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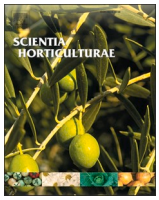

Research Paper

Impact of pre-harvest UVC treatment on powdery mildew infection and strawberry quality in tunnel production in Nordic conditions

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ABSTRACT

Preharvest UVC radiation treatment has emerged as a promising alternative to chemical plant protection methods in plant production systems for preventing fungal diseases. In our study, three strawberry (*Fragaria x ananassa*) cultivars were subjected to nightly UVC treatment (20 s, 0.02 kJ/m^2) delivered through LED technology (with a peak at 276 nm) within polytunnel conditions in Central Finland. The aim was to evaluate the effectiveness of the UVC treatment in inhibiting powdery mildew (caused by *Podosphaera* spp.), as well as to assess its impact on crop yield, fruit quality, firmness, volatile organic compound (VOC) profile, and leaf properties across two consecutive growing seasons. The UVC treatment successfully suppressed the growth of powdery mildew in all three tested strawberry cultivars throughout the experiment, without causing any visible damage to the leaves. The UVC treatment led to an increase in the crop yield of marketable fruits without affecting their size. The impact on fruit quality varied, depending on the specific cultivar, sampling time, and the year under consideration. Fruit firmness following 2–3 days of refrigeration improved due to the UVC treatment. Our findings suggest that UVC treatment can alter the fruit's VOC profile, either directly or indirectly through disease management, affecting its aroma. These findings emphasize the diverse advantages of UVC treatment in enhancing disease resistance and enhancing specific fruit attributes. This suggests the potential for integration of UVC treatment into plant production systems, particularly in tunnel cultivation within Nordic conditions, as a promising approach to improve overall crop management strategies.

1. Introduction

Powdery mildew is a plant disease caused by almost 900 fungal species from 19 genera of Ascomycota. It is considered one of the most economically damaging diseases in plant production systems worldwide (Kusch et al., 2023). The prevailing method for managing powdery mildew is the application of fungicides. Regrettably, the frequent use of fungicides is not only costly but also has adverse effects on the environment and human health and contributes to the development of pathogen resistance (Komarek et al., 2010; Oliveira et al., 2017).

UVC radiation is well-known for its germicidal properties and its ability to damage the DNA and cellular structures of pathogens (Urban et al., 2016). Recent research has suggested that UVC radiation can be harnessed to effectively suppress the growth and proliferation of *Podosphaera aphanis*, the causative agent of powdery mildew on growing strawberry plants (Urban et al., 2016; Peng et al., 2022). Pre-harvest UVC treatment in strawberry production has been explored and employed in various locations around the world as a potential method to control diseases, improve fruit quality, and extend shelf life (Urban et al., 2016; Peng et al., 2022). It has been found that several fungal pathogens can be effectively controlled by exposing the plants to low doses of UVC irradiation, if followed by a period of darkness (Janisiewicz et al., 2016; Suthaparan et al., 2017; Takeda et al., 2019; Pathak et al., 2020).

The effects of UVC radiation on strawberry plants are highly dependent on the dosage, duration, and timing of exposure, which are

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crucial to achieving desired outcomes while minimizing potential negative effects. When plants are exposed to UVC radiation at high intensity and duration, it causes disturbances in cell metabolism, such as damage in DNA, proteins, and membranes, and consequently, reduces photosynthesis, growth, and vigor of plants (Urban et al., 2016). Low UVC doses, in turn, may trigger plant defense responses, such as activation of the antioxidant system and the synthesis of phenolic compounds, resulting in higher stress tolerance (de Oliveira et al., 2016; Severo et al., 2017; Xu et al., 2019). Pre- and postharvest UVC treatment has also been utilized for extending the shelf life of the fruits (Pombo et al., 2011; Xie et al., 2015; 2016). The potential enhancement in phenolic compounds, anthocyanins, and antioxidants holds promise for improving both pathogen resistance and fruit quality across various fruit species (Urban et al., 2016).

The impact of UVC on volatile phytochemicals remains relatively unclear. The volatile compounds of strawberries encompass a range of elements, including esters, alcohols, aldehydes, ketones, acids, terpene compounds, furanones, and lactones, all of which significantly contribute to the fragrance and aroma of strawberries (Nuzzi et al., 2008; Zamorska, 2022). Moreover, these volatile compounds play a crucial role in defending against biotic stress in various parts of the strawberry plant, such as leaves, flowers, and fruits (Amil-Ruiz et al., 2011).

The polytunnel production of strawberries is experiencing a notable surge in popularity across the Nordic countries, driven by the region's challenging climate, characterized by short growing seasons and unpredictable weather patterns (Sønsteby and Karhu, 2005). However, powdery mildew poses a significant challenge in strawberry tunnel cultivation, where the climate and environmental conditions can favor the development of the pathogens. At northern latitudes, flowering and fruit development often occurs in June and July when there is typically a period of twilight or "white nights" rather than complete darkness. In central Finland sunrise occurs at 3am., and at 1am the radiation may be 10–20 W/m^2 (maximum radiation during daytime about 950 W/m^2). Consequently, it's crucial to assess the efficacy of the UVC method, which necessitates a dark period post-treatment, under northern conditions.

Functionality of UVC radiation in preventing fungal diseases in strawberry has been proven in growth chambers (Xu et al. 2017; Sun et al. 2020), greenhouse (Van Hemelrijck et al., 2010; Van Delm et al., 2014; Xie et al., 2016; Forges et al., 2020) and open field (Onofre et al., 2021; Takeda et al., 2021) experiments. To our knowledge, the study presented in this paper is one of the few experiments where impacts of UVC radiation on strawberry crop yield, fruit quality and leaf properties have been studied under tunnel conditions (Janisiewicz et al., 2016; Takeda et al., 2019), employing the LED technique.

The aim of the experiment was to explore the impacts of nightly UVC treatment on (1) effectiveness at suppressing powdery mildew in three strawberry cultivars, (2) crop yield, (3) fruit quality, (4) VOC profile of the fruits, and (5) physiological properties of the leaves.

2. Materials and methods

2.1. Experimental set up

The experiment took place in a strawberry tunnel located in Suonenjoki, Finland (62°39′N, 27°03′E, 142 m above sea level). Two separate experiments were conducted. In 2021, June-bearing strawberry cultivars 'Malling Centenary' and 'Limalexia' were used, while in 2022, 'Malling Centenary' and 'Sonsation' were the chosen varieties. As our aim was to investigate both annual variation in plant responses to UVC radiation and differences in the responses of different strawberry cultivars, we chose to use 'Malling centenary' in both years and to vary the other cultivar. All cultivars used in the experiments are commonly used in tunnel production in Finland. The frigo plants were sourced from the Netherlands, gradually thawed in a chilled storage facility, and

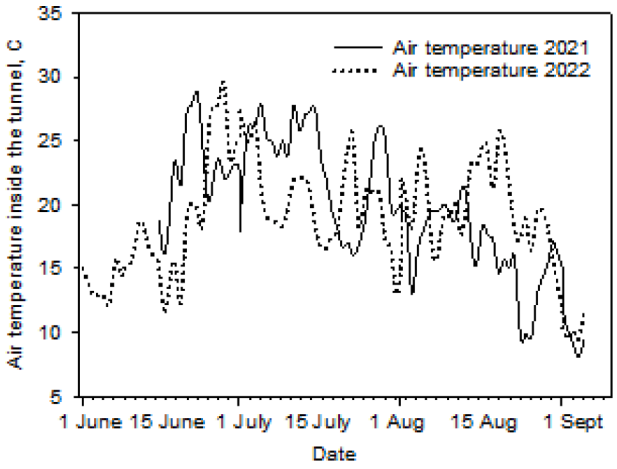

Fig. 1. The air temperature inside the strawberry tunnel was recorded during experiments conducted in 2021 and 2022 in Central Finland. Planting was performed on 15 June 2021 and 1 June 2022. Flowering began in early July, and the first symptoms of powdery mildew were observed after mid-July in both years. Daily mean values were calculated from hourly measurements.

Fig. 2. LED-based UV-exposure equipment developed for research purposes in Suonenjoki, Finland.

subsequently transplanted into the strawberry tunnel in table-tops. Planting occurred on 15 June 2021, and 1 June 2022.

The plants were arranged in a zigzag pattern, with four plants per container (20 cm × 50 cm) containing coconut substrate. Nutrient fertilization was carried out using a nutrient solution composed of Krista K, Calcinit, and Ferticare (7-9-32) (Yara, Vilna, Lithuania). Drip irrigation, consisting of two drippers per container, was employed according to the climatic requirements. Runners were removed weekly.

The experiment included two rows of strawberry plants arranged within the tunnel. One row received nightly UV radiation treatment, while the other row served as the control group. These rows were situated on opposite sides of the tunnel and were separated by a plastic partition. The distance between the rows was approximately 4 m. In the second year of the experiment, the placement of the treatments was switched to mitigate the influence of microclimate variations inside the tunnel. Each row comprised 16 containers of 'Malling Centenary' plants in both 2021 and 2022, along with 15 containers of 'Limalexia' (in 2021) or 'Sonsation' (in 2022). This resulted in a total of 60 to 64 plants per cultivar per treatment. The cultivars were arranged sequentially in the rows, and the rows themselves were divided into four blocks, each containing four containers of each cultivar. Air temperature inside the tunnel was recorded with Hobo loggers (Fig. 1). Upon development of flower buds (starting at the end of June) two bumblebee (*Bombus terrestris*) boxes (Agrobio, Almería, Spain) were installed in the tunnel for

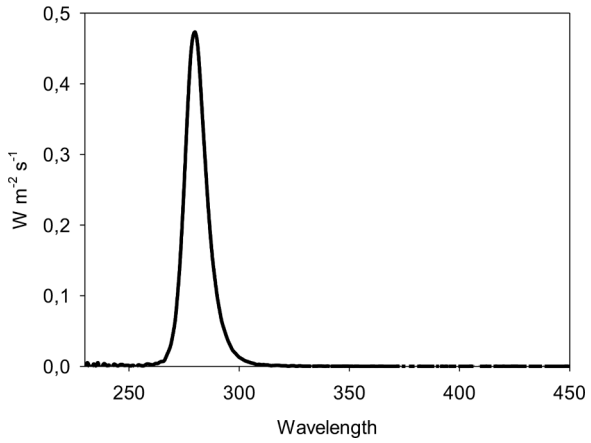

Fig. 3. Spectral composition of UV radiation used for the experiments.

pollination.

In both years, the remaining half of the tunnel was utilized for growing strawberry plants for various purposes, creating a high disease pressure environment. Natural powdery mildew infection symptoms were first observed in mid-July in both years, with a stronger occurrence in the 2021 growing season.

2.2. UV exposure

UVC exposure was conducted nightly with a custom-built apparatus designed for research purposes (Fig. 2). UV LED chips (peaking at 276 nm, Shenzhen Hanhua Opto Co., Ltd., Shenzhen, China) were embedded within a semicylindrical metal structure measuring 68 cm in width, 50 cm in height (ELSOR, Suonenjoki, Finland). The apparatus was positioned so that the LEDs were approximately 10 cm above the plant canopy, and the LED panel was raised as the plants grew during the growing season to ensure a consistent UV dosage. The automated apparatus moved along metal poles situated above the plants (Fig. 2), making intermittent stops above each container to subject the plants to 20 s of UV radiation. This exposure regimen extended from planting until the conclusion of the experiment in mid-September.

Each night, the UVC dosage delivered to each container was 0.02 kJ m^{-2}, resulting in a cumulative total of 1.54 and 1.82 kJ m^{-2} during the growing seasons 2021 and 2022, respectively. A similar apparatus, lacking UV LEDs, was deployed, and operated above the control row. These devices were in operation every night from 11:00PM to 11:15PM. The intensity and duration of UVC exposure were determined through preliminary tests on *Botrytis cinerea* cultivated in Petri dishes, as well as a pre-experiment conducted during the 2020 growing season using the same UVC device (unpublished results). The spectral distribution of light was measured using a spectroradiometer (AvaSpec-ULS2048 Starline, Avantes BV, Apeldoorn, The Netherlands, Fig. 3). The UVC radiation dose was measured using a digital UVC radiometer (RM-22, Opsytec Dr. Gröbel GmbH, Ettlingen, Germany) located in the central part of the irradiation zone. The LEDs also emitted radiation within the UVB range, accounting for 41 % of the energy output.

2.3. Fruit harvesting

Fruit harvesting occurred at regular intervals, typically every three to four days, spanning the entire cropping period. In 2021, this period extended from 19 July to 2 September, while in 2022, it ranged from 14 July to 31 August. In 2021, fruits were classified into two groups: marketable and low quality (identified by a diameter of < 18 mm, malformation, mold, mechanical damage, or powdery mildew infection). In 2022, an extra category was created for fruits affected specifically by powdery mildew. For each category, measurements were taken for fresh mass and the number of fruits. These data were then used to calculate the yield per individual plant, and an average fruit size.

2.4. Determination of Brix, acidity, total phenolics, and total anthocyanins

Sampling to assess fruit chemical properties, including total soluble solid content (Brix), acidity, total phenols, and total anthocyanins, was conducted biannually. For 'Malling Centenary', the samplings took place on 19 July and 2 August 2021, and on 14 July and 28 July 2022. In the case of 'Limalexia', the sampling occurred on 29 July and 9 August 2021, while for 'Sonsation', it was on 18 July and 28 July 2022. Approximately four to five mature fruits were selected from each container for analysis and frozen immediately after sampling.

Frozen fruits were defrosted in a microwave oven using the defrost setting and subsequently homogenized for 3 min with a centrifugal juicer. From this homogenized mixture, two-milliliter subsamples of juice were extracted, then centrifuged at 16,100 g for 5 min before being utilized for further analysis.

Brix values were determined using the juice, while acidity was measured from a 1:50 dilution of the juice, employing a Pocket Brix-acidity meter, PAL-BX|ACID F5, manufactured by ATAGO CO., LTD, Japan.

The total phenolic content was assessed through the Folin-Ciocalteu method, as described by Singleton and Rossi (1965). Two technical replicates were conducted for each sample. The juice was diluted at a ratio of 1:40 with distilled water, and 200 µl of this dilution was combined with 1 ml of a 10 % Folin-Ciocalteu reagent. Subsequently, 800 µl of a 7.5 % sodium carbonate solution was added, and the mixture was thoroughly vortexed. After an incubation period of 120 min in the dark at room temperature, the samples were mixed once more, and 200 µl subsamples were pipetted into a 96-well plate.

Absorbances at 765 nm were determined using a VICTOR3 1420 multilabel plate reader (PerkinElmer, Inc., the United States). Total phenolic concentrations were quantified utilizing a gallic acid standard curve, and the results are expressed as milligrams of gallic acid equivalents (GAE) per 100 ml of juice (mg GAE / 100 ml juice).

The total anthocyanin content was determined using the pH differential method outlined by Lee et al. (2005). Two technical replicates were performed for each sample. To prepare the samples, dilutions (1:20) of the juice were made in pH 1 and pH 4.5 buffers, and their absorbances were measured at 510 nm and 700 nm using a spectrophotometer within a 20 to 50 min time frame.

To calculate the concentrations of total anthocyanins, the molar absorption coefficient ($\mathcal{E} = 15{,}600$ M-1cm^{-1}) and the molecular weight (MW = 433.4 g mol^{-1}) of pelargonidin-3-glucoside (P3g) were employed. P3g is the primary anthocyanin identified in strawberries, as documented by Tonutare et al. (2014). The results are expressed as milligrams of P3g equivalents per 100 ml of juice (mg P3gE / 100 ml juice).

2.5. Ascorbic acid concentration

Five mature fruits were collected for total ascorbic acid analyses from each container on 25 July 2022. The analysis of ascorbic acid was performed using the Megazyme Ascorbic Acid Assay Kit (L-Ascorbate) (K-ASCO) and absorbance was measured at 578 nm with a well plate reader (FLUOstar Omega, BMG Labtech GmbH, Germany) following the kit instructions. To determine the total ascorbic acid content, dehydroascorbic acid was converted into ascorbic acid by adding DTT to the sample at a final concentration of 1 mM and incubating the mixture for 10 min.

2.6. Fruit firmness

Fruit firmness assessments were conducted using a penetrometer (T.

R. Turoni srl, Forli, Italy) equipped with a 'star' plunger specifically designed for strawberries (model 53207, Turoni, Forlì, Italy). Five strawberries from each container were collected on 18 July ('Malling centenary') and on 22 July 2022 ('Sonsation') and stored in cool boxes (five strawberries/box). These boxes were refrigerated at +8 °C until the strawberries' firmness was evaluated after two days for Malling centenary and three days for 'Sonsation'. The fruits were halved longitudinally and the penetrometer measurements were taken at the thickest part of each half. The results were recorded in grams.

2.7. VOC analyses

The analysis of volatile organic compounds (VOCs) from fruit samples was conducted on 4 August 2022, to assess the impact of *P. aphanis* infection and UVC-treatment on emissions, as well as to characterize the volatile profiles of 'Malling Centenary' and 'Sonsation' cultivars under UVC and control conditions. Three fully ripe fruits, exhibiting typical visual characteristics, were sampled from six systematically selected containers within the rows of the tunnel for each cultivar and treatment combination. Subsequently, these collected fruits were placed into cool boxes and transported to the University of Eastern Finland in Kuopio on the same day for the VOC analysis.

The severity of *P. aphanis* infection was classified using the following criteria: no visible infection (0), initial symptoms of infection in one or two seeds (1), and clear infection covering 20–80 % of the surface area (2). Additionally, the fresh mass of the fruits was recorded during the sampling process (Table S1).

VOC collection was conducted under laboratory conditions using a bench-based dynamic headspace sampling system with six sampling lines. The bench temperature was 20–22 °C. The fruits were placed in 1 L glass jars that had been cleaned with water and ethanol and baked in an incubator at 120 °C to remove impurities. Purified inlet air was generated with a zero-air generator (Aadco Instruments, 747-30, Cleves, OH, USA), humidified and introduced via Teflon tubing into the jars at approx. 325 ml min^{-1}. The jars were flushed for 5 min and then VOCs were collected from an outlet port for 30 min into Stainless steel tubes filled with 200 mg of Tenax TA adsorbent (Markes International Ltd., Llantrisant, UK) at a flow rate of approx. 225 ml min^{-1}. Air was pulled through the Stainless-steel tubes with a vacuum pump (D-79112, KNF, Germany) connected via Silicone tubing. A blank sample was collected using the same method, but with an empty jar. Inlet and outlet air flows were calibrated with a mini-Buck calibrator (AP Buck Inc., Orlando, FL, USA).

VOC analysis was performed by gas chromatography-mass spectrometry (GC–MS) (Agilent 7890A GC and 5975C VL MSD; New York, USA). Trapped compounds were desorbed with a thermal desorption unit (TD-100; Markes International Ltd.) at 300 °C for 10 min and then cryofocused at −10 °C. The compounds were transferred in split mode to an HP-5MS UI capillary column (60 $m \times 0.25$ mm; film thickness 0.25 μm) with helium as a carrier gas. The oven temperature was held at 40 °C for 1 min, then programmed to increase by 5 °C min^{-1} to 125 °C and then by 10 °C min^{-1} to 260 °C with a column flow of 1.2 ml min^{-1}. Mass spectra were obtained by scanning from 33 to 400 m z^{-1}.

Compounds were identified and quantified with help of MSD Chemstation Data Analysis software (Agilent) and Wiley275 and NIST20 databases. Authentic standards were available for linalool, cis-3-hexenol

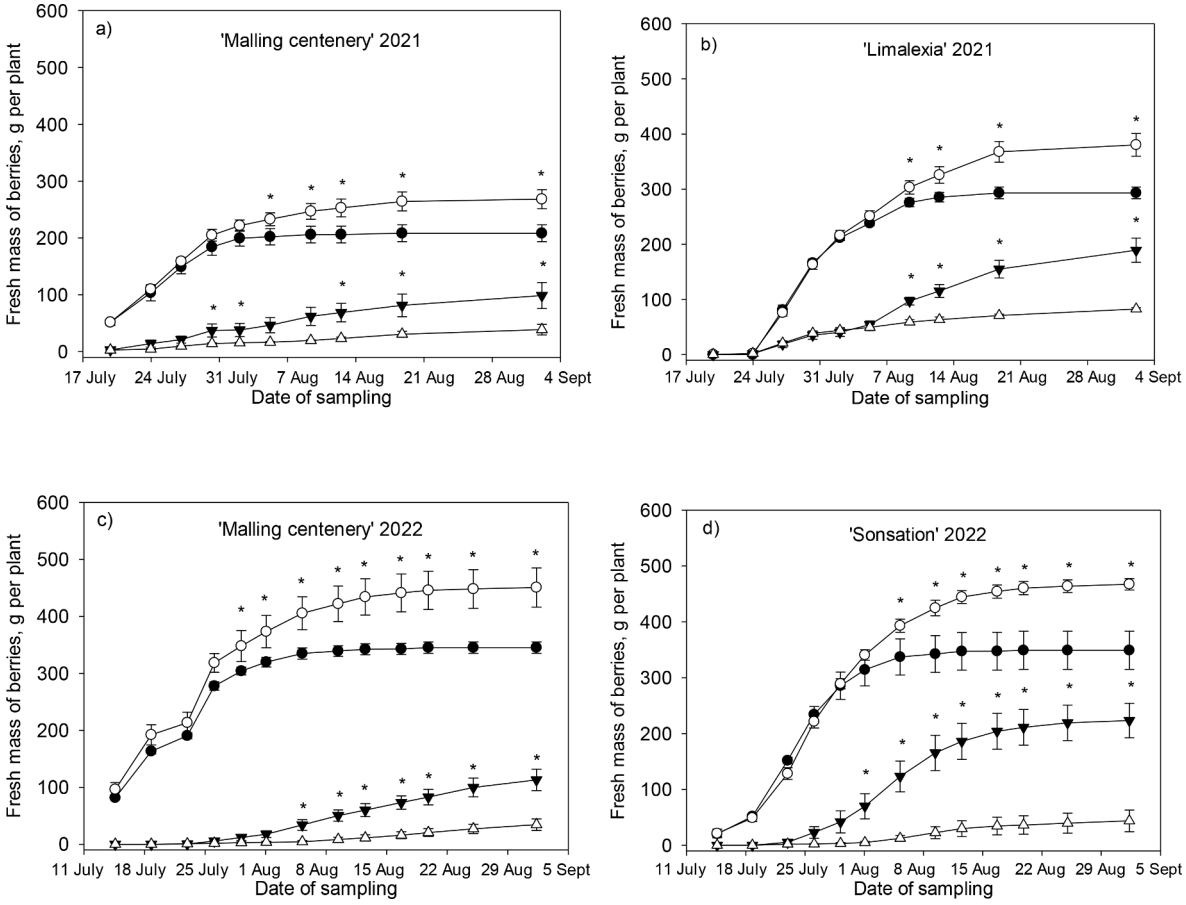

Fig. 4. Cumulative yield of marketable (UVC-treated white circles, controls black circles) and non-marketable (UVC-treated white triangles, controls black triangles) yield (±SE) in strawberry cultivars 'Malling centenary' (b) and 'Limalexia' (b) grown in a tunnel in growing seasons 2021, and marketable and powdery mildew infected fruits in 'Malling centenary' (c) and 'Sonsation' (d) in 2022. Statistically significant differences between the UVC-treated and control plants are indicated by asterisks.

Table 1
Effect of UVC radiation on the average (±SE) fresh mass of the fruits, total yield (sum of marketable and non-marketable fruits) and the proportions of marketable, low quality and powdery mildew infected (only in 2022) fruits in strawberry cultivars 'Malling centenary' (MC), 'Limalexia' (L) and 'Sonsation' (S) grown in a strawberry tunnel during the growing seasons 2021 and 2022 in Central Finland. P values for the main effect of treatment (T) and interaction of treatment and cultivar (T×C) are shown.

Cultivar, year	Treatment	Average fruit size, g	Tot. yield per plant, g	Marketable fruits, %	Low quality fruits, %	Powdery mildew infected fruits, %
MC, 2021	Control	14.3 (0.3)	306.9 (17.8)	68.5 (0.5)	31.5 (6.3)	NM
MC, 2021	UVC	13.8 (0.4)	307.0 (18.3)	87.5 (2.7)	12.5 (2.7)	NM
L, 2021	Control	12.9 (0.3)	482.6 (11.9)	61.0 (3.6)	39.0 (3.6)	NM
L, 2021	UVC	12.5 (0.7)	463.1 (22.7)	82.1 (0.5)	17.9 (0.5)	NM
P value	T	0.288	0.563	0.012	0.012	NM
	T×C	0.854	0.506	0.521	0.521	NM
MC, 2022	Control	16.1 (0.6)	488.1 (17.2)	71.2 (3.1)	6.3 (0.5)	22.5 (3.2)
MC, 2022	UVC	16.5 (0.5)	505.5 (24.4)	87.3 (2.8)	4.4 (0.8)	8.3 (2.0)
S, 2022	Control	14.1 (0.4)	617.2 (24.3)	52.9 (3.7)	7.2 (0.8)	39.8 (3.7)
S, 2022	UVC	13.5 (0.4)	563.8 (15.9)	82.6 (3.0)	8.0 (0.6)	9.4 (2.6)
P value	T	0.813	0.227	<0.001	0.987	<0.001
	T×C	0.324	0.032	0.031	0.008	0.003

MN = not measured.

and methylsalicylate. α-Humulene was used for quantifying sesquiterpenes, cis-3-hexenol for alcohols, aldehydes, acids and ketones and cis-3-hexenyl isobutyrate for esters and other compounds. Quantification was based on Total Ion Counts (TIC). Emissions from blanks were subtracted from fruit emissions. Emission rates were calculated as follows:

$$E = Fx(C2 - C1)/m$$

where E is Emission rate (ng g^{-1} (FW) h^{-1}), F is the flow rate to the collection chamber (L min^{-1}), C2 is the concentration of the outgoing air (ng L^{-1}), C1 is the concentration of the incoming air (ng L^{-1}), m is the berries' FW (g). C1 was considered to be 0 because the incoming air was filtered, and the quantities of VOCs determined from blank samples were subtracted from the fruit emissions.

2.8. Leaf measurements

Symptoms of powdery mildew in leaves were scored on 2 August and 8 August 2022 according to scale modified from Simpson (1987), where scores denote: (0) a healthy plant with no visible disease symptoms, (1) slight leaf curling with no visible mycelium, (2) leaf curling and mottling, (3) severe leaf curling, redding and visible damage to lower leaf surface and (4) severe necrosis and some leaf death.

A Dualex fluorimeter Dualex® Scientific (Force-A, Orsay, France) was used to measure chlorophyll, epidermal flavonol and nitrogen balance (NBI, calculated as chlorophyll/flavonols, describing leaf nitrogen status) indexes. The measurements were made from the two youngest mature, visibly intact leaflets from each plant on 2 August 2022.

Leaf samples for assessing dry matter content were gathered on 8 September 2022, with two leaflets collected from each plant. The fresh mass (FM) and dry mass (DM) of these leaflets were recorded, and an average value was computed for each container.

Following the FW measurements, leaflets were scanned using a flatbed scanner (Epson Perfection V700Photo). The areas of both the leaflets and any holes in them were quantified using the tools available in ImageJ 1.53c. Subsequently, the leaflets were subjected to drying at a constant temperature of +60 °C. Specific leaf area (SLA) was calculated by dividing the leaf area by the dry mass. Additionally, the dry mass content of the leaves and the area of feeding damage (holes) were determined.

2.9. Statistical analyses

The analysis of marketable and non-marketable fruit yield data utilized Linear Mixed Models ANOVA, with sampling time, cultivar, and treatment designated as fixed factors. Random factors used in the analysis were treatment and container, while blocks were considered as subjects to acknowledge the interdependence of measured treatments and containers across multiple samplings. Data-analyses of fruit chemical properties were carried out individually for each sampling date. Non-significant random factors were removed from the model. Subsequent examination of interactions was conducted using the Sidak test.

Principal Component Analysis (PCA) was initially employed to delineate variances in cultivar volatile profiles (Supplementary information). Subsequently, separate PCA analyses were conducted for each cultivar to explore distinctions between treatments or *P. aphanis* infection. To delve deeper into the effects of cultivar, treatment, and *P. aphanis* infection class on the volatile blend, T-tests of PC scores were executed. To streamline the analysis, for 'Malling centenary', infection classes 1 and 2 were amalgamated due to the limited samples in class 2 (Table S1). In the case of 'Sonsation', infection classes were amalgamated in two ways: distinguishing between no infection (0) versus any infection (1 and 2), and a separate comparison between severely infected (2) versus others (0 and 1). PCA was conducted using Simca 17.0.1, while all other analyses were performed using SPSS 29.0. A significance level of $P < 0.05$ was adopted for determining statistical significance.

3. Results

3.1. Fruit production and crop yield

In both years, the cumulative yield of marketable fruits from the UVC-treated plants was significantly higher, and the yield of non-marketable fruits lower than those from the control plants (Fig. 4). In 2021, the total yield of fruits was equivalent in both treatments. However, in 'Sonsation' in 2022, there was a slight decrease in the total yield in the UVC-treated plants compared to the controls (Table 1). The average size of the fruits was not affected by the treatments (Table 1). The cumulative yield of non-marketable fruits in control plants started to exceed that from the UVC plants between late July and early August, soon after the first symptoms of powdery mildew were detected in the canopy on 23 July 2021 and on 27 July 2022. In 2022, the total fresh mass of powdery mildew affected fruits picked separately from low-quality fruits was 2.7- and 4.2-fold higher in control plants than in the UVC-plants, in 'Sonsation' and 'Malling centenary', respectively (Table 1). The differences in treatment effects on the proportion of marketable, non-marketable, and low-quality fruits were more pronounced in 'Sonsation' than in 'Malling Centenary'.

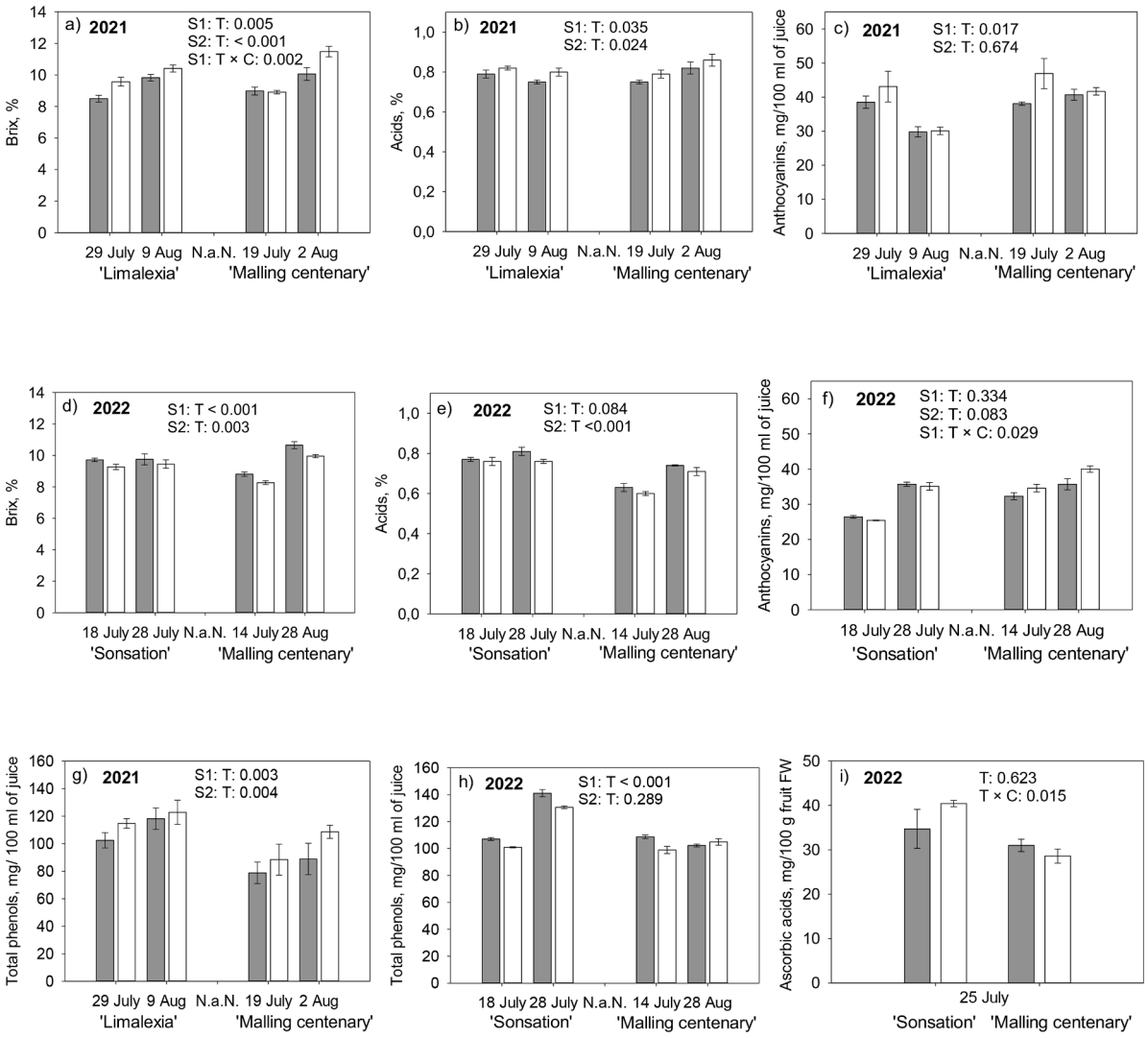

Fig. 5. Quality properties of fruits (±SE) collected from control (gray bars) and UVC-treated (white bars) plants of strawberry cultivars 'Limalexia' and 'Malling centenary' in 2021 (a–c, g) and 'Sonsation' and 'Malling centenary' in 2022 (d–f, h, i), sampled twice (S1 and S2) during each growing season within a strawberry tunnel in Central Finland. Main effects of treatment (T) and statistically significant interactions of T and cultivar (C) derived from mixed model ANOVA are shown.

3.2. Brix, acidity, total phenolics, total anthocyanins, and ascorbic acid concentration

The impact of UVC treatment on fruit quality varied depending on the year, sampling time, and specific cultivar under consideration.

In 2021, fruits treated with UVC showed elevated brix levels, although in 'Limalexia', this effect was observed solely during the first sampling (treatment × cultivar, $P = 0.002$) (Fig. 5a). However, in 2022, brix levels were lower in fruits treated with UVC compared to the control group (Fig. 5d).

UVC increased acid levels in 2021 across both samplings (Fig. 5b). Yet, in 2022, acid levels were lower in UVC-treated fruits compared to the controls, although this difference was only marginally significant in the first sampling (Fig. 5e).

In 2021, UVC treatment increased anthocyanin concentration in the first sampling, while no treatment effect was found in the second sampling (Fig. 5c). In 2022, anthocyanins were higher in UVC-treated fruits in 'Malling centenary', although the increase was significant only in the first sampling (treatment × cultivar $P = 0.029$ and 0.064 in the first and second sampling, respectively) (Fig. 5f).

In 2021, UVC treatment resulted in an increase in total phenolics during both samplings, with a more pronounced effect observed in 'Malling centenary' during the second sampling (Fig. 5g). However, in 2022, total phenolics decreased in the first sampling due to UVC treatment, while their concentration remained unchanged during the second sampling (Fig. 5h).

Regarding ascorbic acid concentration, fruits exposed to UVC treatment showed higher levels in 'Sonsation' (treatment × cultivar $P = 0.015$), whereas no treatment effect was observed in 'Malling centenary' (Fig. 5i).

Table 2
Average values (±SE) for fruit firmness, measured in grams using a penetrometer after two days ('Malling Centenary', MC) or three days ('Sonsation') in the refrigerator.

Cultivar	Treatment	Firmness (g)
MC	Control	312.8 (21.6)
MC	UVC	390.3 (35.4)
'Sonsation'	Control	333.5 (26.2)
'Sonsation'	UVC	368.2 (13.5)

3.3. Fruit firmness

Following refrigeration for either two days ('Malling centenary') or

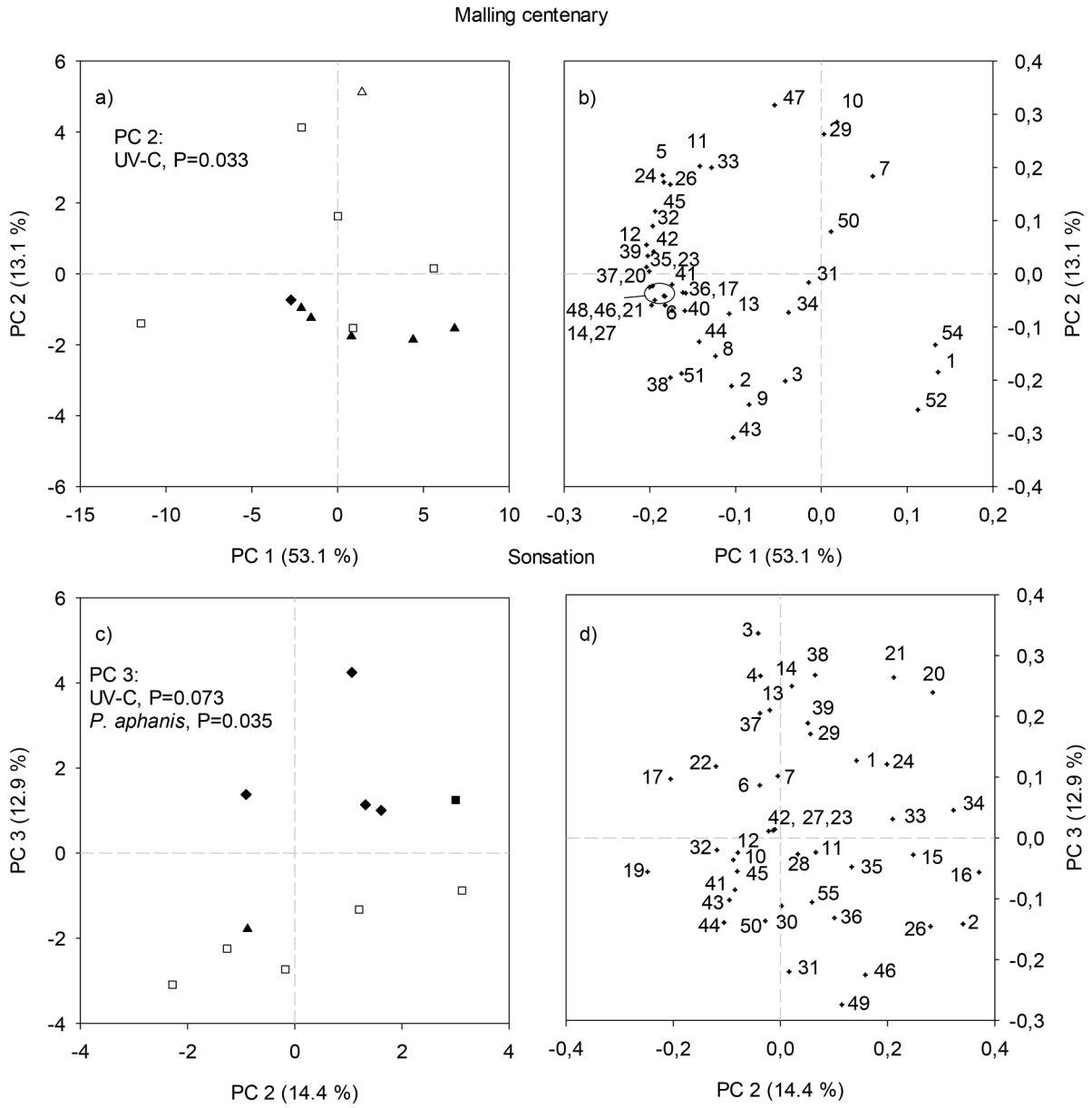

Fig. 6. PCA score plots (a,c) and loading plots (b,d) illustrating the volatile compound profiles of strawberry cultivars 'Malling Centenary' (a,b) and 'Sonsation' (c,d) subjected to either UVC exposure (white symbols) or kept under control conditions (black symbols). Shapes denote different sample conditions: squares represent visibly intact samples, triangles indicate samples with initial signs of *P. aphanis* infection, while diamonds represent those with severe *P. aphanis* infection. The percentages denote the variation in data explained by principal components (PCs), with numbers corresponding to various compounds: 1. Methyl acetate, 2. Ethyl acetate, 3. Methyl propionate, 4. Isopropyl acetate, 5. Isopropyl acetate+1-butanol, 6. S-methyl thioacetate, 7. Methyl butyrate, 8. Dimethyl sulfide, 9. Methyl crotonate, 10. Methyl isovalerate + Methyl −2-methylbutyrate (coeluted), 11. Ethyl butyrate, 12. Butyl acetate, 13. Methyl valerate, 14. Isopropyl butyrate, 15. Ethyl 2-methylbutyrate, 16. Ethyl isovalerate, 17. (*E*)−2-hexenal, 18. (*Z*)−3-hexenol, 19. 2-Methyl butyric acid, 20. Isoamyl acetate, 21. 2-methylbutyl acetate, 22. Methyl 3-methylvalerate, 23. Two co-eluted compounds, the other potentially methyl thiobutyrate, 24. Propyl butyrate, 25. Ethyl valerate, 26. Amyl acetate, 27. Methyl caproate, 28. Unknown, 29. Isobutyl butyrate, 30. Methyl 2-hexenoate, 31. Sulcatone, 32. Butyl butyrate, 33. Ethyl caproate, 34. (*Z*)−3-hexenyl acetate, 35. 1-Hexyl acetate, 36. (*E*)−2-hexenyl acetate, 37. Isopropyl caproate, 38. Butyl isovalerate, 39. Isoamyl butyrate, 40. Amyl butyrate, 41. Mesifurane, 42. Linalool, 43. Methyl caprylate, 44. Benzyl acetate, 45. Butyl caproate, 46. (*E*)−2-hexenyl butyrate, 47. Methyl salicylate, 48. Octyl butyrate, 49. Linalyl isobutyrate, 50. Geranyl acetone, 51. γ-Decalactone, 52. Germacrene-D, 53. (*E, E*)-α-farnesene,54. α-Muurolene, 55. Nerolidol. Emission rates of the compounds are shown in Table S2.

three days ('Sonsation'), fruits subjected to UVC treatment exhibited increased firmness compared to the control fruits (main effect of treatment $P = 0.004$) (Table 2).

3.4. UVC and P. aphanis effects on VOC profile

The application of UVC treatment significantly influenced the VOC profile of 'Malling centenary' (Fig. 6a, b). Specifically, the fruits exposed to the UVC treatment exhibited increased emission rates of methyl salicylate, methyl isovalerate + methyl-2-methylbutyrate, isobutyl butyrate, ethyl butyrate, and ethyl caproate compared to the control group (Fig. 6b). Conversely, emissions of methyl caprylate, methyl crotonate, and germacrene-D were lower in the UVC treated fruits (Fig. 6b). Notably, the presence of *P. aphanis* did not yield a significant effect on the VOC profile.

In 'Sonsation', PC 1 accounted for 43.8 % of the variance in the data, showing no significant influence of either the UVC treatment or *P. aphanis* infection (data not shown). PC 2 explained 14.4 % of the

Table 3
Symptoms of powdery mildew in leaves of strawberry cultivars 'Malling centenary' (MC) and 'Sonsation', scored on 2 August and 8 August 2022 according to scale modified from Simpson (1987).

Cultivar	Treatment	Score 2 August	Score 8 August
MC	Control	0.4	1.1
MC	UVC	0	0
'Sonsation'	Control	1.3	2.1
'Sonsation'	UVC	0	0.1

variation, while PC 3 explained 12.9 % (Fig. 6c, d). The impact of the UVC treatment on the VOC profile was marginally significant (Fig. 6c), whereas severe *P. aphanis* infection (class 2 vs. class 0 and 1) significantly affected PC3 (Fig. 6c). Samples exhibiting severe *P. aphanis* infection displayed higher emissions of methyl propionate, butyl isovalerate, 2-methylbutyl acetate, isopropyl butyrate, isopropyl acetate, and isoamyl acetate (Fig. 6d). Conversely, samples from the UVC treatment and those with no or very mild symptoms of *P. aphanis* infection showed increased emissions of linalyl isobutyrate, (*E*)−2-hexenyl butyrate, and sulcatone (Fig. 6d).

3.5. Leaf properties

Symptoms of powdery mildew were stronger in control plants than in UVC-treated plants (Table 3, Fig. 7). The treatment exhibited no significant influence on the chlorophyll index. However, flavonols and leaf dry mass content were higher in control plants, whereas NBI and SLA were lower when compared to UVC-treated plants (Table 4). The feeding damage in the leaves remained unaffected by the treatment (data not shown).

4. Discussion

Throughout the experiment, the growth of *P. aphanis* in all three tested strawberry cultivars was effectively restrained by the nightly application of UVC treatment from planting to the final picking. The application of UVC treatment resulted in a higher overall marketable crop yield without altering the average size of the fruits. In previous experiments where plants were irradiated from flowering to the final harvest, crop yield was either remained unaffected (Janisiewicz et al., 2016 [0.012 kJ/m^2 once a week]; Forges et al., 2020 [once a week 1.7 kJ/m^2]) or decreased (de Oliveira et al., 2016 [0.5 kJ/m^2 every four days]). The variability in results could stem from differing experimental conditions, including the intensity and duration of UVC exposure, as well as the specific strawberry cultivars used. As the plants were irradiated every night, our findings do not provide sufficient evidence to determine the maximum irradiation interval that would effectively prevent Powdery mildew.

In our experiment, the cumulative UVC dose was 1.54 kJ/m^2 in 2021 (over 11 weeks of exposure) and 1.82 kJ/m^2 in 2022 (spanning 13 weeks of exposure). Notably, the single exposure dose of 0.02 kJ/m^2 utilized in our experiment is considerably smaller than the doses employed in the majority of previous experiments involving strawberries, conducted either in controlled conditions (Xu et al., 2017; Sun et al., 2020; Takeda et al., 2021) or in greenhouses (Van Hemelrijck et al., 2010; Van Delm et al., 2014; Xie et al., 2016; Forges et al., 2020). The UVC dose administered in our experiment aligns more closely with the doses of 0.068–0.170 kJ/m^2, applied 1–2 times per week in an open field experiment (Onofre et al., 2021), the dose of 0.012 kJ/m^2 applied twice weekly in tunnel conditions (Janisiewicz et al., 2016), and some of the doses of 0.030–120 kJ/m^2 applied three times a week in a glasshouse (Verwoort et al., 2020). It's noteworthy that we did not observe UVC-induced leaf injuries in our experiments. In contrast, Van Delm et al. (2014) reported leaf burning, while de Oliveira et al. (2016) observed reduced photosynthetic efficiency, leaf biomass, and crop yield in strawberry plants following exposure to a dose of 0.5 kJ/m^2 applied four times per week. Interestingly, Forges et al. (2020) found that a UVC dose of 1.70 kJ/m^2 applied once a week did not reduce photosynthetic capacity in strawberry leaves. The discrepancies observed among various experiments underscore the influence of environmental conditions on plant responses to UVC irradiation. The complexity of the interactions makes it difficult to interpret the results.

The rapid growth of strawberry plants during the growing seasons led to the development of dense canopies. Due to the short wavelength composition of UVC radiation, it does not penetrate deeply into the canopy or inside the plant tissues (Stevens et al., 1998). Therefore, the UV treatment's direct impact on *P. aphanis* was only possible on the surfaces of leaves and fruits not covered by other plant parts. This suggests that UVC treatment may have stimulated induced plant resistance against powdery mildew. Previous studies have demonstrated that in response to low-dose UVC irradiation, plants produce reactive oxygen species (ROS) that can initiate signaling pathways responsible for activating various defense mechanisms (Urban et al., 2016; Xu et al., 2019; Forges et al., 2020; Takeda et al., 2021). Xu et al. (2019) found that UVC significantly induced an overexpression of a set of genes involved in plant pathogen interaction in leaves of strawberry plants. In our experiment, the observed elevation in leaf epidermal flavonols and reduction in specific leaf area and NBI within the control plants might be linked to the timing of the sampling in early August, coinciding with the visible presence of fungal biomass on the leaf surface within the control treatment. Plants are known to synthesize flavonoids in response to microbial infection (Górniak et al., 2019).

The phytochemical composition of strawberry fruit has been shown to be influenced by UVC irradiation, whether applied preharvest (de Oliveira et al., 2016; Severo et al., 2017; Xu et al., 2017) or postharvest (Pombo et al., 2011; Li et al., 2014; Severo et al., 2015). In our experiment, the effect of UVC treatment on fruit quality showed inconsistencies between the two experimental seasons. Interestingly, in 2021, UVC-treated plants showed increased brix levels, acidity, and total phenols in their fruits. However, these responses to UVC treatment were reversed in 2022. These variations may be attributed to differences in growth conditions (Fig. 1) and sampling dates between the experimental years. Planting was initiated two weeks earlier in 2022 than in 2021, coinciding with markedly higher air temperatures in 2021. Different early-season conditions may also contribute to the observed lower crop yield in 2021 relative to 2022. Also, in previous experiments on strawberries, the responses of phytochemical compounds to UVC preharvest treatment appear to be contingent upon factors such as UVC dose (de Oliveira et al., 2016; Xu et al., 2017), cultivar (Xie et al., 2015; Forges et al., 2018), and season (Xie et al., 2016).

In our experiment, the effect of UVC irradiation on anthocyanin concentration varied depending on the cultivar, with the concentration either increasing or remaining unchanged due to the UVC treatment. Anthocyanins, pivotal for the vibrant range of reds, purples, or blues in strawberries, contribute significantly not only to coloration but also to antioxidant properties and potential health advantages (Li et al., 2017). Previous studies have indicated that UVC exposure has the potential to induce a redder hue in strawberries (Xie et al., 2016; Forges et al., 2020). The observed increase in ascorbic acid concentration in 'Limalexia' due to UVC treatment lends support to the notion of preharvest UVC treatment potentially enhancing the nutritional value of the crop, as supported by findings in other experiments (Severo et al., 2017; de Oliveira et al., 2016; Xu et al., 2019).

Preharvest UVC treatment can impact the shelf life of strawberries by inhibiting microbial growth and stimulating their secondary metabolism (de Oliveira et al., 2016; Xu et al., 2017; 2018). In our experiment, the higher firmness values observed in UVC-treated fruits after 2–3 days of refrigeration suggests a potential delay in fruit softening. This result is consistent with earlier research that suggests a delay in the softening of strawberries as a result of UVC treatment (Xie et al., 2015; 2016).

Fig. 7. Strawberry plants cultivated within a tunnel in Central Finland were photographed on 15 September 2021, and 15 September 2022. In 2021 (a) and 2022 (c), one portion of the plants was exposed to a nightly UVC dose of 0.02 kJ/m^2 from the time of planting until the final harvest, while the other half of the plants acted as control groups in 2021 (b) and 2022 (d). The presence of powdery mildew symptoms is evident, manifested as leaf curling and a reddish discoloration.

However, it contrasts with some other research outcomes (de Oliveira et al., 2016; Severo et al., 2017).

The alterations noted in the VOC profile indicate that UVC treatment has the potential to impact aroma compounds. For instance, compounds like ethyl butyrate and methyl-2-methylbutyrate, which increased due to UVC exposure, play a role in creating the fruity strawberry aroma (Ulrich et al., 1997; Nuzzi et al., 2008). Currently, the direct volatile emissions from *P. aphanis* or the metabolic alterations it triggers in strawberries are yet to be fully understood. However, the altered emission profile characterized by increased methyl propionate, butyl isovalerate, 2-methylbutyl acetate, isopropyl butyrate, isopropyl acetate, and isoamyl acetate, alongside decreased linalyl isobutyrate, (*E*)−2-hexenyl butyrate, and sulcatone, may contribute to an unpleasant taste in fruits affected by powdery mildew disease. Notably, sulcatone's aroma has been linked to the pleasant, sweet taste of strawberries (Fan et al., 2021). Information regarding the impact of preharvest UVC

Table 4
Impact of UVC radiation on leaf chlorophyll and flavonoid indexes, and Nitrogen Balance Index (NBI) obtained by Dualex ®, leaf dry mass content and specific leaf area (SLA) (±SE) of strawberry cultivars 'Malling centenary' (MC) and 'Sonsation' cultivated within a strawberry tunnel in Central Finland and sampled on 2 August 2022. P values for the main effects of treatment obtained from mixed model ANOVA are shown.

Cultivar	Treatment	Chlorophyll	Flavonols	NBI	Leaf dry mass content, %	SLA, cm^2/g
MC	Control	31.6 (0.4)	1.44 (0.02)	22.3 (0.3)	33.2 (0.3)	7.3 (0.19)
MC	UVC	32.0 (0.8)	1.35 (0.02)	24.1 (0.4)	31.4 (0.4)	8.3 (0.13)
'Sonsation'	Control	30.1 (2.0)	1.57 (0.03)	19.5 (0.8)	33.8 (0.8)	7.6 (0.23)
'Sonsation'	UVC	30.9 (0.8)	1.44 (0.03)	21.9 (1.0)	31.6 (0.1)	8.5 (0.23)
P value	Treatment	0.942	<0.001	0.005	0.020	<0.001

ns, not significant.

irradiation on the sensory attributes of strawberries is limited. Forges et al. (2020) found that preharvest UVC treatment did not alter the taste of the fruits compared to the control group.

Methyl salicylate is synthesized from salicylic acid, which is induced by various biotic and abiotic factors, including UVC exposure. This compound offers protection against *P. aphanis* infection (Fragnière et al., 2011; Feng et al., 2020; Gondor et al., 2022). The presence of methyl salicylate solely in the 'Malling Centenary' cultivar, along with increased emissions under UVC treatment, may have contributed to UVC's protective role against powdery mildew disease. This phenomenon might also explain the reduced susceptibility of 'Malling Centenary' to *P. aphanis* infection compared to 'Sonsation'.

In many experiments investigating the effects of UVC irradiation on preventing microbial growth in growing plants or fruits after harvest, low-pressure mercury vapor lamps have been utilized. Their irradiance peaks at 254 nm, which has been recognized as the optimal wavelength for maximum germicidal action (Singh et al., 2021). Although UVC LEDs are still expensive and under development, we employed UVC irradiation using LED technology to develop a custom-made device for research purposes. The LED type available during the construction of our device has its peak irradiance at 276 nm and emits radiation within the UVB range as well. While UVB is recognized for its ability to stimulate secondary metabolism, bolster plant defenses, and disinfect microbes, its efficacy typically requires prolonged exposure spanning several hours or days (Urban et al., 2018). Furthermore, in our preliminary test, we examined the impacts of varying UV-wavelength ranges and exposure durations on grey mold (*Botrytis cinerea*) and Scleroderris canker (*Gremmeniella abietina*) through agar plate experiments. Contrary to UVC irradiation, our findings indicate that UVB irradiation had no discernible effect on the dry mass or conidial germination of either species (unpublished results). While acknowledging the potential impact of UVB radiation on the parameters examined in this experiment, our findings suggest that the plant responses to the irradiation treatment were predominantly influenced by UVC range exposure. Advancements in the development of UVC LEDs, specifically those peaking closer to 254 nm, could potentially facilitate shorter durations for each UVC treatment.

5. Conclusions

Our findings indicate that the UVC irradiation method is not only effective in preventing powdery mildew but also has the potential to enhance the nutritional value and prolong the shelf life of fruits. The treatment can modify the sensory attributes of the fruit, either directly or indirectly, by altering its VOC profile through disease management. These outcomes collectively demonstrate the diverse benefits of UVC treatment, illustrating its ability to improve disease resistance and enhance specific fruit characteristics.

We conclude that powdery mildew prevention can be effectively achieved through pre-harvest, short-duration UV irradiation peaking at the border between UVC and UVB spectra. The expected decrease in prices of UVC LEDs over time is likely to lead to their increased integration into practical plant disinfection solutions, owing to their adaptability and energy efficiency.

Declaration of competing interest

Authors declare that they have no conflict of interest.

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CRediT authorship contribution statement

Johanna Riikonen: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Hanna Ruhanen:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Anne Uimari:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Marja Poteri:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Anna Toljamo:** Writing – review & editing, Investigation. **Harri Kokko:** Writing – review & editing, Investigation. **James D. Blande:** Writing – review & editing, Investigation. **Raija Kumpula:** Writing – review & editing, Investigation. **Minna Kivimäenpää:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Johanna Riikonen reports financial support was provided by The Centre for Economic Development, Transport and the Environment, North Savo. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2024.113706.

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