Methane output in dairy cows in response to long-term feeding of grass-based diets supplemented with linseed or rapeseed

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1   Aphids at crossroads: when branch architecture alters aphid infestation patterns in the apple

2   tree

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16   Running title: Branch architecture and aphid infestation

17 **Abstract**

18 1. Plant architecture highly constrains pest infestation but is rarely considered in studies on

19   plant-insect interactions. We analysed the relationships between apple tree architectural

20   traits manipulated by tree training and within-branch development of *Dysaphis*

21   *plantaginea* (rosy apple aphid, RAA), a major apple pest, during its multiplication

22   wingless phase in spring. We hypothesised that the degree of branching had an effect on

23   RAA within-branch infestation.

24 2. In an experimental apple orchard, the infestation by aphid wingless forms was surveyed in

25   two consecutive spring seasons within branches manipulated to design contrasted

26   architectures differing in shoot numbers, shoot density and branching orders.

27 3. Whatever the branch management system, aphid infestation was higher on long vs. short,

28   fruiting vs. vegetative, and growing vs. non-growing shoots. Either less infested shoots or

29   less severe infestation were observed in the most branched system. A pattern of within-

30   branch short-distance infestation was confirmed. Moreover, the number of branching

31   points between two shoots exerted a high constraint on this infestation pattern.

32 4. Beside possible trophic effects due to plant growth patterns already documented in the

33   literature, a high degree of branching is likely to be a key-architectural trait to constrain

34   within-branch aphid infestation. This opens new perspectives on the manipulation of

35   branch architecture as a mean giving partial control of pests towards sustainable fruit

36   production.

37

38 **Key-words**: branching order, *Dysaphis plantaginea* (rosy apple aphid), habitat complexity,

39 infestation pattern, *Malus* x *domestica*, plant architecture

40 **INTRODUCTION**

41   Training of fruit trees is used by growers to enhance yield, fruit quality and return-

42 bloom in orchards (Wertheim 2005a; 2005b). Tree spatial and temporal organisation, i.e. tree

43 architecture (Bell 1991; Hallé et al. 1978), is therefore periodically modified through pruning,

44 branch bending and selective removal of fruiting and/or vegetative shoots to distribute fruits

45 and increase light penetration within the tree canopy (Costes et al. 2006; Lauri et al. 2004;

46 Lauri and Laurens 2005; Lauri et al. 2009). Because plant architecture shapes the habitat and

47 living conditions of pests and their natural enemies (Lawton 1983; Price et al. 1980), an

48 alteration of the population dynamics of pests is expected from tree training performed by

49 growers. However, this latter topic is still little documented (Kührt et al. 2006; Simon et al.

50 2007a; Stoeckli et al. 2008a).

51   Some studies on the topic revealed significant effects of fruit tree architecture

52 manipulation or aspect and height on pest and disease development (Grechi et al. 2008; Holb

53 et al. 2001; Mani et al. 1995; Prokopy et al. 2001; Simon et al. 2006; Simon et al. 2007b;

54 Stoeckli et al. 2008a), with favourable or unfavourable effects on infestation or infection

55 rates, depending on the studied pest or disease. Most of these experimental studies were

56 descriptive only. Despite proposed hypotheses to explain the observed results, mechanisms

57 were rarely investigated in fruit trees (Simon et al. 2007a). Literature on other plant models

58 (e.g. Pistacia, Martinez and Wool 2003; Cotton, Anderson and Agrell 2005; Birch, Riihimäki

59 et al. 2006) can help identifying the underlying processes which include growth patterns:

60 plant sectoriality (Araújo et al. 2006; Larson and Whitham 1997; Marquis 1996; Orians and

61 Jones 2001), habitat complexity (Finke and Denno 2006; Langellotto and Denno 2004;

62 Lawton 1983) and connectivity (Hanan et al. 2002; Skirvin and Fenlon 2003). In apple, which

63 is one of the most documented fruit tree production, effects of tree architecture were reported

64 on codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), (Simon et al. 2007b;

65 Stoeckli et al. 2008a) and the rosy apple aphid (RAA), *Dysaphis plantaginea* (Passerini)

66 (Hemiptera: Aphididae) (Simon et al. 2006). Both are major pests of apple trees, which may

67 cause serious damages to fruits (codling moth), shoots, fruits and branches (RAA;

68 Bonnemaison 1959; Deberardinis et al. 1994). These pests require pesticide use to be kept

69 under control. Hypotheses to explain results were related to microclimate and fruit phenology

70 for the flying pest, i.e. the codling moth, (Stoeckli et al. 2008a) and within–branch shoot

71 distribution in spring for the walking wingless RAA pest (Simon et al. 2006). Indeed, RAA

72 winter eggs laid in autumn by aphids re-emigrating on their primary host, the apple tree, hatch

73 around March in the area, and stem mothers infest buds before bloom. During a

74 parthenogenesis phase, primary and then secondary colonies develop on trees and cause

75 damage, mainly through severe leaf curling during fruit and shoot growth in spring

76 (Bonnemaison 1959). At this time, because winged forms are not present before infestation

77 peak and/or fly away from apple towards their secondary host-plant *Plantago* spp.

78 (Plantaginaceae) (Bonnemaison 1959), founders of new colonies within the branches are

79 mainly 'pedestrians' which can be seen walking on the branch axes. Branch architecture, as

80 defined by structural and growth traits, is expected to constrain the RAA's movement patterns

81 in its walking behaviour.

82   Here we aim to identify some of the architectural parameters affecting RAA within-

83 tree development in spring before it flies to its secondary host. The approach is based on the

84 study of RAA development within branches belonging to the same apple cultivar but with two

85 pruning strategies to design contrasted branch architectures. The two experimented branch

86 managements belonging to known tree training systems are first presented and their effects on

87 branch architecture assessed. Then architectural parameters of both branch managements are

88 analysed for their effects on RAA development. Our main hypothesis was that the degree of

89 branching is a relevant architectural trait to alter RAA movement in its dissemination phase in

90 spring when walking from one leafy shoot to another. Lastly, the potential of tree architecture

91 manipulation as a method giving partial control of orchard pests is discussed.

92

93 **MATERIALS AND METHODS**

94   The study was carried out in May 2007 and 2008 at the INRA (National Institute for

95 Agricultural Research) Gotheron experimental unit in South-East France (44°58'33" North,

96 4°55'45" East). Located in the middle Rhône Valley, the area has a continental climate with

97 summer Mediterranean influences. The soil in the area has a sandy-loam shallow and stony

98 structure derived from old washed out sediments of the Rhône river.

99

100 **1. Experimental orchard and tree training systems**

101   The experimental orchard was planted in 2001 with cv. 'Pitchounette' (INFEL® 3318), a

102 scab *Vf*-resistant cultivar, grafted onto M9, which is moderately susceptible to RAA

103 (Parveaud et al. 2010). One tree out of ten was a pollinator tree. Tree density was 1110

104 trees.ha^{-1} with 4.5 m between-row and 2 m within-row planting distances. Each of the eight

105 North-South oriented rows of the orchard included 15 trees. All trees had a similar pest and

106 disease management, watering, fertilising, within-row chemical weeding and grass mowing in

107 the orchard alleys. During the first four years after planting, i.e. from 2001 to 2004, all trees

108 were trained to the original solaxe system (OS; Lauri and Lespinasse 2000; Willaume et al.

109 2004). In brief, the OS system is based on three main rules: a vertical trunk up to 2.5 m or

110 more, a regular distribution of 10 to 15 main branches, i.e. issued from the trunk, on average

111 along and around the trunk from 1m onwards (branches in excess are completely removed)

112 and the bending below the horizontal of all branches. There was no pruning within each

113 individual branch, except the removal of vigorous shoots ('water shoots') which may appear

114 on the bent portions of branches and trunk. In 2005, four blocks of two contiguous rows were

115   designed and each row within a block was assigned at random to one of the following training

116   systems:

117   (i) Original solaxe as in previous years,

118   (ii) Centrifugal training (CT; Lauri et al. 2004; Lauri et al. 2007) with the thinning-out of

119   young fruiting shoots in all sites where they have a poor development due to low light

120   level that is on the underside and on the proximal part of the main branches, and around

121   the trunk. This procedure, called extinction pruning (Lauri 2009), aimed at decreasing

122   branching density along the main axes of the branches to improve both the development

123   of the remaining shoots and light penetration within the tree.

124   The two training systems therefore led to trees which did not differ in their cylindrical shape,

125   but rather in their internal architecture with a contrasted spatial distribution of shoots within

126   the branches. Within each row two infested branches, four- to five-year-old, directly issued

127   from the trunk were selected on two 'Pitchounette' trees, one branch per tree, after petal fall

128   in late April of years 2007 and 2008. This yielded to a total of eight branches per training

129   system. These branches were selected at similar height from the ground (1 m-1.5 m) and were

130   representative of each training system in terms of volume and branching. They belonged to

131   trees which had no RAA infestation symptoms on other branches. All branches of adjacent

132   trees touching the studied branches were removed. Each selected branch was considered as an

133   independent repetition and was subjected to architectural description and RAA assessment.

134   As aphid infestation naturally occurred in the orchard and could be unevenly distributed

135   between inner and outer parts of the orchard after the return-flight of aphids from their

136   secondary host, a block design was preferred to account for a possible infestation gradient.

137

138   **2. Description of branch architecture**

6

139   Branch architecture was described by recording the position of each current-year shoot on

140   which RAA could potentially develop within the branch (Fig. 1). More precisely, two

141   concepts were used in our recording: branching order and rank of insertion on the main axis

142   of the branch.

143   - The branching order of a current-year shoot is the number of branching points between the

144   main axis of the branch and this shoot. Namely, the main axis of the branch has a branching

145   order of 0, a sub-branch inserted on the main axis has a branching order of 1, a sub-branch

146   inserted on a 'order 1'-sub-branch has a branching order of 2, etc.

147   - The rank of insertion numbers each shoot along the main axis of the parent branch from the

148   proximal, i.e. near the trunk, to the distal parts of the branch. Each current-year shoot is then

149   characterised by a list of numbers giving the rank of insertion of each intermediate sub-branch

150   between the main axis of the branch and this shoot. For example, a current-year shoot

151   numbered '5-1' is the first shoot inserted on the fifth sub-branch inserted on the main axis of

152   the branch when counting from the proximal part of the branch (Fig. 1). This description

153   permitted identification of the topological proximity of shoots and recording of the number of

154   branching points between the apices of two adjacent shoots. As an example, on Figure 1, the

155   two nearest (adjacent) neighbour shoots of '1-2' shoot (order 2) are '1-1-1' (order 3) and '1-3'

156   (order 2) in proximal and distal topological positions, respectively, and the number of

157   branching points that a walking aphid would meet from the apex of '1-1-1' shoot to '1-2'

158   apex is 3. In parallel to its topological position, each shoot was described and assigned to the

159   following groups: length category (short, < 5 cm; long, ≥ 5 cm), growing status (yes/no, i.e.

160   presence of newly emitted leaves or not if growth has stopped), and reproductive status

161   (yes/no).

162

163   **3. Pest management and assessment of the RAA development**

164   RAA control consisting of one mineral oil and one acetamiprid applied before bloom was

165   required in all systems to permit tree growth and preserve orchard longevity. Other

166   compounds applied during the period of aphid assessments were thinning products:

167   Naphthaleneacetamide (NAD), Naphthaleneacetic acid (NAA) and carbaryl (also being

168   classified as insecticide) in 2007; NAD alone in 2008.

169   The infestation dynamics were described on the 8 selected branches per training system at

170   two consecutive dates after petal fall: at the beginning of RAA multiplication and

171   dissemination phase in spring (D1) and at RAA infestation peak (D2), i.e. 10 to 12 days after

172   the first assessment date depending on the year. Because the studied branches were isolated

173   and selected on trees with no other symptoms (see Materials and methods, section 1), the

174   observed infestation events could be considered to be mainly due to RAA within-branch

175   movements. As 2008 assessments started at the very beginning of RAA dissemination phase,

176   initial infestation levels were lower in 2008 than in 2007. Because infestation was naturally

177   occurring in the orchard, trees and branches that were assessed were different in 2007 and

178   2008. For each one-year shoot within a branch, RAA population was assigned into four

179   infestation classes: 0, no aphids; 1, only individual aphids and no progeny; 2, small colony,

180   i.e. restricted to 1 or 2 leaves; 3, large colony, spreading over 3 leaves or more. The

181   infestation severity of each branch was the mean infestation class of all shoots on that branch.

182   The percentage of RAA-infested shoots of each branch was also calculated. All other aphids,

183   mainly the *Aphis* spp. complex (*Aphis pomi* de Geer, *A. spiraecola* Patch) (Aphididae) were

184   recorded by a presence/absence index. However, as infestation levels by *Aphis* spp. were very

185   low and similar whatever the date and the training system (infestation peaked at 4.2% infested

186   shoots in 2007 and 1.7% in 2008), only RAA infestation was considered in the present

187   analysis. As natural enemies of RAA were very scarce (pers. obs.) at the time of aphid

188 assessment, their effect on RAA development was considered to be null or very low in the

189 present study.

190

191 **4. Data analysis**

192 The effect of the training system, our main studied factor, on (i) the branch architectural

193 traits and (ii) RAA infestation, was investigated through successive steps involving in each

194 case a different set of variables.

195 A first step of the analysis considered each branch as a repetition. An ANOVA (studied

196 factor: tree training; block factor) was carried out on the four following architectural and

197 infestation variables: the number of shoots per branch, shoot density (total number of current-

198 year shoots of a branch per unit of length of the main axis of this branch, number of shoots.m$^-$

199 ^{1}), RAA infestation level (% infested shoots) and mean severity of the branch. Percentage data

200 were arcsin-transformed before ANOVA. The general conditions of parametric ANOVA (i.e.

201 normal distribution and independence of residuals, homoscedasticity) were checked from the

202 graph of the residuals plotted against the predicted values and Shapiro-Wilks test (Dagnélie

203 1975). A second step in the analysis considered the current-year shoots as elementary units. A

204 χ^2 test was used to analyse the distribution of shoots pooled per training system (CT/OS) in

205 the three following analyses: combined shoot descriptive categories (length x reproductive

206 status x growth status), yielding to different degrees of freedom since not all combinations

207 existed; branching orders and infestation course patterns between D1 and D2. Independently

208 of the training system (shoots pooled whatever the training system), a χ^2 test was also used to

209 analyse if infestation was similar (in proportion) between the two status of each descriptor

210 considered separately, e.g. were short vs. long shoots similarly infested? Statistical analysis

211 was done with Statgraphics software (Statistical graphics Corp., Rockville, MD, USA).

212   A regression analysis was used to analyse the short-distance infestation pattern of RAA

213   within the branch. To do so, the RAA infestation severity class of a given shoot (target shoot)

214   at date 2 (dependent variable at D2) was plotted against the mean infestation severity class of

215   its nearest adjacent shoots at date 1 (independent variable at D1). These adjacent shoots were

216   those inserted immediately in proximal and distal topological position (see Materials and

217   methods, Section 2) of this given shoot; two shoots (general case) or only one shoot (no distal

218   adjacent shoot in the case of apices, no proximal adjacent shoot for the nearest of the tree

219   trunk) were thus considered. Because shoot numbers within the different infestation classes

220   were too low to develop this analysis at branch level, calculations were made per training

221   system. The mean infestation class at D2 (Y-axis) was computed per training system for each

222   group of target shoots (when three or more shoots) having the same mean infestation class of

223   their adjacent shoots at D1 (X-axis).

224   To test our hypothesis of an effect of the number of branching points (independent

225   variable) on RAA infestation within the branch (dependent variable), the infestation severity

226   class of a given shoot at D2 was plotted against the infestation severity class of its proximal

227   shoot at D1 considering the number of branching points between these paired shoots. In our

228   topological description, considering only the proximal (and not distal) adjacent shoot was

229   supported by the fact that apices of any current-year shoot (e.g. shoot '1' on Fig. 1) had no

230   distal shoot which would lead to exclude up to 376 shoots from this regression analysis in

231   2007. As our aim was to highlight a possible effect of branching *per se* on RAA within-

232   branch development (i.e. independently of the training system), this analysis was carried out

233   on the pooled data of the 16 study branches. The mean infestation class was computed at D2

234   (Y-axis) for each group of target shoots (when three or more shoots) whose proximal shoots

235   had the same infestation class at D1 (X-axis) in the case of 1, 2, etc. branching points between

236   the considered paired shoots.

237 These latter two regression analyses were done using the Ordinary Least Square (OLS)

238 regression method which is appropriate for fitting bivariate lines in allometry with the

239 hypothesis of a predictive relationship between the independent variable, here in the X-axis,

240 and the dependent variable, here in the Y-axis (SMATR software, Falster et al. 2006; Warton

241 et al. 2006). Comparisons between regression lines were carried out following two steps.

242 First, slopes of all lines were compared to determine if there was a common slope, i.e. a same

243 scaling coefficient, among groups. Second, in the case slopes did not change across groups,

244 tests for shift in elevation (intercept, i.e. allometric constant) and shift along the common axis

245 were computed.

246

247 **RESULTS**

248 **1. Architectural traits shaped by branch manipulation**

249 In 2007, 2030 shoots from 8 OS branches (1104 shoots) and 8 CT branches (926 shoots),

250 were assessed (Table 1). In 2008, 3470 shoots from 8 OS branches (1282 shoots) and 8 CT

251 branches (2188 shoots) were surveyed (Table 1). There were significant differences between

252 training systems for the proportion of shoots within combined categories of descriptors

253 whenever existing (short/long x growing/stopped x fruiting/vegetative). More precisely, in

254 2007, higher proportions of fruiting shoots (including long growing and short shoots) together

255 with a lower proportion of short vegetative stopped shoots were observed in the OS compared

256 to the CT system ($\chi^2 = 266.73$, 6 d.f., $P < 0.001$). In 2008, the proportion of vegetative

257 growing shoots was higher in OS compared to CT branches ($\chi^2 = 82.43$, 5 d.f., $P < 0.001$).

258 Higher proportions of growing shoots with (2007) or without (2008) fruits were thus observed

259 in OS compared to CT branches. The number of shoots per branch (Table 1) was significantly

260 higher in CT than OS branches in 2008 (ANOVA, $F_{1,8} = 11.02$, $P < 0.05$). Shoot density

261 (Table 1) was also higher in CT compared to OS trees in 2008 (ANOVA, $F_{1,8} = 22.67$, $P <$

262 0.01). There was no significant difference between training systems (ANOVA, $P > 0.05$) in

263 2007 for these two architectural variables and no block effect in any year.

264   The distribution of shoots according to their branching order (Fig. 2a, b) displayed strong

265 differences between training systems in both years (2007, order 3 and 4 shoots pooled: $\chi^2 =$

266 244.43, 2 d.f., $P < 0.001$; 2008: $\chi^2 = 337.52$, 3 d.f., $P < 0.001$). Apart from the training system,

267 the proportion of shoots in the highest orders was higher in 2008 compared to 2007 (Fig. 2a,

268 b) attesting to the increased branching process which accompanies branch ageing between the

269 two years. But the proportion of shoots in branching orders 3 and 4 was higher in CT than in

270 OS branches in both years.

271

272 **2. Effect of the training system on shoot infestation by RAA**

273 2.1. RAA infestation and severity at branch level

274   The percentage of RAA-infested shoots and severity (Table 2) increased between the

275 two assessment dates (D1, D2) in both years. In 2007, large variations were observed between

276 branches within the same training system: RAA infestation rate at D1 was between 2.6% and

277 67.7% infested shoots in OS branches, and between 1.3% and 80.4% in CT branches. In 2008,

278 the infestation at D1 was at its beginning and the assessed branches were more

279 homogeneously infested with 0.4% to 4.7% infested shoots in CT and 0.4% to 10.0% infested

280 shoots in OS branches. Because of this high intra-training system variability, no significant

281 difference between training systems was displayed whatever the infestation variable (i.e.

282 percent infested shoots or severity) in any study year (ANOVA, $P > 0.05$). No significant

283 block effect or interaction block-training system could be displayed either.

284

285 2.2. RAA infestation dynamics at shoot level

12

286   Although at a given date no differences in infestation were displayed between training

287   systems in both study years, infestation courses of shoots between D1 and D2 were

288   significantly different between training systems in 2007 (Fig. 3a). Especially the proportion of

289   newly infested shoots between D1 and D2 assessment dates ("Peak only") was higher in OS

290   than in CT branches ($\chi^2 = 25.07$, 3 d.f., $P < 0.001$): 28.4% vs. 20.8% shoots get infested

291   between D1 and D2 in the CT and OS systems, respectively. However in 2008 (Fig. 3b), with

292   less infestation, the infestation courses were similar for both training systems: 77.0% of the

293   shoots remained non-infested, 1.8% were infested at both assessment dates and 21.2%

294   became infested between D1 and D2.

295

296   2.3. RAA infestation according to the shoot category

297   Whatever the training system, RAA infestation was higher on long vs. short shoots, on

298   fruiting vs. vegetative shoots, and on growing vs. non-growing shoots. Indeed, considering

299   pooled shoots per year there were significant differences in the distribution of shoots within

300   'infestation status x descriptive categories' (1 d.f.) whatever the year (2007 length: $\chi^2 = 17.68$,

301    $P < 0.001$; 2007 reproductive status: $\chi^2 = 5.19$, $P < 0.05$; 2007 growth status: $\chi^2 = 23.40$, $P <$

302   0.001; 2008 length: $\chi^2 = 9.21$, $P < 0.01$; 2008 reproductive status: $\chi^2 = 58.87$, $P < 0.001$; 2008

303   growth status: $\chi^2 = 28.79$, $P < 0.001$).

304

305   **3. Effect of tree training on RAA short-distance infestation within branches**

306   The relation between the infestation severity of a given shoot at D2 and the infestation

307   severity of its adjacent shoots at D1 (Fig. 4a, b) attested to short-distance patterns of RAA

308   infestation along the branch in both years whatever the training system: the infestation of a

309   shoot was all the more severe at D2 if adjacent shoots were severely infested at D1. This

310   relationship generally fitted with a linear regression of same slope for the two training

311 systems in 2007 and 2008 ($P > 0.05$). Whereas there was no significant difference between

312 intercepts of OS and CT branches in 2007, OS branches had a higher intercept than CT

313 branches in 2008 (Wald statistic = 3.966, $P < 0.05$). This latter result indicated that whatever

314 the infestation severity of adjacent shoots at D1, the infestation severity of the target shoot at

315 D2 was higher in OS than in CT branches. This held true whatever the infestation severity of

316 the target shoot at D1.

317 In 2007 the infestation severity at D2 of a given shoot according to the infestation

318 severity of its proximal adjacent shoot at D1 was dependent upon the number of branching

319 points decreasing between the '1 branching point' and '4 branching points' cases (Fig. 5;

320 significant difference in slopes, likelihood ratio statistic = 3.069, $P < 0.05$). The low

321 infestation level at D1 in 2008 did not permit a similar analysis.

322

323 **DISCUSSION**

324 **1) Tree training affects RAA infestation through its effects on branch architecture**

325 Aphid infestation dynamics were affected by branch architecture modulated by tree

326 training. A strong effect of extinction pruning was displayed on: (i) shoot proportions in

327 descriptive categories (length, and growth and reproductive status); and (ii) within-branch

328 shoot architecture. The extinction pruning procedure decreased the number of shoots in a

329 given year but provoked an increase in the number of shoots of higher branching order on the

330 remaining laterals in the following years. This led to an increase in shoot density, i.e. the

331 number of shoots per unit of length of the main branch axis. Such effect is not directly aimed

332 but induced by the extinction procedure. It has not been previously described and has to be

333 differentiated from the known effect of winter heading cut (Barritt 1992) which reduces the

334 length of current season- and one-year-old wood and stimulates the growth of new long

335 shoots (e.g. Grechi et al. 2008).

336   Superimposed to aggregation (Lathrop, 1928), a strong structuring effect of

337   architecture through the number of branching points between 2 shoots was observed on the

338   dispersal of individuals to colonize new shoots. Within-branch RAA infestation dynamics

339   relied on two superposed processes: within-branch aphid dissemination and/or multiplication

340   rates, which were likely to prevail since only wingless RAA forms were present along the

341   experiment in (at least partly) isolated branches. Moreover, as all training practices were

342   similar in both training systems and no or scarce competitors (other aphids) or regulators

343   (natural enemies) were observed, differences in aphid infestation were only due to the

344   intrinsic properties of the branch architecture shaped by the training system. We investigated

345   two infestation processes under natural and not controlled infestation conditions for different

346   levels of initial RAA infestation: (i) short-distance dissemination according to branching in

347   2007 when a wide range of infestation levels occurred (Fig. 5), and (ii) short-distance

348   infestation patterns according to the training system, under a low infestation background

349   (2008, Fig. 4b). These differences in initial infestation can explain different infestation

350   patterns between 2007 and 2008: the proportion of newly infested shoots between D1 and D2

351   differed in OS and CT branches in 2007 (Fig. 3a) for a similar severity increase (Fig. 4a). The

352   opposite was observed in 2008: the proportion of infested shoots was similar (Fig. 3b), but

353   severity differed (Fig. 4b). We may hypothesise that at least two interacting processes

354   occurred:

355   (i) The resource hypothesis: less propitious feeding resources, e.g. related to leaf nitrogen

356   content as well as a lower proportion of shoots suitable for aphid development (Grechi et al.

357   2010) induce a lower multiplication rate of aphids. The highest infestation of long growing

358   and fruiting shoots of our study is also related to well-known trophic relationships. This result

359   is consistent with the preferential development of fruit tree aphids on growing shoots (Grechi

360   et al. 2008) and more especially when they are long (Stoeckli et al. 2008b) in the peach -

361   *Myzus persicae* (Sulzer) (Aphididae) and apple - *A. pomi* cases studies, respectively. Sap

362   nutrient quality mediated by source-sink processes (also altered by sap-consumer aphids) can

363   explain such prevalence of aphids on growing and/or fruiting shoots (Larson and Whitham

364   1997). This resource hypothesis, which was not directly investigated in the present study, is

365   documented in literature.

366   (ii) The structural hypothesis: the dispersal process is constrained by both a higher degree of

367   branching and a higher shoot density. Such constrain may explain both a lower proportion of

368   newly infested shoots (2007, Fig. 3a) and a less severe RAA infestation at D2 (2008, Fig. 4b)

369   in CT compared to OS branches because of a delayed arrival of aphids on the newly infested

370   shoots. This hypothesis is supported by a lower infestation progress when aphid pathway from

371   one shoot to its distal neighbour had 4 compared to 1 branching points (Fig. 5). To the best of

372   our knowledge, as there is no previous study establishing differences in trophic resources

373   related to the degree of branching in a fruit tree (see Fig. 5, drawn independently of the

374   training system), the structural hypothesis warrants further comments.

375

376   2) Insect movement in complex habitats and applications for aphid control

377   In the structural hypothesis, each branching point can be seen as a node from a

378   geometrical point of view but as a crossroads for pedestrian foraging aphids. The number of

379   crossroads related to the branching degree affects the probability of reaching the target

380   resource, i.e. whether next or a more distant shoot (Neuvonen 1999). At 0.5 probability for

381   each direction at a crossroads, successive crossroads along the aphid pathway will then result

382   in a very low probability of reaching a topologically distant shoot, without counting increased

383   travel time due to unsuccessful forward and backward movements along the branch. Patterns

384   of connectivity (Hannunen 2002; Randlkofer et al. 2010) seen as the measure of physical

385   contacts between shoots may also interfere although not under focus in our study. The theory

386   of dendritic networks applied to population dynamics (Campbell Grant et al. 2007) may help

387   to represent the within-branch movement and colonisation of aphids, and the significance of

388   shoots, sub-branches and crossroads (nodes). Branches may be seen as composed of suitable

389   habitats (shoots) and pathways of dispersal (main axes and axes of sub-branches) that may

390   present more or fewer crossroads according to the degree of branching. This also comes back

391   to plant heterogeneity and sectoriality (Orians and Jones 2001) as underlying processes

392   constraining aphid population dynamics within apple tree branches. This opens a field of

393   research to investigate these mechanisms via the study of within-tree 3D topology and

394   geometry (structural aspect) and nutritional status (physiological aspect) of shoots in relation

395   to branch architecture and RAA infestation rates.

396   At orchard level, tree architectural traits are both genetically determined for the

397   general tree habit (Lespinasse and Delort 1986; Lauri and Laurens 2005; Costes et al 2006)

398   and manipulated by cultural practices, namely tree training and pruning (Lauri 2002). Tree

399   architecture manipulation can contribute to modify (i) resource availability and access (plant-

400   mediated 'bottom up' processes) and (ii) natural enemies' attractiveness and success in prey

401   localisation (natural enemies-mediated 'top down' processes). Natural enemies were not

402   active in the present study, most probably because of their late arrival. But when considering

403   the complete apple pest complex, another important step would include tri-trophic interactions

404   among plant, pests and natural enemies. It has also to be considered that natural enemies may

405   be less efficient in complex habitats (Gingras and Boivin 2002; Legrand and Barbosa 2003;

406   Randlkofer et al. 2010; Riihimäki et al. 2006) despite increased abundance (Langellotto and

407   Denno 2004). Previous studies have demonstrated the benefits of CT for yield and fruit

408   quality (Lauri et al. 2007) and to lower aphid damage on apples (Simon et al. 2006). Although

409   expected benefits of tree training to control RAA are partial only, tree training appears to be a

410   relevant lever to consider and to combine with other protection methods. The identification of

411 architectural traits detrimental to pests thus contributes to design scientifically-based tree

412 training systems to decrease pesticide dependence in orchards and to contribute to sustainable

413 fruit production.

414

422

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545

546

547   Table 1. Architectural parameters measured at D1 (i.e. start of *Dysaphis plantaginea*

548   multiplication phase) at branch level in original solaxe (OS) and centrifugal training (CT)

549   branches in both years

550

Architectural parameters	2007		2008	
	OS	CT	OS	CT
Shoot number per branch	138.00 ± 14.46	115.75 ± 25.24	159.50 ± 23.55	272.63 ± 45.14
% long shoots[1]	30.83 ± 3.39	21.87 ± 2.67	9.98 ± 1.83	6.71 ± 1.98
% fruiting shoots	54.92 ± 4.88	21.39 ± 4.38	8.27 ± 4.76	12.04 ± 4.59
% growing shoots	33.28 ± 3.91	24.28 ± 4.30	25.00 ± 1.34	20.31 ± 1.41
Shoot density[2]	78.04 ± 3.92	80.86 ± 13.29	93.60 ± 7.86	144.08 ± 14.96

551   Each value is mean ± SE on 8 infested branches

552   [1] Length categories: short, < 5 cm; long, ≥ 5 cm

553   [2] Total number of current-year shoots of a branch per unit of length of the main axis of this branch (number of

554   shoots.m^{-1})

555

556   Table 2. *Dysaphis plantaginea* infestation at branch level in the original solaxe (OS) and

557   centrifugal training (CT) systems at D1 (i.e. start of *D. plantaginea* multiplication phase) and

558   D2 (*D. plantaginea* infestation peak) on apple in spring 2007 and 2008

559

Monitored variables	Year	OS		CT	
		D1	D2	D1	D2
Infested shoots (%)	2007	28.60 ± 9.30	53.88 ± 12.04	41.02 ± 10.83	59.44 ± 12.85
Infestation severity score	2007	0.36 ±0.12	0.77 ± 0.20	0.50 ± 0.13	0.85 ± 0.20
Infested shoots (%)	2008	2.77 ± 1.15	31.66 ± 10.90	1.70 ± 0.54	25.61 ± 7.60
Infestation severity score	2008	0.04 ± 0.02	0.45 ± 0.17	0.03 ± 0.01	0.31 ± 0.09

560   Each value is mean ± SE on 8 infested branches

561

562   Figure 1. Topological annotation of a simplified branch taking into account branching order

563   and rank of insertion. Two shoots inserted at the same topological place (e.g. two "bourse

564   shoots" on the same flower cluster such as shoot '5' and shoot '5bis') are considered to have

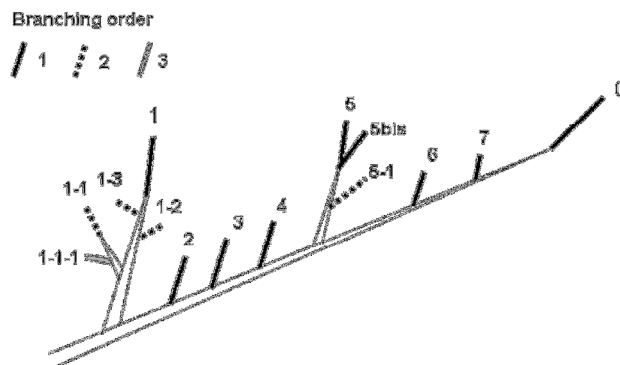565   similar branching order and one branching point between them.

566

567

568   Figure 2. Proportions of shoots per branching order in the original solaxe (OS) and centrifugal

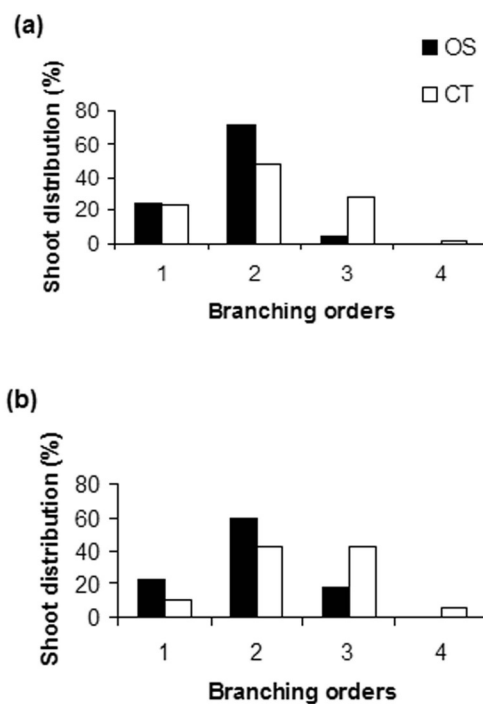569   training (CT) branches in (a) 2007 and (b) 2008

570

571   Figure 3. Infestation course between start and peak of spring *Dysaphis plantaginea* infestation

572   of shoots on apple in the original solaxe (OS) and centrifugal training (CT) branches in (a)
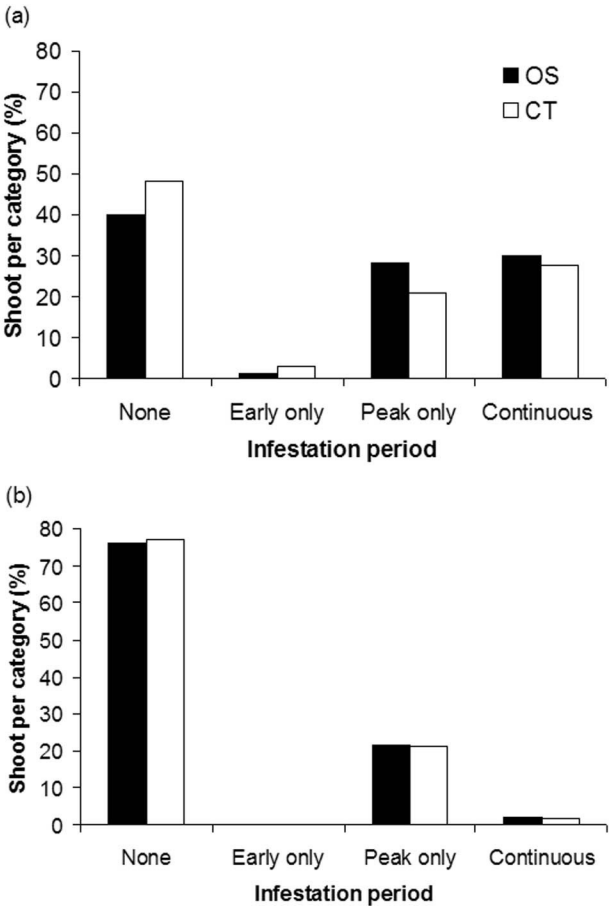
573   2007 and (b) 2008.

574

575   Figure 4. Relationships between *Dysaphis plantaginea* infestation severity of a target shoot at

576   D2 (i.e. infestation peak) and the mean infestation severity of its nearest adjacent shoots

577   (mean severity among 1 to 2 adjacent shoots) at D1 (start of *D. plantaginea* multiplication

578   phase) on apple in years (a) 2007 and (b) 2008 in the original solaxe (OS) and centrifugal

579   training (CT) branches. Symbols are means per severity class when three shoots or more.

580   When larger than symbols lines above or below symbols are standard errors. Regression lines

581   are computed for (a) 2007 OS (y = 0.5787x + 0.8075, r² = 0.7165, n = 6; plain line) and CT (y

582   = 1.0804x + 0.3298, r² = 0.9898, n = 6; dash line) systems; (b) 2008 OS (y = 0.899x + 0.8116,

583   r² = 0.6717, n = 5; plain line) and CT y = 0.8281x + 0.3829, r² = 0.8505, n = 4; dash line)
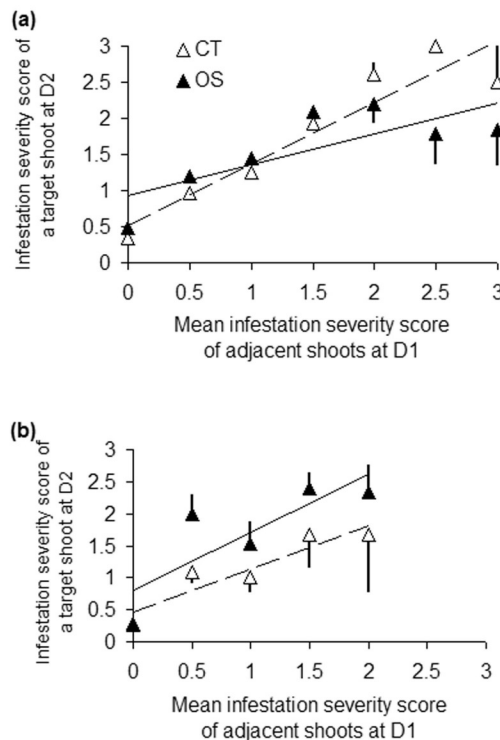
584

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586

587   Figure 5. Relationships between *Dysaphis plantaginea* infestation severity of a target shoot at

588   D2 (infestation peak) and the infestation severity of its nearest proximal shoot at D1 (start of

589   *D. plantaginea* multiplication phase) on apple for different numbers of branching points

590   between the two shoots (2007, all shoots pooled). Symbols (means per severity class when

591   two shoots or more) and regression lines (n = 4) are represented for 1 (dotted line), 2 (dash

592   line), 3 (plain line) and 4 (bold line) branching points. When larger than symbols lines above

593   or below symbols are standard errors

594