Powell et al. (2006)), aphid specialists reject more
358 easily and efficiently non-host plants than generalists do.

359 Chesnais et al. (2014) evaluated the intrinsic rate of increase of the same four aphid species as
360 the ones tested in this study and it clearly appeared that *M. x giganteus* was less suitable for
361 each aphid species than their respective rearing host plants. Accordingly, their feeding
362 behaviour was also drastically affected on *M. x giganteus* in comparison to what is reported in
363 the literature when they feed on their host plant (Boquel et al., 2012; Gabrys et al., 1997;
364 Powell and Hardie, 2001; Slesak et al., 2001). The unsuitability of *M. x giganteus* is also
365 supported by the presence of stress indicators such as a high xylem sap consumption and the
366 occurrence of stylet derailments (Prado and Tjallingii, 1997; Sauge et al., 2002).

367

368 **4.2. Suitability of the three *Miscanthus* species to *R. padi***

369 Two main basic modalities of plant resistance to insects have been defined by Panda and
370 Khush (1995) and Painter (1951): Antixenosis affects insect behavior by deterring or reducing
371 the colonization process whereas antibiosis affects insect life history traits (survival,
372 development, fecundity). Our study revealed that *M. x giganteus* and *M. sinensis* exhibited a
373 higher resistance level to *R. padi* than *M. sacchariflorus* thanks to a combination of both
374 resistance mechanisms.

375 Indeed, on a susceptible host plant such as *Hordeum vulgare*, the high population rate of
376 increase of *R. padi* was associated with a high duration of phloem feeding (58 % of the

377 12 hour recording) (Schliephake et al., 2013). Compared to such data obtained on susceptible
378 plants, our study suggested the occurrence of an antixenosis resistance mechanism through a
379 drastic reduction of phloem sap ingestion of *R. padi* on *M. sinensis* and *M. x giganteus*, and to
380 a lesser extent on *M. sacchariflorus*, (9.3, 3.7 and 16.5 % of the 8-hour recording
381 respectively). This data was consistent with the demographic performance results which
382 showed a high antibiosis resistance mechanism when *R. padi* was reared on *M. x giganteus*
383 and *M. sinensis*. Accordingly, Huggett et al. (1999) demonstrated that *R. padi* was unable to
384 reproduce and to exhibit prolonged feeding on *M. sinensis*. In our study, *M. sacchariflorus*
385 was a more susceptible host for *R. padi* than *M. x giganteus* and *M. sinensis*. However, the
386 suitability of *M. sacchariflorus* to *R. padi* remained moderate as only three *R. padi* nymphs
387 out of the 31 individuals tested reached the adult stage. In contrast, Pointeau et al. (2014)
388 demonstrated that *Rhopalosiphum maidis* was able to develop and reproduce and exhibited
389 long phases of phloem sap ingestion on the three *Miscanthus* species (23 % to 40 % of the
390 time over the duration of probing depending on the *Miscanthus* species). This could be
391 explained by the fact that, contrary to *R. padi*, the corn leaf aphid *R. maidis* is also adapted to
392 feed on C4-plants (Blackman and Eastop, 2000).

393

394 **4.3. Epidemiologic and agronomic implications**

395

396 The inability of *A. fabae*, *M. persicae*, *B. brassicae* and even *R. padi* to produce nymphs that
397 could reach the adult stage on *M. x giganteus* does not allow conferring to this plant the status
398 of reservoir as defined by Spencer and Raghu (2009). *M. x giganteus* has therefore to be
399 considered as a “transitional plant” that would allow the aphids to survive through the
400 consumption of xylem sap and low quantities of phloem sap. The existence of such refuge

401 perennial plants is crucial for aphid pests that use annual plant crops that are harvested in
402 summer. Moreover, as the four aphid species studied cannot complete their life cycle on
403 *M. x giganteus*, they can be considered as non-colonizing or transient species (Fereres and
404 Moreno, 2009; Irwin et al., 2007). In the context of plant virus spreading, transient aphid
405 species alighting on non-host plants are known to transmit non-persistent viruses before
406 taking off in search of a suitable host plant (Boquel et al., 2012; Gray et al., 2010; Radcliffe
407 and Ragsdale, 2002). Our EPG study clearly showed that the four aphid species performed the
408 brief intracellular punctures (potential drop waveforms) which are directly involved in the
409 transmission of non-persistent viruses (Martín et al., 1997). To our knowledge, only the work
410 by Grisham et al. (2012) reported that *M. sinensis* could be infected by the non persistent
411 Sorghum mosaic virus (SrMV) which is not present in Europe.

412 The observation of sustained phloem ingestion phase, particularly for *R. padi*, also makes the
413 transmission of persistent viruses theoretically possible (Martín et al., 1997). Christian et al.
414 (1994) and Huggett et al. (1999) demonstrated that *M. sinensis* could be susceptible to some
415 persistent viruses such as the barley yellow dwarf virus (BYDV), and could therefore be a
416 perennial reservoir of phytoviruses. However, another study by Drechsler et al. (2014) shows
417 that different *M. x giganteus* cultivars were resistant to the persistent Maize streak
418 virus (MSV).

419

420 Thus, the introduction of miscanthus in the north of France could not only have an effect on
421 the spread of phytoviruses related to Poaceae but also on those related to the other
422 conventional crops. Indeed, *Miscanthus* spp. could constitute a tall barrier which may reduce
423 potential virus dissemination by aphid vectors when aphid vectors migrate between crops.
424 Hooks and Fereres (2006) propose that barrier plants may act as a sink for non-persistent
425 viruses. After landing on the barrier crop, the viruliferous aphid loses its virus “charge” by

426 making a few brief probes on the plant. Consequently, a virus-free aphid entering an area with
427 susceptible primary crops will no longer be able to transmit a viral disease. For example,
428 Fereres (2000) studied the use of sorghum and maize as barrier crops to protect pepper plants
429 against the potato virus Y (PVY) and the cucumber mosaic virus (CMV). He concluded that
430 these tall barrier plants did not reduce the number of vectors entering in pepper habitats but
431 protected the pepper plant by acting as a natural sink for non-persistent viruses. In Picardy,
432 the agricultural landscape being mainly dominated not only by cereal crops but also by crops
433 such as rapeseed, potato, legumes (typically beans and peas), sugar beet, turnips, carrots and
434 lettuce, attention should be paid to where miscanthus is being planted. Miscanthus could be
435 used as a virus sink to prevent the dissemination of non persistent viruses of Brassicaceae
436 (e.g., *Cauliflower mosaic virus*, CaMV, the Turnip yellow mosaic virus, TuMV), Solanaceae
437 (*Potato virus Y* PVY) and Cucurbitaceae (*Cucumber mosaic virus*, CMV). However, it should
438 not be planted as a barrier crop nearby arable crops such as wheat or maize, as in this case it
439 could possibly act as a reservoir for the BYDV.

440 **5. Conclusion**

441
442 Despite the probable modification of the equilibrium of local agrosystems, the introduction of
443 miscanthus in northern France may not contribute to creating a new reservoir for aphid pests
444 issued from susceptible crops. Moreover, its possible role as a barrier crop could also limit
445 aphid movements between crops, reducing the risk of virus spreading. Our work also
446 demonstrates that, the most interesting species for biomass production, *M. x giganteus*, is also
447 the species which exhibited the highest level of resistance towards *R. padi* in comparison to
448 its parents *M. sinensis* and *M. sacchariflorus*.

449 In the future, field surveys should continue to be used to predict aphid pest problems before
450 they develop in the miscanthus crop. Indeed, our study did not take into account the genetic

451 variability of *R. padi*. Within the same geographic location, Lushai et al. (2002) revealed two
452 genetic profiles of the grain aphid, *Sitobion avenae* (Fabricius) that exhibited different levels
453 of specialization towards different grasses and cereals. Therefore, some other natural
454 populations of *R. padi* may be adapted to feed and reproduce on *Miscanthus* spp. Otherwise,
455 even if *R. maidis* populations are negligible in the northern France, their abundance is likely
456 to increase in cooler regions in response to climate warming (Harrington, 2007), which could
457 in turn enhance its pest status of Poaceae such as *Miscanthus* spp.

458
459

460 **Acknowledgments**

461 We would like to acknowledge the financial support from the Picardie region (research
462 project MISCPIC). Shân Williams (Maison des langues / Université de Picardie Jules Verne)
463 and Alain Corbière (College of Arts / Université de Picardie Jules Verne) are also thanked for
464 their critical proof-readings of the manuscript especially concerning the English language.

465

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603

604

605 **Table 1** - Species and total number of alate aphids from yellow water traps placed in three
606 *Miscanthus x giganteus* fields of northern France in 2011 (from May 2nd to July 29th) and in
607 2014 (from May 7th to July 2nd). Among the 50 species identified, the eleven most abundant
608 pest species were numbered.

Species	Common name	Total collected in 2011	Total collected in 2014	Total collected in 2011 and 2014	Percentage collected in 2011 and 2014
<i>Myzus persicae</i>	Green peach aphid	175	845	1020	41.87
<i>Aphis fabae</i>	Black bean aphid	239	72	311	12.77
<i>Brevicoryne brassicae</i>	Cabbage aphid	231	3	234	9.61
<i>Cavariella aegopodii</i>	Willow-carrot aphid	53	15	68	2.79
<i>Acyrtosiphon pisum</i>	Pea aphid	20	25	45	1.85
<i>Rhopalosiphum padi</i>	Birdcherry-oat aphids	25	1	26	1.07
<i>Hyperomyzus lactucae</i>	Blackcurrant-sowthistle aphid	24	19	43	1.77
<i>Sitobion avenae</i>	Grain aphid	16	1	17	0.70
<i>Macrosiphum euphorbiae</i>	Potato aphid	4	7	11	0.45
<i>Nasonovia ribisnigri</i>	Lettuce aphid	0	2	2	0.08
<i>Cavariella theobaldi</i>	Willow - carrot aphid	4	1	5	0.21
Others		414	240	654	26.85
Total		1205	1231	2436	100.00

609

610 **Table 2** - Electrical penetration graph parameters (means \pm SEM) calculated for four aphid species during an 8-h monitoring session on
 611 *Miscanthus x giganteus* plants.

EPG classes	Kruskal- Wallis test	<i>A. fabae</i>	<i>B. brassicae</i>	<i>M. persicae</i>	<i>R. padi</i>
	H(P)	n = 22	n = 20	n = 24	n = 23
General probing behaviour					
1. Number of probes	16.06 (**)	22.70 \pm 2.20 a	21.50 \pm 3.10 ab	25.80 \pm 2.00 a	14.70 \pm 1.20 b
2. Total duration of probing (min)	30.4 (***)	295.10 \pm 14.58 b	202.33 \pm 17.90 c	314.85 \pm 16.82 ab	357.28 \pm 12.34 a
Pathway phase					
3. Number of pathway phases	15.92 (**)	28.20 \pm 2.10 b	28.00 \pm 3.60 b	44.40 \pm 4.00 a	29.72 \pm 1.50 b
4. Total duration of pathway phases	19.11 (***)	185.01 \pm 12.78 ab	137.79 \pm 13.49 c	161.49 \pm 9.75 bc	219.12 \pm 11.52 a
5. Mean number of potential drops (pd)	21.26 (***)	110.27 \pm 9.2 b	70.16 \pm 9.97 c	119.25 \pm 10.68 b	146.52 \pm 8.55 a
Phloem phase					
6. Time of first phloem phases (min)	13.23 (***)	279.71 \pm 33.44 a	186.58 \pm 43.71 ab	151.76 \pm 34.88 b	101.64 \pm 9.41 b
7. Total duration of phloem phases (salivation E1+ ingestion E2) (min)	20.41 (***)	3.81 \pm 0.99 c	8.11 \pm 2.96 bc	29.21 \pm 9.54 ab	21.27 \pm 7.55 a
8. Total duration phloem sap ingestion (E2) (min)	3.71 (NS)	1.60 \pm 0.44	3.96 \pm 1.80	9.52 \pm 3.35	17.83 \pm 7.45
Other parameters					
9. Total duration of xylem ingestion (G) (min)	15.52 (*)	100.41 \pm 11.93 a	58.13 \pm 11.98 b	78.62 \pm 9.28 ab	90.79 \pm 6.52 a
10. Total duration of stylet derailment (F) (min)	7.40 (NS)	9.13 \pm 4.63	14.07 \pm 8.21	54.64 \pm 12.53	40.88 \pm 16.72

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

613 different letters indicate significant differences (pairwise comparisons using Mann-Whitney U test).

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617 **Table 3** - Mean (\pm SEM) population parameter values of four aphid species reared on *Miscanthus x giganteus*.

	Kruskal-Wallis test	<i>A. fabae</i>		<i>B. brassicae</i>		<i>M. persicae</i>		<i>R. padi</i>	
Adults	H(P)	n = 34		n = 38		n = 40		n = 31	
Survival (days)	25.73 (***)	4.49 \pm 0.25	a	2.58 \pm 0.23	b	4.44 \pm 0.36	a	4.18 \pm 0.26	a
Fecundity	71.75 (***)	1.39 \pm 0.30	b	0.04 \pm 0.04	c	0.56 \pm 0.24	bc	6.75 \pm 0.68	a
Nymphs		n = 38		n = 58		n = 24		n = 32	
Survival (days)	26.52 (***)	2.16 \pm 0.09	ab	2	b	2	b	2.69 \pm 0.17	a

618 Asterisks indicate a significant difference: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ associated with H (Kruskal-Wallis test); within a row,619 different letters indicate significant differences (pairwise comparisons using Mann-Whitney U test).

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629 **Table 4** - Mean (\pm SEM) performance parameter values of *Rhopalosiphum padi* on the three miscanthus species (*Miscanthus x giganteus*,
630 *Miscanthus sacchariflorus* and *Miscanthus sinensis*).

	Kruskal-Wallis test	<i>Miscanthus x giganteus</i>	<i>Miscanthus sacchariflorus</i>	<i>Miscanthus sinensis</i>
Adults	H(P)	n = 28	n = 25	n = 27
Survival (days)	41.20 (***)	4.18 \pm 0.26 b	9.28 \pm 0.76 a	4.04 \pm 0.27 b
Fecundity	20.11 (***)	6.75 \pm 0.68 a	8.88 \pm 0.85 a	3.67 \pm 0.65 b
Nymphs		n = 32	n = 31	n = 25
Survival (days)	12.55 (**)	2.69 \pm 0.17 b	4.71 \pm 0.7 a	2.4 \pm 0.16 b

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

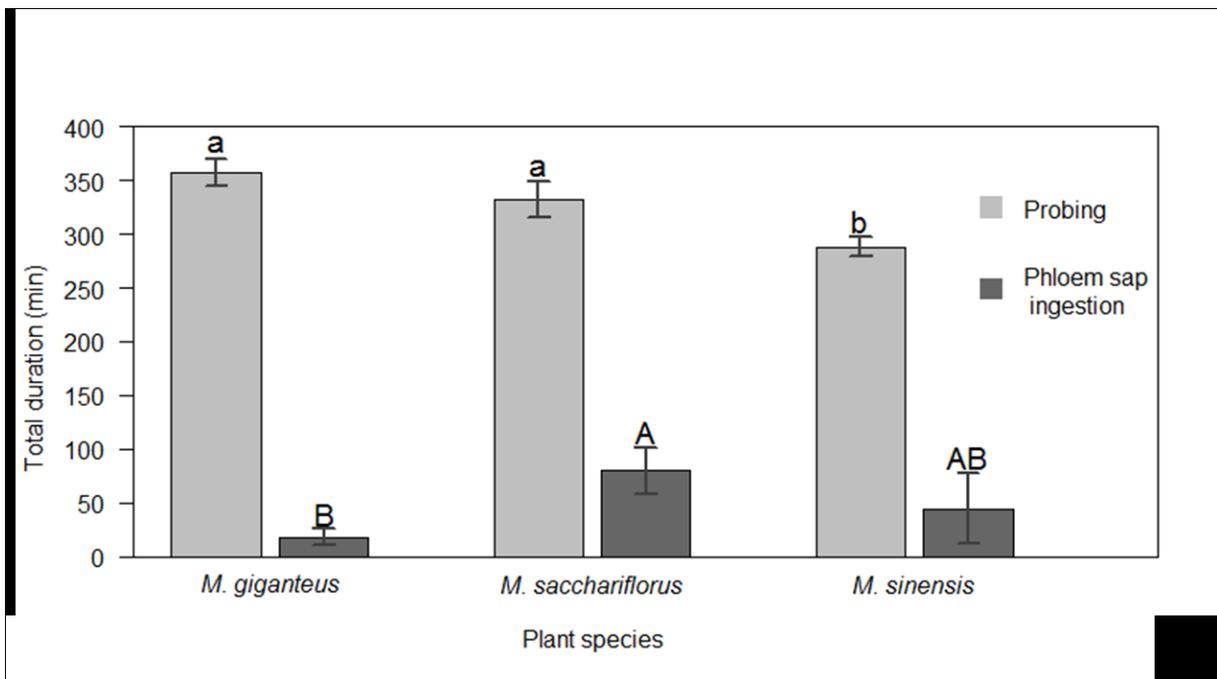
632 different letters indicate significant differences (pairwise comparisons using Mann-Whitney U test).

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635 **Fig. 1** - Two electrical penetration graph parameters (total duration of probing \pm SEM in light
636 grey bars and total duration of phloem sap ingestion \pm SEM in dark grey bars) calculated for
637 *Rhopalosiphum padi* during an 8 h monitoring session on the three miscanthus species
638 (*Miscanthus x giganteus*, *Miscanthus sacchariflorus* and *Miscanthus sinensis*).

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