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

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

Abstract

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

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

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

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

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

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

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

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

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

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

Materials and Methods

Plant material

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

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

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

UV-C treatments

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

The dose applied to the plants was calculated based on light intensity and time of exposure. Light intensity measurements were performed with a radiometer positioned 40 cm below the ceiling lights. The UV-C dose selected was 1.70 kJ/m² (*i.e.,* a treatment time of 4 min 08 sec) according to a study carried out by Forges *et al*. (2018).

Strawberry plants were treated once a week after two weeks of adaptation in the greenhouse. Several modes of application were tested:

- Before flowering, “BEFORE” (1 x 1.70 kJ/m² = 1.70 kJ/m²),

- After flowering, “AFTER” (5 x 1.70 kJ/m² = 8.50 kJ/m²),

144 - During growth “DURING” (6 x 1.70 kJ/m² = 10.20 kJ/m²),

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 µmol/m²/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.

Morphological analysis during plant growth

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

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

Fungal material and pathological tests on leaves and fruit

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

Fruit (n = 18 per treatment modality) were inoculated with a spore suspension of Bc1 dosed at 10^6 spores/mL thanks to Malassez counting cell. Each fruit was wounded on the epidermal surface with a sterile needle, and 10 µL of spore suspension was applied. The inoculated fruit were stored in plastic boxes at 21 °C in the dark. The disease development was estimated by counting the number of diseased fruit and by taking pictures for 5 days after inoculation and calculating the fruit lesion area by using ImageJ software.

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

Quality analysis of fruit during post-harvest storage

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

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

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

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

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

Data Analysis

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

Results

Impact of UV-C treatments on strawberry plant development

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

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

Impact of UV-C treatments on strawberry fruit development

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

Subsequently, green fruit were counted each week until harvest (Figure 4). The 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**

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

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

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

Impact of UV-C treatments on fruit quality

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

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

Discussion

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

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

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

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

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

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

Conclusion

In conclusion, pre-harvest UV-C treatments had some significant effect on plant and reduced the natural occurrence of diseases, such as powdery mildew on leaves. Concerning fruit, pre-harvest UV-C treatments had some significant effect on color and there was a strong 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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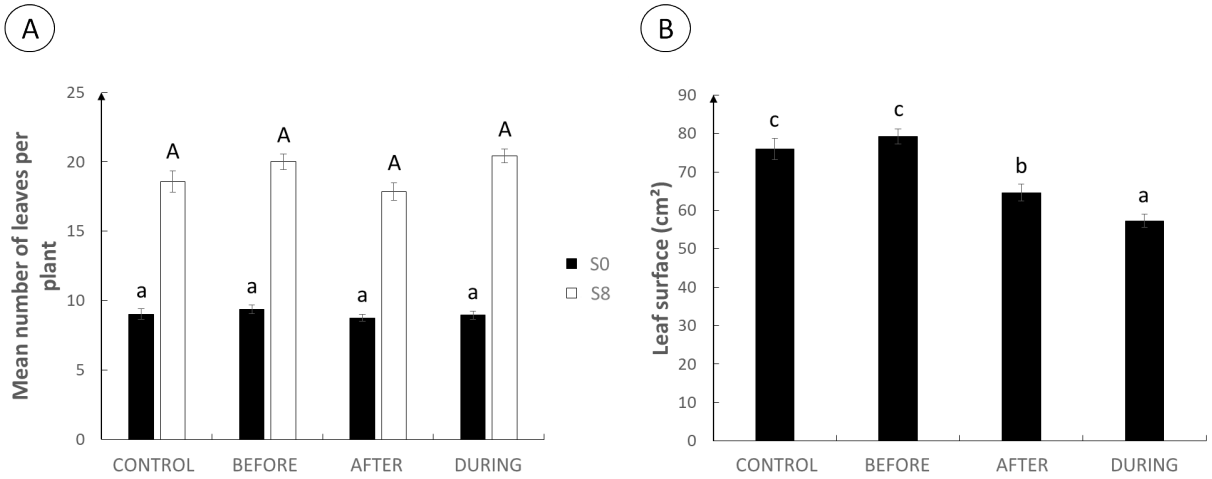

Figure 1: **Effect of UV-C treatment on (A) the number of leaves per plant and (B) the leaf surface at harvest.** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" 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-Vi) / (1-Vj)	**3.23**	**-3.48**	0.20
1 - (F4/Fm)	**-2.97**	-0.78	-0.90
Vk / Vj	**-9.66**	**-7.60**	**-4.29**

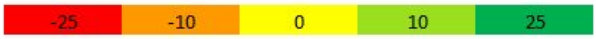

Figure 2: **Relative fluorescence of chlorophyll a of strawberry plant at the harvest day.** "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds to UV-C treatment realized throughout the crop. The selected 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).

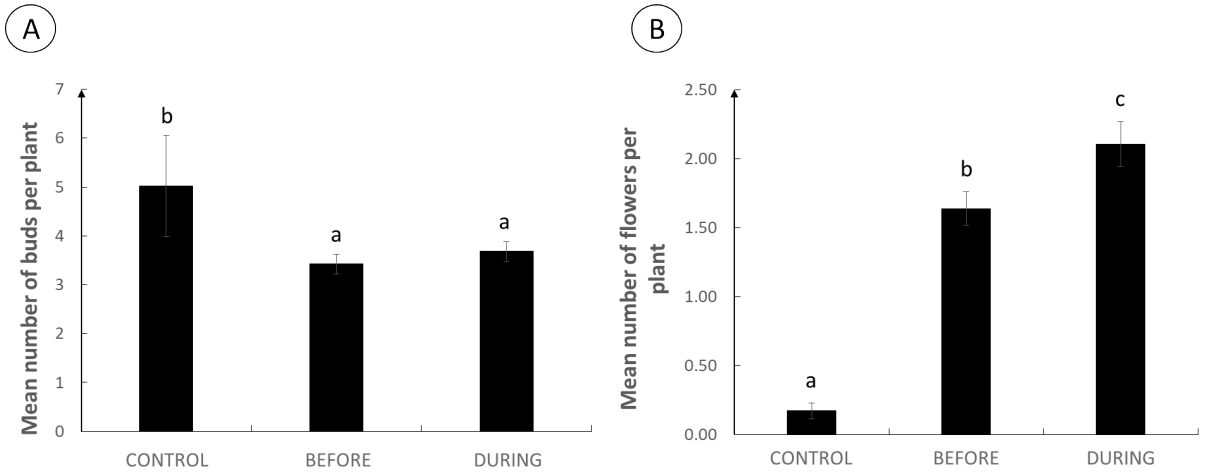

Figure 3: **Effect of UV-C treatment on the number of (A) buds and (B) flowers per plant (counted one week after the first UV-C treatment).** This count was done before flower apparition (n = 47). "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before 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.

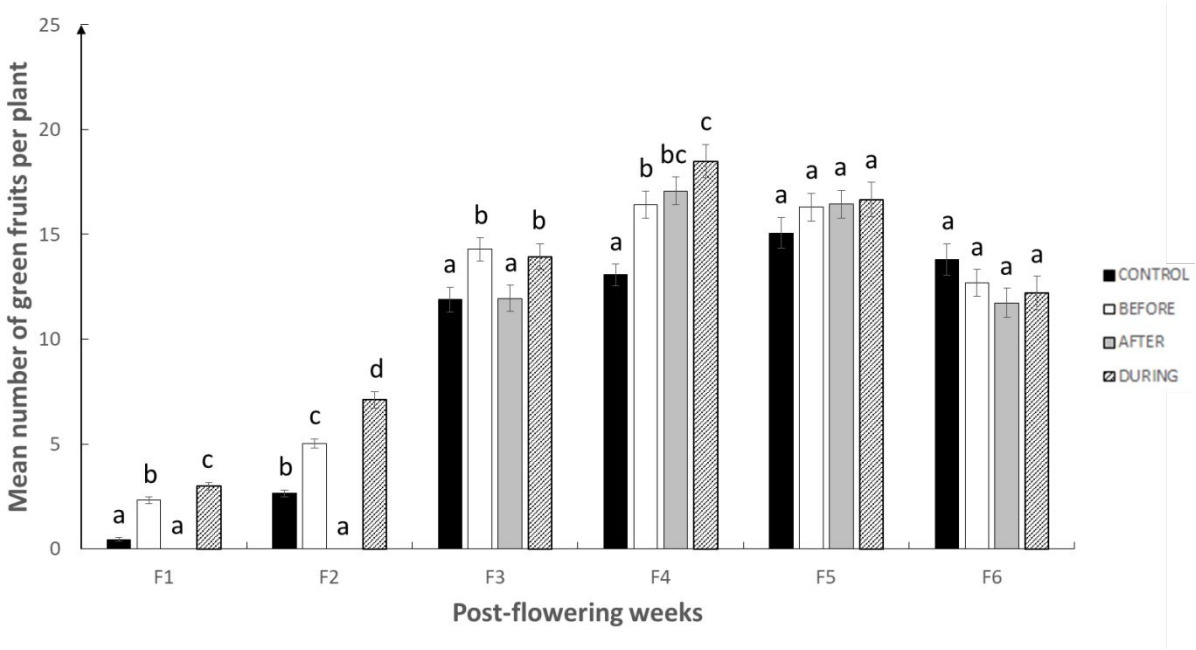

Figure 4: **Mean number of green fruit produced per strawberry plant during the cultivation.** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds to 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.

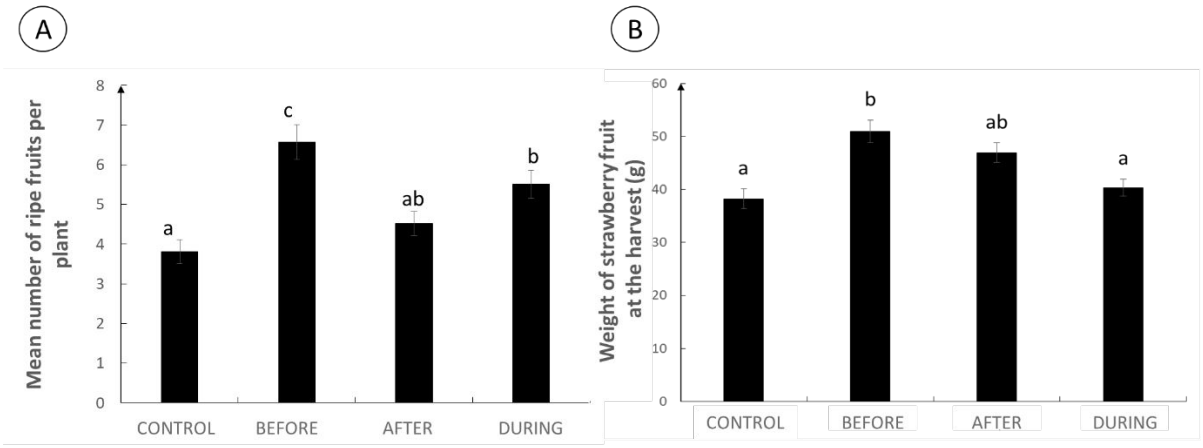

Figure 5: **(A) Number of ripped fruit per strawberry plant at harvest (one week after the last UV-C treatment). (B) Effect of UV-C treatment on the weight of strawberry fruit at harvest (one week after the last UV-C treatment).** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds 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.

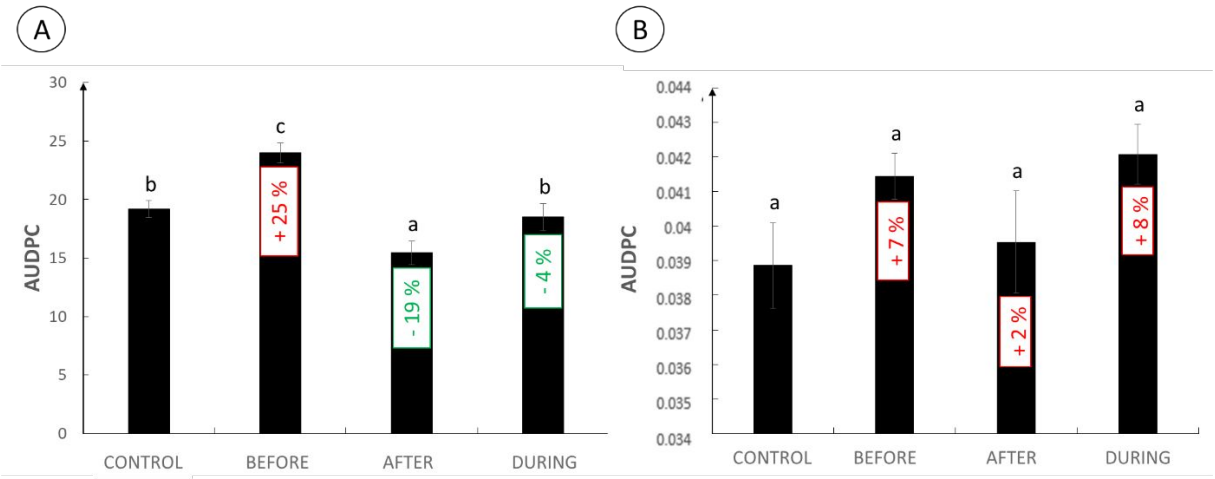

Figure 6: **Susceptibility of strawberry leaves (A) and strawberry fruit (B) to *B. cinerea*.** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds 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 deposing 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 10^6 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.

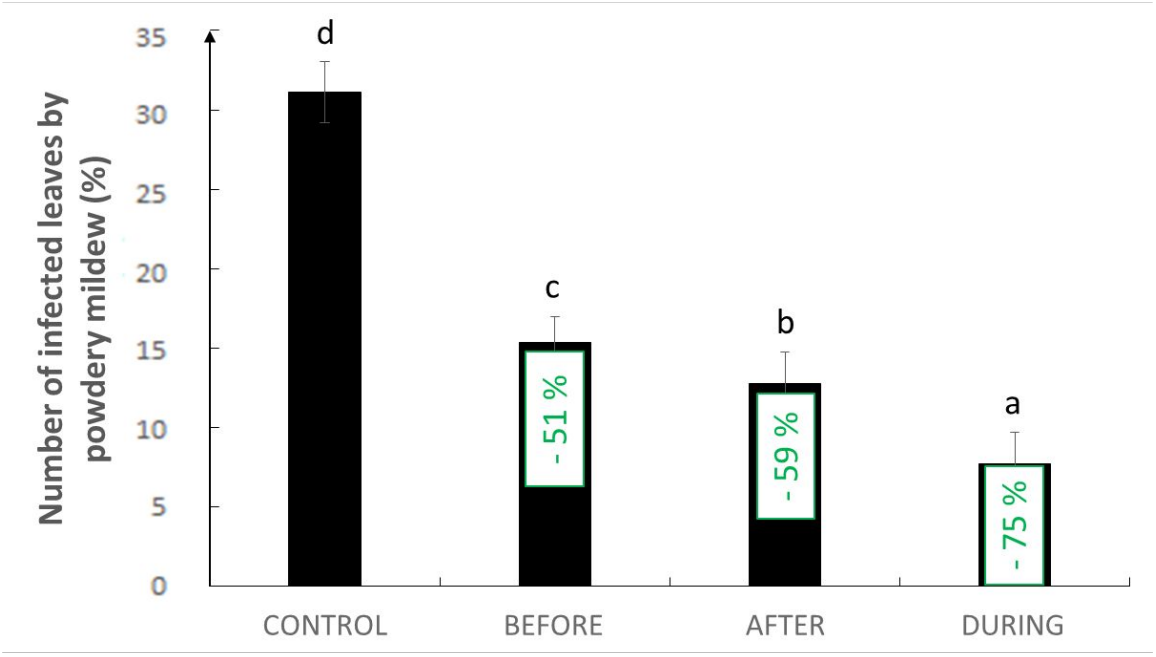

Figure 7: **Susceptibility of strawberry leaves to powdery mildew.** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds to UV-C treatment realized 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.

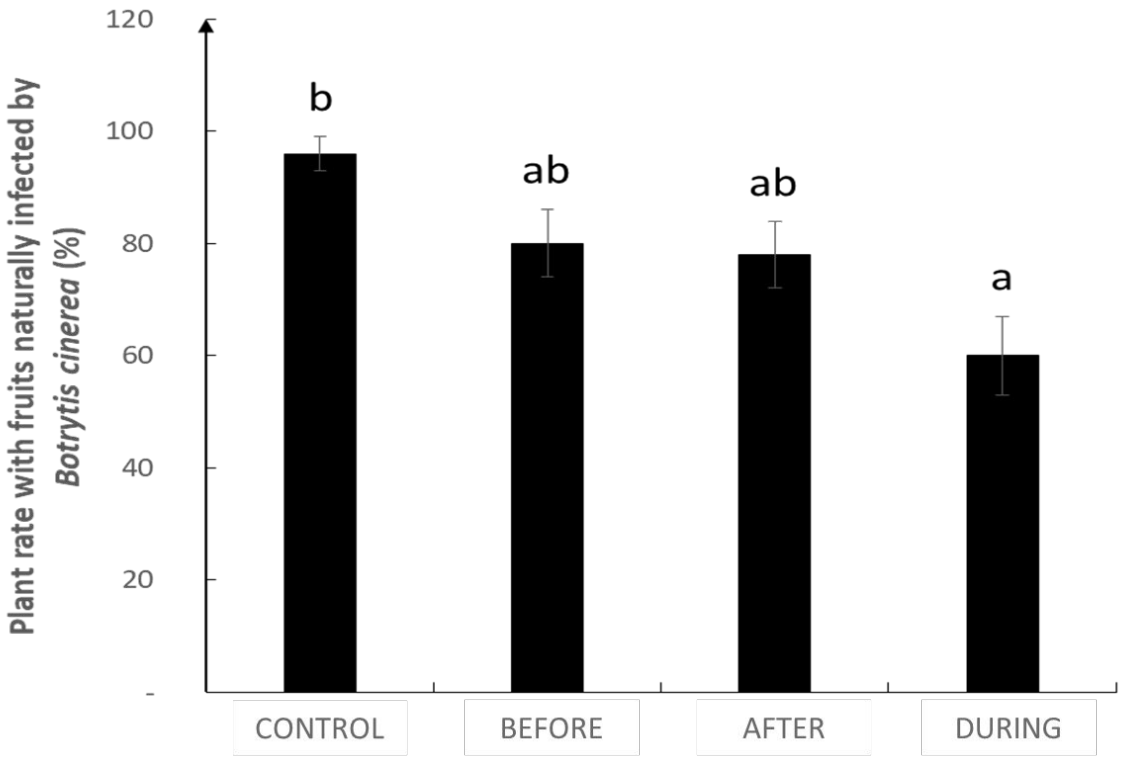

Figure 8: **Plants with fruit naturally infected by *B. cinerea* (%).** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds to UV-C treatment realized 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 Khi² test at p-value < 0.05.

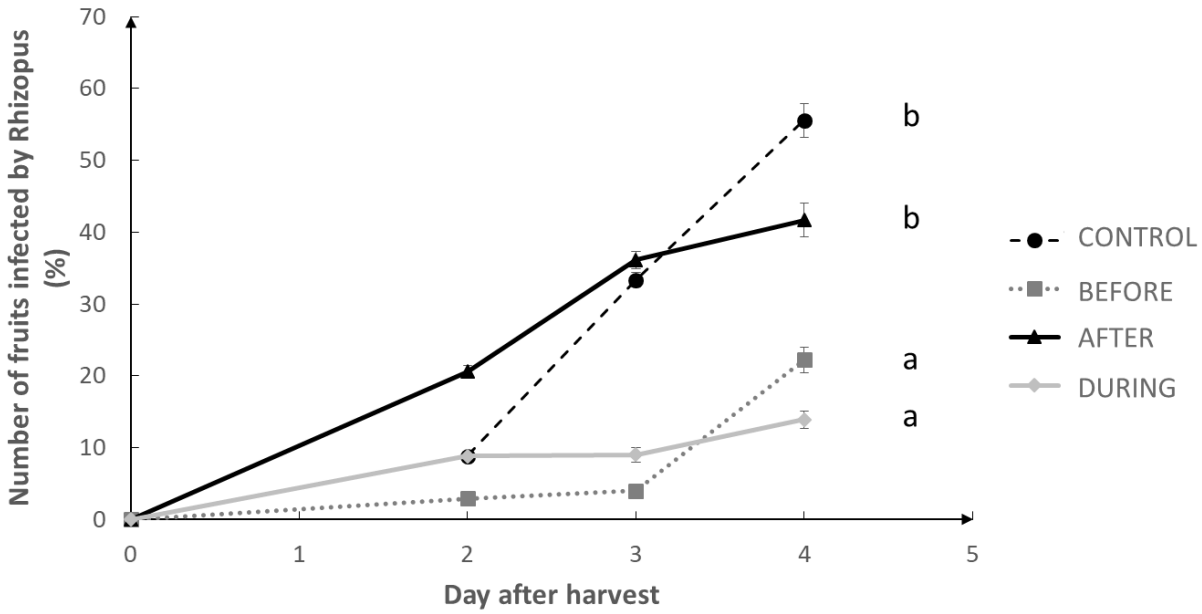

Figure 9: **Susceptibility of strawberry fruit to *Rhizopus* sp. during fruit storage.** "CONTROL" corresponds to plants without treatment, "BEFORE" corresponds to UV-C treatment realized before flowering, "AFTER" corresponds to UV-C treatment realized after flowering and "DURING" corresponds to UV-C 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