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# 1 Nature Abhors a Vacuum: Deciphering the Vegetative Reaction of 2 the Mango Tree to Pruning

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18  
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20 vegetative growth

21  
22 **Declarations of interest: none**

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26

27 **Abstract**

28 Pruning is an important horticultural practice that generally promotes vegetative growth.  
29 However, the precise characterization of vegetative growth after pruning and of the factors  
30 affecting it are little known. The objective of this study was to decipher the vegetative  
31 response to pruning in a tropical evergreen species, the mango tree. Pruning was characterized  
32 by two factors: pruning intensity, defined at the tree scale as the amount of fresh biomass  
33 removed per unit volume of canopy, and pruning severity, defined at the axis scale as the  
34 distance between the pruning point and the distal end of the axis. Vegetative growth after  
35 pruning was broken down into structural (burst rate, vegetative growth intensity, leaf area  
36 produced) and temporal (burst date) variables, and the effects of pruning were evaluated on  
37 these variables at a local scale on pruned axes and at a distant scale on unpruned axes. Burst  
38 rate and leaf area produced increased with pruning intensity (pruned and unpruned axes),  
39 pruning severity (pruned axes), axis diameter (pruned and unpruned axes) and proximity to  
40 pruned axes (unpruned axes). Vegetative growth intensity increased with pruning severity  
41 (pruned axes) and axis diameter (pruned and unpruned axes) but was not affected by pruning  
42 intensity. For these three variables, local responses were more important than distant  
43 responses. The dynamics of vegetative growth was affected by pruning intensity and severity.  
44 Results depicted the complexity of mango tree response to pruning at different scales. As a  
45 general rule, more extensive pruning led to larger and more synchronous vegetative growth.

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## 52 **1. Introduction**

53

54 Pruning is an important horticultural practice whose purpose is to control the size of fruit  
55 trees, to improve the distribution of light within the canopy and the orchard, and to facilitate  
56 cultivation practices and harvest (Oosthuysen, 1994). Depending on the studies, yield can be  
57 higher (Avilán et al. 2003; Bhagawati et al., 2015; Reddy and Kurian 2011), similar  
58 (Albarracín et al., 2017; Oosthuysen, 1994) or lower (Oosthuysen, 1997) on pruned trees than on  
59 unpruned trees. The three cases can be reported for a single species such as the mango tree  
60 (Menzel and Le Lagadec, 2017). Even though pruning has often been studied, the reasons for  
61 these contrasted effects of pruning on yield are not well understood. This could be because  
62 these studies focused on the effects of tree pruning on yield, and were not designed to  
63 decipher the tree response to pruning.

64 From a structural point of view, the effects of pruning on yield are probably indirect. Pruning  
65 leads to numerous modifications that could be a benefit (improvement of light interception) or  
66 a disadvantage (reduction of the number of potential flowering sites, loss of leaf area, loss of  
67 wood containing carbohydrate reserves) for yield. Numerous studies have shown that pruning  
68 stimulates vegetative growth (Fumey et al., 2011; Jonkers, 1962; Oosthuysen, 1994). This  
69 vegetative growth can then affect the ensuing flowering and fruiting since it has been shown  
70 in several species that morphological, structural and temporal characteristics of vegetative  
71 growth can affect subsequent flowering and fruiting (Dambreville et al., 2013a; Gaaliche et  
72 al., 2011; Lauri and Trottier, 2004; Normand et al., 2009). The structural (how much and  
73 where?) and temporal (when?) characteristics of vegetative growth in response to pruning  
74 thus appear to be key issues to better understand the variable effects of pruning on yield.

75 Pruning represents the removal of a part of the above-ground biomass, and generates an  
76 imbalance between above- and below-ground biomass within the tree. These two biomasses

77 are isometrically related within a wide range of woody and non-woody species (Niklas, 2005),  
78 and their ratio, often referred to as the shoot:root ratio, is considered as a functional  
79 equilibrium within the plant for a given environment, leading to a balance in the uptake of the  
80 various resources (Brouwer, 1962; Grechi et al., 2007). If a disturbance like pruning modifies  
81 this ratio, the plant adapts both shoot and root growth rates in order to re-establish the  
82 shoot:root ratio that existed before the disturbance. Even if the mechanisms that regulate the  
83 partitioning between roots and shoots are still poorly understood, hormonal and nutritional  
84 controls have been suggested (Brouwer, 1962). We consider the shoot:root ratio framework in  
85 order to predict the structural and temporal vegetative responses of a tree to pruning. If we  
86 assume that the main driver of vegetative growth after pruning is the recovery of the tree  
87 balance between below- and above-ground biomass, and that the period for vegetative growth  
88 is limited, for example, by favorable environmental conditions, then more extensive pruning  
89 probably leads to larger number of buds that burst and to early bud burst after pruning,  
90 allowing a longer period for vegetative growth. We also assume that the removal of biomass  
91 at the branch scale creates a local imbalance and that the local reaction at the pruning point  
92 follows the same rules as at the tree scale. On the basis of these hypotheses at the tree and at  
93 the local scales, we can expect that the more biomass that is removed, the larger and earlier  
94 the local vegetative growth will be, and that vegetative growth will be greater and earlier on  
95 unpruned axes when pruning is extensive. The spatial (local reaction on pruned axes vs.  
96 distant reaction on unpruned axes) and temporal dimensions are important points for  
97 deciphering how a tree canopy reacts to pruning.

98 The objective of our study was to test these hypotheses on the mango tree (*Mangifera indica*).  
99 This fruit crop is very popular in tropical and subtropical areas where it is of economic and  
100 nutritional importance (Mukherjee and Litz, 2009). It rates fifth in terms of worldwide fruit  
101 production (Gerbaud, 2015). Contrary to deciduous fruit trees like the apple tree or the peach

102 tree for which the main pruning occurs in winter and concerns wood only, the mango tree is  
103 an evergreen tree and pruning therefore leads to removal of both wood and leaves. Another  
104 major difference with temperate fruit trees is that mango tree pruning occurs after harvest,  
105 during the hot and rainy season, with environmental conditions that allow a rapid regrowth  
106 after pruning. From a practical point of view, we applied contrasted degrees of pruning at the  
107 tree scale and at the pruned axis scale and characterized vegetative growth on the pruned axes  
108 (local effect) and on unpruned axes (distant effect) according to the structural and temporal  
109 dimensions.

110

## 111 **2. Materials and methods**

### 112 **2.1 Plant material**

113 The study was carried out in 2016 and 2017 in an experimental orchard located at the French  
114 Agricultural Research Center for International Development (CIRAD) station in Saint-Pierre,  
115 Reunion Island (21°19'S, 55°29'E, 125 m a.s.l). The soil is a brown ferralitic soil, with a  
116 depth of about 1.5 m, a low spatial heterogeneity and a good available water capacity (130  
117 mm.m<sup>-1</sup>) (Raunet, 1991). Trees were planted in 2004 with a distance of 6 m between rows and  
118 5 m between trees within a row. The orchard was composed of 153 trees of the Floridian  
119 cultivar 'Cogshall', grafted onto the rootstock 'Maison Rouge'. Tree biomass and its  
120 distribution between above- and below-ground parts were not determined. Davie and Stassen  
121 (1997) and Normand et al. (2006) recorded an average tree dry mass of 121.4 kg and 178.4  
122 kg, and a shoot:root ratio of 3.3 and 2.3, for 11- and 13-year-old mango trees, respectively.

123 Trees were not fertilized because of the good and deep soil in the orchard and to avoid  
124 affecting vegetative growth during the experiment. The last pruning in the orchard was in  
125 2014, meaning that the observed trees had not been pruned for at least two years before the  
126 experiment in order to avoid a potential long-term effect of previous pruning. Trees were drip-

127 irrigated on an evapotranspiration basis ( $5 \text{ mm.d}^{-1}$ ) as of flowering, i.e., from about 6 months  
128 before pruning until rainfall was sufficient to maintain soil moisture, i.e., five and three weeks  
129 after pruning in 2016 and 2017, respectively. Weeds were cut every four weeks with a flail  
130 mulcher. No phytosanitary treatment was performed during the experiment since vegetative  
131 growth is not susceptible to pests and diseases. Average yield was very low during the 2015-  
132 2016 growing cycle ( $2.2 \pm 3.8$  fruits/tree), whereas it was higher during the 2016-2017  
133 growing cycle ( $69.6 \pm 84.8$  fruits/tree).

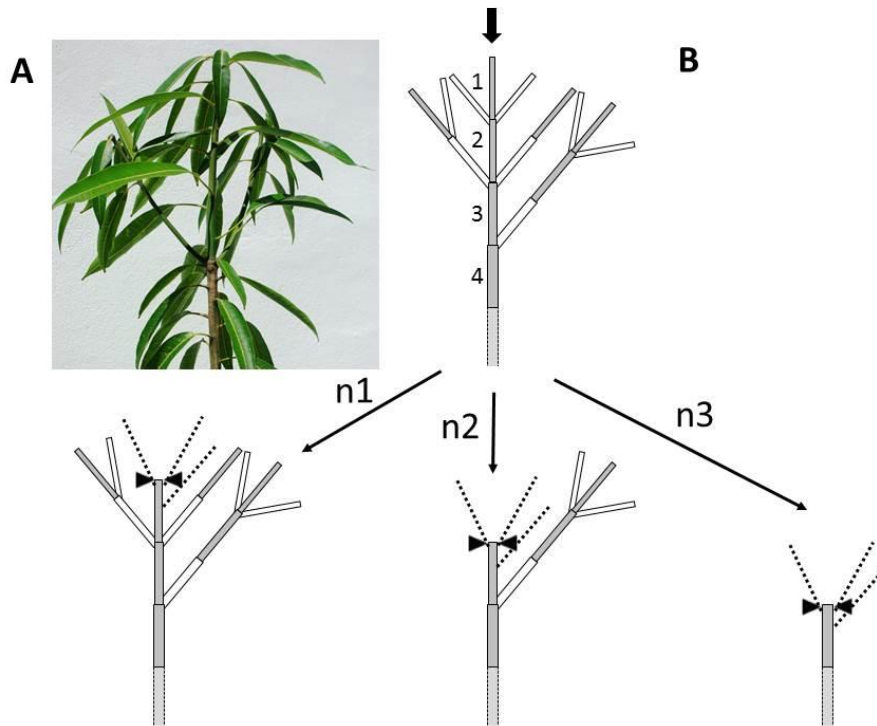
134 Climatic data were recorded by a nearby CIRAD automatic weather station. The average daily  
135 temperatures for the 70 days after pruning were similar between the two years  
136 (Supplementary data, Figure S1), with an average temperature of  $26.1^{\circ}\text{C}$  for both years. The  
137 total rainfall for the 70 days after pruning was 442 mm in 2016 and 274 mm in 2017. The  
138 weekly distribution of rainfall differed between the two years (Supplementary data, Figure  
139 S1). In 2016, a first episode of heavy rainfall occurred during the second week after pruning,  
140 and then from the fourth to the sixth week after pruning. In 2017, heavy rainfall occurred  
141 during the week after pruning, and then during the sixth week after pruning.

142 Under the subtropical climate of Reunion Island, vegetative growth of mango trees occurs  
143 mainly after harvest during the hot and rainy season from January to May. Vegetative growth  
144 is characterized by flushes, defined as short episodes of growth during which growth units  
145 (GUs) develop. A GU is defined as a portion of an axis developed during an uninterrupted  
146 period of growth (Hallé and Martin, 1968; Figure 1A). We used kinship terminology to  
147 describe the topological and temporal relationships between adjacent GUs: a mother GU can  
148 bear one or several daughter GUs, which can themselves become mother GUs and produce  
149 daughter GUs. A GU can be in an apical or lateral position with respect to its mother GU. An  
150 apical GU stems from the apical bud of the mother GU and a lateral GU stems from an  
151 axillary bud of the mother GU (Figure 1).

152 Pruning was characterized by two factors, pruning intensity and pruning severity. Pruning  
153 severity was defined at the axis scale as the distance between the pruning point and the distal  
154 end of the axis (Figure 1B). Because of the mango rhythmic growth, we considered the  
155 number of GUs as a measurement unit, rather than the length of the removed part of the axis  
156 (Jonkers, 1982; Negrón et al., 2015). Three modalities were considered: pruning under the last  
157 (n1), second to last (n2) or third (n3) GU from the distal end of the axis. If GUs branched at  
158 the selected pruning point, the point was moved to below the branching GUs in order to  
159 remove them as well (Figure 1B). For convenience, GUs pruned according to these modalities  
160 of pruning severity are referred to as n1 GUs, n2 GUs and n3 GUs, respectively. Pruning  
161 intensity was defined at the tree scale as the amount of fresh biomass (leaves and wood)  
162 removed per unit volume of tree canopy. Three modalities of pruning intensity were  
163 considered: unpruned control (C), lightly pruned (LP) and intensely pruned (HP), referred to  
164 as C trees, LP trees and HP trees, respectively. Pruning intensity and severity were applied on  
165 each pruned tree. Control C trees were not pruned and were therefore not concerned by the  
166 pruning severity factor.

167





168

169 Figure 1: Photograph of mango growth units showing a mother growth unit bearing three  
 170 daughter growth units, one in apical position in the middle and two in lateral position (A), and  
 171 schematic representation of the three modalities of pruning severity, n1, n2 and n3 (B).  
 172 Rectangles represent growth units (leaves are not represented). Apical growth units are gray  
 173 and lateral growth units are white. Top scheme: initial mango axis. The arrow indicates the  
 174 distal end of the axis and the numbers are the rank of the growth units along the axis. The axis  
 175 after pruning, according to pruning severity n1, n2 or n3, is represented below. Black triangles  
 176 indicate the pruning point where the diameter was measured after pruning. Three daughter  
 177 growth units, which appear after pruning, are represented by dotted lines on each pruned  
 178 growth unit.

179

180 Before pruning, the canopy volume of each tree was calculated as the product of canopy  
 181 height and canopy width in the row and between rows (rectangular cuboid). Fresh biomass  
 182 was removed by initially pruning 60 axes for LP trees and 180 axes for HP trees. Removed  
 183 biomass was collected and weighed. Then, to take differences in canopy volume among the

184 trees into account, additional axes were possibly pruned on each tree so that pruning intensity  
185 was adjusted to  $0.14 \pm 0.02$  kg of biomass removed per  $m^3$  of canopy for LP trees, and  $0.51 \pm$   
186  $0.05$  kg of biomass removed per  $m^3$  of canopy for HP trees. For both the initial pruning step  
187 and the subsequent step to adjust pruning intensity, pruned axes were fairly distributed per  
188 modality of pruning severity and within the tree canopy. Each modality of pruning intensity  
189 was repeated on four trees, i.e., a total of 12 trees, randomly sampled in the orchard. The  
190 experimental design was the same in 2016 and 2017 but different trees were pruned each year.  
191 Pruning was done at the end of the harvest, on January 14, 2016, and on February 1 and 2,  
192 2017.

193

## 194 **2.2 Data collection**

195 Vegetative growth after pruning was monitored on each tree on pruned (except on C trees)  
196 and unpruned GUs in order to assess the local and the distant effects of pruning, respectively.  
197 Thirty pruned GUs, 10 per modality of pruning severity, evenly distributed within the tree  
198 canopy, were sampled on the day of pruning on each LP and HP tree, and their diameter was  
199 measured at the pruning point. The leaf area ( $LA$ ,  $dm^2$ ) removed locally by pruning was  
200 estimated from the cross-sectional area of the pruned GUs at the pruning point ( $x$ ,  $mm^2$ ),  
201 considered as a circular section, according to the allometric relationship:

$$202 \quad LA = \exp(1.093 \ln x - 2.146) \quad (\text{Eq. 1})$$

203 Parameter values for the ‘Cogshall’ cultivar in Equation 1 are from Normand and Lauri  
204 (2012).

205 Thirty unpruned terminal GUs were sampled on each C, LP and HP tree on the day of  
206 pruning. Since GU position affects GU morphology and vegetative growth (Dambreville et  
207 al., 2013a; Normand et al., 2009), these unpruned terminal GUs were divided into 15 apical  
208 and 15 lateral GUs. Their basal diameter was measured. To assess if the presence of close

209 pruned GUs affected vegetative growth of unpruned GUs, the number of pruned GUs close to  
210 each unpruned GU was recorded in 2017, as well as their individual distance to the unpruned  
211 GU. The distance was measured in number of GUs along the axes between pruned and  
212 unpruned GUs. A pruned GU was considered close to an unpruned GU if the distance  
213 between them was less than or equal to 12 GUs. This threshold of 12 GUs was chosen in  
214 order to have a sufficient number of unpruned GUs in LP and HP trees with at least one close  
215 pruned GU and representing a wide range of distance between them. This threshold was also  
216 chosen to be not excessively high to suggest a potential direct or indirect effect of pruned GUs  
217 on unpruned GUs.

218 On pruned and unpruned GUs, burst date of each daughter GU (Figure 1B) was recorded  
219 every week during the period of vegetative growth, from the date of pruning up to June. Burst  
220 date was the date corresponding to the phenological stage C, i.e. bud opening, when leaves  
221 begin to spread out and GU axis is not yet apparent (Dambreville et al., 2015). This stage is  
222 easily identifiable and lasts one day, allowing a precise determination of the burst date. On  
223 pruned GUs, daughter GUs appeared at the axil of leaves or leaf scars, indicating that they  
224 stemmed from dormant axillary buds, and not from buds that were neofomed as a response to  
225 pruning. The number of daughter GUs per pruned or unpruned GU was calculated from these  
226 data. The number of leaves as well as the length ( $L$ ) and maximum width ( $l_{max}$ ) of the median  
227 leaf were recorded for each daughter GU at the end of the period of vegetative growth. The  
228 area of each median leaf ( $la$ , dm<sup>2</sup>) was estimated from its length and maximum width (cm)  
229 using the following relationship (Dambreville et al., 2013b):

$$230 \quad la = 0.0074 L l_{max} \quad (\text{Eq. 2})$$

231 The leaf area of a daughter GU was estimated as the product of its number of leaves and the  
232 area of its median leaf. The total leaf area produced by a pruned or an unpruned GU was the  
233 sum of the leaf area of its daughter GUs. The total leaf area of a GU that did not burst after

234 the date of pruning was zero.

235

### 236 **2.3 Data analysis**

237 Statistical analyses were carried out at the GU scale. At this scale, vegetative growth was  
238 studied through three response variables: (i) the occurrence of vegetative growth (burst rate),  
239 a binary variable corresponding to whether or not the GU produces at least one daughter GU;  
240 (ii) the intensity of vegetative growth, a discrete variable corresponding to the number of  
241 daughter GUs per bursting GU; and (iii) the total leaf area produced by a GU, a continuous  
242 variable. This third variable depends on the two previous response variables and on the  
243 morphology of the daughter GUs. For pruned GUs, a binary response variable corresponding  
244 to whether or not the total leaf area produced by the GU compensated for the leaf area  
245 removed by pruning (i.e., total leaf area produced  $\geq$  leaf area removed) was computed.

246 The factors considered to explain variability in these response variables were those controlled  
247 in the experiment (pruning intensity, pruning severity and GU position for unpruned GUs), as  
248 well as complementary factors corresponding to measured variables such as GU diameter or  
249 distance between pruned and unpruned GUs. Despite the high correlation between pruning  
250 severity and GU diameter at the pruning point (see Results, part 3.1), the effects of both  
251 factors were considered because of their different meaning from a biological point of view.  
252 Since pruning severity corresponds to pruning depth along the axis, it appears to be mainly  
253 related to the age of the buds close to the pruning point and probably related to the light  
254 environment of these buds. Diameter at the pruning point is mainly related to the amount of  
255 removed biomass and leaf area (Normand and Lauri, 2012) and to the local capacity for  
256 carbohydrate storage. For unpruned GUs, basal diameter was considered as a factor because a  
257 larger basal diameter indicates a larger leaf area for photosynthesis and a larger stem volume

258 for carbohydrate storage (Normand and Lauri, 2012), suggesting a higher availability of  
259 carbohydrates for vegetative growth.

260 Statistical analyses were carried out in successive steps in order to test the effects of the  
261 factors studied on each response variable. In the first step, the effects of pruning intensity,  
262 pruning severity and their interaction were tested on each response variable for pruned GUs,  
263 and the effects of pruning intensity, GU position and their interaction were tested on each  
264 response variable for unpruned GUs for each year. The year effect was then tested for pruned  
265 and unpruned GUs on each response variable on LP and HP trees. In the second step, the  
266 effects of complementary factors were tested in three ways. First, the effects of GU diameter  
267 at the pruning point for pruned GUs and of the basal diameter for unpruned GUs were tested  
268 on each response variable for each year. If a significant relationship was observed between the  
269 response variable and the GU diameter, the effects of pruning intensity and of pruning  
270 severity on the relationship were tested for pruned GUs. For unpruned GUs, only the effect of  
271 pruning intensity was tested on the relationship. Second, for unpruned GUs in 2017, the  
272 effects of the distance (in number of GUs) between the unpruned GU and the closest pruned  
273 GU, on the one hand, and of the number of pruned GUs close to the unpruned GU (at a  
274 distance  $\leq 12$  GUs), on the other, were tested on each response variable. If a significant  
275 relationship was found between the response variable and one of the two factors, the effect of  
276 pruning intensity was tested on the relationship. In the third step, the response variables were  
277 compared for each year between pruned and unpruned GUs on LP trees and on HP trees.

278 The dynamics of vegetative growth, a discrete variable corresponding to the duration,  
279 expressed in days, between the date of pruning and the date of burst of the first daughter GU  
280 of a pruned or an unpruned GU, was characterized and analyzed separately. Only the burst  
281 date of the first daughter GU to appear was considered because all the daughter GUs of a  
282 sampled GU burst in a short period of less than 10 days, and because it gave the same weight

283 to each pruned and unpruned GU in the dynamics fitting, independently of their number of  
284 daughter GUs. Vegetative growth after pruning occurred in one or two flushes, which were  
285 modeled as a weighed sum of two Gaussian distributions:

$$286 \quad d(t) = p N(\mu_1, \sigma_1)(t) + (1-p) N(\mu_2, \sigma_2) (t) \quad (\text{Eq. 3})$$

287 where  $d(t)$  is the density value at time  $t$ ,  $N(\mu, \sigma)$  is the Gaussian distribution with mean  $\mu$  and  
288 standard deviation  $\sigma$ , and  $p \in [0, 1]$  is the relative weight of the first flush. Parameters  $\mu_1, \sigma_1,$   
289  $\mu_2, \sigma_2$  and  $p$  were estimated from the data with a nonlinear method that maximizes log-  
290 likelihood. The effects of pruning intensity, pruning severity and type of GU (pruned vs.  
291 unpruned) on the dynamics of vegetative growth were determined by fitting Equation 3 for  
292 each modality of these factors. The duration of vegetative growth was estimated as the  
293 difference between quantiles 0.05 and 0.95 of the recorded data, i.e., 5% of the tails were  
294 removed on each side of the distribution. Similarly, the beginning of vegetative growth, or  
295 earliness, was calculated as the 0.05 quantile of the recorded data. Since pruning intensity  
296 affected vegetative growth dynamics, these variables were calculated each year for pruned  
297 and unpruned GUs within each pruning intensity, and for each pruning severity within each  
298 pruning intensity.

299 Statistical analyses were performed with R software, version 3.2.5 (R Development Core  
300 Team, 2016). Generalized Linear Models with appropriate distribution followed by Type-II  
301 analysis of deviance with a Wald chi-square test (Anova function of the ‘car’ package, Fox  
302 and Weisberg, 2011) were used to test the effects of the different factors on the response  
303 variables. When a significant effect of pruning intensity or pruning severity was found on a  
304 response variable, multiple comparisons were performed with the glht function of the  
305 ‘multcomp’ package (Hothorn et al., 2008). The nlm function was used to estimate the  
306 parameters of the mixture of Gaussian distributions to model dynamics of vegetative growth  
307 (Eq. 3). Because of the large sample size (> 100 GUs) and to highlight the main factors

308 affecting the response variables, the significance level was set at  $P=0.01$ . For better legibility  
309 of the results, the P-value of the tests is given only if  $P > 0.01$ , and non-significant  
310 interactions are not presented.

311

### 312 **3. Results**

313

314 No vegetative growth occurred on unpruned control trees (C) after the date of pruning of the  
315 LP and HP trees in 2016. Consequently, C trees were not included in the analyses in 2016 and  
316 pruning intensity had two modalities in 2016 (LP and HP trees) and three modalities in 2017  
317 (C, LP and HP trees).

318

#### 319 **3.1 Effect of pruning on GU diameter and proximity between unpruned and pruned** 320 **GUs**

321 The average diameter of pruned GUs at the pruning point significantly increased with pruning  
322 severity (Table 1). Average diameters of n1, n2 and n3 GUs were significantly different from  
323 each other for both years. For each modality of pruning severity, average diameters were  
324 similar in 2016 and 2017.

325

326 Table 1: Diameter (mean  $\pm$  standard deviation, mm) of pruned growth units at the pruning  
327 point according to pruning severity (n1, n2, n3) and year. Means in the same row followed by  
328 different letters are significantly different (Tukey test at the overall  $P=0.01$  level).

Year	Pruning severity		
	n1	n2	n3
2016	7.0 $\pm$ 1.7 c	9.6 $\pm$ 2.6 b	13.5 $\pm$ 3.6 a
2017	6.9 $\pm$ 1.6 c	9.5 $\pm$ 2.5 b	13.1 $\pm$ 3.4 a

329

330

331 The percentage of unpruned GUs with at least one close pruned GU was significantly higher  
 332 on HP trees (88%) than on LP trees (53%). For these unpruned GUs, the number of close  
 333 pruned GUs significantly increased with pruning intensity (LP trees:  $1.3 \pm 0.6$  GUs; HP trees:  
 334  $2.6 \pm 1.5$  GUs). However, the average distance, expressed in number of GUs, between these  
 335 unpruned GUs and their closest pruned GU was not significantly different on LP trees and on  
 336 HP trees (LP trees:  $7.6 \pm 2.5$  GUs; HP trees:  $6.9 \pm 2.1$  GUs;  $P=0.32$ ).

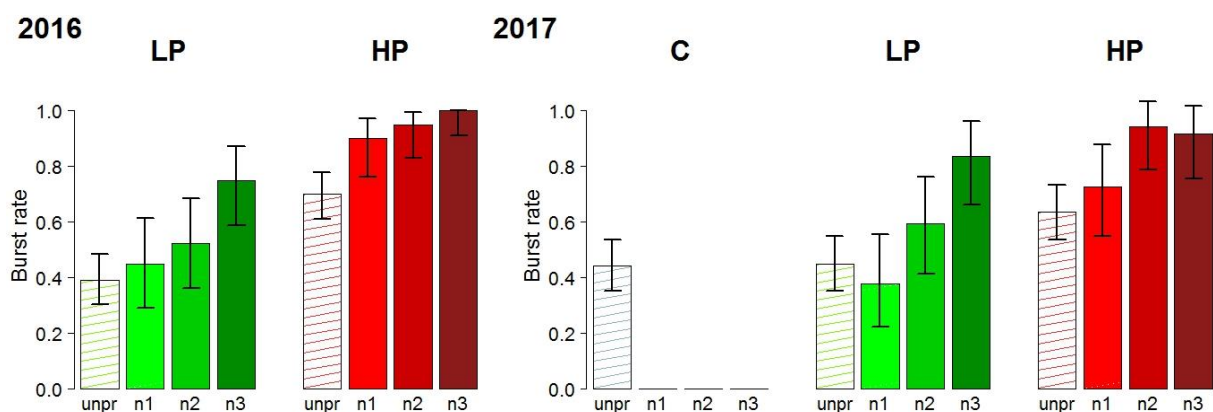
337

### 338 3.2 Effect of pruning on vegetative growth occurrence: GU burst rate

#### 339 3.2.1 Pruned GUs

340 The burst rate of pruned GUs was significantly higher on HP trees (2016: 0.95; 2017: 0.80)  
 341 than on LP trees (2016: 0.58; 2017: 0.56) and significantly increased with pruning severity  
 342 (Figure 2). Burst rate was significantly higher on n3 GUs (2016: 0.88; 2017: 0.81) than on n1  
 343 GUs (2016: 0.68; 2017: 0.51), and n2 GUs had intermediate values (2016: 0.74; 2017: 0.71).  
 344 On HP trees, the burst rate of pruned GUs was significantly higher in 2016 than in 2017 but  
 345 there was no significant difference between years on LP trees ( $P=0.79$ ).

346



347

348 Figure 2: Burst rate (mean  $\pm$  95% confidence interval) of unpruned growth units (unpr) and  
 349 pruned growth units according to pruning severity (n1, n2 and n3) for unpruned control trees  
 350 (C), lightly pruned trees (LP) and intensely pruned trees (HP) in 2016 and 2017. The



351 unpruned control trees did not produce vegetative growth after the pruning date of LP and HP  
352 trees in 2016 (no C tree modality).

353

354 The diameter at the pruning point had a significant and positive effect on the burst rate of  
355 pruned GUs. Pruning intensity significantly affected the relationship between burst rate and  
356 GU diameter. For the same diameter, the burst rate of pruned GUs on HP trees was higher  
357 than the one on LP trees. Pruning severity did not affect the relationship between burst rate  
358 and GU diameter in 2016 ( $P=0.74$ ) and in 2017 ( $P=0.67$ ), indicating a relationship  
359 independent of pruning severity.

360

### 361 **3.2.2 Unpruned GUs**

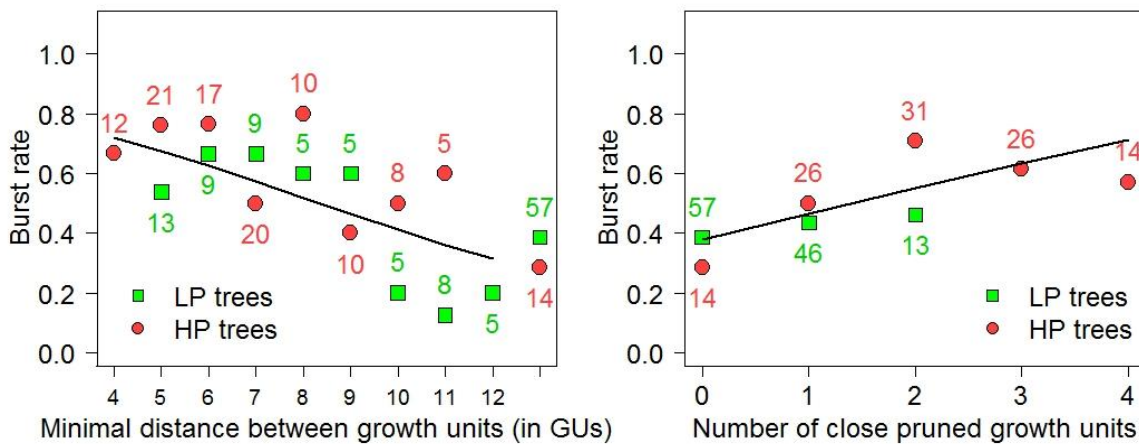
362 In 2016, the burst rate of unpruned GUs was significantly higher on HP trees than on LP trees  
363 (Figure 2). In 2017, the effect of pruning intensity on burst rate was barely significant  
364 ( $P=0.014$ , Figure 2). As in 2016, the burst rate of unpruned GUs was significantly higher on  
365 HP trees than on LP trees, and the burst rate on C trees had intermediate values. The position  
366 of unpruned GUs did not affect their burst rate in 2016 ( $P=0.52$ ) and in 2017 ( $P=0.83$ ). The  
367 burst rate of unpruned GUs was similar between the two years on both LP ( $P=0.69$ ) and HP  
368 ( $P=0.08$ ) trees.

369 In 2016, the burst rate was not related to the basal diameter of unpruned GUs ( $P=0.46$ ). In  
370 2017, GU basal diameter had a significant and positive effect on burst rate. Pruning intensity  
371 affected this relationship (Supplementary data, Figure S2). The relationship was rather linear  
372 for LP and HP trees. For the same diameter, unpruned GUs on HP trees had a higher burst  
373 rate than unpruned GUs on LP trees. The relationship was logistic for C trees. Unpruned GUs  
374 on C trees had a lower burst rate than unpruned GUs on LP and HP trees for diameters  
375 smaller than about 5.6 mm, and a similar burst rate for larger diameters (Figure S2).

376 The proximity of pruned GUs had a significant effect on unpruned GU burst rate. The closer  
 377 an unpruned GU was to a pruned GU, the higher its burst rate was (Figure 3A). Pruning  
 378 intensity did not affect the relationship between burst rate and distance between pruned and  
 379 unpruned GUs ( $P=0.05$ ). For unpruned GUs that were far from a pruned GU (distance  $> 12$   
 380 GUs, Figure 3A), burst rate was similar ( $P=0.48$ ) to the one of unpruned GUs on C trees  
 381 (Figure 2). The number of pruned GUs close to an unpruned GU had a significant and positive  
 382 linear effect on the burst rate of unpruned GUs (Figure 3B). Pruning intensity did not affect  
 383 this relationship ( $P=0.04$ ).

384 The burst rate was significantly higher on pruned GUs than on unpruned GUs on HP trees  
 385 (Figure 2). On LP trees, the burst rate was significantly higher on pruned GUs than on  
 386 unpruned GUs in 2016, but not in 2017 ( $P=0.28$ ; Figure 2).

387



388

389

390 Figure 3: Average burst rate of unpruned growth units (GUs) according to pruning intensity  
 391 and to the minimal distance (in number of GUs) between the unpruned GU and the closest  
 392 pruned GU (A), and according to pruning intensity and to the number of pruned GUs close to  
 393 the unpruned GU (distance  $\leq 12$  GUs; B). The lines represent the linear regression of burst  
 394 rate on the distance and on the number of close pruned GUs, independently of the pruning

395 intensity ( $P > 0.01$ ). Unpruned GUs with the closest pruned GUs at a distance greater than 12  
396 GUs were not taken into account in the linear regression between burst rate and minimal  
397 distance between GUs since this class did not correspond to a particular distance value. Points  
398 represent the average burst rate observed per class of distance or number of close pruned  
399 GUs. Numbers above or below the points correspond to sample size. Only sample sizes larger  
400 than 4 GUs are represented.

401

### 402 **3.3 Effect of pruning on the number of daughter GUs per bursting GU: vegetative** 403 **growth intensity**

#### 404 **3.3.1 Pruned GUs**

405 Pruning intensity did not affect the vegetative growth intensity of pruned GUs, which was  
406 remarkably stable (2016: LP trees:  $3.4 \pm 2.2$  GUs, HP trees:  $3.4 \pm 2.1$  GUs,  $P=0.96$ ; 2017: LP  
407 trees:  $3.4 \pm 2.4$  GUs, HP trees:  $3.4 \pm 2.2$  GUs,  $P=0.94$ ; Figure 4). In contrast, pruning severity  
408 had a significant effect on vegetative growth intensity, where n3 GUs (2016:  $4.2 \pm 2.6$  GUs;  
409 2017:  $3.9 \pm 2.6$  GUs) had significantly more daughter GUs than n1 GUs in 2016 and 2017  
410 (2016:  $3.2 \pm 1.8$  GUs; 2017:  $2.6 \pm 1.8$  GUs) and than n2 GUs in 2016 only (2016:  $2.7 \pm 1.4$   
411 GUs; 2017:  $3.4 \pm 2.1$  GUs). Vegetative growth intensity was similar between the two years on  
412 both LP ( $P=0.96$ ) and HP trees ( $P=0.84$ ; Figure 4).

413 The diameter of pruned GUs had a significant and exponential effect on vegetative growth  
414 intensity. Pruning intensity did not affect this relationship (2016:  $P=0.16$ ; 2017:  $P=0.37$ ).  
415 Pruning severity affected this relationship in 2016 but not in 2017 ( $P=0.26$ ). In 2016, for the  
416 same diameter, n2 GUs had a significantly lower vegetative growth intensity than n1 GUs,  
417 and n3 GUs had intermediate values.

418

#### 419 **3.3.2 Unpruned GUs**

420 Pruning intensity did not affect vegetative growth intensity of unpruned GUs (Figure 4). In  
 421 contrast, the position of unpruned GUs affected the vegetative growth intensity: apical  
 422 unpruned GUs produced significantly more daughter GUs (2016:  $1.6 \pm 1.1$  GU; 2017:  $1.7 \pm$   
 423  $1.3$  GUs) than lateral unpruned GUs (2016:  $1.2 \pm 0.5$  GUs; 2017:  $1.3 \pm 0.6$  GUs). Vegetative  
 424 growth intensity of unpruned GUs was similar between the two years on both LP (2016:  
 425  $P=0.25$ ) and HP trees (2016:  $P=0.12$ ; Figure 4).

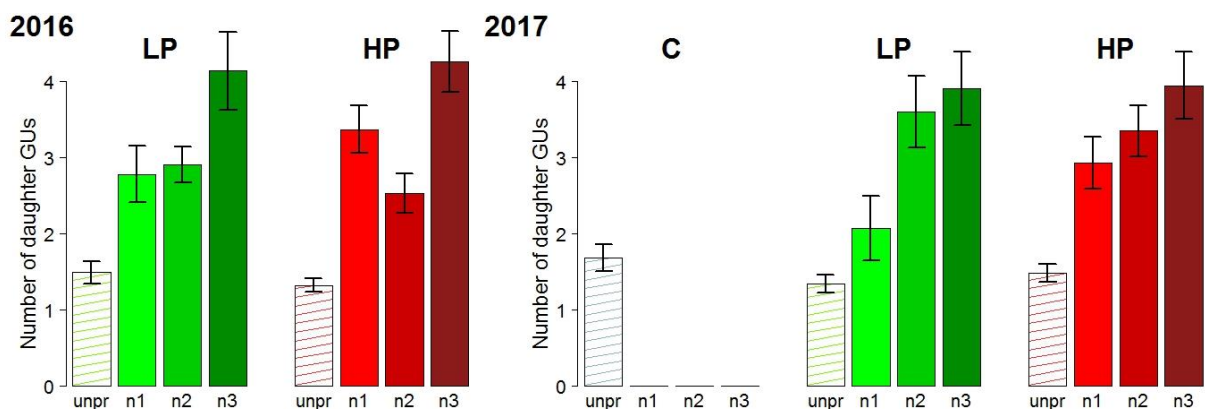
426 The basal diameter of unpruned GUs had a significant and exponential effect on vegetative  
 427 growth intensity. Even though pruning intensity did not affect vegetative growth intensity of  
 428 unpruned GUs in 2016 and in 2017, it affected the relationship between vegetative growth  
 429 intensity and the basal diameter of unpruned GUs in 2017, but not in 2016 ( $P=0.16$ ). For the  
 430 same diameter, unpruned GUs of C trees had significantly lower vegetative growth intensity  
 431 than those of LP and HP trees.

432 The presence of pruned GUs close to unpruned GUs did not affect the vegetative growth  
 433 intensity of the latter (effect of the minimum distance between the unpruned GU and the  
 434 closest pruned GU:  $P=0.23$ ; effect of the number of close pruned GUs:  $P=0.50$ ).

435 Vegetative growth intensity was significantly higher on pruned GUs than on unpruned GUs  
 436 on both LP and HP trees (Figure 4).

437

438



439

440 Figure 4: Number (mean  $\pm$  standard error) of daughter growth units (GUs) of unpruned GUs  
 441 (unpr) and pruned GUs according to pruning severity (n1, n2 and n3) for unpruned control  
 442 trees (C), lightly pruned trees (LP) and intensely pruned trees (HP) in 2016 and 2017. The  
 443 unpruned control trees did not produce vegetative growth after the pruning date of LP and HP  
 444 trees in 2016 (no C tree modality).

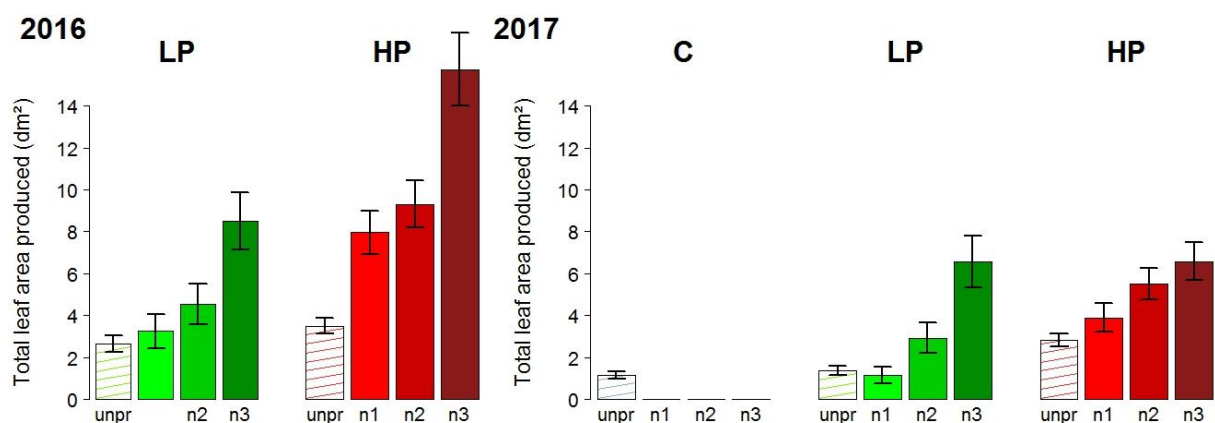
445

### 446 3.4 Effect of pruning on the total leaf area produced per pruned and unpruned GU

#### 447 3.4.1 Pruned GUs

448 The total leaf area produced per pruned GU increased with pruning intensity and pruning  
 449 severity (Figure 5). Pruned GUs produced more leaf area on HP trees (2016:  $11.0 \pm 9.0$  dm<sup>2</sup>,  
 450 2017:  $5.3 \pm 5.1$  dm<sup>2</sup>) than on LP trees (2016:  $5.4 \pm 7.1$  dm<sup>2</sup>; 2017:  $3.6 \pm 5.8$  dm<sup>2</sup>) in both  
 451 years. In 2016, n3 GUs produced more leaf area than n1 and n2 GUs. In 2017, the difference  
 452 between n3 and n2 GUs was barely significant (P=0.014). Pruned GUs on HP trees produced  
 453 more leaf area in 2016 than in 2017. The same trend was observed on LP trees, but the  
 454 difference was not significant (P=0.02).

455



456

457 Figure 5: Total leaf area (mean  $\pm$  standard error, dm<sup>2</sup>) produced per unpruned growth unit  
 458 (unpr) and pruned growth unit according to pruning severity (n1, n2 and n3) for unpruned  
 459 control trees (C), lightly pruned trees (LP) and intensely pruned trees (HP) in 2016 and 2017.

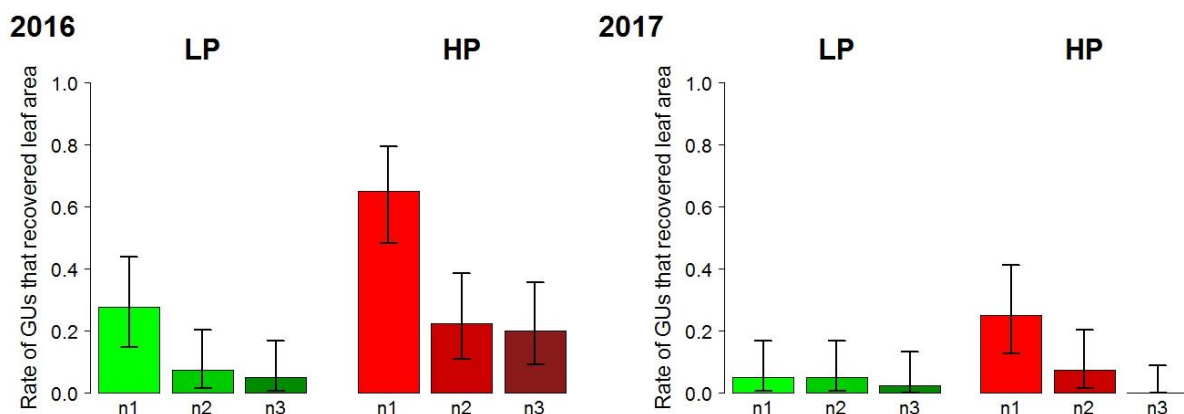
460 The unpruned control trees did not produce vegetative growth after the pruning date of LP and  
461 HP trees in 2016 (no C tree modality).

462

463 The diameter of pruned GUs had a significant and positive linear effect on the leaf area  
464 produced. Pruning intensity had a significant effect on this relationship in 2016, whereas the  
465 effect was barely significant in 2017 ( $P=0.013$ ). For the same diameter, pruned GUs produced  
466 more leaf area on HP trees than on LP trees. Pruning severity had no effect on this  
467 relationship (2016:  $P=0.06$ ; 2017:  $P=0.44$ ).

468 In 2016, pruning intensity and pruning severity had a highly significant effect on the capacity  
469 of the pruned GUs to recover the leaf area removed by pruning (Figure 6). The more intensely  
470 the tree was pruned, the higher the rate of pruned GUs that recovered the leaf area removed  
471 was. In contrast, this rate was significantly higher for the less severely pruned n1 GUs  
472 compared to the most severely pruned n2 and n3 GUs. In 2017, the capacity of the pruned  
473 GUs to recover the leaf area removed by pruning was not affected by pruning intensity  
474 ( $P=0.06$ ) and pruning severity ( $P=0.02$ ), despite pronounced differences, in particular on HP  
475 trees (Figure 6).

476



477

478 Figure 6: Rate (mean  $\pm$  95% confidence interval) of pruned growth units (GUs) that recovered  
479 the leaf area removed by pruning according to pruning severity (n1, n2 and n3) for lightly  
480 pruned trees (LP) and intensely pruned trees (HP) in 2016 and 2017.

481

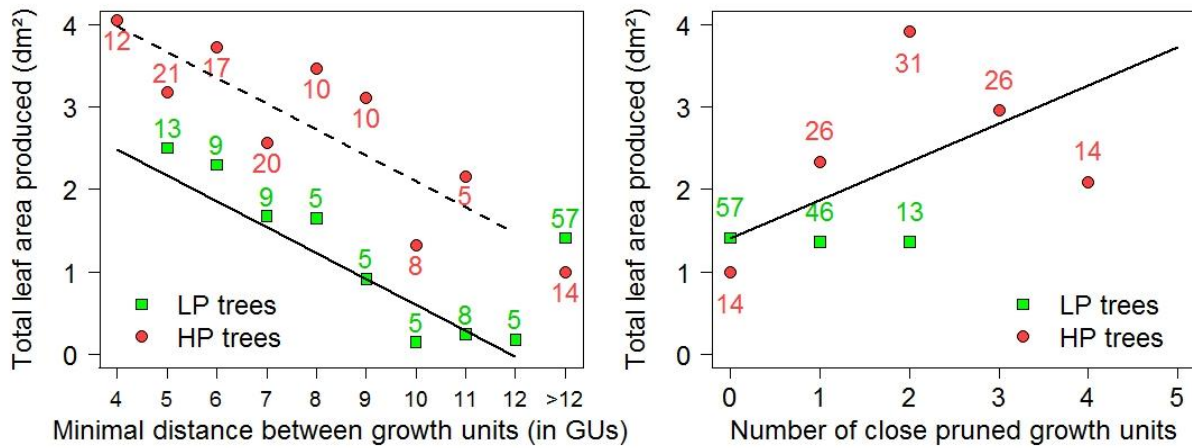
### 482 **3.4.2 Unpruned GUs**

483 Pruning intensity did not affect the total leaf area produced per unpruned GU in 2016  
484 (P=0.10; Figure 5). In contrast, the total leaf area produced by unpruned GUs was higher on  
485 HP trees than on LP and C trees in 2017 (Figure 5). The total leaf area produced was not  
486 affected by the apical or lateral position of unpruned GUs (2016: P=0.06; 2017: P=0.74). The  
487 total leaf area produced by unpruned GUs was significantly higher in 2016 than in 2017 on  
488 LP trees, and was similar in 2016 and 2017 on HP trees (P=0.15; Figure 5).

489 The diameter of unpruned GUs had a significant and positive effect on the total leaf area  
490 produced, and pruning intensity significantly affected this relationship. For the same diameter,  
491 unpruned GUs produced higher total leaf area on HP trees than on LP and C trees (in 2017).

492 The presence of pruned GUs close to an unpruned GU had a significant effect on the total leaf  
493 area produced by the latter. The closer an unpruned GU was to a pruned GU, the larger the  
494 total leaf area produced was (Figure 7A). This relationship was significantly affected by  
495 pruning intensity. For the same minimal distance between pruned and unpruned GUs, the total  
496 leaf area produced was higher for unpruned GUs on HP trees than on LP trees. The number of  
497 pruned GUs close to an unpruned GU had a significant and positive linear effect on the total  
498 leaf area produced by the latter (Figure 7B). Pruning intensity did not affect this relationship  
499 (P=0.02).

500 Unpruned GUs generally produced lower total leaf area than pruned GUs on both LP and HP  
501 trees in 2016 and 2017 (Figure 5).



502

503 Figure 7: Average total leaf area produced by unpruned growth units (GUs) according to

504 pruning intensity and to the minimal distance (in number of GUs) between the unpruned GU

505 and the closest pruned GU (A) and according to pruning intensity and to the number of

506 pruned GUs close to the unpruned GU (distance  $\leq 12$  GUs) (B). Lines represent the linear

507 regressions between total leaf area produced and minimal distance for LP trees (solid line)

508 and HP trees (dotted line) (A), and between total leaf area produced and the number of close

509 pruned GUs, independently of pruning intensity ( $P > 0.01$ ; B). Unpruned GUs with the closest

510 pruned GUs at a distance greater than 12 GUs were not taken into account in the linear

511 regression between leaf area produced and minimal distance between GUs since this class did

512 not correspond to a particular distance value. Points represent the average total leaf area

513 produced per class of distance or number of close pruned GUs. Numbers above or below the

514 points correspond to sample size. Only sample sizes larger than 4 GUs are represented.

515

### 516 3.5 Effect of pruning on the duration between the date of pruning and the date of burst

#### 517 of the first daughter GU to appear: vegetative growth dynamics

##### 518 3.5.1 Pruned GUs

519 In 2016, bud burst occurred on pruned GUs during two main periods, i.e., two flushes, on LP

520 and HP trees (Figure 8). On LP trees, 58% of pruned GUs burst during the first flush,  $23.9 \pm$



521 6.8 d after pruning. The second flush occurred  $49.1 \pm 3.1$  d after pruning. On HP trees, the  
 522 two flushes were closer than on LP trees. The first flush represented 81% of the GUs and  
 523 occurred  $31.7 \pm 5.4$  d after pruning. The second flush was weak and occurred  $41.3 \pm 1.0$  d  
 524 after pruning. In 2017, vegetative growth of pruned GUs occurred in two flushes on LP trees  
 525 and in one flush on HP trees (Figure 8). The first flush on LP trees, representing 57% of the  
 526 GUs, occurred  $17.8 \pm 2.4$  d after pruning, slightly earlier than in 2016. The second flush  
 527 occurred  $28.1 \pm 2.8$  d after pruning, about three weeks earlier than in 2016. The single flush  
 528 on HP trees occurred at  $16.5 \pm 2.6$  d, about two weeks earlier than the first one in 2016 and at  
 529 the same time as the first flush on the LP trees.

530 The two flushes observed on LP trees were partly related to pruning severity (Table 2). In  
 531 2016, daughter GUs of n3 GUs generally appeared during the first flush, whereas daughter  
 532 GUs of n1 GUs exclusively appeared during the second flush. Daughter GUs of n2 GUs  
 533 appeared equally during the two flushes. The same trend was observed in 2017, with less  
 534 pronounced differences between modalities of pruning severity (Table 2).

535

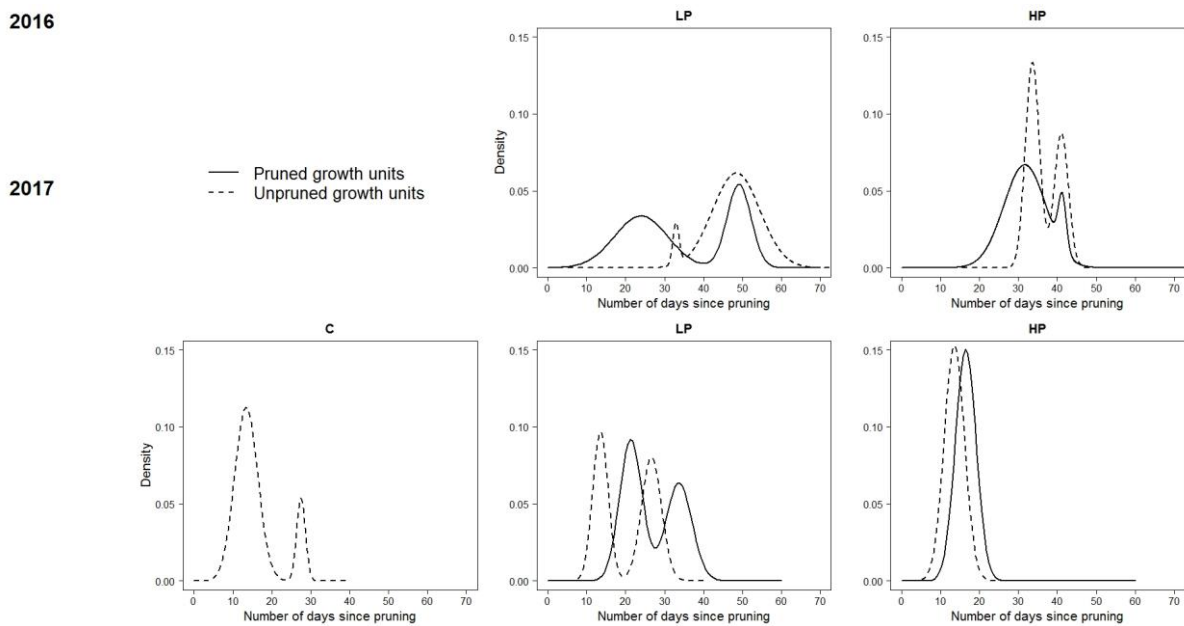
536 Table 2: Parameter values of the mixture of Gaussian models fitted on the distributions of the  
 537 observed durations between pruning and burst of the first daughter growth unit (GU) of  
 538 pruned GUs according to pruning severity and year for lightly pruned trees (p: weight of the  
 539 first distribution;  $\mu_1$  and  $\mu_2$ : means of the first and second Gaussian distributions;  $\sigma_1$  and  $\sigma_2$ :  
 540 standard deviations of the first and second Gaussian distributions; see Equation 3).

<b>Year</b>	<b>Pruning severity</b>	<b>p</b>	<b><math>\mu_1</math></b>	<b><math>\sigma_1</math></b>	<b><math>\mu_2</math></b>	<b><math>\sigma_2</math></b>
<b>2016</b>	n1	0	-	-	48.5	1.4
	n2	0.48	22.8	4.7	48.4	4.1
	n3	0.83	23.0	6.1	48.1	3.1
<b>2017</b>	n1	0.28	14.7	1.5	28.2	3.9
	n2	0.69	19.4	2.9	28.3	0.7
	n3	0.64	17.8	2.1	28.3	2.0

541

542 Vegetative growth of pruned GUs was longer in 2016 than in 2017. It was shorter on HP trees  
 543 (2016: 19.4 d on HP trees vs. 39.6 d on LP trees; 2017: 7.0 d on HP trees vs. 17.4 d on LP  
 544 trees). Vegetative growth duration was short for n1 GUs, intermediate for n2 GUs and long  
 545 for n3 GUs in 2016 on LP and HP trees (data not shown). Differences in vegetative growth  
 546 duration among modalities of pruning severity were small in 2017 and no trend was observed.

547 The beginning of vegetative growth of pruned GUs was earlier on LP trees (13.0 d after  
 548 pruning) than on HP trees (22.7 d after pruning) in 2016. It occurred simultaneously on LP  
 549 (14.3 d after pruning) and HP (13.0 d after pruning) trees in 2017. Vegetative growth began  
 550 early in 2016 on n3 GUs, intermediate on n2 GUs and late on n1 GUs on both LP and HP  
 551 trees (data not shown). In 2017, pruning severity did not affect the beginning of vegetative  
 552 growth on LP and HP trees.



553  
 554 Figure 8: Modeled vegetative growth dynamics of pruned and unpruned growth units (GUs)  
 555 according to pruning intensity (C: unpruned control trees; LP: lightly pruned trees; HP:  
 556 intensely pruned trees) in 2016 and 2017. Curves represent the distributions of the duration  
 557 between the date of pruning and the date of burst of the first daughter GU, fitted with a

558 mixture of Gaussian models. Actual data and modeled dynamics are presented in the  
559 Supplementary data (Figure S3).

560

### 561 **3.5.2 Unpruned GUs**

562 The effect of pruning intensity on vegetative growth dynamics of unpruned GUs differed  
563 between the two years (Figure 8). In 2016, the vegetative growth of unpruned GUs occurred  
564 in two flushes on both LP and HP trees. On LP trees, the first flush was weak (5% of the  
565 GUs) and occurred  $32.9 \pm 0.8$  d after tree pruning. The second flush, representing most of the  
566 GUs, occurred  $48.4 \pm 6.1$  d after pruning. The first flush on HP trees occurred at the same  
567 time as on the LP trees ( $33.7 \pm 1.8$  d after tree pruning), but represented 60% of the GUs. The  
568 second flush occurred earlier and was shorter ( $41.0 \pm 1.8$  d after tree pruning) than on LP  
569 trees. In 2017, vegetative growth of unpruned GUs occurred in one flush on HP trees ( $13.6 \pm$   
570  $2.6$  d after tree pruning), and in two flushes on LP and C trees. Vegetative growth occurred  
571 mostly during the first flush on C trees (85% of the GUs), whereas it was more balanced  
572 between the two flushes on LP trees (48% of the GUs burst during the first flush). The two  
573 flushes on LP trees occurred  $13.5 \pm 2.0$  d and  $26.6 \pm 2.6$  d after tree pruning, at the same time  
574 as the two flushes on C trees, occurring at  $13.4 \pm 3.0$  d and  $27.5 \pm 1.1$  d after LP and HP tree  
575 pruning. The single flush on HP trees occurred at the same time as the first flush on C and LP  
576 trees.

577 In general, vegetative growth duration of unpruned GUs was shorter on HP trees than on LP  
578 and C trees (2016: 12.0 d on HP trees vs. 17.1 d on LP trees; 2017: 8.0 d on HP trees vs. 18.0  
579 d on LP trees and C trees).

580 The beginning of vegetative growth of unpruned GUs was not affected by pruning intensity  
581 (2016: 34.9 d after pruning on LP trees and 31.0 d after pruning on HP trees; 2017: 10.0 d  
582 after pruning on C trees and HP trees, and 12.0 d after pruning on LP trees).

583 Vegetative growth duration of unpruned GUs was shorter in 2016 and similar in 2017 than  
584 that of pruned GUs in both LP and HP trees. The beginning of vegetative growth was earlier  
585 on pruned GUs than on unpruned GUs on LP and HP trees in 2016. Vegetative growth of  
586 pruned and unpruned GUs began almost simultaneously in 2017.

587

#### 588 **4. Discussion**

589

590 The very low fruit load during the 2015-2016 growing cycle led to a generalized flush of  
591 vegetative growth on the trees in November 2015, after the end of flowering. This probably  
592 explained the lack of vegetative growth on C trees during the first year. Consequently,  
593 vegetative growth on LP and HP trees was the vegetative response to pruning in 2016. On the  
594 other hand, regular fruit load on trees during the second year prevented vegetative growth  
595 before the harvest and before pruning. Vegetative growth in 2017 on C trees could therefore  
596 be considered as normal post-harvest vegetative growth on unpruned trees, and the differences  
597 observed between pruned trees (LP and HP trees) and C trees were the response to pruning.  
598 Despite these differences, the results were remarkably stable for the two years of the study.  
599 They are synthesized in Table 3.

600

#### 601 **4.1 Mango tree response to pruning intensity**

602 Pruning intensity was defined and applied at the tree scale and reflected the imbalance  
603 imposed between above- and below-ground biomass. The results showed that pruning  
604 intensity affected vegetative growth at the structural and temporal levels and at the local and  
605 distant scales (Table 3). They globally confirmed the expected effects according to our  
606 assumptions: increasing pruning intensity led to greater and earlier vegetative growth. The  
607 leaf area produced increased with pruning intensity. This could be partly explained by a  
608 positive effect of pruning intensity on bud burst, but not by an effect on vegetative growth

609 intensity. The same effects were observed on pruned and unpruned GUs (except for the leaf  
610 area produced in 2016 on unpruned GUs), indicating that the responses were similar at the  
611 local and at the distant scales. The local response on pruned GUs was, however, greater than  
612 the distant response on unpruned GUs (comparisons between pruned and unpruned GUs in  
613 Table 3).

614 Burst rate, vegetative growth intensity and leaf area produced were positively related to the  
615 diameter at the pruning point for pruned GUs and, in general, to the basal diameter of  
616 unpruned GUs. Similar results were found on fruiting, with a positive effect of basal diameter  
617 of unpruned GUs on their fruiting rates on unpruned trees (Normand et al., 2009). Pruning  
618 intensity affected these relationships (except the relationship between vegetative growth  
619 intensity and pruned GU diameter), indicating that the response at the GU scale, depending on  
620 the diameter, was affected by the global biomass imbalance at the tree scale, so that pruned  
621 and unpruned GUs of more intensely pruned trees produced more vegetative growth and leaf  
622 area for a given diameter. In particular, the shape of the relationship between burst rate and  
623 basal diameter of unpruned GUs in 2017 differed between C trees and pruned trees (LP and  
624 HP), conferring higher burst rates on GUs with a small diameter on pruned trees compared to  
625 C trees (Figure S2). Although pruning intensity did not affect vegetative growth intensity, it  
626 affected the relationship between vegetative growth intensity and basal diameter of unpruned  
627 GUs in 2017. This relationship was similar for pruned trees (LP and HP) and differed from  
628 that of C trees.

629 Pruning intensity affected the relationship between the leaf area produced by unpruned GUs  
630 and the distance to the closest pruned GU (Figure 7A) but not the other proximity  
631 relationships between pruned and unpruned GUs (Figures 3 and 7B). Since the average  
632 distance between an unpruned GU and the closest pruned GU was independent of pruning  
633 intensity, this suggested that pruning intensity had a specific effect on the leaf area produced

634 by unpruned GUs, independently of the distance to the closest pruned GU. This effect was  
635 probably on the leaf area of each daughter GU since their number was independent of the  
636 distance to the closest pruned GU, and pruning intensity did not affect the relationship  
637 between burst rate and the distance to the closest pruned GU (Figure 3A). In this way, it has  
638 been shown in several species that new axes were longer on pruned trees than on unpruned  
639 trees, suggesting a positive effect of pruning on the leaf area produced at the axis scale  
640 (Fumey et al., 2011; Jonkers, 1982; Yeshitela et al., 2005).

641 At the temporal level, pruning intensity synchronized vegetative growth and tended to make it  
642 early (Figure 8). In 2017, vegetative growth occurred in one flush on HP trees and in two  
643 flushes on LP and C trees, the first flush appearing at the same time as the one on HP trees. In  
644 2016, it occurred in two flushes on LP and HP trees. Despite an earlier beginning of  
645 vegetative growth on LP trees, vegetative growth was globally shorter and earlier on HP trees  
646 than on LP trees as a result of closer and more synchronized flushes, with the first flush  
647 representing a higher proportion of GUs and an earlier second flush. More intense pruning  
648 consequently appeared as a powerful trigger of early vegetative growth on the whole tree, on  
649 pruned and unpruned GUs. This is consistent with the predictions related to our assumptions.  
650 These results confirm previous observations of earlier and more synchronous vegetative  
651 growth of pruned mango trees compared to unpruned trees (Davenport, 2006; Oosthuysen,  
652 1994; Uddin et al., 2014). However, we showed that the response depends on the intensity of  
653 pruning. Vegetative growth dynamics were similar between C trees and LP trees in 2017,  
654 indicating that light pruning did not affect the dynamics, compared to unpruned trees. In  
655 contrast, intense pruning (HP trees) modified vegetative growth dynamics compared to C  
656 trees, in particular, in terms of duration and synchronization.

657

## 658 **4.2 Mango tree response to pruning severity**

659 Pruning severity was defined and applied at the axis scale and reflected the local imbalance  
660 related to the removed biomass and leaf area. Pruning severity was correlated to diameter at  
661 the pruning point, and the mean diameter per modality of pruning severity was stable across  
662 the years (Table 1). Since pruning severity was the distance between the pruning point and the  
663 distal end of the axis, expressed in number of GUs, this stability was related to the allometry  
664 of the mango tree branch (Normand et al., 2008).

665 Pruning severity affected vegetative growth at the structural and temporal levels, and  
666 confirmed the expected effects of our assumptions at the local scale. The leaf area produced  
667 by pruned GUs increased with pruning severity as the result of the positive effect of pruning  
668 severity on burst rate and vegetative growth intensity (Table 3). Despite this increase, only a  
669 low rate of severely pruned axes (n3 GUs) recovered the leaf area removed by pruning  
670 compared to n1 and n2 GUs (Figure 6). The leaf area removed on n3 GUs corresponded to the  
671 leaf area of a minimum of three GUs, but for most of the n3 GUs, it was much more because  
672 of branching (Figure 1). The same scheme was valid to a lesser extent for n2 GUs, and to a  
673 much lesser extent for n1 GUs. Even if vegetative growth was earlier on n3 GUs (Table 2 and  
674 below), daughter GUs did not themselves produce new GUs before vegetative rest.  
675 Considering the average burst rates (Figure 2) and the number of daughter GUs (Figure 4), it  
676 appeared unlikely that the removed leaf area of n3 GUs, which had been produced during  
677 three consecutive flushes, be recovered by the leaf area produced in only one flush after  
678 pruning. This was supported by the fact that n3 GUs that recovered leaf area removed by  
679 pruning were mainly those with the lower leaf area removed (data not shown). It was more  
680 probable for n1 GUs to recover removed leaf area because it had been produced during one  
681 flush.

682 Pruning severity did not affect the relationships between response variables and diameter at  
683 the pruning point (except in 2016 for vegetative growth intensity), indicating that the response

684 variables were in fact dependent on the diameter, and not on the distance between the pruning  
685 point and the axis end. Consequently, the local response was probably independent on the age  
686 of the lateral buds below the pruning point, at most, up to three GUs from the axis end.  
687 At the temporal level, pruning severity modified vegetative growth dynamics, and this effect  
688 depended on pruning intensity and year. On LP trees, modeled dynamics showed that most of  
689 the daughter GUs of the n3 GUs appeared earlier than those of the less severely pruned axes  
690 (Table 2). The hypothesis that a more severe pruning of axes leads to earlier burst to have  
691 more time to compensate for the loss of leaf area was also confirmed in 2016 with vegetative  
692 growth duration and earliness calculated on the basis of actual data on LP trees, as well as on  
693 HP trees despite a more synchronous vegetative growth (Table 3). Pruning severity did not  
694 affect vegetative growth duration and earliness in 2017 on either LP or HP trees, indicating a  
695 year effect. This year effect was probably related to the fact that vegetative growth was a  
696 specific response to pruning in 2016, whereas it was a combination of response to pruning and  
697 post-harvest vegetative growth in 2017.

698

### 699 **4.3 Endogenous and environmental factors may also affect vegetative response to** 700 **pruning**

701 Our results suggested that vegetative growth after pruning was also affected by two other  
702 endogenous factors, fruit load and proximity of pruned GUs, and by rainfall. The probable  
703 effects of these factors are worth exploring in future investigations. The higher fruit load on  
704 the trees before pruning in 2017 probably led to the weaker vegetative growth generally  
705 observed that year, in particular on HP trees (Figures 2, 5, 6). This is consistent with the  
706 negative effect of reproductive efforts on the subsequent vegetative growth observed at the  
707 axis scale (Capelli et al., 2016; Issarakraisila et al., 1991) and at the whole tree scale in the  
708 mango tree (Issarakraisila et al., 1997; Normand et al., 2016; Scholefield et al., 1986), as well



709 as in other species (peach tree: Berman and DeJong, 2003; olive tree: Connor and Fereres,  
710 2005; apricot tree: Costes et al., 2000; apple tree: Lauri and Térouanne, 1999; and avocado  
711 tree: Lovatt, 2010).

712 Leaf area produced and burst rate of unpruned GUs were negatively affected by the distance  
713 to the closest pruned GU and positively affected by the number of close pruned GUs,  
714 suggesting a 'remote effect' of pruned GUs on unpruned GUs within a short distance (< 12  
715 GUs). The distance to the closest pruned GU was not dependent on pruning intensity, whereas  
716 the number of close pruned GUs was, and the percentage of unpruned GUs close to at least  
717 one pruned GU increased with pruning intensity. Consequently, the positive effect of pruning  
718 intensity on burst rate and leaf area produced by unpruned GUs was probably related to the  
719 more frequent 'remote effect' in the canopy of intensely pruned trees. Vegetative growth  
720 intensity was not affected by this effect, indicating that close pruned GUs stimulated bud burst  
721 at the unpruned GU scale and not at the bud scale.

722 The dynamics of vegetative growth differed between the two years in terms of number and  
723 period of occurrence of flushes (Figure 8). Pruning intensity and type of GU, pruned or  
724 unpruned, affected this dynamics but did not explain why vegetative growth was globally late  
725 in 2016 and early in 2017 after pruning. The beginning of the different flushes of vegetative  
726 growth seemed to follow a week with heavy rainfall (weeks 2 and 4 to 6 after pruning in  
727 2016, and week 1 after pruning in 2017; Figure S1). Trees were drip-irrigated daily on an  
728 evapotranspiration basis. These coincidences suggest that, despite adapted water availability  
729 and non-limiting conditions, sudden and large rainfall triggers vegetative growth. The early or  
730 late vegetative growth after pruning might therefore be partly explained by rainfall  
731 distribution each year. The remarkable stability of structural response variables between the  
732 two years suggests that they are not affected by the amount and distribution of rainfall.

733

#### 734 **4.4 Hypotheses on the underlying mechanisms**

735 Although it was not the objective of the study, three mechanisms underlying the responses to  
736 pruning could be hypothesized from the results: trophic (nitrogen, carbohydrates), hormonal  
737 and light-related mechanisms. The burst rate of pruned and unpruned GUs and the leaf area  
738 produced were affected by factors at the tree scale (pruning intensity) and factors at the GU  
739 scale (pruning severity, diameter). On the other hand, vegetative growth intensity of pruned  
740 and unpruned GUs was affected by factors at the GU scale only. This suggested that different  
741 mechanisms were involved in the occurrence of burst and in the number of buds that burst on  
742 a GU. The hypothesized mechanisms are probably not exclusive and several of them may be  
743 involved in a particular response.

744 Pruning leads to the removal of leaf area on the pruned GUs, disrupting the hydraulic  
745 functioning of the whole canopy and more locally around pruned GUs. Xylem sap fluxes are  
746 then directed towards the remaining transpiring leaves of unpruned and possibly pruned GUs,  
747 providing these GUs with larger quantities of nutrients, in particular, nitrogen, a trigger of bud  
748 burst (Davenport, 2006; Lobit et al., 2001; Médiène et al., 2002; Normand and Habib, 2001).  
749 This might explain the positive effects of pruning intensity and of the proximity of pruned  
750 GUs on the burst rate of unpruned GUs, or the positive effects of pruning intensity on the  
751 relationships between response variables and GU diameter. On the other hand, GU diameter  
752 of pruned and unpruned GUs was positively related to burst rate, vegetative growth intensity  
753 and leaf area produced and therefore appeared to be an important local factor. As explained in  
754 the Materials and Methods section, this suggested that carbohydrates might be involved in  
755 these responses. The negative effect of fruit load on vegetative growth observed in our 2017  
756 results and in other studies (see above) supports this hypothesis.

757 The hypothesized hormonal mechanism is mostly local, related to the pruned GUs. Apical  
758 dominance is the repression of lateral bud outgrowth by the apical bud (Champagnat, 1965;

759 Cline and Sadeski, 2002; Wilson, 2000) through a basipetal flux of auxin produced by the  
760 latter (Booker et al., 2003; Dun et al., 2006; Liang et al., 2010; Thimann and Skoog, 1933).  
761 Pruning suppresses this flux in the remaining pruned GUs, allowing lateral bud outgrowth and  
762 contributing to the local increase in bud burst and vegetative growth intensity.

763 Light plays a positive role on bud burst. This effect can be direct, with light acting as a signal  
764 perceived by photochromic sensory receptors such as phytochromes (Casal et al., 1990; Evers  
765 et al., 2006), or indirect through an increase of photosynthesis and local availability of  
766 carbohydrates (Girault et al., 2008, 2010; Henry et al., 2011; Rabot et al., 2012; Schaffer and  
767 Gaye, 1989; Sharma et al., 2006). As a result, axes in the shade are less prone to bud burst  
768 than axes in full light. Pruning removes more or less large and numerous branches and  
769 thereby modifies the light environment of the remaining structures and buds. The  
770 hypothesized light-related mechanism is based on this observation, but is not clear and would  
771 need specific light measurements. On the one hand, if an axis with a large diameter is pruned,  
772 the remaining GU would probably be located deep inside the canopy, in the shade. The  
773 consequence would be a low burst rate, which does not fit with our results. On the other hand,  
774 this large diameter corresponds to the removal of a large structure, thus creating a light well  
775 and improving the light environment of the remaining GU and its ability to burst. Similarly,  
776 this light-related mechanism may contribute to the explanation of the positive effect of the  
777 number of close pruned GUs on the burst rate of unpruned GUs.

778

## 779 **5. Conclusion**

780

781 This study provides a better understanding of the vegetative responses of the mango tree, cv.  
782 ‘Cogshall’, to pruning in terms of structure (burst rate, vegetative growth intensity, leaf area  
783 produced) and dynamics. These responses are local on the pruned GUs and distant on the

784 unpruned GUs. They are affected by factors at the tree scale (pruning intensity) and at the GU  
785 scale (pruning severity, GU diameter, proximity to pruned GUs). To increase this complexity,  
786 the effects of pruning intensity and severity can be direct on the response variables or indirect  
787 on the relationships between response variables and GU diameter. The results confirmed the  
788 expected structural and temporal consequences of our assumptions, suggesting that the main  
789 drivers of the vegetative response to pruning were the recovery of the balance between above-  
790 and below-ground biomass at the tree scale, and the recovery of the leaf area removed on  
791 pruned GUs at the local scale. It would be interesting to assess if the leaf area removed by  
792 pruning was recovered by triggered vegetative growth at the whole canopy scale. This  
793 assessment was not possible with our data that represented a sample of the canopy. The  
794 simulation, based on our results, of vegetative growth on a digitized tree could provide part of  
795 the answer.

796 At least five perspectives can be highlighted from the results. First, three mechanisms  
797 underlying the responses to pruning were hypothesized and need to be explored with specific  
798 studies. Second, the objective of this study was to decipher the vegetative responses of one  
799 mango cultivar to pruning over two years in order to evaluate their consistency across years.  
800 Based on these results, it would be interesting to analyze the responses of other cultivars and  
801 to identify common and cultivar-specific responses. Third, the response to pruning in terms of  
802 reproduction (flowering and fruiting) should also be studied. This can be considered directly  
803 through the effects of pruning intensity and severity on reproduction, and indirectly through  
804 the effects of the characteristics of vegetative growth induced by pruning on reproduction.  
805 Fourth, vegetative responses to pruning may be integrated into a functional-structural mango  
806 tree model (Boudon et al., 2017) in order to account for this cultivation practice and its effects  
807 on tree development and yield. Finally, these results may be useful to improve the pruning  
808 techniques of the mango tree.

809

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Table 3: Effects of the factors studied at the scale of pruned and unpruned growth units (GUs) on the structural and temporal variables describing vegetative growth after pruning, and comparison of pruned and unpruned GUs. The sign + or – indicates a significantly positive or negative effect, respectively, of the factor on the response variable; ns indicates a non-significant effect. The sign = indicates that the response variable was quite similar among factor modalities (no statistical test). A positive effect indicates that the response variable increased with pruning intensity or pruning severity. For growth unit position, A > L indicates that the value of the response variable was higher on apical than on lateral GUs. For the factor “GU diameter”, the upper part indicates a significantly positive (+) or negative (-) relationship with the response variable, and the lower part indicates whether or not this relationship was affected by pruning intensity and severity. For the comparison of pruned and unpruned GUs, a positive effect indicates that the value of the response variable was higher on pruned GUs than on unpruned GUs. Year-specific results are given when they differed among years. na: analysis not carried out because of limited or unbalanced data.

Response variables	Pruned growth units			Unpruned growth units					Pruned vs. unpruned GUs
	Pruning intensity	Pruning severity	GU diameter	Pruning intensity	GU diameter	GU position	Distance to the closest pruned GU	Number of close pruned GUs	
Burst rate	+	+	+ Intensity: + Severity: ns	+	ns (2016) + (2017) Intensity: +	ns	- Intensity: ns	+ Intensity: ns	+
Vegetative growth intensity	ns	+	+ Intensity: ns Severity: +/- (2016) ns (2017)	ns	+ Intensity: ns (2016) + (2017)	A > L	ns	ns	+
Total leaf area produced	+	+	+ Intensity: + Severity: ns	ns (2016) + (2017)	+ Intensity: +	ns	- Intensity: +	+ Intensity: ns	+
Vegetative growth dynamics:									
- nb flushes	= (2016) - (2017)	=	na	= (2016) - (2017)	na	na	na	na	=
- duration	-	- (2016) = (2017)	na	-	na	na	na	na	+ (2016) = (2017)
- earliness	- (2016) = (2017)	+ (2016) = (2017)	na	=	na	na	na	na	- (2016) = (2017)