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1 **Impact of UV-C radiation applied during plant growth on pre- and**
2 **post-harvest disease sensitivity and fruit quality of strawberry**

3

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11 *Keywords: strawberry, UV-C, pre-harvest, post-harvest, phytopathology, quality*

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21 **Abstract**

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23 applied during plant growth on pre- and post-harvest disease sensitivity and fruit quality of
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25

26 UV-C radiation is efficient in reducing the development of diseases in many species,
27 including strawberry (*Fragaria x ananassa*). Several studies suggest that UV-C radiation is
28 effective not only because of its disinfecting effect but also because it may stimulate plant
29 defenses. In this study, the effect of pre-harvest UV-C radiation applied during strawberry
30 cultivation on plant growth, fruit quality and susceptibility to major fungal diseases, as gray
31 mold, powdery mildew and soft rot, was evaluated. UV-C treatments had an impact on
32 flowering initiation and fruit development. Flowering occurred earlier for UV-C-treated plants
33 than for non-treated plants. At harvest, a larger amount of fruit was produced by treated
34 plants despite their slight decrease in leaf area. UV-C treatment did not improve strawberry
35 shelf life but did not alter the physical integrity of strawberry fruit. Natural infection of leaves
36 to powdery mildew and of fruit to *Rhizopus* was strongly decrease in response to UV-C
37 treatment.

38

39 Keywords: strawberry, UV-C, pre-harvest, post-harvest, phytopathology, quality

40

41 **Abbreviations**

ANOVA Analysis of variance

AUDPC	Area under disease progression curve
AUFC	Area under fluorescence curve
F_0	Initial fluorescence
F_M	Maximal fluorescence
N	Newton
PAL	Phenylalanine ammonia-lyase
PDA	Potato dextrose agar
PSII	Photosystem II
SOD	Superoxide dismutase
UV-C	Ultraviolet-C

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52 Strawberry is a very popular fruit appreciated by consumers because of its organoleptic
53 characteristics (Li *et al.*, 2017; Lu *et al.*, 2018). In addition, strawberries are one of the richest
54 sources of natural antioxidants and therefore have a highly beneficial effect on human health
55 (Hannum, 2004; Li *et al.*, 2019; Yan *et al.*, 2019). However, many plant pathogenic
56 microorganisms, including fungi, are very damaging to both strawberry plants and fruit. Yields
57 can be strongly affected by these fungi, and strawberries are subjected to rapid degradation,
58 affecting fruit flavor (Perkins-Veazie, 1995). Restrictions on the use of fungicides make it
59 necessary to find alternative phytosanitary tools. Among these tools, physical methods can
60 improve the resistance of plants to pathogens and can increase the synthesis of vitamins,
61 micronutrients and secondary metabolites in fruit (Aghdam *et al.*, 2018; Li *et al.*, 2014;
62 Poiroux-Gonord *et al.*, 2010). Among these physical methods, the application of low doses of
63 ultraviolet-C (UV-C) radiation creates a moderate oxidative stress that can increase the
64 resistance of the plants to plant pathogens (Charles *et al.*, 2008; Mercier *et al.*, 2001; Ouhibi
65 *et al.*, 2015; Vasquez *et al.*, 2017) and improve the nutritional qualities of plant products
66 (Mohammadi *et al.*, 2012; Xu *et al.*, 2019b).

67 The lethal effect of UV-C light has been exploited successfully to control post-harvest
68 diseases, thus extending the shelf life of fruit and vegetables (Charles *et al.*, 2008; Erkan *et al.*,
69 2008; Liu *et al.*, 1993; Maharaj *et al.*, 1999; Mercier *et al.*, 2001; Siddiqui *et al.*, 2011; Urban *et al.*,
70 2016). UV-C irradiation has been extensively studied for its role in the reduction of post-
71 harvest disease spoilage in harvested horticultural products by exerting a direct germicidal
72 effect and/or by eliciting critical defense responses (Duarte-Sierra *et al.*, 2019). For instance,
73 it can induce partial resistance to the plant pathogenic fungus *Botrytis cinerea* on carrots,
74 lettuce, tomatoes and strawberries (Charles *et al.*, 2008; Mercier *et al.*, 1993a,b; Ouhibi *et al.*,
75 2014; Pombo *et al.*, 2011). In the case of strawberry, the enhancement of resistance to *B.*

76 *cinerea* was linked to an increase in the activity of phenylalanine ammonia-lyase (PAL) and
77 polyphenol oxidase and in the expression of pathogenesis-related protein genes (Pombo *et al.*
78 *et al.*, 2011). Moreover, UV-C radiation can induce defense mechanisms, increasing the content
79 of chitinase and superoxide dismutase (SOD) or PAL in various fruit, such as mangoes, peaches
80 and strawberries (El-Ghaouth *et al.*, 2003; Erkan *et al.*, 2008; Gonzalez-Aguilar *et al.*, 2007;
81 Mohammadi *et al.*, 2012; Yang *et al.*, 2014). Several studies have also pointed out that UV-C
82 light can influence the physiology of harvested organs, delaying their senescence and
83 stimulating secondary metabolism (Xu *et al.*, 2018), which is known to play a role in both the
84 health benefits of the harvested organs and the defense of plants against pathogens (Huang
85 *et al.*, 2017; Poiroux-Gonord *et al.*, 2010). UV-C radiation caused modifications in the
86 secondary metabolites of mangoes, grapes and peaches compared to those in non-treated
87 fruit (Freitas *et al.*, 2015; Gonzalez-Aguilar *et al.*, 2001, 2004). In strawberry, UV-C radiation
88 applied at the post-harvest stage induced beneficial effects on the preservation and
89 promotion of fruit quality, including a delay in fruit softening through reduced cell wall
90 degradation (Pombo *et al.*, 2009) or a stimulation of the biosynthesis of bioactive molecules,
91 such as anthocyanins, ascorbic acid and esters (Severo *et al.*, 2015). In addition to these
92 compounds, UV-C radiation applied to strawberry fruit at the post-harvest stage caused
93 variations in the activation of genes involved in fruit firmness, thus allowing an improvement
94 in the shelf life and in the production of volatile compounds, which results in strongly aromatic
95 fruit (Severo *et al.*, 2015).

96 UV-C treatment of growing plants has an effect on the resistance of vegetative organs
97 to pathogens (Obande *et al.*, 2011; Xu *et al.*, 2017b). Janisiewicz *et al.* (2016) demonstrated
98 that pre-harvest UV-C treatment could be an effective way to manage gray mold (caused by
99 *B. cinerea*) in the production of strawberry. On strawberries, UV-C radiation at 12.36 J/m² did

100 not impact photosynthesis or pollen tube germination (Janisiewicz *et al.*, 2016). In geranium
101 (*Pelargonium x hortotum*), low doses of UV-C radiation (0.5 - 5.0 kJ/m²) applied during growth
102 caused photomorphogenic changes such as an increase in biomass and in the number of
103 lateral stems and inflorescences (Darras *et al.*, 2012a).

104 To our knowledge, only a few reports have evaluated the potential of low doses of UV-
105 C applied during plant growth for use in fruit or vegetable and ornamentals quality
106 maintenance (Darras *et al.*, 2012a; Janisiewicz *et al.*, 2016; Obande *et al.*, 2011 ; Severo *et al.*,
107 2016; Xie *et al.*, 2015 ; Xu *et al.*, 2019a). However, a recent comprehensive review by Urban
108 *et al.* (2016) discussed the physiological effects of UV-C radiation and evaluated its agronomic
109 potential at both the pre-harvest and post-harvest stages. It is important to verify that the
110 improvement in plant resistance resulting from UV-C treatments does not negatively impact
111 yield or fruit quality at harvest and during post-harvest storage.

112 The aim of this study was to evaluate the effect of UV-C treatments applied to
113 strawberry plants (i) on the resistance of leaves and fruit to the main fungal pathogens of
114 strawberry as gray mold, powdery mildew and soft rot, (ii) on the vegetative growth of the
115 plant and crop yield and (iii) on the quality of strawberry fruit after harvest.

116

117 **Materials and Methods**

118 **Plant material**

119 Trays of strawberry plants of the cultivar Candiss (single-harvest plants, Ciref, France)
120 supplied by the Martailac nursery (Sainte-Marthe, France), were transplanted in a mixed
121 substrate (60 % compost of TS3 type (Code of Practice) with fine granulometry and 40 % pine

122 bark) and placed in a greenhouse at the end of February. The plants were fertilized with a
123 standard commercial nutrient solution (Soluvég Parme, NPK 16-6-27+3 MgO+OE, Angibaud
124 Derome) with a drip irrigation system (one dripper per pot) at a frequency adapted to the
125 climatic demand. Plants were completely randomized ($n = 188$) and were grown for 3 months
126 from planting to harvesting of mature fruit. Plants were grown for two weeks after
127 transplantation for adaptation to the greenhouse. One week later, flowers appeared.

128 The experiment was carried out twice: in 2017 and 2018. The fruit were harvested at
129 the beginning of May when they reached the stage of commercial maturity (completely
130 developed, intense red color and firm). Strawberry fruit were harvested only once.

131 **UV-C treatments**

132 The device used for UV-C treatments was a luminous ceiling with 9 UV-C lamps (DSP
133 UV-C tube, OSRAM HNL, 24 W; Pascal *et al.*, 2018). The measurement of the spectrum (by a
134 UV sensor, OSI UV-20 TO-8 photodiode) confirmed a major peak at 254 nm. Four plants were
135 processed in the box at the same time at a distance of 40 cm from the UV-C lamps.

136 The dose applied to the plants was calculated based on light intensity and time of
137 exposure. Light intensity measurements were performed with a radiometer positioned 40 cm
138 below the ceiling lights. The UV-C dose selected was 1.70 kJ/m^2 (*i.e.*, a treatment time of 4
139 min 08 sec) according to a study carried out by Forges *et al.* (2018).

140 Strawberry plants were treated once a week after two weeks of adaptation in the greenhouse.

141 Several modes of application were tested:

142 - Before flowering, "BEFORE" ($1 \times 1.70 \text{ kJ/m}^2 = 1.70 \text{ kJ/m}^2$),

143 - After flowering, "AFTER" ($5 \times 1.70 \text{ kJ/m}^2 = 8.50 \text{ kJ/m}^2$),

144 - During growth "DURING" ($6 \times 1.70 \text{ kJ/m}^2 = 10.20 \text{ kJ/m}^2$),

145 - No treatment: "CONTROL".

146 There were 47 strawberry plants per treatment modality. Following each irradiation
147 treatment, the treated plants were kept in the dark overnight.

148 **Chlorophyll a fluorescence**

149 To characterize the impact of the UV-C treatments on the photosystems, chlorophyll a
150 fluorescence was measured, and the OJIP parameters were calculated (Sirbet and Govindge,
151 2011). The OJIP method correspond to different steps (O, K, J, I and P) in the fluorescence
152 kinetic profile, plotted in a logarithmic time scale from the initial fluorescence F_0 to the
153 maximal fluorescence F_M . The objective was to identify the frequency of application of UV-C
154 that was not deleterious for the plants.

155 The chlorophyll a fluorescence was measured with a fluorimeter (Pocket-PEA).
156 Measurements were done once a week from the beginning of experiment (during plant
157 growth) and until harvest day (corresponding to 8 times of measurements). Three
158 measurements per plant were performed ($n = 145$) and were made in morning on non-
159 senescent and fully developed leaves. Leaves were selected: leaf fully developed above the
160 plant cover. A highlight pulse ($3000 \mu\text{mol/m}^2/\text{s}$) was applied to leaves after they underwent
161 dark adaptation for 30 min with clamps placed on the stems supporting the leaves. The period
162 of dark adaptation allowed the electron acceptor of photosystem II (PSII) to be reoxidized
163 gradually until all PSII reaction centers were able to resume photochemistry. This method
164 allows the quantification of the flow of electrons that takes place in the photosynthetic
165 machinery. All the parameters measured in this study were explained by Stirbet and Govindge
166 (2011). The area under the fluorescence curve (AUFC) was calculated during plant growth.

167 **Morphological analysis during plant growth**

168 To characterize strawberry plant growth, the number of leaves on each strawberry
169 plant was counted (n = 47) before the first UV-C treatment (*i.e.*, 15 days after planting the tray
170 plants) and at harvest (after 8 weeks of growth). The leaf area was also measured at harvest
171 on one leaf of each strawberry plant (n = 47). This leaf was selected since the beginning of
172 experiment marked by a ring corresponding to young leaf above the plant cover.

173 For the fruit production phase, counting of buds, flowers and green/turning/mature
174 fruit was carried out each week (from flowering to the harvest day, which gives an
175 enumeration of 6 consecutive weeks) on each strawberry plant (n = 47). These data provide
176 information about the impact of the UV-C treatments on flowering and fruit production. At
177 harvest, the strawberry fruit were weighed (n = 20).

178 **Fungal material and pathological tests on leaves and fruit**

179 Strain Bc1 of *Botrytis cinerea* was used in this study to artificially inoculate leaves and
180 fruit. This strain was chosen because it is very aggressive on strawberry as already observed
181 by Forges *et al.* (2018). Test was done on detached leaves fully developed and above the plant
182 cover. For pathological tests on leaves, the strain was grown for 3 days on PDA medium
183 (potato dextrose agar, 39 g/L, Sigma-Aldrich) at 21 °C (16 h of light and 8 h in dark). Mycelial
184 plugs of 0.5 cm diameter were used as inoculum and deposited on the central veins of leaves
185 (n = 47). Lesions caused by the fungal pathogen were monitored for a whole week on a day-
186 per-day basis by taking pictures and measuring the lesion areas with ImageJ software. The
187 area under the disease progress curve (AUDPC) was then computed to determine the level of
188 sensitivity of the strawberry plants to the pathogen.

189 Fruit (n = 18 per treatment modality) were inoculated with a spore suspension of Bc1
190 dosed at 10⁶ spores/mL thanks to Malassez counting cell. Each fruit was wounded on the
191 epidermal surface with a sterile needle, and 10 µL of spore suspension was applied. The
192 inoculated fruit were stored in plastic boxes at 21 °C in the dark. The disease development
193 was estimated by counting the number of diseased fruit and by taking pictures for 5 days after
194 inoculation and calculating the fruit lesion area by using ImageJ software.

195 Natural infections by pathogens were also observed during the two years of
196 experiments (2017 and 2018) and were evaluated. A natural epidemic of powdery mildew
197 caused by *Podosphaera aphanis* occurred in 2017. During fruit production, the number of
198 leaves with visible typical symptoms of powdery mildew (as exemplified in Bardin and Gullino,
199 2020) was counted, and the percentage of infected leaves (with more than 3 spots on leaves)
200 per plant was computed (n = 47 plants per treatment modality). Natural infection of fruit by
201 *B. cinerea* (see Bardin and Gullino, 2020) was also observed in 2018 and infected fruit were
202 counted on each plant before harvesting. The percentage of strawberry plants with at least
203 one infected fruit was computed (n = 47 plants per treatment modality). During storage, fruits
204 naturally infected by *Rhizopus* sp. were counted during the two years of the experiment, and
205 the percentage of infected fruit was computed (n = 18 fruit per treatment modality).

206 **Quality analysis of fruit during post-harvest storage**

207 The firmness and color of fruit (n = 18 fruit per treatment modality) were estimated
208 after harvest (D0) and after 2 (D2) and 4 days (D4) of storage at 21 °C.

209 Fruit firmness was carried out on the domed part of the strawberry with a penetration
210 probe (5 mm diameter). The force required for the probe to penetrate the fruit was measured

211 by a Penefel texture analyser (Setop Giraud-Technologie, France). The firmness was reported
212 as force in Newtons (N).

213 Fruit color was measured with a chromameter (CR-400, Minolta). The apparatus was
214 calibrated with a white reference plate, and the parameters L^* , a^* and b^* were measured.
215 Hue angle (H° , where 0° = red-purple, 90° = yellow, 180° = bluish-green, and 270° = blue) and
216 chroma (C^* , which represents the intensity of color) were estimated according to McGuire
217 (1992).

218 To evaluate consumer preferences, taste tests were carried out on harvested
219 strawberry fruit. A panel of 30 consumers, with a combination of men and women, tasted
220 strawberry fruit from plants undergoing the various UV-C treatments. Consumers tasted blind
221 and had to indicate their preferences and taste criteria (such as acidity, sweetness or texture).

222 **Data Analysis**

223 All statistical analyses were performed with the software Statistica. First, analysis of
224 data normality was performed using the Shapiro test. If the data were normal, an analysis of
225 variance (ANOVA) was performed. In the case of a significant effect of the test factor, a
226 comparison of means was made with Duncan's test or Newman-Keuls test. In contrast, if the
227 data were not Gaussian, nonparametric tests were used, such as the Kruskal-Wallis test. For
228 each test, a threshold of p-value < 0.05 was used. All statistical analyses were performed on
229 all results obtained in both 2017 and 2018 years.

230

231 **Results**

232 **Impact of UV-C treatments on strawberry plant development**

233 To evaluate the effect of UV-C treatment on the vegetative growth of the strawberry
234 plants, the number of leaves was counted before the first UV-C treatment and at harvest, 8
235 weeks after planting (Figure 1-A). Plant growth was homogeneous before the first UV-C
236 treatment. At harvest, no significant differences in the number of leaves was observed
237 between treated groups and non-treated group. However, leaf area was significantly smaller
238 in the plants treated after flowering (“AFTER” and “DURING”) compared to the non-treated
239 plants (“CONTROL”) and the plants treated once before flowering (“BEFORE”) (Figure 1-B).

240 The parameters associated with the fluorescence of chlorophyll a were measured to
241 evaluate the impact of the UV-C treatments on the plant photosystem (Figure 2). Successive
242 applications of UV-C did not cause any major damage to the photosynthetic apparatus of
243 strawberry plants. In fact, the different percentages observed between each group treated
244 with UV-C and the control group did not exceed 25 %. We observed that the measured
245 parameters associated with the fluorescence of chlorophyll a increased for plants treated
246 before flowering (“BEFORE”) and decreased for plants treated after flowering (“AFTER”) or
247 during cultivation (“DURING”) compared to the non-treated group (“CONTROL”).

248 **Impact of UV-C treatments on strawberry fruit development**

249 The number of buds was significantly lower in the UV-C-treated plants than in the non-
250 treated plants (Figure 3-A). Conversely, at the same time, the number of flowers was
251 significantly higher for strawberry plants that received UV-C treatment (1.5 to 2 flowers per
252 plant depending on the treatment) than in the plants that were not treated (0.25 flowers per
253 plant for the “CONTROL”) (Figure 3-B).

254 Subsequently, green fruit were counted each week until harvest (Figure 4). The
255 number of green fruit per plant was higher in treated plants, *i.e.*, those of the “BEFORE” and

256 “DURING” modalities, than in non-treated plants (“CONTROL”). After 4 weeks, all treated
257 samples, including “BEFORE”, “DURING” and “AFTER” plants, had more green fruit than the
258 control. Then, after 5 weeks, the number of green fruit produced per plant was similar across
259 all modalities.

260 The number of ripe fruit per plant was counted on the day of harvest (Figure 5-A). The
261 amount of ripe fruit was significantly higher for the plants treated with UV-C before flowering
262 (“BEFORE” with a mean of 6.6 ripe fruit per plant) or during the entire cultivation process
263 (“DURING” with a mean of 5.5 ripe fruit per plant) than for the non-treated plants (“CONTROL”
264 with a mean of 3.8 ripe fruit per plant) and those treated after flowering (“AFTER” with a mean
265 of 4.5 ripe fruit per plant). An approximately two-fold increase in the amount of ripe fruit was
266 observed when the plants were UV-C treated. Moreover, UV-C treatment applied before
267 flowering (“BEFORE”) significantly increased the weight of the fruit at harvest (Figure 5-B).

268 **Impact of UV-C treatments on strawberry sensitivity (leaves and fruit) to *B. cinerea***

269 Pathogenicity tests using *B. cinerea* on detached leaves fully developed and above the
270 cover of strawberry plant collected at harvest revealed a significant reduction in the
271 susceptibility to the plant pathogen (19 %) for the plants that were treated with UV-C after
272 flowering (“AFTER”) (Figure 6-A). For plants treated before flowering, the sensitivity to *B.*
273 *cinerea* significantly increased up to 25 % compared to the non-treated plants (“CONTROL”).

274 No difference in the sensitivity to *B. cinerea* between fruit collected from UV-C-treated
275 plants or untreated plants was observed (Figure 6-B). However, a tendency (not significant)
276 for an increase in the sensitivity of strawberry fruit after UV-C treatment was observed.

277 **Impact of UV-C treatments on strawberry sensitivity (leaves and fruit) to spontaneous** 278 **infections**

279 Natural and spontaneous epidemics of powdery mildew (caused by *Podosphaera*
280 *aphanis*) occurred a few days before harvest. We evaluated the level of strawberry resistance
281 against this biotroph by counting the infected leaves (Figure 7). UV-C treatment, regardless of
282 the period of application, significantly decreased the susceptibility of strawberry plants to the
283 pathogen by 51 %, 59 % and 75 % in the “BEFORE”, “AFTER” and “DURING” treatments,
284 respectively.

285 At harvest, some strawberry fruit were infected naturally by *B. cinerea* (Figure 8). The
286 most repeated UV-C treatment, “DURING”, for which UV-C treatment was applied each week
287 during all growth periods, was the most efficient at reducing natural contamination (a
288 reduction of 40%). The decrease observed for the other UV-C-treated samples was not
289 significant compared to the control.

290 Moreover, during storage at 21 °C, strawberry fruit were also naturally infected by
291 *Rhizopus* sp. (Figure 9). After 4 days of storage, contamination with *Rhizopus* sp. was high in
292 the control samples (55 %), and there was no difference with the treatment “AFTER”. The
293 “BEFORE” and “DURING” UV-C treatments significantly reduced the contamination after 4
294 days by 20 % and 12 %, respectively.

295 **Impact of UV-C treatments on fruit quality**

296 The color and firmness of strawberry fruit were analyzed (Table 1). During storage, the
297 hue angle and chroma of groups treated with UV-C were lower than those of the control
298 group. The groups “AFTER” and “DURING” had lower hue angles and chroma values than the
299 control group beginning at two days of storage. After three days of storage, the groups
300 “AFTER”, “DURING” and “BEFORE” had a lower hue angle and chroma than the control group.
301 The firmness slightly decreased during storage for all the samples.

302 Sensory evaluation on strawberry fruit the day before was carried out by blind tests
303 with 30 consumers (Data not shown). UV-C treated fruit from both the “BEFORE” group and
304 the “DURING” group were appreciated at the same level (21 % for each group). The UV-C
305 treated fruit from the “AFTER” group were appreciated by 11 % of consumers. And 47 % of
306 consumers prefer fruit no treated with UV-C radiation.

307

308 **Discussion**

309 This study investigated the impact of pre-harvest application of UV-C radiation on plant
310 growth, the sensitivity of leaves and fruit to major plant pathogens and fruit quality after
311 harvest.

312 One striking result concerns the rate of flowering of strawberry plants between non-
313 treated and UV-C treated plants. Flowering occurred earlier when strawberry plants received
314 UV-C treatments. This result is consistent with two studies conducted by Darras *et al.* (2012a
315 and 2015), who demonstrated that the application of short UV-C radiation improved flowering
316 and even increased the biomass of geranium plants. Early flowering was also observed in
317 strawberry plants treated with a low dose of UV-C at pre-harvest, which could be related to
318 changes in the phytohormone profile (Xu *et al.*, 2017a). If flowering occurs earlier, the
319 production cycle can be completed faster, as shown in our study. Thus, larger amounts of ripe
320 fruit at harvest, especially for the strawberry plants treated before flowering, were counted.
321 It suggests that UV-C treatments were beneficial for flower initiation, allowing greater fruit
322 production. Floral induction results in the transition from the vegetative to the reproductive
323 state of meristem, under the action of a reduction in the gibberellin production. UV-C
324 treatments may have an impact on gibberellin production and thus promote flower induction.

325 Fina *et al.* (2017) demonstrated that UV-B treatments on corn decreased leaf growth and this
326 reduction was correlated with a decrease in the concentration of gibberellins. The floral
327 induction has given way to the floral initiation during which a certain number of stems was
328 initiated, thus determining a production potential. Floral differentiation was the last step. It is
329 this phase that determined flower number per stem and therefore fruit number (CTIFL, 2004).
330 As the flowering process was rapid, UV-C treatments could be beneficial for all stages of
331 flowering, from flower induction to flower differentiation and flower initiation. These results
332 confirm that UV-C radiation can induce a high irradiance response that enhances plant growth
333 and development of fruit (Taiz and Zeiger, 1998).

334 Crop quality is correlated with the accumulation of direct or indirect solar radiation,
335 which is absorbed by the leaves and is dependent on the total area and number of leaves
336 (Marcelis *et al.*, 1998). In this study, we did not find significant differences in the amount of
337 leaves per plant between non-treated and UV-C treated plants. A slight decrease in leaf area
338 was observed for plants treated with UV-C. This result was in line with Darras *et al.* (2012a)
339 who suggest that the UV-C radiation was powerful enough to give maximum benefits so that
340 plants did not need to expand their leaf area to capture more light radiation. Moreover, this
341 slight decrease in leaf area could be related to the flower induction with a decrease in
342 gibberellin content (Fina *et al.*, 2017). In addition, analysis of parameters linked to chlorophyll
343 a fluorescence makes it possible to identify the potential damage caused by repeated and
344 successive UV-C treatments. In this study, we demonstrated that successive UV-C doses of
345 1.70 kJ/m² did not damage the photosynthesis pathway. But the repetition of UV-C treatments
346 may improve the desired effect of UV-C radiation, that is, the stimulation of plant defenses.
347 Plants treated throughout cultivation (6 successive UV-C treatments) were less sensitive to *P.*
348 *aphanis*, *B. cinerea* and *Rhizopus* at the leaf and fruit level than plants treated once before

349 flowering. An application threshold should therefore be found to improve plant resistance
350 without irreversibly damaging the photosynthetic system of plants. With a hormetic dose
351 applied to plants, the photosynthetic apparatus can be impacted, but reparation of this
352 pathway can occur after a few hours due to the photoreactivation of white light (Kunz *et al.*,
353 2006).

354 Only a few reports have evaluated the impact of UV-C radiation when it was applied
355 during plant growth (Darras *et al.*, 2012a; Janisiewicz *et al.*, 2016; Obande *et al.*, 2011; Oliveira
356 *et al.*, 2016; Severo *et al.*, 2016; Xie *et al.*, 2015; Xu *et al.*, 2019a). These studies focused on
357 the evolution of secondary metabolites in fruits and vegetables which is closely related to
358 defense mechanism. But limited knowledge is available regarding fruit responses to
359 pathogens when UV-C radiation are applied before harvesting the fruit. This study investigated
360 the impact of pre-harvest UV-C treatment on the susceptibility of strawberry plants and fruit.
361 UV-C treatment applied after flowering significantly decreased the susceptibility of the
362 strawberry leaves to *B. cinerea* and to *P. aphanis*. For powdery mildew, the occurrence of a
363 natural epidemic does not make it possible to differentiate the part of the direct effect or the
364 induced resistance effect of UV-C in the high level of protection observed. UV-C radiation has
365 a well-known and studied direct antimicrobial effect. For example, Darras *et al.* (2012b) have
366 shown a strong impact of UV-C radiation on the conidial germination of *B. cinerea* and a
367 significant delay of mycelium growth. However, the decrease in the sensitivity of strawberry
368 plants which received a single UV-C radiation (“BEFORE”), long before the appearance of the
369 first symptoms of powdery mildew on untreated control plants, may indicate that induced
370 resistance occurred.

371 Plants treated with UV-C had significantly fewer fruit naturally infected with *Rhizopus*
372 sp. and *B. cinerea*, demonstrating a potential link between pre-harvest treatments and post-
373 harvest conservation. However, after artificial inoculation with *B. cinerea*, we didn't observe
374 any effect of UV-C treatments. The inoculation method of the fruit was probably too invasive,
375 causing *B. cinerea* to grow too quickly on the fruit, and not allowing identification of
376 differences in susceptibility. Our inoculation method and that of Jin *et al.* (2017) were similar
377 in the concentration of *B. cinerea* suspension (10^6 spores/mL by wounding), but they observed
378 that the strawberry fruit treated with UV-C had smaller lesion diameters. At least two
379 hypothesis may explain the differences observed between our study and that of Jin *et al.*: the
380 strains of *B. cinerea* that may have different aggressiveness on strawberry and the
381 temperature of incubation (5 °C vs. 21 °C in our study). At the temperature of 5 °C used by Jin
382 *et al.* (2017), the development of *B. cinerea* is slowed down (compared to the temperature of
383 21 °C used during our experiment), and could explain the differences observed.

384 The sensory and physical qualities of strawberry fruit were evaluated after harvest and
385 during 4 days of storage at 21 °C. Color and firmness are widely used to monitor post-harvest
386 fruit quality and are very well accepted as indicators of complex maturation processes and,
387 therefore, of many physiological mechanisms (Gunness *et al.*, 2009). The UV-C treatments did
388 not alter the physical integrity of the strawberry fruit. In this study, there was no difference in
389 firmness between fruit from control and UV-C-treated plants (from 1.7 to 10.20 kJ/m²). This
390 result is in contradiction with a previous study (Xie *et al.*, 2016) that showed that pre-harvest
391 UV-C treatments (3.6 kJ/m²) improved the firmness of post-harvest strawberry fruit.
392 According to these authors, this result depends on cultivar and season of harvesting that
393 played a more important role in influencing fruit quality than the pre-harvest UV-C treatment.
394 However, strawberry fruit showed a lower hue angle, which indicates that UV-C-treated fruit

395 were redder (lower hue angle) in color than the control group. These results were in
396 agreement with those of Xu *et al.* (2017a), who demonstrated that the higher ABA level in
397 strawberry fruit treated with UV-C of low cumulative dose of 9.6 kJ/m² and mid-level
398 cumulative dose of 15 kJ/m², with more red color, suggests that UV-C dose stimulates the
399 accumulation of pigments such as anthocyanin. Other studies have shown that UV-C radiation
400 applied to plants during cultivation had an impact on the color of post-harvest strawberry
401 fruit. Xie *et al.* (2016) observed a significantly higher value for a*, which indicates redness. In
402 the case of strawberry fruit, these parameters generally indicate an increase in the
403 anthocyanin content and are therefore a marker of the progress of fruit ripening. However,
404 Xie *et al.* (2015) did not observe any effect of pre-harvest UV-C on the anthocyanin content in
405 strawberry fruit.

406 We also conducted blind tests with a panel of 30 consumers to estimate the sensorial
407 qualities of fruit. This study highlighted that UV-C treatment during pre-harvest did not change
408 the taste of fruit compared to the control if we took into account both UV-C treatments
409 (“CONTROL” vs “BEFORE”/“AFTER”/“DURING”). For this test, consumers did not prefer a
410 group, that is to say that strawberry were not sweeter for example as the sweetness is one of
411 the first quality parameter preferred by consumers.

412

413 **Conclusion**

414 In conclusion, pre-harvest UV-C treatments had some significant effect on plant and
415 reduced the natural occurrence of diseases, such as powdery mildew on leaves. Concerning
416 fruit, pre-harvest UV-C treatments had some significant effect on color and there was a strong
417 significant reduction in natural infection with pathogens, such as *Rhizopus* sp. Additional

418 experiments will be done to confirm this encouraging result with artificial inoculum of
419 *Rhizopus* and *P. aphanis*.

420 It seems difficult to find only one UV-C treatment that would be optimal for all
421 parameters measured, such as disease resistance of plants, of fruit or fruit quality. In our
422 study, we showed that it is preferable to apply UV-C treatments before flowering to increase
423 flowering and plant yield but it is preferable to apply UV-C after flowering to reduce the
424 susceptibility of leaves to infection by *B. cinerea*.

425 In addition, UV-C treatments applied pre-harvest seem to be promising in terms of crop
426 quality, but further evaluation is needed to find optimal UV-C treatments that can also have
427 an impact on strawberry fruit.

428

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433

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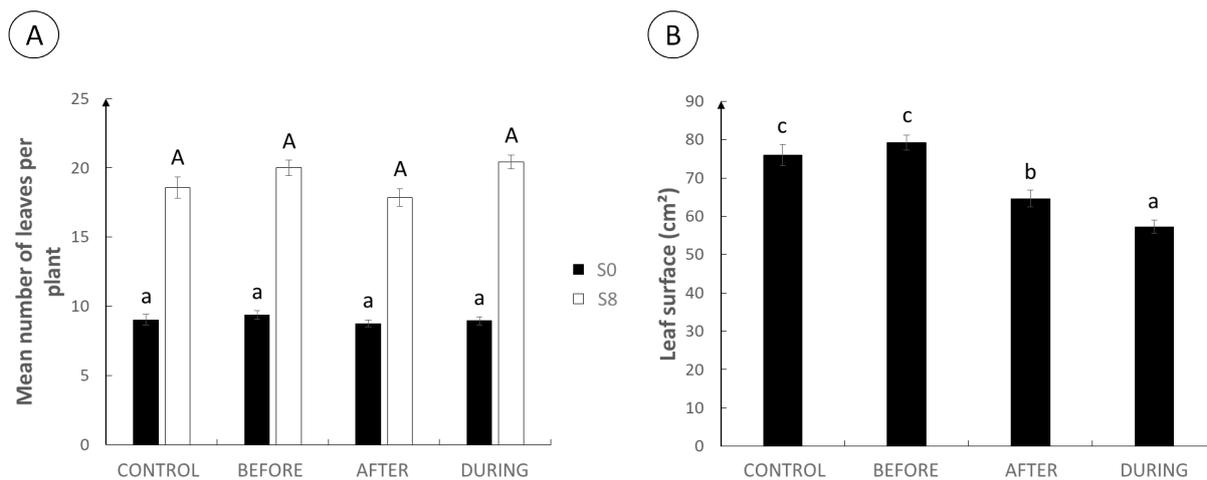


Figure 1: Effect of UV-C treatment on (A) the number of leaves per plant and (B) the leaf surface at harvest. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². (A) Count of leaves was done before the first UV-C treatments, after 15 days of plant growth (S0) and at harvest (S8), after the successive UV-C treatments (n = 47). (B) Leaf surface was measured at harvest day (n = 47). Different letters indicate significant differences according to Newman-Keuls test at p < 0.05.

AUFC	BEFORE	AFTER	DURING
Area	21.63	-16.86	-11.90
F0	0.95	-11.64	-10.57
Fm	-0.18	-13.01	-15.81
Fv	-0.40	-13.28	-16.83
F0 / Fm	1.56	1.71	6.38
Fv / Fm	-0.30	-0.33	-1.24
Fv / F0	-1.35	-1.83	-7.15
Sm	14.85	-4.82	5.53
N	10.91	-10.79	-0.22
ABS / RC	-5.15	-6.08	-4.09
Di0 / RC	-3.69	-4.06	1.77
TR0 / RC	-5.43	-6.48	-5.24
Et0 / RC	-7.58	-7.09	-4.89
Re0 / RC	-4.16	-10.54	-4.83
Pi total	7.08	-1.60	-1.52
$(1-V_i) / (1-V_j)$	3.23	-3.48	0.20
$1 - (F_4/F_m)$	-2.97	-0.78	-0.90
Vk / Vj	-9.66	-7.60	-4.29

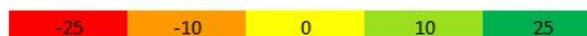


Figure 2: Relative fluorescence of chlorophyll a of strawberry plant at the harvest day. “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². Values represented AUFC (Area Under Fluorescence Curve) and represent difference percentages between each group treated with UV-C compared to the control group (n = 145). A color scale is provided, ranging from red (negative effect of UV-C radiation) to green (positive effect of UV-C radiation). Values in bold and underlined mean significant difference according to the Newman-Keuls test at p-value < 0.05).

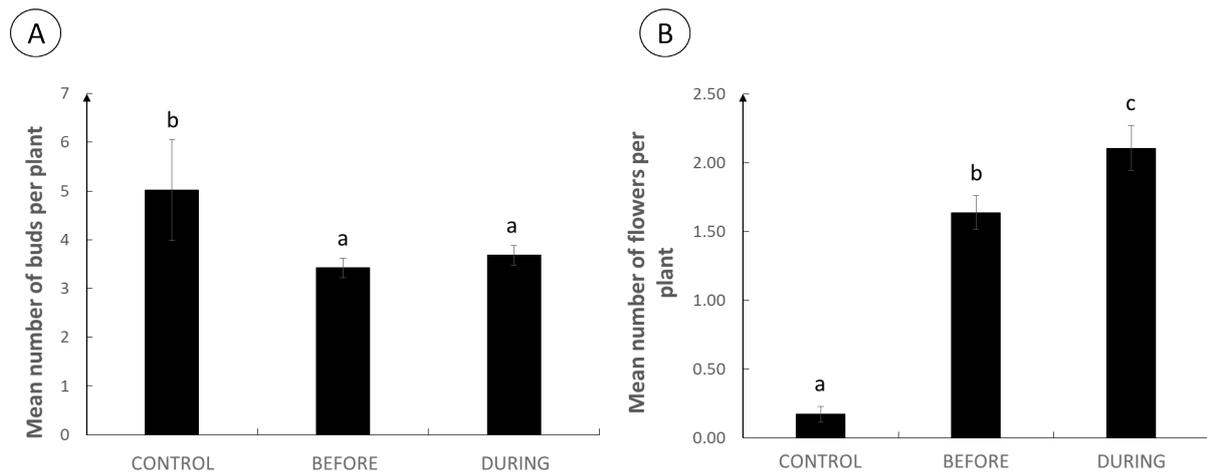


Figure 3: Effect of UV-C treatment on the number of (A) buds and (B) flowers per plant (counted one week after the first UV-C treatment). This count was done before flower apparition (n = 47). “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. Groups “BEFORE” and “DURING” corresponded to the same modality at this level because the count was done before flowering (group “AFTER” didn’t take into account because because it was after UV-C treatment on modalities “BEFORE” and “DURING”). The selected UV-C dose is 1.70 kJ/m². Different letters indicate significant differences according to the Newman-Keuls test at p-value < 0.05.

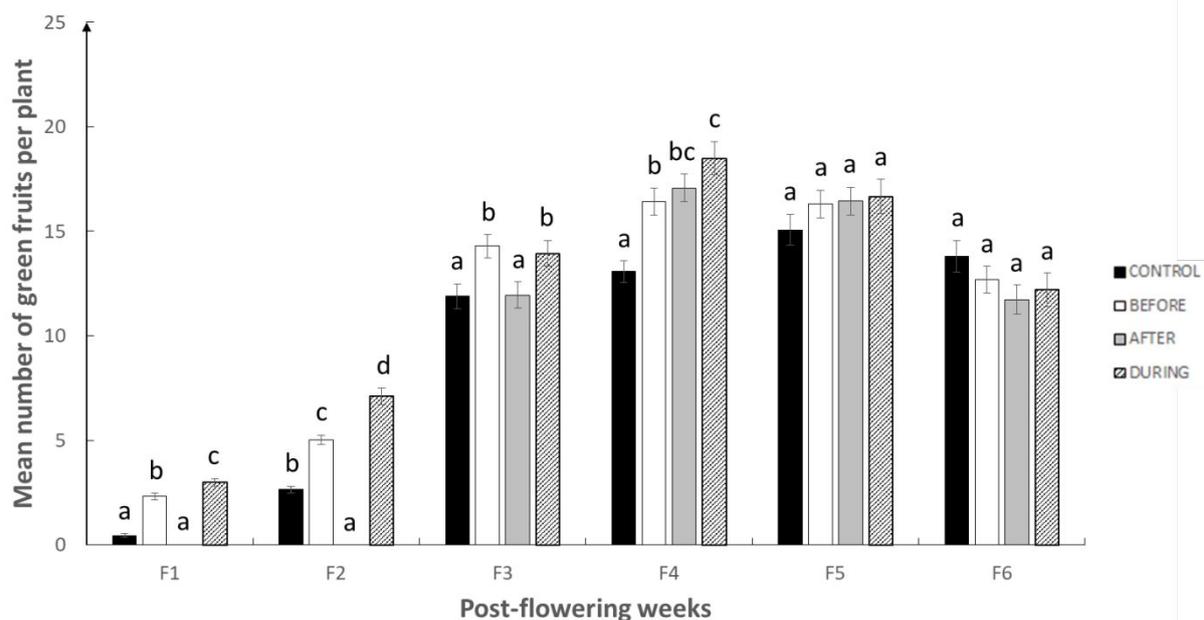


Figure 4: Mean number of green fruit produced per strawberry plant during the cultivation. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². Count was made during 6 weeks just after flowering (post-flowering weeks = F) on each strawberry plant (n = 47). Different letters indicate significant differences according to Newman-Keuls test at p-value < 0.05.

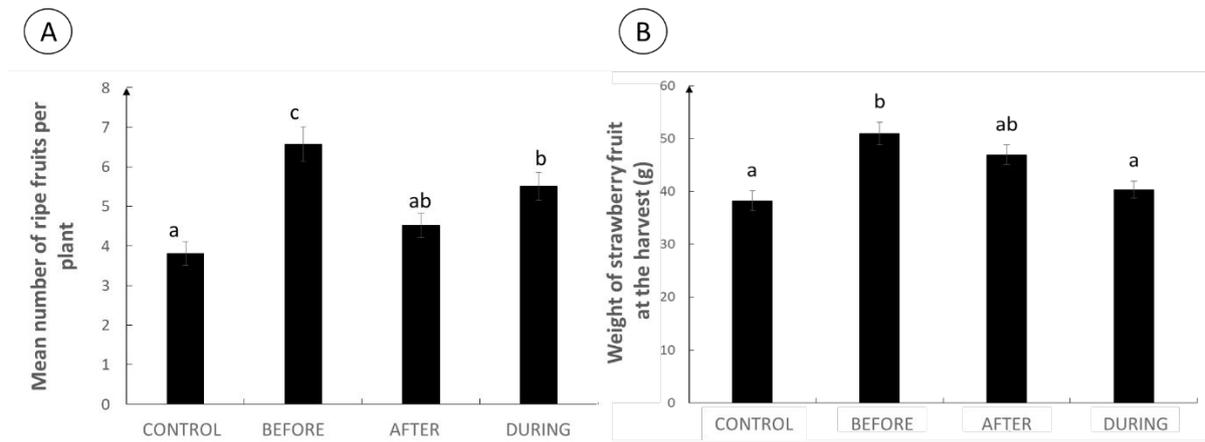


Figure 5: (A) Number of ripped fruit per strawberry plant at harvest (one week after the last UV-C treatment). (B) Effect of UV-C treatment on the weight of strawberry fruit at harvest (one week after the last UV-C treatment). “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². (A) The count was done on each strawberry plant (n = 47) and (B) The weight of strawberry fruit was done on 20 fruit per modality. Different letters indicate significant differences according to Newman-Keuls test at p-value < 0.05.

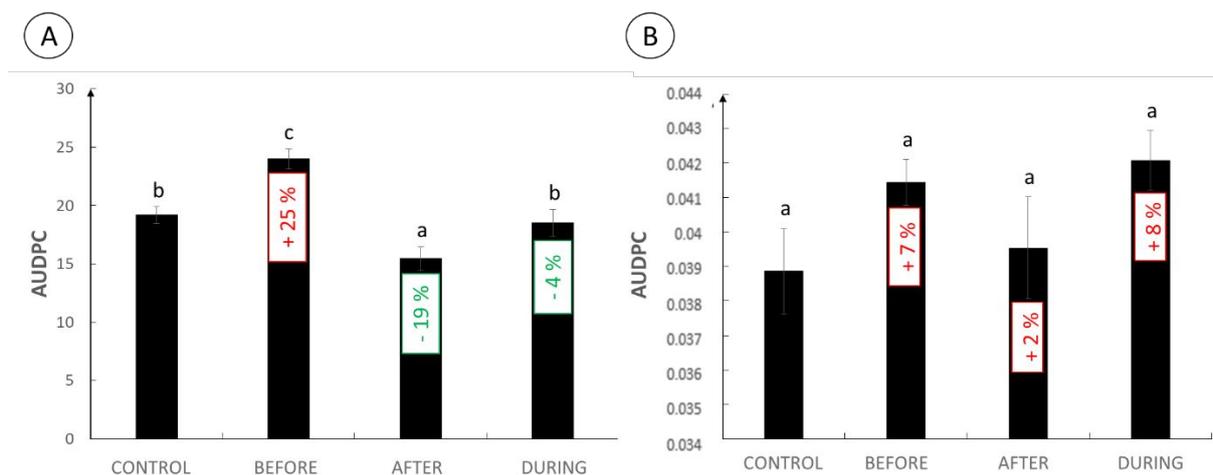


Figure 6: Susceptibility of strawberry leaves (A) and strawberry fruit (B) to *B. cinerea*. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². Inoculation of leaves were made after UV-C treatments by depositing a mycelial plug of *B. cinerea* on the main vein of detached leaves. Surface of necrosis was measured daily for 6 days in order to calculate the AUDPC (Area Under Disease Progression Curve, n = 47). Inoculations of fruit were carried out by depositing a drop of fungus suspension at 10⁶ spore/mL. Measurement of necrosis width was done daily for 4 days in order to calculate AUDPC (n = 18). Percentages correspond to the protection or sensibility level compared to the control group: in red depict acceleration of the disease progression curve and percentages indicated in green its slowing down (protection). Different letters indicate significant differences according to Newman-Keuls test at (A) p-value < 0.01 and (B) p-value = 0.05.

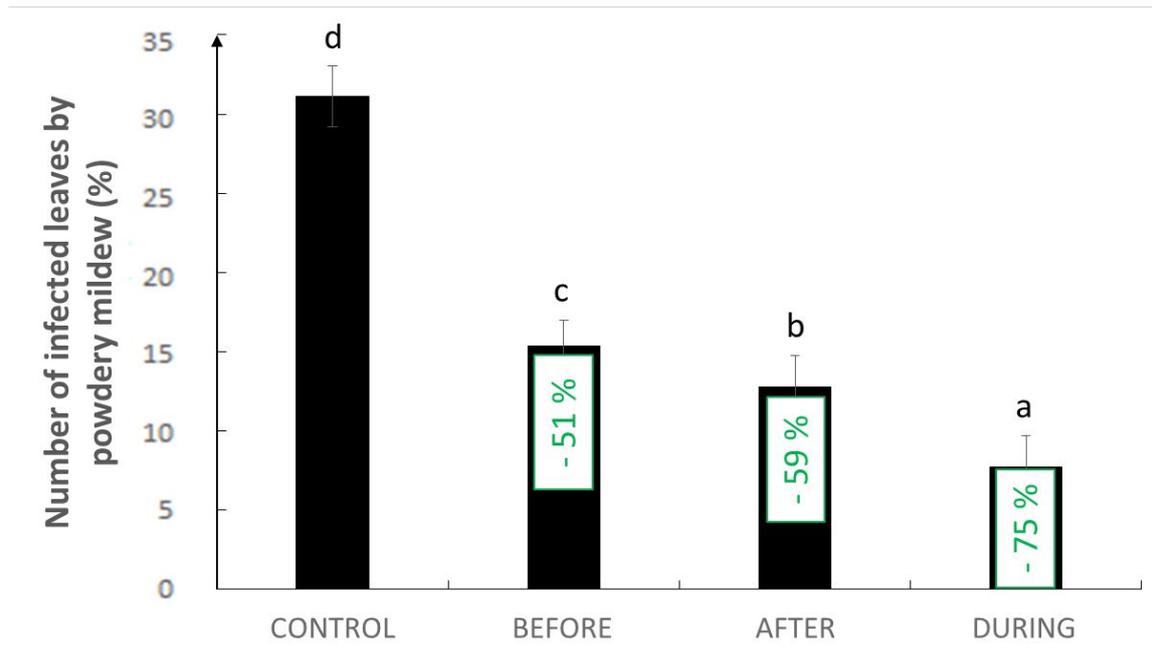


Figure 7: Susceptibility of strawberry leaves to powdery mildew. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². Amount of leaves with symptoms was estimated by appearance of powdery and whitish leaf spots (n = 47). Different letters indicate significant differences according to Newman-Keuls test at p-value < 0.0001.

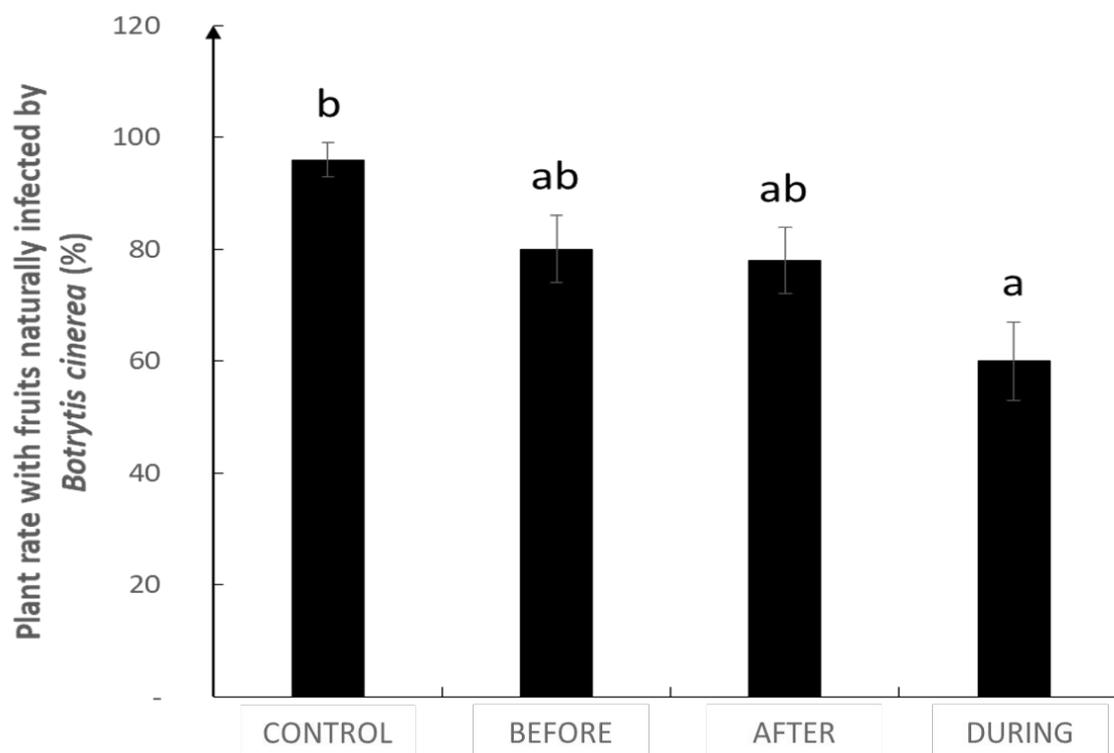


Figure 8: Plants with fruit naturally infected by *B. cinerea* (%). “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². The presence or absence of *B. cinerea* on strawberry fruit was evaluated and the percentage of strawberry plants with at least one infected fruit was computed (n = 47). Different letters indicate significant differences according to K_{hi}² test at p-value < 0.05.

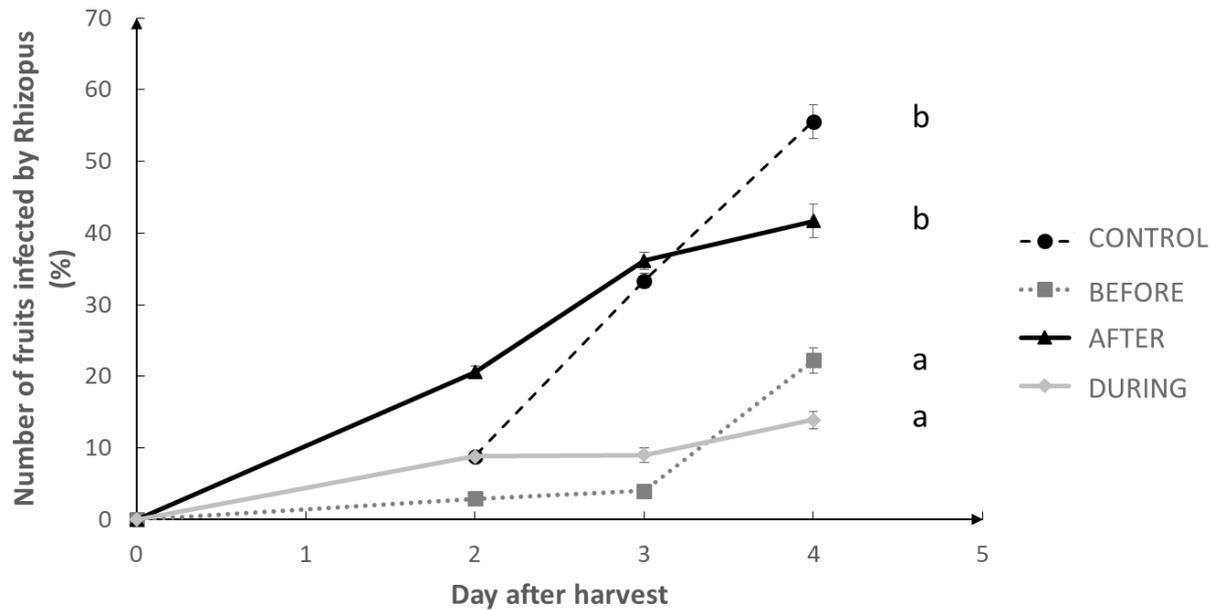


Figure 9: Susceptibility of strawberry fruit to *Rhizopus* sp. during fruit storage. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². A follow-up of fruit infected with *Rhizopus* sp. was carried out every day and the percentage of infected fruit was calculated (n = 18). Different letters indicate significant differences according to Newman-Keuls test at p-value < 0.05.

Table 1: Evolution of color (Hue and Chroma) and firmness of strawberry. “CONTROL” corresponds to plants without treatment, “BEFORE” corresponds to UV-C treatment realized before flowering, “AFTER” corresponds to UV-C treatment realized after flowering and “DURING” corresponds to UV-C treatment realized throughout the crop. The selected UV-C dose is 1.70 kJ/m². The firmness and color were done on 18 fruit per modality. Color were estimated with Hue angle (H°, where 0° = red-purple, 90° = yellow, 180° = bluish-green, and 270° = blue) and Chroma (C*, which represents the intensity of color) thanks to L*a*b* parameters (McGuire, 1992). The (*) shows statistical differences between modalities according to Newman-Keuls test at p-value < 0.05.

	COLOR						FIRMNESS		
	Hue H°			Chroma C*			0	2	4
	0	2	4	0	2	4			
CONTROL	29.2 ±0.8	33.3 ±1.0	34.0 ±1.1	43.1 ±1.0	41.1 ±1.8	46.5 ±1.0	4.2 ±0.6	3.9 ±0.3	3.4 ±0.3
BEFORE	28.3 ±1.3	31.5 ±0.7	30.3* ±0.9	42.3 ±1.0	42.0 ±1.2	43.1 ±0.9	4.4 ±0.7	4.2 ±0.3	3.2 ±0.1
AFTER	26.7 ±1.9	26.0* ±0.5	27.6* ±0.5	38.6 ±1.4	33.5 ±0.9	39.4 ±0.7	4.1 ±0.6	4.1 ±0.3	3.3 ±0.2
DURING	25.8 ±1.2	26.1* ±0.7	25.7* ±1.2	37.7 ±1.3	35.1 ±1.3	40.5 ±1.3	4.2 ±0.4	4.3 ±0.4	3.2 ±0.2