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# Growing under photoselective nets affects the gas exchange and chemical composition of the leaves of highbush blueberry (*Vaccinium corymbosum* L.) before and after harvest

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## ABSTRACT

The use of photoselective nets in highbush blueberry (*Vaccinium corymbosum* L.) orchards could affect the light properties below the nets, along with the plants' physiological processes and the chemical composition of their leaves. In our research, we compared the effects of black, red, yellow, and white exclusion nets with full-sun conditions (control) on light quality and quantity and the performance of blueberry 'Bluecrop' leaves over two consecutive years. The light properties were found to be altered by the nets. The net photosynthesis and leaf gas exchange did not differ among the treatments in 2022. In 2023, the lowest net photosynthesis was measured in the leaves of plants under the control treatment (7.08 μmol $m^{-2}$ $s^{-1}$) before harvest and under the black (3.01 μmol $m^{-2}$ $s^{-1}$) and red nets (3.36 μmol $m^{-2}$ $s^{-1}$) after harvest. At the same time, plants without fruit exhibited significantly lower values of carbon assimilation. The highest chlorophyll fluorescence value was measured in the plants under the red net (0.59) before harvest and under the white exclusion net (0.40) after harvest. Among the measured chloroplast pigments, zeaxanthin increased under the yellow net and the control treatment in 2022, while in 2023, it increased under the red net, white exclusion net, and control treatment before harvest. The total phenolics differed significantly among the treatments across all three sampling dates, with the highest contents measured before harvest in 2023. These promising results indicate that other blueberry cultivars and colored photoselective nets should also be examined in future experiments.

## 1. Introduction

As a consequence of frequent hailstorm events, likely due to global warming, anti-hail nets have been established in blueberry orchards all over the world (Kim et al., 2011; Retamales and Hancock, 2018). The traditionally used black nets are completely opaque, thus reducing the quantity of light reaching the plants below, although the light quality remains unchanged (Ilić, Fallik, 2017; Lobos et al., 2012). Conversely, colored nets, which were developed in 1996 (Ganelevin, 2008), contain specific chromophores that affect the composition of light (Zoratti et al., 2015). Instead of colored nets, the term "photoselective nets" has prevailed and is the standard term used today due to their ability to selectively reflect specific wavelengths of solar radiation (Shahak, 2008).

One of the pests affecting blueberry plants is the spotted-wing drosophila (SWD, *Drosophila suzukii* Matsumara), which lays its eggs in soft-skinned fruit, including blueberries, thus making them unmarketable (McDermott and Nickerson, 2014). Regarding pest management, photoselective nets are considered to be environmentally friendly alternatives to chemical pesticides and are particularly useful in organic farming (Cormier et al., 2015). They have a higher density compared to traditional anti-hail nets (i.e., black nets), which could lead to a greater

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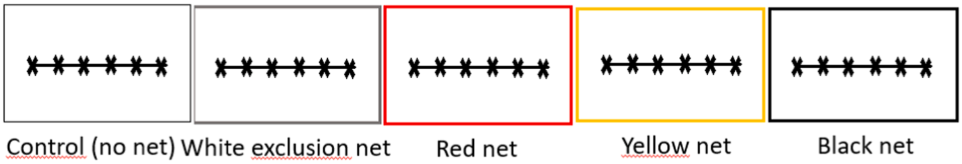

**Fig. 1.** Arrangement of the photoselective nets.

reduction in solar radiation beneath them (Vuković et al., 2022). Consequently, further investigation is necessary to assess the effects of exclusion nets on blueberry plants.

Photoselective nets alter the quantity, quality, and direction of light, modifying the performance of plants (Honorato et al., 2023; Silva et al., 2023). The ability of plants to rapidly adapt to changing environmental conditions is reflected in alteration in the morphological and chemical properties of the leaves and physiological processes. Shaded leaves are usually thinner and have a larger leaf area as well as higher chlorophyll and lower phenolic contents than sunny leaves. Additionally, they have different gas exchange parameters (Lobos et al., 2012; Retamal-Salgado et al., 2017; Smrke et al., 2021). However, Lobos et al. (2012) reported a strong correlation between all of the abovementioned adaptations with a reduction in light quantity rather than quality.

Net photosynthesis is greatly affected by external (environmental) and internal factors. Among the internal factors, a high sink strength, such as fruit development and ripening, leads to enhanced photosynthesis in plants (Demmig-Adams et al., 2017; Smrke et al., 2023).

Nets are currently considered an indispensable measure for intensive blueberry production, especially in less appropriate environments and under an increased pests incidence (Lobos and Hancock, 2015). Despite the promising results regarding the use of photoselective nets in blueberry orchards, discrepancies between different studies still occur (Lobos et al., 2009, 2012, 2013; Milivojević et al., 2016). This suggests that the effects of leaf morphological, chemical, and physiological features on the photoresponse are not yet fully understood. Consequently, the aims of the current study were to (i) define the solar radiation quantity and quality under different photoselective nets; (ii) evaluate the response of highbush blueberry plants to modified light conditions regarding leaf gas exchange parameters and chemical composition; (iii) describe variations in net photosynthesis before and after harvest; and (iiii) determine which photoselective net used in the present study is most suitable for *Vaccinium corymbosum* L. 'Bluecrop'.

## 2. Materials and methods

### 2.1. Field trial

The present study took place in a test field of the Biotechnical Faculty in Ljubljana, Slovenia (latitude: 46 ° 50' N; longitude: 14 °47' E; altitude: 295 m a.s.l.), in 2022 and 2023, using initially 3-year-old plants. Blueberry plants were planted in 40 L black pots in a substrate that was composed of soil, peat, and pine sawdust (1:1:1; v/v/v). For the experiment, 5 treatments with 6 uniform plants (30 altogether) were established: black, red, and yellow photoselective nets, a white exclusion net, and a control (without net) (Fig. 1). The nets were installed on arches that were 4 m wide and 3 m high. The photoselective nets were obtained from Agrintech Srl Italy and were made from high-density polyethylene (mesh size was 2.4 mm x 4.8 mm, shading was 18 % for the black net, 12–18 % for the yellow net, and 17–21 % for the red net). The white exclusion net was purchased from Vetisa, Loznica pri Zalcu, Slovenia (high-density polyethylene, white threads, mesh size of 0.39 mm x 0.83 mm). All nets were placed above the plants from bud swelling to the beginning of flowering and again from the beginning of ripening until leaf senescence. During flowering, the nets were rolled onto the top of the structure to enable optimal pollination.

Each treatment included 6 uniform plants that were placed in one row. The distance between the plants was 0.6 m. The plants in the trial plots were set 4 m apart from each other. Row orientation is south to north, we have therefore estimated that 4 m would be a sufficient distance to avoid shading of the plants by the netting of the neighboring treatment. The ground was covered with black agrotextile to prevent weed growth. The plants were drip-irrigated six times a day for 10 min, using four drippers at each plant and with the flow rate maintained at 900 ml $h^{-1}$ per dripper.

### 2.2. Light measurements

The light spectrum and quantity measurements were performed above the blueberry plants in five replicates for each individual treatment (Spectral Light Meter Optimum SRI-2000-UV, Optimum optoelectronics Corp., Hsinchu, Taiwan). Light spectrum measurements were performed at noon on a clear sunny day (11 September 2023), while diurnal changes in light quantity (photosynthetic photon flux density, PPFD; µmol $m^{-2}$ $s^{-1}$) was measured every hour from 7.00 a.m. to 7.00 p. m.

### 2.3. Net photosynthesis and chlorophyll fluorescence measurements

Before the measurements, one fully developed, intact, and sun-exposed leaf from each plant was selected and labeled. The measurements were carried out in 2022 after harvest (1 August 2022) at 9.00 a. m. to avoid net photosynthesis saturation due to high temperatures or excessive PPFD, while in 2023 they were performed before (19 June 2023) and after harvest (11 August 2023) on a clear, sunny day at noon. The net photosynthesis (Pn; [µmol $CO_2$ $m^{-2}$ $s^{-1}$]) was measured in ambient conditions without artificial modifications of the environmental circumstances using a CI-340 handheld photosynthesis system (CID Bio-Science, Camas, Washington, USA). At the same time, environmental conditions (air and leaf temperatures [°C], photosynthetic photon flux density (PPFD; [µmol $m^{-2}$ $s^{-1}$]), transpiration (E; [mmol $H_2O$ $m^{-2}$ $s^{-1}$]), and stomatal conductance (gs; [mmol $H_2O$ $m^{-1}$ $s^{-1}$]) were recorded.

Chlorophyll fluorescence, i.e., actual PS II efficiency ($F_v$'/$F_m$'), was estimated simultaneously with the net photosynthesis measurements using an LI-600 (Li-Cor, Lincoln, USA) portable porometer/fluorometer in 2023. The measurements were performed on light-adapted leaves under ambient conditions by applying an irradiance pulse of 10000 µmol $m^{-2}$ $s^{-1}$ to the leaves prior to the measurements. $F_m$' is the maximal fluorescence yield of a light-adapted leaf after additionally applying a saturating light pulse on top of the ambient light. $F_v$' is the variable fluorescence yield of a light-adapted leaf. Together with the $F_v$'/$F_m$' value, the gs value, E value, leaf temperature, leaf vapor pressure deficit (VPDl; [kPa]), and photosynthetic photon flux density (PPFD; [µmol $m^{-2}$ $s^{-1}$]) were measured.

### 2.4. Leaf sampling

In parallel with the measurements, leaf sampling for photosynthetic pigment and phenolic compound extractions was performed in both years. Eight randomly chosen, fully developed, and sun-exposed leaves were selected from each plant, put into a paper bag, and immediately frozen in liquid nitrogen to prevent any degradation of individual compounds. For each treatment, 6 replicateswere made. The samples

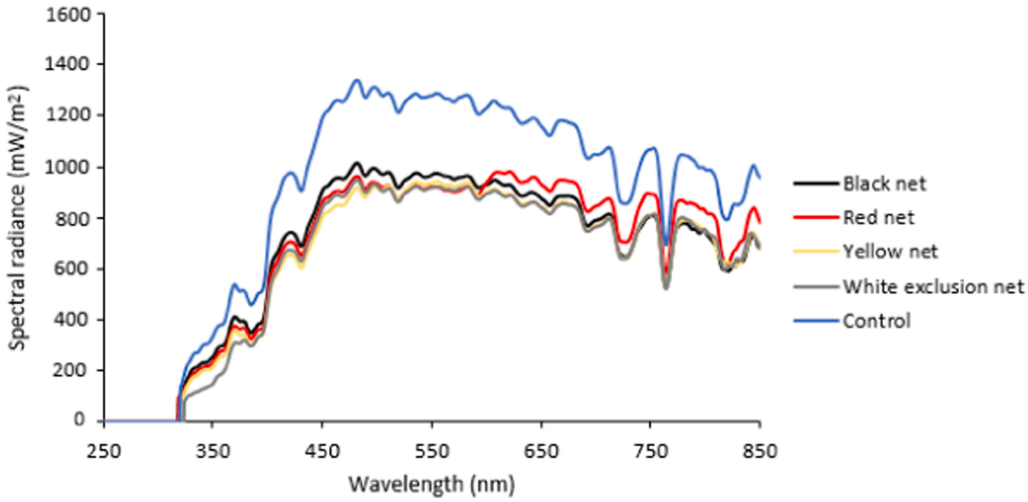

**Fig. 2.** Spectral composition of light (250–850 nm) under the photoselective nets and the control treatment.

were transferred directly into a freeze dryer until they reached a constant weight and then thoroughly ground with a cooled grinder into fine powder. The samples were stored in firmly sealed plastic containers at −20 °C until extraction.

### *2.5. Photosynthetic pigment extraction and analysis*

Photosynthetic pigments were extracted under reduced light in a laminar flow cabinet (LED bulb) according to a previously established method (Tausz et al., 2003). The leaf powder (0.2 g) was mixed with ice-cold 100 % acetone (4 ml) in glass test tubes. Each sample was mixed for 30 s with an Ultra-Turrax T25 homogenizer (IKA, Staufen, Germany), followed by filtration through polyamide filters (Minisart, SRP 15, PTFE, Sartorius Stedim Biotech, Göttingen, Germany) directly into vials. The samples were immediately subjected to high-performance liquid chromatography (HPLC) for analysis.

Photosynthetic pigments were analyzed using HPLC-DAD (Thermo Finnigan, San Jose, California, USA). Separation took place on a Spherisorb S5 ODS-2 column (250 × 4.6 mm) with an S5 ODS-2 (50 × 4.6 mm) precolumn (Alltech Associates, Inc., Deerfield, Illinois, USA). The flow rate was maintained at 1 ml min$^{-1}$ and detection was performed at 440 nm. Mobile phase A contained acetonitrile, water, and methanol (100/10/5; v/v/v), while mobile phase B contained acetone and ethyl acetate (2/1; v/v). The gradient used was as follows: from 10 % B to 75 % B (0–18 min), from 75 % B to 70 % B (18–25 min), from 70 % B to 100 % B (25–30 min), and back to the initial conditions (30–32 min) (Tausz et al., 2003). The pigment concentrations were calculated using individual peak areas and their corresponding external standards and expressed in mg g$^{-1}$ of DW.

### *2.6. Phenolic compound extraction and analysis*

The extraction of phenolic compounds from the previously prepared leaf samples was performed in five replicates per treatment according to an established method (Mikulic-Petkovsek et al., 2010). For the extraction, 0.7 g of sample was transferred into a 10 ml test tube and mixed with 5 ml of pure methanol. Then, we mixed the samples by vortexing and placed them in a cooled (0 °C) ultrasonic bath for 1 h. After the ultrasonic extraction, the samples were centrifuged (9000 *g* at 4 °C for 10 min; 5810 R, Eppendorf centrifuge, Hamburg, Germany) and filtered through polyamide filters (0.2 µm pores, Chromafil AO-20/25, Macherey-Nagel, Düren, Germany) into the vials. The samples were then stored at –20 °C until the HPLC analyses.

The Dionex UltiMate 3000 HPLC (Thermo Scientific, Waltham, Massachusetts, USA) system was used for individual phenolic separation and detection. Each sample was analyzed for 50 min at a flow rate maintained at 0.6 ml min. The injection volume was set to 20 µl and absorbance was detected between 280 nm and 350 nm. The column temperature was held at 25 °C and the autosampler temperature at 10 °C. Mobile phase A consisted of 3 % acetonitrile and 0.1 % formic acid in bi-distilled water (v/v/v), and mobile phase B consisted of 3 % bi-distilled water and 0.1 % formic acid in acetonitrile (v/v/v). The gradient used was, sequentially, 5 % solvent B from 0 to 15 min, 5–20 % B from 15 to 20 min, 20–30 % B from 20 to 30 min, 30–90 % B from 30 to 35 min, 90–100 % B from 35 to 45 min, and 100–5 % B from 45 to 50 min.

An LTQ XL linear ion trap mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) was used to identify individual phenolics based on mass fragmentation. At the same time, their retention times were compared with the external standards for HPLC analysis (Mikulic-Petkovsek et al., 2010). The mass spectrometer operated in the negative ion mode with electrospray ionization and *m/z* scanning from 115 to 1600. The capillary temperature was maintained at 250 °C, the source voltage at 4 kV, the sheath gas at 20 units, and the auxiliary gas at 8 units. The flow rate of the samples was 0.6 ml min$^{-1}$, and the injection volume was 10 µL. The individual phenolic content was calculated using their corresponding or most similar external standard and expressed in mg g$^{-1}$ of dry weight (DW).

### *2.7. Statistical analyses*

Statistical analyses of the data were performed using R Commander (4.3.2). Statistically significant differences were determined using one-way analysis of variance (ANOVA) at the confidence level $\alpha < 0.05$. Significant differences between the two sampling dates in 2023 were determined using a mixed model. Principal component analysis and correlation analysis were performed for the individual photosynthetic pigments.

## 3. Results

### *3.1. Solar radiation*

All nets reduced light quantity compared to the control (Fig. 2). The red net increased the light quantity from approximately 600 nm to 700 nm onward (the red part of visible light) and throughout the IR spectrum (Fig. 2). Under the yellow net, higher values were measured from approximately 500 nm onward. The white exclusion net reduced light quantity only in the UV portion of the specter (from 250 nm to approximately 400 nm).

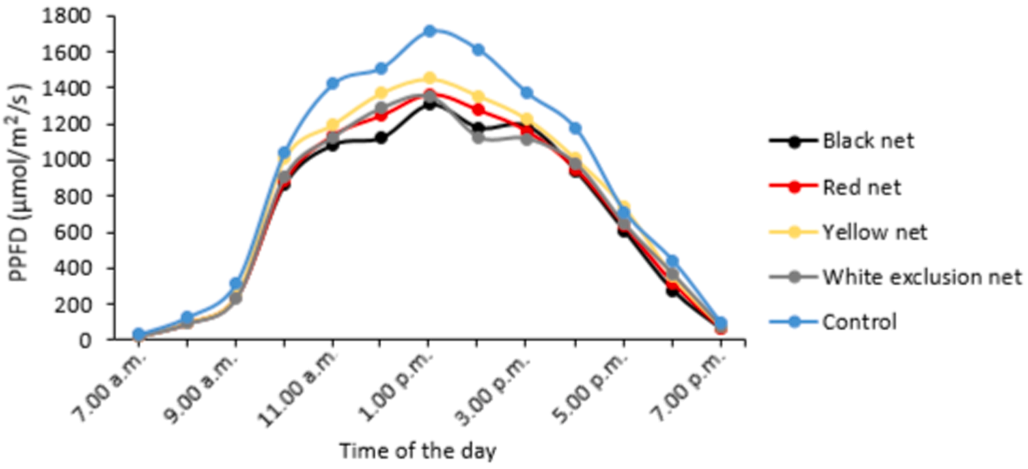

**Fig. 3.** Photosynthetic photon flux density (PPFD, µmol $m^{-2}$ $s^{-1}$) under the photoselective nets and the control treatment from 7.00 a.m. to 7.00 p.m.

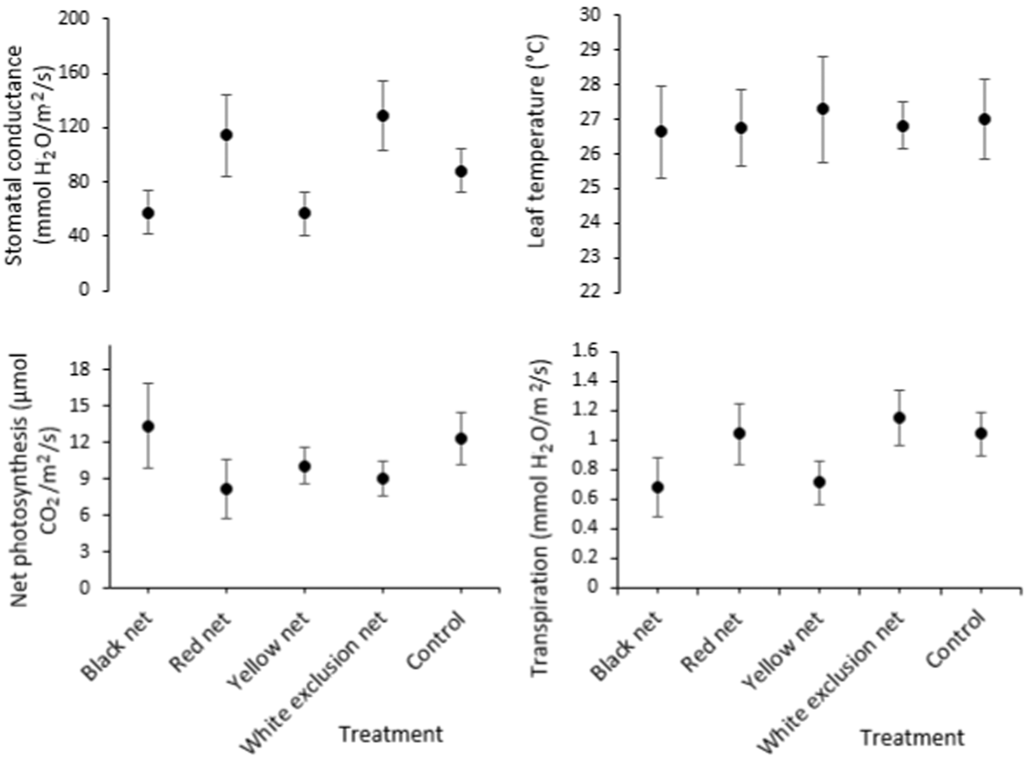

**Fig. 4.** Net photosynthesis, stomatal conductance, transpiration, and leaf temperature under photoselective nets and the control treatment after harvest in 2022. The figure presents the average values with the standard errors calculated from six replicates per treatment. Differences between the treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.

The highest PPFD was measured under full-sun conditions, followed by the yellow photoselective net (Fig. 3). The black, red, and white exclusion nets showed similar values during the day, except at 12.00 p.m.

### 3.2. Net photosynthesis and leaf gas exchange

In 2022, no significant differences in net photosynthesis, stomatal conductance, leaf transpiration, or temperature were detected (Fig. 4). In 2023, before harvest, the lowest net photosynthesis (7.08 µmol $m^{-2}$ $s^{-1}$) and stomatal conductance (44.84 mmol $H_2O$ $m^{-2}$ $s^{-1}$) were measured in the plants from the control treatment, while no significant difference was observed between the plants under the nets (Fig. 5A). No significant difference was determined between all treatments in terms of transpiration and leaf temperature, while a significantly higher VPD was measured under full-sun conditions. After harvest, significant differences were observed in the net photosynthesis of the plants under the yellow and black nets, ranging between 3.01 µmol $m^{-2}$ $s^{-1}$ and 6.42 µmol $m^{-2}$ $s^{-1}$, respectively (Fig. 5B). A similar performance was observed in stomatal conductance and transpiration rate. The VPD was significantly higher in the plants of the control treatment.

When we compared the measurements before and after harvest, significant differences in net photosynthesis, stomatal conductance, and transpiration were determined across all five treatments (Table 1), with the highest values obtained before harvest. Leaf temperature did not differ significantly before and after harvest in neither treatment, and ranged between 38.17 °C and 40.47 °C before harvest and between 36.72 °C and 38.95 °C after it.

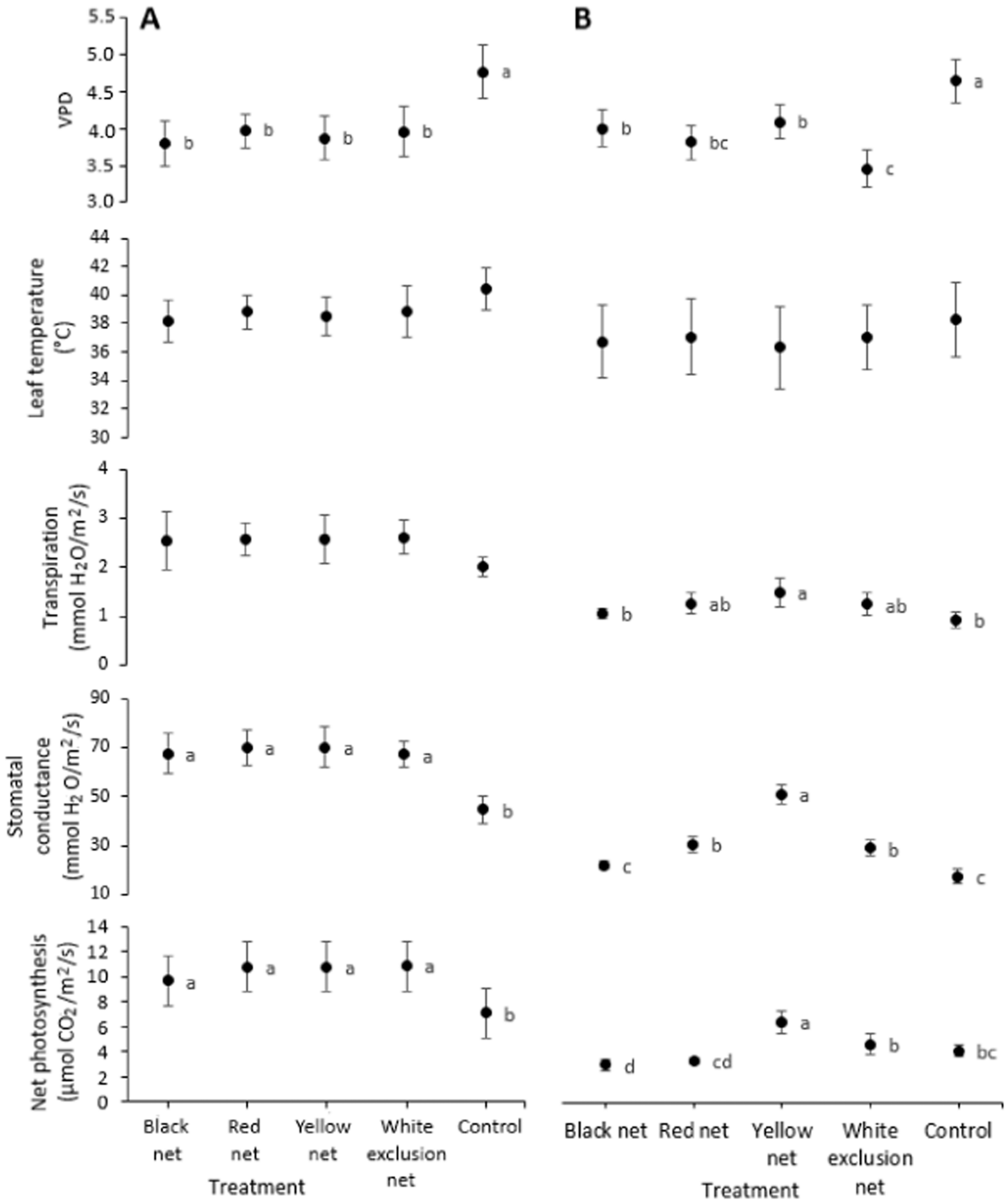

**Fig. 5.** Net photosynthesis, stomatal conductance, transpiration, leaf temperature, and VPD under the photoselective nets and the control treatment before (A) and after (B) harvest in 2023. The figure presents the average values with the standard errors calculated from six replicates per treatment. Differences between the treatments (a-d) were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.

**Table 1**

Significant differences in net photosynthesis, stomatal conductance, transpiration, and leaf temperature between the two sampling dates in 2023 (before and after harvest) for the plants under the photoselective nets and the control treatment.

| | Black net | Red net | Yellow net | White exclusion net | Control |
|---|---|---|---|---|---|
| Net photosynthesis | *** | *** | *** | *** | *** |
| Stomatal conductance | *** | *** | *** | *** | *** |
| Transpiration | *** | *** | *** | *** | *** |
| Leaf temperature | NS | NS | NS | NS | NS |

Differences between the treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.

[***] , $p < 0.001$; NS, not significant.

### 3.3. *Chlorophyll fluorescence*

Before harvest, the highest chlorophyll fluorescence (Fv'/Fm') value was measured in the leaves under the red net (0.59), while the other treatments did not differ significantly from each other (Fig. 6A). On the other hand, similar values in leaf stomatal conductance were measured between the treatments, where a significant difference was only observed between the white exclusion net and the control treatment. The highest transpiration was measured under the yellow net (2.82 mmol $H_2O$ $m^{-2}$ $s^{-1}$) and white exclusion net (3.17 mmol $H_2O$ $m^{-2}$ $s^{-1}$). The VPDl values, where a significant difference was only measured between the control treatment (3.50) and the black net (3.08), were inconsistent with the photosynthesis measurements. Regarding the fluorescence measurements after harvest, the highest values were measured under the white exclusion net (0.4) and the lowest values under the black net (0.18) and the control treatment (0.22) (Fig. 6B). The lowest stomatal conductance and transpiration rates were measured

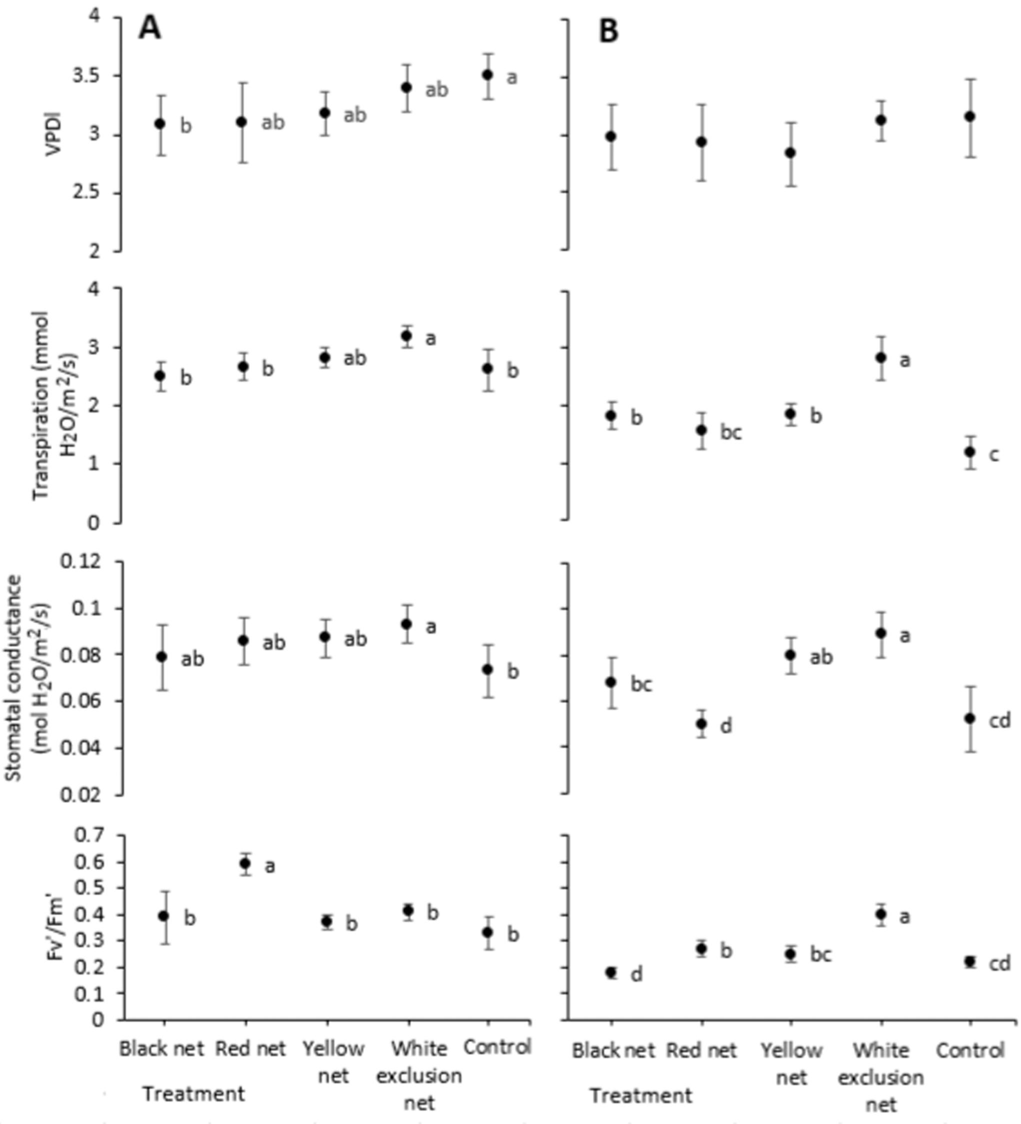

**Fig. 6.** Chlorophyll fluorescence (Fv'/Fm'), stomatal conductance, transpiration, and leaf vapor pressure deficit under the photoselective nets and the control treatment before (A) and after (B) harvest in 2023. The figure presents the average values with the standard errors calculated from six replicates per treatment. Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$ (a-d).

**Table 2**
Significant differences in chlorophyll fluorescence (Fv'/Fm'), stomatal conductance, transpiration, leaf vapor pressure deficit, and leaf temperature between the two sampling dates in 2023 (before and after harvest) under the photoselective nets and the control treatment.

| | Black net | Red net | Yellow net | White exclusion net | Control |
|---|---|---|---|---|---|
| Fv'/Fm' | *** | *** | *** | NS | ** |
| Stomatal conductance | NS | *** | NS | NS | * |
| Transpiration | *** | *** | *** | NS | *** |
| VPDl | NS | NS | * | * | NS |
| Leaf temperature | NS | NS | NS | NS | NS |

Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.
*, $p < 0.05$;
**, $p < 0.01$;
***, $p < 0.001$; NS, not significant.

under the red net and the control treatment. No significant difference was determined in terms of VPDl.

Regarding chlorophyll fluorescence, significant differences between measuring days were determined among all treatments, except for the white exclusion net (Table 2).

### 3.4. Photosynthetic pigments

In the first year of the experiment, the lowest violaxanthin and the highest zeaxanthin contents were measured under the yellow net and the control treatment (Table 3). A negative correlation between the zeaxanthin and violaxanthin contents was also obtained in the principal component analysis (Supplementary Figure S1) and confirmed by the correlation analysis (r = -0.9084) (Table 5). The AZ/VAZ ratio was highest in the leaves under the yellow net and the control treatment. The total chlorophyll content (chlorophyll $a + b$) was highest under the black net and lowest under the yellow net (Table 3). The correlation analysis showed a positive correlation between these two compounds (r = 0.6604) (Table 5). The lowest chlorophyll $a/b$ ratio was measured in the plants under the black and red photoselective nets.(Tables 4 and

**Table 3**
Contents of individual photosynthetic pigments in blueberry leaves under the photoselective nets and the control treatment after harvest in 2022.

| | After harvest in 2022 | | | | | |
|---|---|---|---|---|---|---|
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neoxanthin | 0.13 ± 0.01 a | 0.12 ± 0.01 ab | 0.11 ± 0.00 b | 0.12 ± 0.00 ab | 0.11 ± 0.01 b | ** |
| Violaxanthin | 0.077 ± 0.004 a | 0.080 ± 0.005 a | 0.058 ± 0.011 b | 0.087 ± 0.006 a | 0.053 ± 0.005 b | *** |
| Antheraxanthin | 0.063 ± 0.015 | 0.063 ± 0.003 | 0.065 ± 0.003 | 0.077 ± 0.006 | 0.061 ± 0.008 | NS |
| Zeaxanthin | 0.13 ± 0.01 bc | 0.11 ± 0.01c | 0.15 ± 0.02 ab | 0.12 ± 0.01c | 0.16 ± 0.01 a | *** |
| Lutein | 0.41 ± 0.02 | 0.40 ± 0.02 | 0.37 ± 0.01 | 0.39 ± 0.01 | 0.37 ± 0.04 | NS |
| Chlorophyll *a* | 3.02 ± 0.08 | 2.99 ± 0.11 | 2.87 ± 0.09 | 2.97 ± 0.09 | 2.98 ± 0.14 | NS |
| Chlorophyll *b* | 1.37 ± 0.05 a | 1.31 ± 0.08 ab | 1.16 ± 0.05c | 1.26 ± 0.06 abc | 1.18 ± 0.07 bc | ** |
| β-carotene | 0.28 ± 0.01 | 0.27 ± 0.01 | 0.25 ± 0.01 | 0.26 ± 0.02 | 0.26 ± 0.02 | NS |
| VAZ | 0.27 ± 0.02 | 0.26 ± 0.01 | 0.28 ± 0.01 | 0.28 ± 0.01 | 0.28 ± 0.02 | NS |
| AZ/VAZ | 0.72 ± 0.02 b | 0.69 ± 0.03 b | 0.79 ± 0.04 a | 0.69 ± 0.02 b | 0.81 ± 0.01 a | *** |
| Chlorophyll $a + b$ | 4.40 ± 0.13 a | 4.30 ± 0.17 ab | 4.03 ± 0.13 b | 4.22 ± 0.14 ab | 4.16 ± 0.18 ab | * |
| Chlorophyll $a/b$ | 2.20 ± 0.03c | 2.29 ± 0.12 bc | 2.48 ± 0.05 ab | 2.36 ± 0.08 abc | 2.52 ± 0.13 a | *** |
| VAZ/Chlorophyll $a + b$ | 0.12 ± 0.01 | 0.11 ± 0.01 | 0.11 ± 0.00 | 0.12 ± 0.00 | 0.11 ± 0.01 | NS |
| β-carotene/Chlorophyll $a + b$ | 0.064 ± 0.001 | 0.063 ± 0.002 | 0.062 ± 0.001 | 0.061 ± 0.001 | 0.062 ± 0.003 | NS |

The average values with the standard errors, calculated from six replicates per treatment, are presented. Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$ (a-c).

$^{*}$, $p < 0.05$;
$^{**}$, $p < 0.01$;
$^{***}$, $p < 0.001$; NS, not significant.

**Table 4**
Contents of individual photosynthetic pigments in blueberry leaves under the photoselective nets and the control treatment before and after harvest in 2023.

| | Before harvest in 2023 | | | | | |
|---|---|---|---|---|---|---|
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neoxanthin | 0.12 ± 0.01 | 0.12 ± 0.02 | 0.12 ± 0.02 | 0.12 ± 0.01 | 0.10 ± 0.01 | NS |
| Violaxanthin | 0.064 ± 0.009 a | 0.043 ± 0.003 b | 0.033 ± 0.004c | 0.035 ± 0.005 bc | 0.029 ± 0.004c | *** |
| Antheraxanthin | 0.058 ± 0.009 ab | 0.065 ± 0.007 a | 0.057 ± 0.007 ab | 0.064 ± 0.005 ab | 0.052 ± 0.005 b | * |
| Zeaxanthin | 0.11 ± 0.02c | 0.17 ± 0.03 ab | 0.16 ± 0.01 b | 0.18 ± 0.02 ab | 0.20 ± 0.01 a | *** |
| Lutein | 0.39 ± 0.03 a | 0.40 ± 0.02 a | 0.38 ± 0.02 ab | 0.39 ± 0.02 a | 0.34 ± 0.03 b | ** |
| Chlorophyll *a* | 3.05 ± 0.12 | 3.04 ± 0.18 | 2.80 ± 0.33 | 3.04 ± 0.15 | 2.75 ± 0.19 | * |
| Chlorophyll *b* | 1.26 ± 0.06 ab | 1.30 ± 0.08 a | 1.17 ± 0.05 bc | 1.22 ± 0.08 ab | 1.07 ± 0.07c | *** |
| β-carotene | 0.35 ± 0.02 a | 0.34 ± 0.03 ab | 0.33 ± 0.04 ab | 0.33 ± 0.03 ab | 0.30 ± 0.03 b | * |
| VAZ | 0.23 ± 0.03 b | 0.28 ± 0.03 a | 0.26 ± 0.02 ab | 0.28 ± 0.02 a | 0.28 ± 0.02 a | ** |
| AZ/VAZ | 0.72 ± 0.04c | 0.85 ± 0.02 b | 0.87 ± 0.02 ab | 0.87 ± 0.02 ab | 0.90 ± 0.01 a | *** |
| Chlorophyll $a + b$ | 4.31 ± 0.15 a | 4.34 ± 0.25 a | 3.97 ± 0.34 ab | 4.27 ± 0.22 a | 3.83 ± 0.25 b | ** |
| Chlorophyll $a/b$ | 2.41 ± 0.11 | 2.35 ± 0.11 | 2.39 ± 0.28 | 2.49 ± 0.12 | 2.57 ± 0.12 | NS |
| VAZ/Chlorophyll $a + b$ | 0.10 ± 0.01 b | 0.12 ± 0.02 a | 0.11 ± 0.02 ab | 0.11 ± 0.01 ab | 0.11 ± 0.01 ab | * |
| β-carotene/Chlorophyll $a + b$ | 0.081 ± 0.002 | 0.079 ± 0.008 | 0.083 ± 0.01 | 0.077 ± 0.007 | 0.078 ± 0.003 | NS |
| | After harvest in 2023 | | | | | |
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neoxanthin | 0.11 ± 0.01 a | 0.11 ± 0.01 a | 0.10 ± 0.01 ab | 0.09 ± 0.01 b | 0.08 ± 0.01 b | *** |
| Violaxanthin | 0.035 ± 0.004 a | 0.032 ± 0.006 ab | 0.028 ± 0.004 bc | 0.024 ± 0.004c | 0.025 ± 0.003 bc | *** |
| Antheraxanthin | 0.038 ± 0.003 a | 0.035 ± 0.005 ab | 0.034 ± 0.003 ab | 0.035 ± 0.003 ab | 0.031 ± 0.004 b | * |
| Zeaxanthin | 0.09 ± 0.01 | 0.09 ± 0.01 | 0.10 ± 0.01 | 0.10 ± 0.01 | 0.09 ± 0.01 | NS |
| Lutein | 0.35 ± 0.02 a | 0.35 ± 0.03 a | 0.33 ± 0.02 ab | 0.32 ± 0.02 ab | 0.29 ± 0.02 b | ** |
| Chlorophyll *a* | 2.88 ± 0.13 a | 2.96 ± 0.19 a | 2.74 ± 0.28 ab | 2.67 ± 0.12 ab | 2.51 ± 0.15 b | ** |
| Chlorophyll *b* | 1.16 ± 0.10 ab | 1.21 ± 0.08 a | 1.09 ± 0.10 abc | 1.06 ± 0.03 bc | 0.96 ± 0.06c | *** |
| β-carotene | 0.27 ± 0.02 a | 0.27 ± 0.02 a | 0.25 ± 0.02 ab | 0.24 ± 0.02 ab | 0.22 ± 0.02 b | ** |
| VAZ | 0.16 ± 0.01 a | 0.16 ± 0.02 a | 0.16 ± 0.01 a | 0.16 ± 0.01 a | 0.14 ± 0.01 b | * |
| AZ/VAZ | 0.78 ± 0.03c | 0.80 ± 0.04 bc | 0.83 ± 0.02 ab | 0.85 ± 0.03 a | 0.83 ± 0.02 ab | *** |
| Chlorophyll $a + b$ | 4.04 ± 0.19 ab | 4.17 ± 0.27 a | 3.83 ± 0.37 abc | 3.73 ± 0.37 bc | 3.46 ± 0.21c | *** |
| Chlorophyll *a*/b | 2.50 ± 0.22 | 2.44 ± 0.09 | 2.51 ± 0.12 | 2.51 ± 0.10 | 2.62 ± 0.07 | NS |
| VAZ/Chlorophyll $a + b$ | 0.06 ± 0.01 a | 0.07 ± 0.01 a | 0.07 ± 0.00 a | 0.07 ± 0.01 a | 0.05 ± 0.00 b | * |
| β-carotene/Chlorophyll $a + b$ | 0.066 ± 0.005 | 0.064 ± 0.003 | 0.066 ± 0.003 | 0.063 ± 0.005 | 0.064 ± 0.003 | NS |

The average values with the standard errors, calculated from six replicates per treatment, are presented. Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$ (a-c).

$^{*}$, $p < 0.05$;
$^{**}$, $p < 0.01$;
$^{***}$, $p < 0.001$; NS, not significant.

5).

Before the harvest in 2023, the highest violaxanthin and the lowest zeaxanthin contents were found in the leaves under the black net. The negative correlation between violaxanthin and zeaxanthin was high (r = -0.7902). The results regarding the total chlorophyll content were similar to the results in 2022. The *β*-carotene content differed significantly between the treatments in the second experimental year, with the highest contents measured in the plants under the nets. After the harvest in 2023, the results regarding the individual pigments were similar to the results before the harvest. An exception was the content of zeaxanthin, where no significant difference was determined.

The principal component analysis based on individual chloroplast pigments did not show any grouping of data by treatments (Supplementary Figures S1, S2, and S3).

**Table 5**
Correlation analysis of individual photosynthetic pigments in blueberry leaves.

| | Antheraxanthin | β-carotene | Chlorophyll *a* | Chlorophyll *b* | Lutein | Neoxanthin | Violaxanthin | Zeaxanthin |
|---|---|---|---|---|---|---|---|---|
| After harvest in 2022 | | | | | | | | |
| Antheraxanthin | | 0.1886 | 0.3281 | 0.1451 | 0.4698 | 0.3888 | 0.5018 | −0.3419 |
| β-carotene | | | 0.7654** | 0.8593*** | 0.8869*** | 0.8735*** | 0.4294 | −0.2578 |
| Chlorophyll *a* | | | | 0.6604* | 0.7544** | 0.7423** | 0.3998 | −0.3176 |
| Chlorophyll *b* | | | | | 0.8571*** | 0.8906*** | 0.5977 | −0.4795 |
| Lutein | | | | | | 0.9448*** | 0.5908 | −0.4068 |
| Neoxanthin | | | | | | | 0.6661* | −0.5628 |
| Violaxanthin | | | | | | | | −0.9084*** |
| Zeaxanthin | | | | | | | | |
| Before harvest in 2023 | | | | | | | | |
| Antheraxanthin | | 0.5441* | 0.6434** | 0.5772* | 0.7157*** | 0.7045*** | 0.1265 | 0.1491 |
| β-carotene | | | 0.3284 | 0.7441*** | 0.7761*** | 0.7671*** | 0.3939 | −0.2090 |
| Chlorophyll *a* | | | | 0.6586** | 0.5675* | 0.4895 | 0.4769 | −0.2262 |
| Chlorophyll *b* | | | | | 0.8425*** | 0.7440*** | 0.5776* | −0.2923 |
| Lutein | | | | | | 0.8562*** | 0.4145 | −0.1399 |
| Neoxanthin | | | | | | | 0.4099 | −0.1469 |
| Violaxanthin | | | | | | | | −0.7902*** |
| Zeaxanthin | | | | | | | | |
| After harvest in 2023 | | | | | | | | |
| Antheraxanthin | | 0.7088*** | 0.6518** | 0.5494* | 0.7206*** | 0.6865*** | 0.5957** | 0.0421 |
| β-carotene | | | 0.7942*** | 0.8705*** | 0.9143*** | 0.9450*** | 0.7008*** | 0.0853 |
| Chlorophyll *a* | | | | 0.8530*** | 0.7942*** | 0.7974*** | 0.8315*** | −0.0728 |
| Chlorophyll *b* | | | | | 0.9121*** | 0.9086*** | 0.7099*** | 0.0661 |
| Lutein | | | | | | 0.9654*** | 0.6881*** | 0.1059 |
| Neoxanthin | | | | | | | 0.7356*** | 0.0160 |
| Violaxanthin | | | | | | | | −0.4190 |
| Zeaxanthin | | | | | | | | |

Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.
*, $p < 0.05$;
**, $p < 0.01$;
***, $p < 0.001$; NS, not significant.

**Table 6**
Significant differences in individual photosynthetic pigments in blueberry leaves between the two sampling dates in 2023 (before and after harvest) under the photoselective nets and the control treatment.

| | Black net | Red net | Yellow net | White exclusion net | Control |
|---|---|---|---|---|---|
| Neoxanthin | * | NS | NS | ** | ** |
| Violaxanthin | *** | ** | NS | *** | NS |
| Antheraxanthin | ** | *** | *** | *** | *** |
| Zeaxanthin | * | *** | *** | *** | *** |
| Lutein | * | * | ** | *** | * |
| Chlorophyll *a* | * | NS | NS | *** | * |
| Chlorophyll *b* | NS | NS | NS | ** | * |
| β-carotene | *** | *** | ** | *** | *** |
| VAZ | *** | *** | *** | *** | *** |
| AZ/VAZ | * | * | * | NS | *** |
| Chlorophyll $a + b$ | * | NS | NS | *** | * |
| Chlorophyll $a/b$ | NS | NS | NS | NS | NS |
| VAZ/Chlorophyll $a + b$ | *** | *** | ** | *** | *** |
| β-carotene/Chlorophyll $a + b$ | *** | ** | * | ** | *** |

Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.
*, $p < 0.05$;
**, $p < 0.01$;
***, $p < 0.001$; NS, not significant.

The significant differences between the two sampling dates in 2023 are presented in Table 6. Antheraxanthin and zeaxanthin differed across all five treatments, being the highest values detected before harvest. Similar results were observed regarding the total chlorophyll content.

### 3.5. *Phenolic compounds*

In 2022, the total flavonol content was highest under the control treatment and the black net, and the total phenolic content was highest under the control treatment and the black and yellow nets (Table 7). Among flavonols, nine individual compounds were identified, namely, myricetin and quercetin derivatives, being myricetin derivatives the most abundant. In 2023, before harvest, chlorogenic acid and, therefore, total hydroxycinnamic acids were highest under the control treatment (Table 8). Similar results were obtained regarding flavan-3-ols. Conversely, the total content of flavonols did not differ significantly between treatments before harvest. After harvest, the contents of chlorogenic acid and total phenolic compounds in the leaves were the same for all treatments (Table 8). Among the individual phenolic compounds, chlorogenic acid, procyanidin B2, myricetin pentoside, and the majority of quercetin derivatives differed significantly between the sampling dates in 2023 across all five treatments (Table 9), and the highest values of total phenolic compounds were measured before harvest.

## 4. Discussion

Colored photoselective nets alter light quality through the absorption, transmittance, and scattering of light. A black net transmit light through the entire radiation spectrum and does not scatter light, while the red net transmits a higher light quantity in the red and far-red parts of the spectrum. Under the yellow net, higher light quantity were measured from approximately 500 nm onward, resulting in the increased absorption of light in the UV and blue spectra (Shahak, 2008). The white exclusion net only absorbed UV radiation, which is in agreement with the results published by Lobos et al. (2012).

Environmental conditions, such as light and temperature, are the main factors affecting carbon assimilation in plants (Retamal-Salgado et al., 2017; Smrke et al., 2023). In 2023, before harvest, higher net photosynthesis was expected in plants under the red net due to a higher transmittance in the red part of the spectrum, in which chlorophylls showed the highest absorbance. However, this was not the case in the

**Table 7**
Contents of individual phenolic compounds in blueberry leaves under the photoselective nets and the control treatment after harvest in 2022.

| | After harvest in 2022 | | | | | |
|---|---|---|---|---|---|---|
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neochlorogenic acid | 3.70 ± 0.10 a | 3.26 ± 0.11 ab | 3.18 ± 0.19 ab | 3.01 ± 0.16 b | 3.40 ± 0.46 ab | * |
| 5-galloylquinic acid | 1.51 ± 0.33 | 1.61 ± 0.14 | 1.90 ± 0.19 | 1.61 ± 0.14 | 1.67 ± 0.12 | NS |
| di-caffeoylquinic acid | 0.77 ± 0.10 b | 0.85 ± 0.09 ab | 0.97 ± 0.06 a | 0.96 ± 0.07 a | 0.92 ± 0.07 ab | * |
| p-coumaroylquinic acid | 0.66 ± 0.05 b | 0.72 ± 0.08 b | 0.88 ± 0.08 a | 0.90 ± 0.06 a | 0.94 ± 0.08 a | *** |
| Chlorogenic acid | 50.99 ± 2.51 a | 42.02 ± 3.24 b | 52.96 ± 5.41 a | 45.50 ± 2.31 ab | 49.84 ± 4.48 ab | ** |
| Cryptochlorogenic acid | 2.83 ± 0.38 bc | 2.33 ± 0.30c | 3.19 ± 0.17 ab | 2.85 ± 0.36 bc | 3.60 ± 0.27 a | *** |
| Total hydroxycinnamic acids | 60.46 ± 3.05 a | 50.79 ± 3.58 b | 63.08 ± 5.58 a | 54.82 ± 2.20 ab | 60.36 ± 5.01 a | ** |
| Procyanidin B1 | 1.66 ± 0.24 a | 1.10 ± 0.15 b | 1.30 ± 0.07 b | 1.09 ± 0.07 b | 1.17 ± 0.19 b | *** |
| Procyanidin B2 | 8.90 ± 0.64 bc | 7.97 ± 0.50c | 10.63 ± 0.81 a | 10.12 ± 0.44 ab | 9.10 ± 0.56 bc | *** |
| Catechin | 4.32 ± 0.07 ab | 4.55 ± 0.38 a | 4.51 ± 0.31 a | 3.67 ± 0.11 b | 4.21 ± 0.48 ab | ** |
| Epicatechin | 3.40 ± 0.61 | 2.91 ± 0.22 | 3.23 ± 0.39 | 3.02 ± 0.08 | 3.11 ± 0.60 | NS |
| Total flavan−3-ols | 18.28 ± 1.31 ab | 16.52 ± 0.79 b | 19.67 ± 0.60 a | 17.90 ± 0.52 ab | 17.59 ± 1.11 b | ** |
| Myricetin−3-galactoside | 6.77 ± 0.57 a | 5.86 ± 0.45 b | 5.83 ± 0.26 b | 4.20 ± 0.36c | 6.70 ± 0.34 ab | *** |
| Myricetin−3-glucoside | 5.22 ± 0.51 b | 5.06 ± 0.95 b | 5.51 ± 0.36 ab | 4.84 ± 0.28 b | 6.57 ± 0.35 a | ** |
| Myricetin-pentoside | 0.98 ± 0.23 | 0.95 ± 0.14 | 0.89 ± 0.10 | 0.83 ± 0.09 | 0.97 ± 0.09 | NS |
| Myricetin-hexoside | 1.47 ± 0.16 a | 1.26 ± 0.16 a | 1.23 ± 0.18 a | 0.87 ± 0.07 b | 1.31 ± 0.10 a | *** |
| Quercetin−3-rutinoside | 0.10 ± 0.01 | 0.10 ± 0.01 | 0.10 ± 0.01 | 0.09 ± 0.01 | 0.10 ± 0.01 | NS |
| Quercetin−3-galactoside | 2.88 ± 0.18 b | 2.59 ± 0.22 bc | 2.83 ± 0.12 b | 2.24 ± 0.21c | 3.33 ± 0.15 a | *** |
| Quercetin−3-glucoside | 0.88 ± 0.13 bc | 1.05 ± 0.16 b | 0.79 ± 0.08c | 1.85 ± 0.12 a | 0.69 ± 0.04c | *** |
| Quercetin−3-arabinopyranoside | 0.84 ± 0.11 a | 0.69 ± 0.04 b | 0.80 ± 0.05 a | 0.70 ± 0.05 b | 0.83 ± 0.06 a | * |
| Quercetin−3-acetylhexoside | 0.92 ± 0.08 | 0.91 ± 0.11 | 0.91 ± 0.09 | 1.04 ± 0.14 | 0.96 ± 0.14 | NS |
| Total flavonols | 20.07 ± 0.43 ab | 18.47 ± 0.82 b | 18.88 ± 0.68 b | 16.66 ± 0.73c | 21.46 ± 1.03 a | *** |
| Total phenolic compounds | 98.81 ± 3.82 ab | 85.78 ± 4.47c | 101.6 ± 6.04 a | 89.39 ± 1.53 bc | 99.42 ± 5.03 a | *** |

The average values with the standard errors, calculated from six replicates per treatment, are presented. Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$ (a-c).

[*] , $p < 0.05$;

[**] , $p < 0.01$;

[***] , $p < 0.001$; NS, not significant.

present study. The light saturation point for photosynthesis in highbush blueberries was reported to reach approximately 500–800 μmol $m^{-2}$ $s^{-1}$ (Moon et al., 1987; Petridis et al., 2018) depending on the cultivar, leading to the conclusion that the reduction in light under the photoselective nets was not a limiting factor for carbon assimilation. Since the leaf temperature did not differ between the treatments, excessive solar radiation and significantly higher VPD under full-sun conditions led to the closure of leaf stomata and, consequently, the reduction in stomatal conductance and net photosynthesis. This is in accordance with the results reported by Shahak et al. (2004) on 'Golden Delicious' apples, but contradictory with the results published by Kim et al. (2011) on 'Bluecrop' blueberries; the differences in leaf temperature between the treatments probably contributed to the opposing results. A higher stomatal conductance enables a higher $CO_2$ intake into the leaf, which facilitates carbon assimilation, indicating a strong correlation between these two factors (Hao et al., 2019). The absence of significant differences in the transpiration rate between the treatments, together with the reduced stomatal conductance in the control treatment, suggests that plants activate a defense mechanism to cope with stressful growing conditions (Zheng et al., 2017). After harvest, the VPD values showed an increase in the plants in the control treatment. VPD is affected by air temperature (NS, data not shown) and relative humidity (not measured in the current study) (Ferlan et al., 2016). Since there was no significant difference measured in air and leaf temperature between the treatments, the higher VPD values probably resulted from the lower relative humidity in the control treatment, which was also confirmed in other studies using photoselective nets (Milivojević et al., 2016; Solomakhin and Blanke, 2010).

In addition to environmental factors, carbon assimilation highly depends on a plant's sink demand. A high sink strength, among other fruit growth and ripening factors, leads to an upregulation of photosynthesis (Fatichi et al., 2014), whereas fruit removal leads to its downregulation (Duan et al., 2016).

Chlorophyll fluorescence have proven to be a reliable tool for assessing the effects of plant stress (Chen et al., 2012), wherelower values indicate more stressful conditions (Maxwell and Johnson, 2000; Smrke et al., 2023). In addition to light and temperature, plant physiological processes depend on other environmental factors such as $CO_2$ availability, relative humidity, and Rubisco activity (Hao et al., 2019; Sage, 1990). All of these factors can fluctuate very quickly under natural conditions (Smrke et al., 2023), which explains the slightly inconsistent values for leaf gas exchange properties between the net photosynthesis and chlorophyll fluorescence measurements. Regarding the fluorescence measurements after harvest, the highest values were measured under the white exclusion net and the lowest values under the black net and the control treatment, indicating that the plants under the latter two treatments grew under the most stressful conditions. According to Kim et al. (2011) and Retamal-Salgado et al. (2017), chlorophyll fluorescence decreases as PPFD increases, which was only partly confirmed in this study. However, similar to photosynthesis, chlorophyll fluorescence depends on various environmental factors, which may have influenced the outcomes of the present experiment (Li et al., 2024; Maxwell and Johnson, 2000).

The main functions of chloroplast pigments in plant tissues are to capture solar radiation for the carbon assimilation process and, at the same time, protect the photosynthesis apparatus from photo-oxidative damage through the elimination of excess energy and reactive oxygen species (Simkin et al., 2022). Violaxanthin transforms into zeaxanthin through antheraxanthin in the xanthophyll cycle as a result of stressful environmental conditions, such as excessive solar radiation. This means that the content of zeaxanthin increases at the expense of a decrease in violaxanthin, which we confirmed by the multivariate and correlation analyses. Zeaxanthin dissipates excessive light energy that is absorbed in the photosynthesis apparatus in order to protect the photosynthetic reactive center from photoinhibition or even from irreversible damages (Faraloni et al., 2021; Šircelj et al., 2007). Similarly to zeaxanthin, antheraxanthin also helps to dissipate excessive solar energy as heat (Yin et al., 2010), which explains the increased AZ/VAZ ratio in the leaves under the yellow net and the control treatment. The total chlorophyll content (chlorophyll a + b) was highest under the black net and lowest under the yellow net, which was associated with the amount of light reaching the plants (Retamal-Salgado et al., 2017). The increase in total

**Table 8**
Contents of individual phenolic compounds in blueberry leaves under the photoselective nets and the control treatment before and after harvest in 2023.

| | Before harvest in 2023 | | | | | |
|---|---|---|---|---|---|---|
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neochlorogenic acid | 3.61 ± 0.68 | 3.73 ± 0.81 | 3.13 ± 0.09 | 3.62 ± 0.61 | 4.25 ± 0.83 | NS |
| 5-galloylquinic acid | 1.06 ± 0.20 | 0.98 ± 0.11 | 1.05 ± 0.14 | 1.05 ± 0.20 | 0.94 ± 0.19 | NS |
| di-caffeoylquinic acid | 0.69 ± 0.06 a | 0.72 ± 0.17 a | 0.74 ± 0.11 a | 0.74 ± 0.06 a | 0.46 ± 0.07 b | *** |
| p-coumaroylquinic acid | 0.77 ± 0.05 b | 1.08 ± 0.13 a | 1.10 ± 0.12 a | 1.10 ± 0.16 a | 1.28 ± 0.13 a | *** |
| Chlorogenic acid | 54.39 ± 4.81 b | 55.58 ± 4.76 b | 53.23 ± 3.76 b | 53.92 ± 5.44 b | 64.68 ± 5.16 a | ** |
| Cryptochlorogenic acid | 2.61 ± 0.48 ab | 3.25 ± 0.59 a | 2.79 ± 0.19 ab | 3.14 ± 0.29 a | 2.33 ± 0.48 b | ** |
| Total hydroxycinnamic acids | 63.13 ± 5.52 b | 65.32 ± 4.48 b | 62.04 ± 3.81 b | 63.59 ± 5.75 b | 73.95 ± 5.40 a | ** |
| Procyanidin B1 | 0.78 ± 0.19 a | 0.70 ± 0.19 ab | 0.93 ± 0.18 a | 0.84 ± 0.14 a | 0.48 ± 0.10 b | ** |
| Procyanidin B2 | 5.37 ± 0.99c | 7.43 ± 0.98 bc | 9.01 ± 0.96 b | 10.11 ± 1.42 b | 31.88 ± 4.16 a | *** |
| Catechin | 4.18 ± 0.49 | 4.11 ± 0.41 | 4.64 ± 0.55 | 4.32 ± 0.57 | 4.57 ± 0.70 | NS |
| Epicatechin | 2.65 ± 0.46 b | 3.17 ± 0.50 b | 3.26 ± 0.42 b | 2.89 ± 0.25 b | 4.03 ± 0.46 a | *** |
| Total flavan−3-ols | 12.99 ± 1.53c | 15.41 ± 1.17 bc | 17.84 ± 1.33 b | 18.16 ± 1.75 b | 40.96 ± 5.04 a | *** |
| Myricetin−3-galactoside | 6.35 ± 0.78 a | 5.76 ± 0.66 abc | 5.34 ± 0.65 bc | 4.82 ± 0.47c | 6.31 ± 0.31 ab | *** |
| Myricetin−3-glucoside | 3.89 ± 0.50 b | 4.13 ± 0.69 b | 4.60 ± 0.14 b | 5.84 ± 0.34 a | 3.96 ± 0.39 b | *** |
| Myricetin-pentoside | 0.96 ± 0.14 | 0.92 ± 0.16 | 1.05 ± 0.09 | 0.96 ± 0.12 | 0.82 ± 0.11 | NS |
| Myricetin-hexoside | 1.12 ± 0.15 | 0.94 ± 0.15 | 1.20 ± 0.31 | 0.89 ± 0.13 | 1.08 ± 0.21 | NS |
| Quercetin−3-rutinoside | 0.09 ± 0.01 | 0.10 ± 0.01 | 0.11 ± 0.01 | 0.10 ± 0.02 | 0.10 ± 0.01 | NS |
| Quercetin−3-galactoside | 2.52 ± 0.36 | 2.41 ± 0.17 | 2.39 ± 0.15 | 2.58 ± 0.35 | 2.71 ± 0.22 | NS |
| Quercetin−3-glucoside | 1.08 ± 0.17 a | 1.04 ± 0.14 a | 1.10 ± 0.20 a | 0.70 ± 0.09 b | 0.73 ± 0.07 b | *** |
| Quercetin−3-arabinopyranoside | 1.00 ± 0.09 ab | 1.15 ± 0.12 a | 1.16 ± 0.18 a | 0.93 ± 0.07 b | 0.87 ± 0.09 b | *** |
| Quercetin−3-acetylhexoside | 1.24 ± 0.10 ab | 1.26 ± 0.17 a | 1.42 ± 0.11 a | 1.42 ± 0.15 a | 1.04 ± 0.07 b | *** |
| Total flavonols | 18.27 ± 0.75 | 17.72 ± 1.49 | 18.37 ± 0.95 | 18.24 ± 0.91 | 17.63 ± 0.75 | NS |
| Total phenolic compounds | 94.38 ± 6.52 b | 98.45 ± 4.45 b | 98.25 ± 3.29 b | 99.99 ± 7.13 b | 132.5 ± 9.35 a | *** |
| | After harvest in 2023 | | | | | |
| | Black net | Red net | Yellow net | White exclusion net | Control | Significance |
| Neochlorogenic acid | 2.42 ± 0.50 | 2.24 ± 0.15 | 2.35 ± 0.42 | 3.04 ± 0.87 | 2.54 ± 0.44 | NS |
| 5-galloylquinic acid | 1.28 ± 0.13 ab | 1.11 ± 0.11 b | 1.17 ± 0.12 b | 1.38 ± 0.10 a | 1.19 ± 0.14 ab | ** |
| di-caffeoylquinic acid | 0.77 ± 0.09 | 0.77 ± 0.05 | 0.76 ± 0.10 | 0.88 ± 0.11 | 0.81 ± 0.13 | NS |
| p-coumaroylquinic acid | 0.75 ± 0.15 | 0.75 ± 0.09 | 0.75 ± 0.08 | 0.79 ± 0.16 | 0.78 ± 0.06 | NS |
| Chlorogenic acid | 33.57 ± 2.45 | 34.06 ± 3.88 | 35.23 ± 3.35 | 35.58 ± 3.18 | 36.83 ± 2.71 | NS |
| Cryptochlorogenic acid | 2.96 ± 0.64 a | 2.13 ± 0.35 b | 2.54 ± 0.50 ab | 2.61 ± 0.37 ab | 2.37 ± 0.21 ab | * |
| Total hydroxycinnamic acids | 41.75 ± 2.27 | 41.06 ± 3.95 | 42.80 ± 3.42 | 44.28 ± 4.51 | 44.52 ± 3.11 | NS |
| Procyanidin B1 | 0.82 ± 0.10 ab | 0.69 ± 0.13 bc | 0.66 ± 0.06 bc | 0.90 ± 0.14 a | 0.64 ± 0.09c | ** |
| Procyanidin B2 | 13.35 ± 1.60 a | 11.28 ± 0.96 bc | 11.38 ± 1.32 abc | 12.28 ± 1.23 ab | 9.86 ± 0.73c | *** |
| Catechin | 4.66 ± 0.32 | 4.35 ± 0.57 | 4.27 ± 0.26 | 4.73 ± 0.37 | 4.17 ± 0.39 | NS |
| Epicatechin | 3.07 ± 0.29 ab | 2.75 ± 0.40 b | 2.64 ± 0.47 b | 2.71 ± 0.40 b | 3.40 ± 0.44 a | * |
| Total flavan−3-ols | 21.91 ± 1.64 a | 19.08 ± 1.55 bc | 18.94 ± 1.77 bc | 20.62 ± 1.24 ab | 18.07 ± 0.49c | *** |
| Myricetin−3-galactoside | 6.16 ± 0.50 b | 4.59 ± 0.36c | 5.08 ± 0.67c | 4.95 ± 0.63c | 7.18 ± 0.56 a | *** |
| Myricetin−3-glucoside | 4.44 ± 0.55 b | 4.01 ± 0.42 b | 4.17 ± 0.71 b | 5.57 ± 0.33 a | 4.30 ± 0.68 b | *** |
| Myricetin-pentoside | 0.69 ± 0.11 | 0.65 ± 0.06 | 0.65 ± 0.04 | 0.58 ± 0.05 | 0.59 ± 0.13 | NS |
| Myricetin-hexoside | 1.05 ± 0.10 ab | 0.87 ± 0.09 bc | 0.85 ± 0.14 bc | 0.79 ± 0.11c | 1.14 ± 0.19 a | *** |
| Quercetin−3-rutinoside | 0.07 ± 0.01 | 0.07 ± 0.01 | 0.08 ± 0.00 | 0.08 ± 0.01 | 0.08 ± 0.00 | NS |
| Quercetin−3-galactoside | 2.51 ± 0.20 ab | 2.06 ± 0.15 b | 2.28 ± 0.23 ab | 2.57 ± 0.38 ab | 2.78 ± 0.54 a | * |
| Quercetin−3-glucoside | 0.62 ± 0.07 a | 0.38 ± 0.06c | 0.41 ± 0.06 bc | 0.44 ± 0.03 bc | 0.50 ± 0.09 b | *** |
| Quercetin−3-arabinopyranoside | 0.61 ± 0.06 abc | 0.62 ± 0.04 | 0.67 ± 0.07 a | 0.53 ± 0.04c | 0.54 ± 0.06 bc | *** |
| Quercetin−3-acetylhexoside | 0.80 ± 0.14 a | 0.87 ± 0.17 a | 0.85 ± 0.11 a | 0.55 ± 0.07 b | 0.80 ± 0.09 a | *** |
| Total flavonols | 16.95 ± 0.35 ab | 14.13 ± 0.98c | 15.05 ± 1.25 bc | 16.05 ± 1.08 abc | 17.91 ± 1.72 a | *** |
| Total phenolic compounds | 80.61 ± 3.45 | 74.26 ± 5.92 | 76.78 ± 4.10 | 80.95 ± 6.06 | 80.50 ± 4.96 | NS |

The average values with the standard errors, calculated from six replicates per treatment, are presented. Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$ (a-c).

[*] , $p < 0.05$;

[**] , $p < 0.01$;

[***] , $p < 0.001$; NS, not significant.

chlorophyll content under the black net is associated with an elevated chlorophyll *b* content, whose main role is light harvesting and transferring its energy to chlorophyll a (Johnson et al., 2005). The chlorophyll a/b ratio indicates the amount of shade/sun in which plants are located (2.2 – 4.2, shade–sun) (Fernández-Marín et al., 2018). This agrees with our results, where the lowest ratio was measured in the plants under the black and red photoselective nets, which also transmitted the highest light quantity.

Before the harvest in 2023, the highest violaxanthin and lowest zeaxanthin contents were found in the leaves under the black net, leading to the conclusion that those plants were least exposed to stressful conditions. The same conclusion was implied by the AZ/VAZ ratio. One of the main roles of β-carotene in plants is the protection of the photosystem from oxidative damage, which is most commonly associated with reactive oxygen species that are formed under extreme stress (Ledford and Niyogi, 2005). In our study, the β-carotene content differed significantly between the treatments in the second experimental year, with the highest contents measured in the plants under the nets. Antheraxanthin and zeaxanthin probably managed to remove excessive solar energy from the photosynthesis apparatus in the plants under the full-sun conditions; therefore, an increase in $\beta$-carotene content was not necessary.

The variation of the xanthophyll cycle pigments in blueberry leaves along the different phenophases of the plants has not yet been investigated and explained. Our results showed significant differences before and after harvest in antheraxanthin and zeaxanthin contents across all five treatments, with the highest values detected before harvest. Similar results were observed regarding the total chlorophyll content. Similar results were obtained in apple(Wünsche et al., 2005) and olive trees (Proietti, 2001). A decrease in total chlorophyll content in the leaves

**Table 9**
Significant differences in individual phenolic compounds in blueberry leaves between the two sampling dates in 2023 (before and after harvest) under the photoselective nets and the control treatment.

| | Black net | Red net | Yellow net | White exclusion net | Control |
|---|---|---|---|---|---|
| Neochlorogenic acid | ** | ** | *** | NS | ** |
| 5-galloylquinic acid | * | NS | NS | ** | * |
| di-caffeoylquinic acid | NS | NS | NS | * | *** |
| p-coumaroylquinic acid | NS | *** | *** | ** | *** |
| Chlorogenic acid | *** | *** | *** | *** | *** |
| Cryptochlorogenic acid | NS | ** | *** | * | NS |
| Total hydroxycinnamic acids | *** | *** | *** | *** | *** |
| Procyanidin B1 | NS | NS | ** | NS | * |
| Procyanidin B2 | *** | *** | ** | * | *** |
| Catechin | NS | NS | NS | NS | NS |
| Epicatechin | NS | NS | * | NS | * |
| Total flavan−3-ols | *** | *** | NS | * | *** |
| Myricetin−3-galactoside | NS | ** | NS | NS | ** |
| Myricetin−3-glucoside | NS | NS | NS | NS | NS |
| Myricetin-pentoside | ** | ** | *** | *** | ** |
| Myricetin-hexoside | NS | NS | * | NS | NS |
| Quercetin−3-rutinoside | * | *** | *** | * | *** |
| Quercetin−3-galactoside | NS | ** | NS | NS | NS |
| Quercetin−3-glucoside | *** | *** | *** | *** | *** |
| Quercetin−3-arabinopyranoside | *** | *** | *** | *** | *** |
| Quercetin−3-acetylhexoside | *** | ** | *** | *** | *** |
| Total flavonols | ** | *** | *** | ** | NS |
| Total phenolic compounds | ** | *** | *** | *** | *** |

Differences between treatments were determined using Tukey's test and were found to be significant at $\alpha < 0.05$.
* , $p < 0.05$;
** , $p < 0.01$;
*** , $p < 0.001$; NS, not significant.

after harvest reduced the absorption of incident light in order to protect the photosynthetic apparatus from photoinhibition and injuries, since carbon assimilation decreased with fruit removal (Jorquera-Fontena et al., 2016).

The synthesis of phenolic compounds is usually stimulated by high UV and visible light amount (Winkel-Shirley, 2002). Consequently, the shading of plants has been reported to reduce the contents of chlorogenic acid and flavonoids in blueberry leaves (Smrke et al., 2023). In line with this, our results showed that in the second year of the experiment before harvest, chlorogenic acid and, therefore, total hydroxycinnamic acids were highest under the control treatment (Klem et al., 2019), which is in agreement with one of the main functions of chlorogenic acid in leaves, namely, conferring protection from high UV radiation (Soviguidi et al., 2022). Similar results were obtained regarding flavan-3-ols. However, this function could be more relevant during the fruiting phenophase, as after harvest, the contents of chlorogenic acid and total phenolic compounds in the leaves were the same for all treatments. Other environmental factors besides light could affect the secondary metabolism of plants individually and simultaneously (Naikoo et al., 2019).

## 5. Conclusions

The quality and quantity of the light reaching the plants were altered by the photoselective nets. The net photosynthesis, leaf gas exchange, and chlorophyll fluorescence differed significantly between the treatments. In general, the plants in the control treatment exhibited the lowest values, while the results do not suggest a better performance of a certain net color. Regarding the chemical composition, higher values of compounds indicating stressful conditions were measured in the leaves under the control treatment, while the results regarding netting were inconclusive. Significant differences were also detected between the sampling dates before and after harvest, with higher values of net photosynthesis, pigments, and phenolics being measured before harvest. The current experiment obtained some promising results regarding the physiological processes and chemical composition of blueberry 'Bluecrop' leaves under full sun and black, red, yellow, and white photoselective nets before and after fruit harvest. In future experiments, the inclusion of other blueberry cultivars and other colors of photoselective nets is recommended. At the same time, higher amount of plants should be included.

## CRediT authorship contribution statement

**Jakopic Jerneja:** Writing – review & editing, Supervision, Conceptualization. **Laznik Ziga:** Writing – review & editing, Funding acquisition, Data curation. **Sircelj Helena:** Writing – review & editing, Validation, Methodology, Funding acquisition, Conceptualization. **Grohar Mariana Cecilia:** Writing – review & editing, Formal analysis, Data curation. **Veberic Robert:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Smrke Tina:** Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.eja.2025.127565.

## Data availability

Data will be made available on request.

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