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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 CO<sub>2</sub> 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 C<sub>4</sub>  
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 2<sup>nd</sup> to July 29<sup>th</sup> and a second time in 2014 from May 7<sup>th</sup> to July 2<sup>nd</sup>. 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”).  
149

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<sup>®</sup> 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<sup>®</sup> 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](http://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

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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 2<sup>nd</sup> to July 29<sup>th</sup>) and in  
607 2014 (from May 7<sup>th</sup> to July 2<sup>nd</sup>). 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
<b>Total</b>		<b>1205</b>	<b>1231</b>	<b>2436</b>	<b>100.00</b>

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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
<b>General probing behaviour</b>					
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
<b>Pathway phase</b>					
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
<b>Phloem phase</b>					
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
<b>Other parameters</b>					
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>	
<b>Adults</b>	H(P)	n = 34		n = 38		n = 40		n = 31	
<b>Survival (days)</b>	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
<b>Fecundity</b>	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
<b>Nymphs</b>		n = 38		n = 58		n = 24		n = 32	
<b>Survival (days)</b>	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>
<b>Adults</b>	H(P)	n = 28	n = 25	n = 27
<b>Survival (days)</b>	41.20 (***)	4.18 $\pm$ 0.26 b	9.28 $\pm$ 0.76 a	4.04 $\pm$ 0.27 b
<b>Fecundity</b>	20.11 (***)	6.75 $\pm$ 0.68 a	8.88 $\pm$ 0.85 a	3.67 $\pm$ 0.65 b
<b>Nymphs</b>		n = 32	n = 31	n = 25
<b>Survival (days)</b>	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,

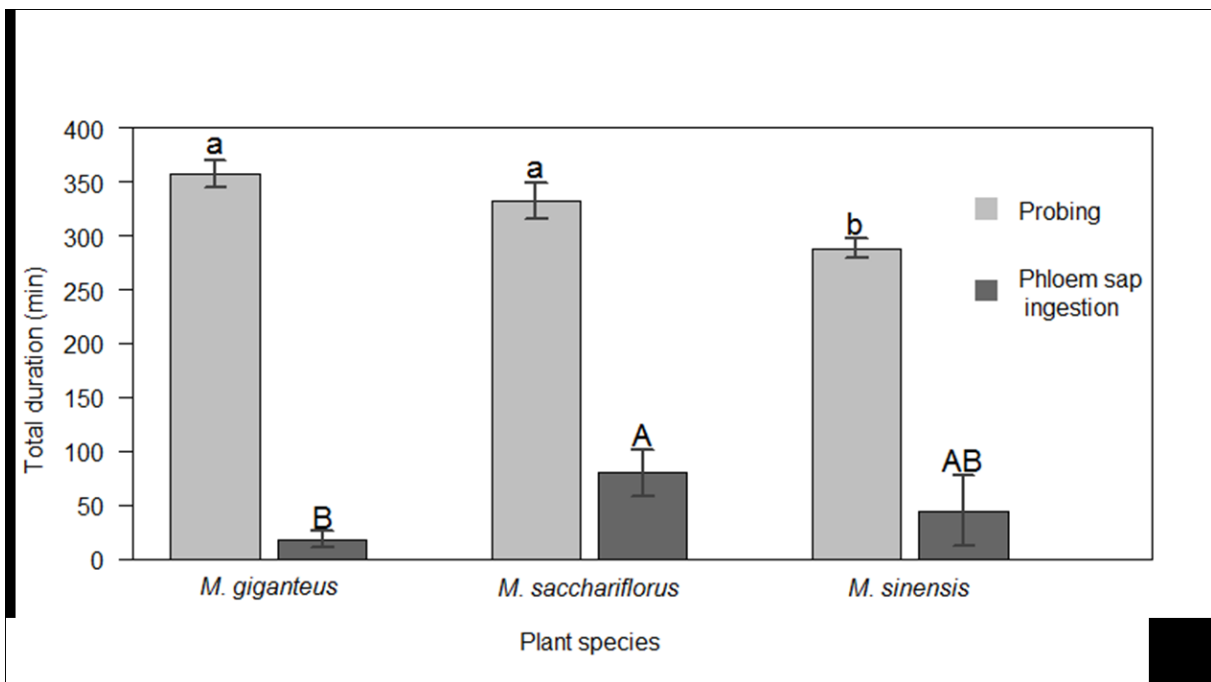
632 different letters indicate significant differences (pairwise comparisons using Mann-Whitney  $U$  test).

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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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