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# 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

3

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16 Running title: Branch architecture and aphid infestation

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## 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;

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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 Bonnemaïson 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 (Bonnemaïson 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) (Bonnemaïson 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<sup>®</sup> 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<sup>-1</sup> 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**

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,  $\geq$  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**



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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<sup>-1</sup>),  
199 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  $\chi^2$  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  $\chi^2$  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).

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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

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

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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

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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

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418 experimental unit and B. Hucbourg (GRCETA Basse-Durance) for their contribution to tree  
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420 (Supagro Montpellier) for stimulating discussions, and to David Biron for his helpful advice  
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422

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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 <sup>1</sup>	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 <sup>2</sup>	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 <sup>1</sup> Length categories: short, < 5 cm; long, ≥ 5 cm

553 <sup>2</sup> 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<sup>-1</sup>)

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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

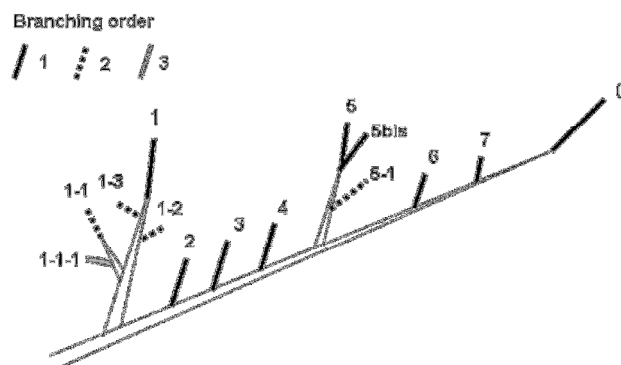
560 Each value is mean ± SE on 8 infested branches

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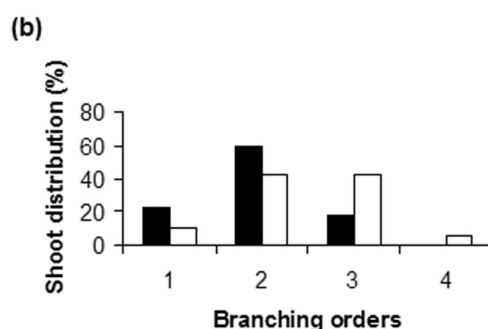
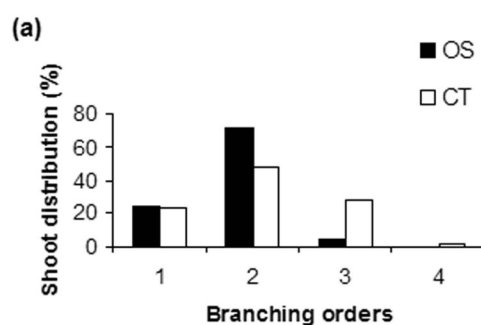
562 Figure 1. Topological annotation of a simplified branch taking into account branching order  
563 and rank of insertion. Two shoots inserted at the same topological place (e.g. two “bourse  
564 shoots” on the same flower cluster such as shoot ‘5’ and shoot ‘5bis’) are considered to have  
565 similar branching order and one branching point between them.



566

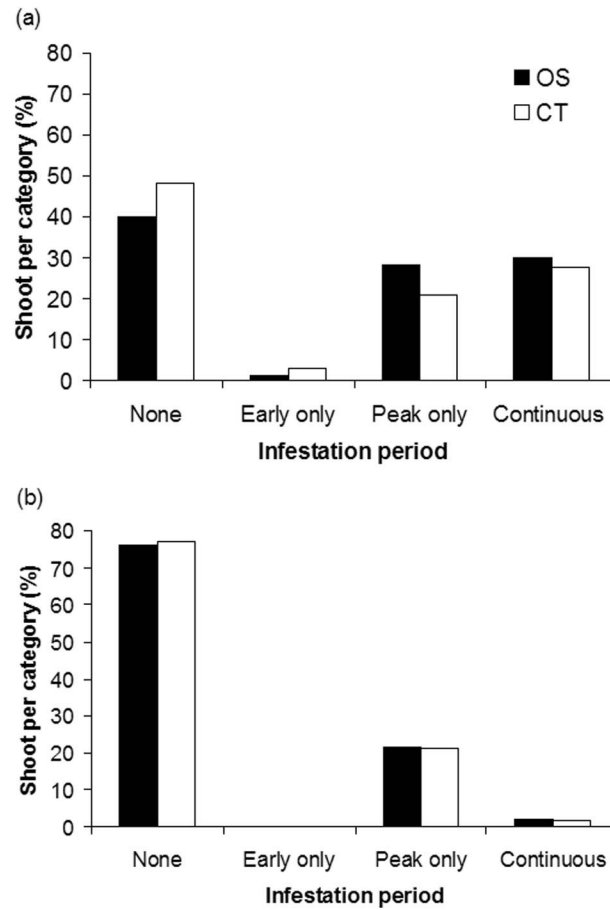
567

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.

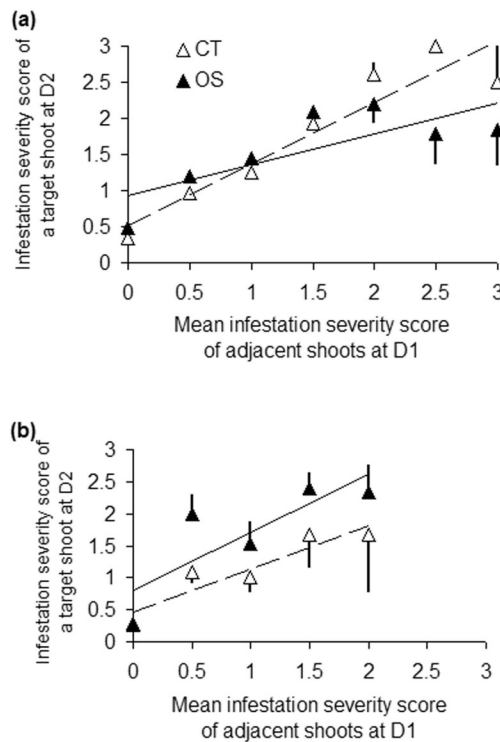


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575 Figure 4. Relationships between *Dysaphis plantaginea* infestation severity of a target shoot at  
576 D2 (i.e. infestation peak) and the mean infestation severity of its nearest adjacent shoots  
577 (mean severity among 1 to 2 adjacent shoots) 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 ( $y = 0.5787x + 0.8075$ ,  $r^2 = 0.7165$ ,  $n = 6$ ; plain line) and CT ( $y$   
582  $= 1.0804x + 0.3298$ ,  $r^2 = 0.9898$ ,  $n = 6$ ; dash line) systems; (b) 2008 OS ( $y = 0.899x + 0.8116$ ,  
583  $r^2 = 0.6717$ ,  $n = 5$ ; plain line) and CT  $y = 0.8281x + 0.3829$ ,  $r^2 = 0.8505$ ,  $n = 4$ ; dash line)  
584



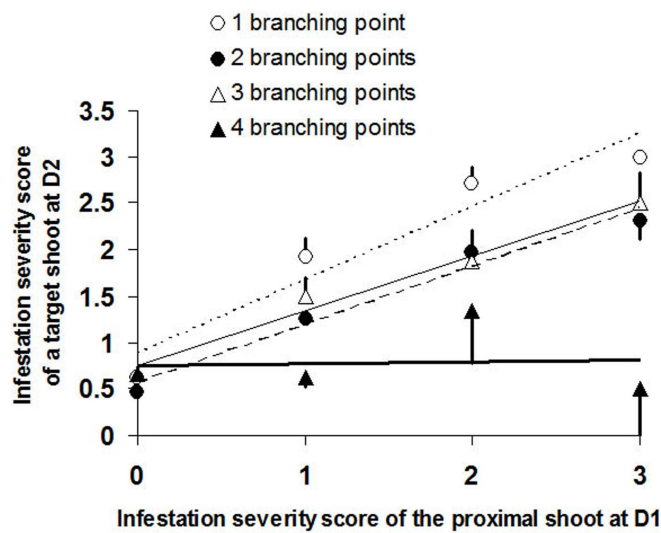
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587 Figure 5. Relationships between *Dysaphis plantaginea* infestation severity of a target shoot at  
588 D2 (infestation peak) and the infestation severity of its nearest proximal shoot at D1 (start of  
589 *D. plantaginea* multiplication phase) 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