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Storage Morphological and Biochemical Performance of Highbush Blueberries (*Vaccinium corymbosum* L.) Grown Under Photoselective Nets

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Abstract

The use of photoselective nets has gained interest in highbush blueberry production systems in recent years. Although some work has been conducted on their effects on the growth and development of the fruit, the performance of fruit grown under those nets after harvest has not been addressed yet. Here we focus on the performance of fruit grown under photoselective nets (exclusion, red, yellow, black) during long cold storage for the first time. The experiment was performed in two different years, monitoring morphological parameters, as well as primary and secondary metabolites using HPLC-MS and GC-MS. Minimal differences between treatments were noticed in fruit color, firmness and total soluble solids contents (TSS). In terms of fruit metabolism, two different periods were described during storage, with an inflection point at 14 days; in the first period, an increase in sugar content and a decrease in volatile content was observed, while after that, we found the opposite behavior. Overall, fruit grown under red nets showed the highest retention of secondary metabolites and the highest sugar/organic ratio, probably associated with a higher antioxidant capacity promoted by an increased red light proportion during the growth season. On the other hand, yellow nets showed the least favorable storage performance, as the light quality did not significantly improve the metabolism.

Keywords: 'Bluecrop'; anti-insect net; light modification; phenolics; volatiles; sugars; organic acids; HPLC-MS; GC-MS

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1. Introduction

Blueberries (*Vaccinium corymbosum* L.) are known worldwide as superfoods due to their high contents of health-promoting metabolites [1,2]. Among primary metabolites, they are especially low in sugar content, which is a clear advantage in diets with low-calories requirements [3]. At the same time, higher organic acids content regulates the sugar/organic acid ratio, resulting in flavors acceptable to consumers [3,4]. Among secondary metabolites, blueberries are rich in phenolic compounds, especially anthocyanins and quercetin derivatives, which significantly contribute to the antioxidative properties of the fruit [5]. A cocktail of volatile organic compounds significantly contributes to the fruit's typical aroma, such as ethyl acetate, ethyl 2-methylbutanoate and methyl 3-methylbutanoate among esters; (E)-2-hexenal, hexanal and 2-methylbutyraldehyde among aldehydes; linalool, 1-octen-3-ol and geraniol among alcohols; and linalool, β-caryophyllene oxide and eucalyptol among terpenes [6,7]. Both primary and secondary metabolite profiles vary with

many intrinsic (ripening, cultivar) and extrinsic (temperature, relative humidity, growing systems) factors [5,8–13].

Research interest has been shifting towards pre-harvest technologies that could improve not only the yield but also the content of such compounds. Lately, attention has been drawn to the use of different types of nets, which are today indispensable in blueberry production as protection from biotic [14,15] and abiotic [13,16,17] factors. They modify the quality and quantity of the light that reaches the plant [18], their photosynthetic activity [19], and consequently the development of the fruit [9,13,16]. Black nets, which are the dominant net type in commercial orchards, are completely opaque, which rather decrease light intensity without affecting light quality [20]. On the other hand, colored photoselective nets contain different chromophores that have a reflective function and filter only specific wavelengths of solar radiation [21]; red nets transmit light in the red and far-red part of the spectrum, while yellow nets transmit in the green, yellow, red and far red [22]. Under a white exclusion net, higher photosynthetic photon flux density (PPFD) was measured compared with the black net, since black nets absorb light by the same amount throughout the entire spectrum, whilst the exclusion net absorbs only ultraviolet radiation [9,16].

Blueberry is a seasonal fruit with a relatively short shelf life; up to 18 days in cold storage with 90–95% relative humidity and a non-modified atmosphere [23,24]. In order to maintain blueberry quality parameters (visual appearance, firmness, color, optimal sugar/organic acid ratio, high phenolics content) at a high level for a prolonged period of time, new pre-harvest production methods, such as the usage of the appropriate photoselective net, should be intensively tested.

The effect of different photoselective nets on fruit quality preservation during storage was already examined on mandarins [25], herbs [26] and various vegetable species, proving to be a useful pre-harvest tool to improve storage performance in length and fruit quality preservation, especially by improving secondary metabolism [27,28]. For blueberries, colored nets have been proven to influence fruit ripening, leading to differences in yield, as well as color and metabolite content, although the effect of each net color and type is variably evident depending on the season's climatic conditions [9,21,29]. However, no studies have been yet performed on the storage performance of blueberries that were produced under different photoselective nets. Here, we focus for the first time on the postharvest storage behavior of blueberry cv. 'Bluecrop' produced under different nets (exclusion net, red, yellow and black net), analyzing different fruit quality parameters at the morphological and metabolic levels. With this approach, we aim to understand how light conditions during the growing season influence fruit performance during storage, which contributes to the optimization of the storage length and the preservation of the fruit quality throughout its duration.

2. Materials and Methods

2.1. Plant Material and Experimental Setup

The experiment was conducted on blueberry cultivar 'Bluecrop' harvested at the Biotechnical Faculty in Ljubljana, Slovenia (latitude, 46°50′ N; longitude, 14°47′ E; altitude, 295 m a.s.l.) during two consecutive years, 2022 and 2023. Five treatments with six 2-year-old plants each, growing in 40 L pots, were established: no net, black, red, yellow and white exclusion net. Black net also serves as a control, since it is standardly used in blueberry commercial orchards. Standard irrigation and fertilization management was performed for the whole experiment set (for details see [9]).

2.2. Fruit Harvest and Storage Conditions

In 2022, fruit were harvested at full maturity (100% of dark skin coloration) and analyzed from all five established treatments, while in 2023, only fruit from plants covered with nets were included, due to a hailstorm event, which destroyed all of the fruit from plants without netting (control). Maturity parameters and metabolite content measurements at harvest have already been published and are here included in the results only as a reference for comparison with the subsequent storage period [9].

At harvest peak, approximately 100 g of fruit were randomly chosen from an average sample of each treatment and put into a plastic container. Three replicates were made for each treatment and were stored together in a polyethylene bag at 2 °C and 95% relative humidity. In 2022, maturity parameters (see Section 2.3) were measured on 5 fruit per treatment on the 18th, 29th and 37th day of storage, when visible fruit decay occurred (mold growth). In 2023, measurements and samplings were made every 7 days, while the storage was finished after 28 days due to mold growth. Weight and maturity parameters were measured at each sampling date on 5 fruit from each treatment. Additionally, twelve fruit per treatment were removed and stored at −20 °C for the extraction of primary and secondary metabolites (sugars, organic acids, phenolic compounds and volatile organic compounds).

2.3. Fruit Maturity Parameters

For both considered harvest/storage periods (2022 and 2023), standard fruit maturity parameters (color, firmness, total soluble solids or TSS) were evaluated to assess the fruit performance during storage. Blueberry peel color was measured once on each fruit on the fruit equator by a colorimeter (Konica Minolta CR-10 portable colorimeter, Tokyo, Japan), which measures color in a CIELAB tridimensional system: L^* (0—black to 100—white), C^* (color intensity, increasing with higher values) and h° (hue angle, 0–90° is red towards yellow, 90–180° is yellow towards green, 180–270° is green towards blue and 270–360° is blue towards red).

Individual fruit firmness was measured with a 1 mm diameter tip (digital penetrometer, TR, Turini, Italy; N). Total soluble solids (TSS) were measured by a digital refractometer (MA885 wine refractometer, Milwaukee Electronics, Szeged, Hungary).

2.4. Extraction and Analysis of Sugars, Organic Acids and Phenolic Compounds

In 2023, additional analyses of metabolic content were included to assess the performance of fruit during storage. Sugars, organic acids, and phenolic compounds were extracted from fruit at different time points during storage following previously established methods by using liquid chromatography and mass spectroscopy [9,10]. All chemicals used for the analyses were HPLC-MS grade, purchased at Sigma Aldrich (Staufen, Germany).

2.5. Analysis of Volatile Organic Compounds

The volatile profile of blueberry fruits was analyzed in 2023 using headspace gas chromatography-mass spectrometry (HS-GC-MS; Shimadzu GC-MS QP2020, Kyoto, Japan) equipped with a single-quadrupole MS and an electron impact (EI) detector. Frozen fruit samples were finely ground using liquid nitrogen and an analytical mill (IKA A11 basic, Staufen, Germany). Subsequently, 2 g of the sample, along with 10 µL of internal standard (3-nonanone, 2.7 mg/mL in acetonitrile), were placed in 20 mL glass vials and sealed tightly with screw caps containing PTFE silicone septa. Each treatment was performed in quintuplicate. The vials were then loaded into a Shimadzu AOC-20s autosampler (Kyoto, Japan) and incubated at 50 °C with continuous stirring at 250 rpm for 10 min. A 2000 µL headspace sample was injected into the GC port for 0.4 min at 250 °C in split

mode (1:10). The injection rate was set at 25 mL/min. Separation of the volatile compounds was carried out using a ZB-wax PLUS capillary column (30 m × 0.25 mm × 0.5 µm) from Phenomenex (Torrance, CA, USA), with helium as the carrier gas at a flow rate of 1 mL/min. The temperature program started at 45 °C for 3 min, followed by an increase to 150 °C at 4 °C/min, and then to 220 °C at 10 °C/min, where it was held for 5 min. The scan rate was 2.0 scans/second, with the interface and ion source temperatures set at 240 °C. Ionization was performed at 70 eV, and mass scanning was performed in the 50–500 m/z range. Volatile compounds were identified based on their retention indices (RIs) and comparison with commercial spectral libraries (NIST 11 and FFNSC 4), including compounds identified with an accuracy of more than 90%. Semi-quantification was conducted by considering the peak areas of each compound, as well as both sample and internal standard weights [9].

2.6. Statistical Analyses

Statistical analysis of the data was performed in R commander i386 4.3.2. Significant differences between different photoselective nets and different sampling dates were determined by one-way analysis of variance (ANOVA), using an HSD test ($\alpha < 0.05$). Significant differences are presented by different letters. Heatmaps were performed using Euclidean distance between treatments for each variable separately.

3. Results

3.1. Maturity Parameters

Maturity parameters of blueberry fruit (color, firmness, TSS) varied differently throughout the storage period during both years of the experiment (Tables 1 and 2). In 2022, despite initial differences between treatments, there was scarcely any difference in color lightness (L^*) within the same storage date, except after 29 days, when black, red and yellow nets shifted towards a darker color. In 2023, however, the performance was different, since the initial material was homogeneous, but significant differences between treatments were found later during most storage time points. After 28 days, differences in lightness were blurred. Similar results were acquired regarding color intensity (C^*) in 2022, in which, despite initial differences in fruit material, the storage homogenized its values between treatments in the first 2 weeks of storage. In 2023, slight significant differences were detected only after 30 days of storage between yellow and exclusion nets. Hue angle (h°) showed a different performance. In 2022, despite the initial homogeneity of the material, significant differences between treatments were found at all three storage time points, while no significance between treatments was detected during storage in 2023. Considering all variables together, the storage affected fruit color towards darker tones.

No significance between treatments was observed in fruit firmness in 2022, while in the second year of the experiment, differences were found only at harvest and after 7 days of storage, the highest values being found in fruit from black and exclusion nets at harvest, and from exclusion and yellow nets after 7 days in storage. The content of TSS in 2022 was initially significantly different between treatments, which was maintained for 18 days of storage. After that period, no difference in TSS was found. On the other hand, in 2023, significant differences in TSS between treatments occurred only after 21 days of storage, with the highest TSS content in fruit from black and exclusion nets.

Table 1. Blueberry peel color parameters (L^*, C^* and h°), fruit firmness and total soluble solids (TSS) from black, red, yellow and exclusion nets and control at harvest and individual storage duration in 2022.

		2022				
Treatment	**Storage Duration**	***L****	***C****	***h*°**	**Firmness (N)**	**Total Soluble Solids (°Brix)**
Black net	Harvest	30.76 ± 2.18 b AB	1.41 ± 0.55 b B	291.8 ± 21.35 A	0.22 ± 0.09 AB	11.43 ± 1.30 bc
Red net		33.66 ± 1.92 a	2.55 ± 0.58 a AB	278.6 ± 10.53	0.20 ± 0.07	10.97 ± 1.07 c
Yellow net		31.32 ± 2.72 ab A	1.69 ± 0.49 b A	290.5 ± 23.35 A	0.29 ± 0.15	11.73 ± 0.68 bc
Exclusion net		31.78 ± 2.69 ab	1.59 ± 0.71 b AB	266.8 ± 62.55 AB	0.22 ± 0.09	13.43 ± 1.62 a
Control		32.00 ± 2.22 ab AB	1.98 ± 0.53 ab AB	276.1 ± 10.68 B	0.23 ± 0.11	12.39 ± 1.13 ab
Significance		*	***	NS	NS	***
Black net	18 days	40.58 ± 20.72 A	3.27 ± 2.81 A	233.8 ± 8.92 b B	0.31 ± 0.11 A	11.22 ± 0.92 b
Red net		37.45 ± 17.70	2.97 ± 2.38 A	274.3 ± 7.90 ab	0.25 ± 0.06	11.63 ± 0.95 ab
Yellow net		30.91 ± 2.76 A	1.90 ± 0.92 A	281.5 ± 21.7 a A	0.24 ± 0.05	11.99 ± 1.69 ab
Exclusion net		35.65 ± 18.39	2.57 ± 2.63 A	295.8 ± 24.3 a AB	0.23 ± 0.08	12.81 ± 1.93 a
Control		38.19 ± 17.30 A	3.14 ± 2.28 A	276.7 ± 9.34 ab B	0.24 ± 0.09	12.37 ± 1.37 ab
Significance		NS	NS	**	NS	*
Black net	29 days	26.92 ± 2.78 bc B	1.51 ± 0.97 B	302.8 ± 28.76 a A	0.24 ± 0.11 AB	11.55 ± 1.48
Red net		28.48 ± 1.79 abc	1.67 ± 0.82 BC	303.5 ± 79.33 a	0.22 ± 0.08	11.25 ± 1.19
Yellow net		26.37 ± 2.41 c B	1.27 ± 1.05 AB	290.8 ± 25.57 b B	0.33 ± 0.14	11.31 ± 1.63
Exclusion net		29.19 ± 2.34 ab	1.51 ± 0.47 AB	286.4 ± 17.40 b B	0.30 ± 0.14	12.27 ± 2.11
Control		29.46 ± 1.89 a B	1.36 ± 0.59 BC	288.9 ± 23.77 b B	0.32 ± 0.15	12.09 ± 1.32
Significance		***	NS	**	NS	NS
Black net	37 days	30.60 ± 1.86 AB	0.73 ± 0.37 b B	308.1 ± 15.92 ab A	0.20 ± 0.07 B	11.29 ± 1.12
Red net		31.88 ± 2.28	1.20 ± 0.31 a C	289.4 ± 14.62 b	0.28 ± 0.06	11.02 ± 1.34
Yellow net		29.78 ± 1.23 A	0.87 ± 0.28 b B	299.6 ± 15.29 b A	0.22 ± 0.06	10.87 ± 1.19
Exclusion net		30.35 ± 2.19	0.95 ± 0.37 ab B	307.7 ± 27.83 ab A	0.27 ± 0.07	11.73 ± 1.43
Control		30.99 ± 1.93 AB	0.75 ± 0.27 b C	322.3 ± 26.84 a A	0.25 ± 0.08	11.16 ± 1.59
Significance		NS	**	**	NS	NS
Sign. black net		**	***	***	*	NS
Sign. red net		NS	**	NS	NS	NS
Sign. yellow net		***	**	***	NS	NS
Sign. exclusion net		NS	*	*	NS	NS
Sign. control		*	***	***	NS	NS

Data are means ± standard errors calculated from five replicates per treatment. Different lowercase letters (a–c) indicate significant differences between treatments (i.e., net colors) within the same storage duration, and uppercase letters (A–C) between storage durations within the same treatment (HSD test, $\alpha < 0.05$). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant. Sign., significance. Harvest data have been published before [9] and are here included only as a reference.

Table 2. Blueberry peel color parameters (L^*, C^* and h°), fruit firmness and total soluble solids (TSS) from black, red, yellow and exclusion nets at harvest and individual storage duration in 2023.

		2023				
Treatment	**Storage Duration**	***L****	***C****	***h*°**	**Firmness (N)**	**Total Soluble Solids (°Brix)**
Black net	Harvest	31.60 ± 2.18 A	2.59 ± 0.61	296.3 ± 12.78 B	0.16 ± 0.02 a A	10.80 ± 1.06
Red net		32.21 ± 1.89	2.44 ± 0.46 B	285.2 ± 16.55 C	0.13 ± 0.03 bc AB	10.57 ± 1.75 A
Yellow net		31.69 ± 2.56	2.41 ± 0.65 B	284.4 ± 17.08 B	0.12 ± 0.03 c B	10.46 ± 1.68 A
Exclusion net		33.27 ± 2.22 A	2.65 ± 0.94	299.6 ± 25.68	0.16 ± 0.05 a AB	9.98 ± 0.77
Significance		NS	NS	NS	**	NS
Black net	7 days	29.28 ± 1.32 b AB	2.17 ± 0.80	317.0 ± 17.84 AB	0.15 ± 0.00 b AB	9.91 ± 1.21
Red net		31.58 ± 2.28 ab	2.49 ± 0.82 AB	325.2 ± 21.81 AB	0.16 ± 0.05 b AB	9.80 ± 1.00 AB
Yellow net		33.53 ± 1.93 a	2.87 ± 0.65 AB	319.7 ± 11.81 A	0.21 ± 0.05 a A	8.97 ± 1.06 B
Exclusion net		31.80 ± 2.83 ab AB	3.50 ± 1.97	321.1 ± 25.04	0.17 ± 0.03 ab AB	9.80 ± 0.99
Significance		**	NS	NS	*	NS
Black net	14 days	28.37 ± 2.35 b B	1.81 ± 1.11	307.4 ± 27.50 AB	0.14 ± 0.04 AB	10.50 ± 1.26
Red net		31.56 ± 2.80 a	2.56 ± 0.54 AB	306.7 ± 26.84 BC	0.14 ± 0.06 AB	9.47 ± 1.42 AB
Yellow net		32.47 ± 1.74 a	2.92 ± 1.06 AB	308.0 ± 27.88 A	0.18 ± 0.06 A	9.27 ± 0.96 AB
Exclusion net		31.12 ± 0.86 a AB	3.17 ± 1.61	311.0 ± 32.93	0.18 ± 0.06 A	9.88 ± 0.82
Significance		**	NS	NS	NS	NS

Table 2. *Cont.*

Treatment	Storage Duration	2023				
		*L**	*C**	*h*°	Firmness (N)	Total Soluble Solids (°Brix)
Black net	21 days	28.29 ± 2.91 b B	2.64 ± 1.74	331.0 ± 24.97 A	0.17± 0.05 A	9.71 ± 1.72 a
Red net		32.51 ± 2.89 a	3.88 ± 1.44 A	345.0 ± 12.76 A	0.17 ± 0.03 A	8.38 ± 0.20 b B
Yellow net		32.12 ± 1.62 a	3.32 ± 1.93 AB	323.4 ± 12.71 A	0.16 ± 0.03 AB	8.38 ± 0.78 b B
Exclusion net		30.41 ± 1.60 ab B	2.44 ± 0.85	317.8 ± 28.18	0.16 ± 0.03 AB	9.63 ± 0.73 ab
Significance		**	NS	NS	NS	**
Black net	28 days	29.13 ± 1.89 AB	2.58 ± 1.16 ab	327.0 ± 22.92 A	0.12 ± 0.04 B	9.59 ± 0.82
Red net		30.69 ± 3.45	3.07 ± 1.83 ab AB	328.9 ± 22.44 AB	0.11 ± 0.03 B	9.02 ± 0.97 B
Yellow net		31.59 ± 1.76	3.91 ± 1.27 a A	330.3 ± 19.44 A	0.12 ± 0.04 B	8.64 ± 0.73 B
Exclusion net		31.22 ± 0.74 AB	2.10 ± 0.55 b	312.1 ± 26.34	0.11 ± 0.03 B	9.39 ± 0.39
Significance		NS	*	NS	NS	NS
Sign. black net		**	NS	**	*	NS
Sign. red net		NS	*	***	*	**
Sign. yellow net		NS	*	***	***	***
Sign. exclusion net		**	NS	NS	*	NS

Data are means ± standard errors calculated from five replicates per treatment. Different lowercase letters (a–c) indicate significant differences between treatments within the same storage duration, and uppercase letters (A–C) between storage durations within the same treatment (HSD test, $\alpha < 0.05$). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant. Sign., significance. Harvest data have been published before [9] and are here included only as a reference.

3.2. Primary Metabolites

Primary metabolism, comprising sugars and organic acids, was also affected by storage. The highest values of total sugar content (Table 3) were detected after 14 days of storage in fruit from black and red nets, which coincides with the content of glucose and fructose, the two most abundant sugars in blueberries. Despite initial differences in sugar content between treatments, 7-day storage equaled them, but longer storage duration accentuated the differences again, with fruits from yellow nets the ones with the lowest content.

Table 3. Sugar content (mg g^{-1} FW) in blueberry fruit from black, red, yellow and exclusion nets at harvest and during storage in 2023.

Treatment	Storage Duration	Sucrose	Glucose	Fructose	Total
Black net	Harvest	7.34 ± 0.38 c B	33.75 ± 1.74 a B	32.64 ± 1.53 a AB	73.73 ± 3.07 a C
Red net		9.46 ± 0.48 b C	28.60 ± 0.99 b C	27.95 ± 1.47 b C	66.00 ± 2.44 b C
Yellow net		10.96 ± 0.20 a BC	24.80 ± 0.69 c C	24.18 ± 0.81 c B	59.94 ± 1.40 c C
Exclusion net		9.95 ± 0.34 b CD	27.70 ± 0.79 b D	27.13 ± 1.08 b C	64.87 ± 1.86 b D
Significance		***	***	***	***
Black net	7 days	10.62 ± 0.96 A	32.41 ± 1.40 B	31.31 ± 2.46 ab B	74.34 ± 3.54 BC
Red net		12.35 ± 0.77 A	30.63 ± 1.73 BC	28.89 ± 3.21 b BC	71.87 ± 4.91 BC
Yellow net		10.63 ± 1.06 BC	31.14 ± 0.37 A	29.95 ± 0.37 b A	71.73 ± 1.30 AB
Exclusion net		11.32 ± 0.42 AB	32.22 ± 1.92 BC	36.00 ± 0.78 a A	79.54 ± 1.35 AB
Significance		NS	NS	*	NS
Black net	14 days	12.04 ± 0.89 A	37.84 ± 1.81 a A	35.23 ± 0.99 a A	85.11 ± 3.17 a A
Red net		11.66 ± 0.89 AB	34.66 ± 1.96 ab A	37.43 ± 1.90 a A	83.75 ± 0.92 a A
Yellow net		12.67 ± 0.46 A	31.43 ± 0.85 b A	30.66 ± 0.82 b A	74.76 ± 1.34 b A
Exclusion net		12.31 ± 0.48 A	36.34 ± 0.77 a A	34.82 ± 0.95 a A	83.47 ± 1.55 a A
Significance		NS	**	**	***
Black net	21 days	11.65 ± 0.49 ab A	35.32 ± 0.66 a AB	34.42 ± 0.88 a AB	81.34 ± 1.85 a AB
Red net		10.42 ± 0.14 c BC	32.88 ± 1.03 b AB	33.95 ± 1.26 a AB	77.24 ± 2.12 a AB
Yellow net		11.88 ± 0.35 a AB	29.08 ± 0.75 c B	30.37 ± 1.21 b A	71.32 ± 2.27 b AB
Exclusion net		10.67 ± 0.64 bc B	33.51 ± 0.27 ab B	33.61 ± 1.15 a A	77.78 ± 0.46 a BC
Significance		**	***	**	**

Table 3. *Cont.*

Treatment	Storage Duration	Sucrose	Glucose	Fructose	Total
Black net	28 days	8.68 ± 0.30 b B	33.52 ± 0.40 a B	35.36 ± 0.24 a A	77.56 ± 0.73 a BC
Red net		8.95 ± 0.43 b C	31.76 ± 1.68 ab ABC	33.62 ± 1.71 a AB	74.33 ± 3.25 ab B
Yellow net		10.30 ± 0.81 a C	27.88 ± 0.48 c B	29.51 ± 0.40 b A	67.69 ± 1.55 c B
Exclusion net		9.42 ± 0.17 ab C	29.79 ± 0.96 bc CD	30.87 ± 0.78 b B	70.08 ± 1.57 bc D
Significance		**	***	***	**
Sign. black net		***	***	**	***
Sign. red net		***	**	***	***
Sign. yellow net		*	***	***	***
Sign. exclusion net		**	***	***	***

Data are means ± standard errors calculated from five replicates per treatment. Different lowercase letters (a–c) indicate significant differences between treatments within the same storage duration, and uppercase letters (A–D) between storage durations within the same treatment (HSD test, $\alpha < 0.05$). * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS, not significant. Sign., significance. Harvest data have been published before [9] and are here included only as a reference.

Organic acid content was also affected by storage (Table 4). For each treatment separately, total organic acids content increased until 14 (exceptionally, 21 in the yellow net) days of storage, while after that period, it decreased to initial levels. Comparing the treatments, despite initial differences between them, storage time blurred them during the first 14 days. After that period, differences started to be more evident, with the red and exclusion nets the ones with the lowest content of organic acids.

After 28 days of storage, the highest total organic acid content was detected in fruit from the yellow and exclusion nets, which is mostly determined by citric acid, the most abundant individual organic acid.

Variations in sugar and acid content affected the sugar/acid ratio (Figure 1), especially in fruit from the red net, which increased with storage duration. In fruit from the yellow net, the sugar/organic acid ratio was the lowest and less variable during storage. In fruit from the exclusion net, the same performance was observed until 21 days of storage, while after that, it was restored back to the initial values. Fruit from the black net showed the opposite performance: it decreased during the first 21 days of storage but increased to initial values after 28 days.

Table 4. Organic acids content (mg g^{-1} FW) in blueberry fruit from black, red, yellow and exclusion nets during storage in 2023.

Treatment	Storage Duration	Citric Acid	Tartaric Acid	Malic Acid	Shikimic Acid	Total
Black net	Harvest	8.07 ± 0.62 c B	0.65 ± 0.07 B	0.79 ± 0.04 c CD	0.04 ± 0.004	9.55 ± 0.66 c D
Red net		9.32 ± 0.29 b AB	0.68 ± 0.07	0.87 ± 0.05 bc	0.04 ± 0.005	10.92 ± 0.40 b AB
Yellow net		11.36 ± 0.43 a	0.62 ± 0.17 B	0.96 ± 0.08 ab C	0.04 ± 0.005	12.98 ± 0.55 a
Exclusion net		11.02 ± 0.79 a A	0.73 ± 0.05	1.02 ± 0.10 a A	0.04 ± 0.005	12.80 ± 0.92 a A
Significance		***	NS	***	NS	***
Black net	7 days	9.72 ± 0.91 A	0.71 ± 0.10 AB	0.71 ± 0.05 c D	0.04 ± 0.006	11.18 ± 1.05 BC
Red net		10.59 ± 0.58 A	0.74 ± 0.05	0.94 ± 0.09 ab	0.04 ± 0.004	12.31 ± 0.46 A
Yellow net		11.09 ± 1.09	0.85 ± 0.11 AB	1.05 ± 0.09 a BC	0.03 ± 0.002	13.02 ± 1.18
Exclusion net		10.07 ± 0.46 AB	0.66 ± 0.04	0.81 ± 0.06 bc B	0.04 ± 0.003	11.57 ± 0.51 AB
Significance		NS	NS	**	NS	NS
Black net	14 days	11.24 ± 0.66 A	0.74 ± 0.12 AB	0.87 ± 0.09 b BC	0.04 ± 0.006	12.89 ± 0.68 A
Red net		10.68 ± 1.25 A	0.73 ± 0.13	0.94 ± 0.09 b	0.04 ± 0.002	12.40 ± 1.38 A
Yellow net		11.61 ± 0.53	0.85 ± 0.12 AB	1.15 ± 0.04 a AB	0.04 ± 0.001	13.66 ± 0.61
Exclusion net		10.76 ± 0.35 A	0.69 ± 0.02	0.96 ± 0.03 b AB	0.04 ± 0.002	12.44 ± 0.35 A
Significance		NS	NS	**	NS	NS

Table 4. *Cont.*

Treatment	Storage Duration	Citric Acid	Tartaric Acid	Malic Acid	Shikimic Acid	Total
Black net	21 days	10.39 ± 0.18 b A	0.75 ± 0.05 b AB	0.98 ± 0.06 b AB	0.03 ± 0.003	12.16 ± 0.29 b AB
Red net		8.89 ± 0.57 c B	0.58 ± 0.04 b	0.80 ± 0.04 c	0.04 ± 0.004	10.31 ± 0.61 c B
Yellow net		11.66 ± 0.58 a	1.16 ± 0.29 a A	1.17 ± 0.02 a AB	0.04 ± 0.002	14.04 ± 0.87 a
Exclusion net		9.03 ± 0.48 c B	0.66 ± 0.06 b	1.02 ± 0.07 b A	0.04 ± 0.003	10.75 ± 0.37 bc B
Significance		***	**	***	NS	***
Black net	28 days	7.58 ± 0.11 b B	0.90 ± 0.03 A	1.08 ± 0.03 a A	0.04 ± 0.003	9.60 ± 0.12 b CD
Red net		8.44 ± 0.35 b B	0.66 ± 0.03	0.93 ± 0.06 b	0.04 ± 0.003	10.07 ± 0.43 b B
Yellow net		10.45 ± 0.70 a	0.77 ± 0.12 AB	1.22 ± 0.05 a A	0.04 ± 0.003	12.47 ± 0.76 a
Exclusion net		9.91 ± 0.26 a AB	0.85 ± 0.16	1.10 ± 0.07 a A	0.03 ± 0.003	11.90 ± 0.48 a AB
Significance		***	NS	**	NS	***
Sign. black net		***	**	**	NS	**
Sign. red net		**	NS	NS	NS	**
Sign. yellow net		NS	***	**	NS	NS
Sign. exclusion net		***	NS	***	NS	**

Data are means ± standard errors calculated from five replicates per treatment. Different lowercase letters (a–c) indicate significant differences between treatments within the same storage duration, and uppercase letters (A–D) between storage durations within the same treatment (HSD test, $\alpha < 0.05$). ** $p < 0.01$; *** $p < 0.001$; NS, not significant. Sign., significance. Harvest data have been published before [9] and are here included only as a reference.

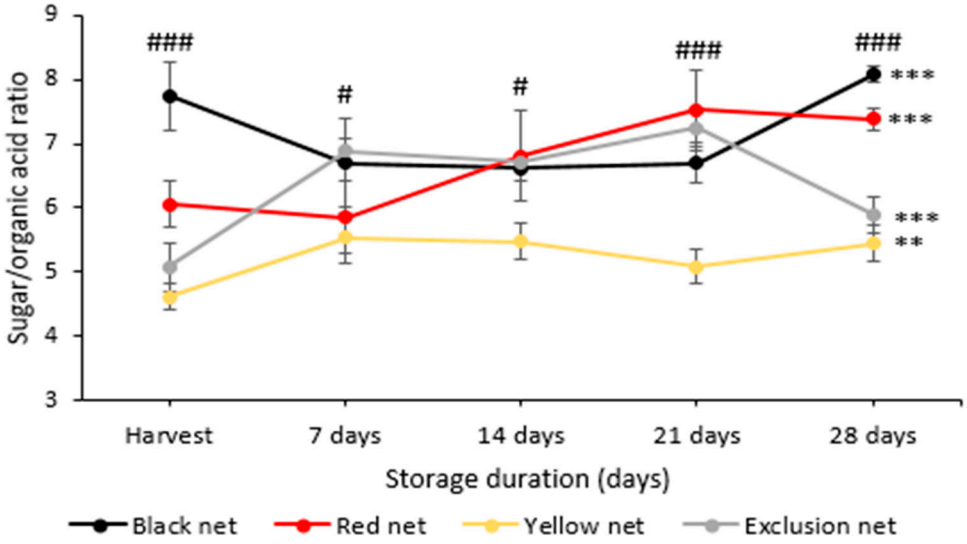

Figure 1. Sugar/organic acid ratio in blueberry fruit from black, red, yellow and exclusion nets at harvest and during storage in 2023. Data are means ± standard errors calculated from five replicates per treatment (HSD test, $\alpha < 0.05$). #, $p < 0.05$; ###, $p < 0.001$ (significant differences between treatments within the same storage duration). **, $p < 0.01$; ***, $p < 0.001$ (significant differences between storage durations within individual treatment). Harvest data have been published before [9] and are here included only as a reference.

3.3. Phenolic Compounds

The content of phenolic compounds showed a significant variation during storage, and from 14 days of storage forward, the highest contents were measured in fruit from the red net (Figure 2, Tables S6–S10).

After 7 days of storage, most of the individual flavonols (quercetin derivatives and isorhamnetin-3-*O*-hexoside) had their highest contents in fruit from the yellow net, after 14 days in fruit from the red net, and after 21 days from the red and yellow nets. After 28 days of storage, no difference in total flavonol content was detected between different treatments.

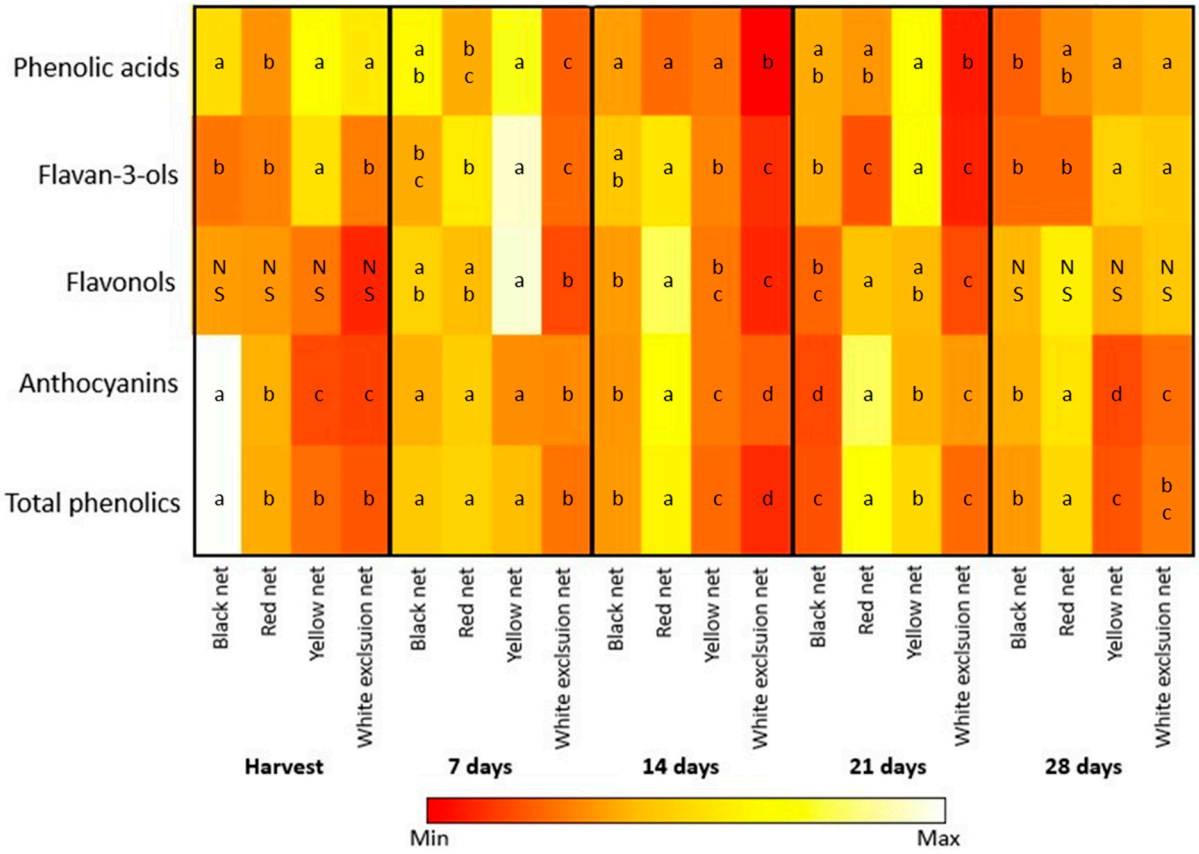

Figure 2. Heatmap for the contents of phenolic acids, flavan-3-ols, flavonols, anthocyanins and total phenolics in blueberry fruit from black, red, yellow and exclusion nets at harvest and during storage in 2023. Different letters (a–d) indicate significant differences between nets within each storage date (HSD test, $\alpha < 0.05$); NS, not significant. The color scale indicates variation in content within each phenolic group throughout all storage dates. Harvest data have been published before [9] and are here included only as a reference.

Among flavan-3-ols, three compounds were identified: two procyanidin dimers and epicatechin. At harvest, the highest contents of all three compounds were measured in fruit from the yellow net, while after 14 days, different treatments showed the maximum contents of individual compounds at each storage point. The exclusion net mostly exhibited the lowest contents, especially at harvest.

After 7 days of storage, the highest content of total phenolic acids was measured in fruit from the black and yellow nets, after 14 and 21 days also under the red net, and at the end of storage in fruit harvested from the red, yellow and exclusion nets. The prevailing compound among phenolic acids was chlorogenic acid, followed by nechlorogenic and cryptochlorogenic acids. The other nine compounds from this phenolic group presented only a smaller share of the total content. At harvest, the highest content of chlorogenic acid was measured in fruit from the yellow and exclusion nets, while under the black net, neochlorogenic acid had the highest total content.

Among anthocyanins, the most abundant compound was petunidin-3-*O*-glucoside, accounting for almost half of the total anthocyanins content. Seven other compounds were detected, although with lower contents. At harvest, fruit from the black net showed significantly the highest content of anthocyanins, followed by fruit from the red net. In contrast, yellow and exclusion nets had the lowest content, almost 70% lower than fruit from the black net. During storage, differences between contents were no longer so marked and fluctuated around 1000–2000 mg/kg FW. However, at all timepoints during storage,

fruit from the red net showed the highest anthocyanin content, followed almost always by fruit from the black net.

3.4. Volatile Compounds

According to our results, 17 volatile compounds were identified in 'Bluecrop' blueberries, which were classified into six groups: alcohols, aldehydes, hydrocarbons, ketones, lactones and monoterpenes. For most of the treatments, the total content of volatiles increased during storage. No significant difference in total volatile content was detected between treatments at harvest, despite significant differences in the majority of the individual compounds (Tables S1–S5). However, over the storage period, significant differences became evident. Fruit from the red net showed among the highest contents of total volatiles at all time points. Fruit from the black net was also frequently among the highest contents. After 28 days of storage, fruit from black and red nets showed the highest content, while fruit from yellow and exclusion nets showed almost a 50% lower content.

Regarding volatile groups, significant fluctuations in their content were detected throughout the storage duration for all treatments in 2023 (Figure 3). Aldehydes, which were the most abundant group of volatiles in the fruit, were the highest in fruit from the red net throughout the storage period. The black net reached it towards the end of the storage period, while staying low in fruit from yellow and exclusion nets. The lowest contents of aldehydes and, consequently, total volatiles, were reached after 21 days in fruit from the exclusion net (Table S4) and after 28 days in fruit under the yellow and exclusion nets (Table S5). Among aldehydes, (E)-2-Hexenal and hexanal contributed the most to the total aldehyde content (Tables S1–S5).

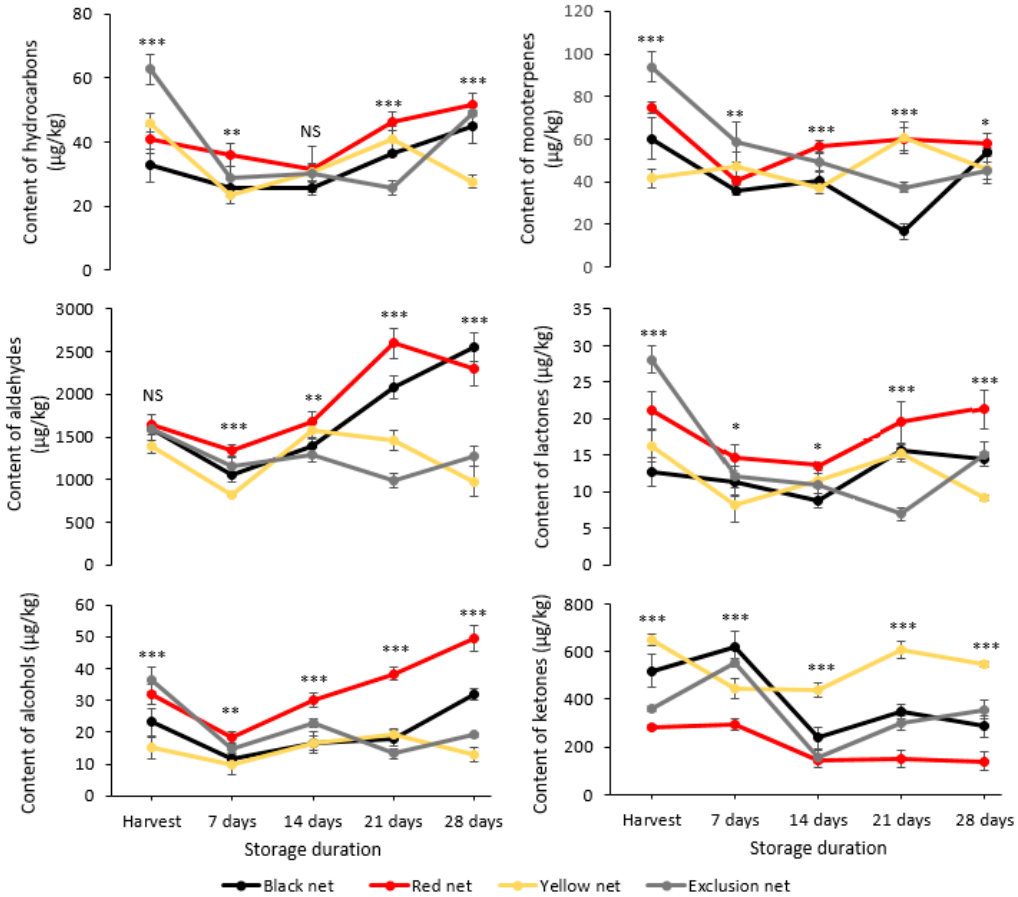

Figure 3. Contents of groups of volatile compounds in blueberry fruit from black, red, yellow and exclusion nets at harvest and during storage in 2023. Data are means ± standard errors calculated

from five replicates per treatment (HSD test, $\alpha < 0.05$). Asterisks indicate statistical differences between treatments at each sampling point. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; NS, not significant. Harvest data have been published before [9] and are here included only as a reference.

The opposite occurred in the second most abundant group of volatiles and ketones, and, consequently, in 2-Methyl-2-cyclopenten-1-one content, the prevailing compound among them. Their content was, significantly, the highest in fruit from the yellow net after 14 days of storage onwards (Figure 3).

4. Discussion

Color nets affect leaf performance directly, as they modify the light quality and quantity. Indirectly, they also affect fruit ripening on the plant, as a higher photosynthetic activity results in higher energy production, which can result in modified primary and secondary metabolism in the sink organs, such as the fruit [9]. Although even more indirectly, they can affect the performance of the fruit during storage, as the metabolism has different initial conditions to cope with oxidative stress related to senescence. Many changes at the morphologic and metabolic levels of blueberries have been described under different storage conditions [30–32].

Our results show that during storage, differences in the numeric analysis of color between different nets were significant, however minor and hard to detect with the naked eye, as was described before for other blueberry cultivars [30], as well as for other fruit species [25]. In blueberries, anthocyanins and flavanols are the phenolic compounds responsible for the fruit color. Our results show that the anthocyanin content changes only slightly during the initial stages of storage, coinciding with previous results [30], which explains the minor shifts in fruit color.

Primary metabolism also showed variability among nets. The initial differences in their content at harvest were a direct consequence of the differential photosynthetic activity during the growth season in response to different light quality under colored nets [9], which determined the amount of primary metabolites synthesized in the leaves and translocated to the sink organs. Interestingly, storage had a homogenizing effect on the primary metabolites, since fruit from almost all treatments had similar contents during storage. The most explicit exception was the fruit from the yellow net, which had the lowest sugar and the highest acid content both at harvest and during the whole storage period. Yellow nets typically transmit yellow and green light, which are the least efficient in the photosynthetic activity [9], which could determine a lower synthesis of primary metabolites that could be transported to the fruit.

Although during ripening organic acids and sugars are negatively correlated [9,21], that does not seem to be the case during storage. The sugar to acid (S/A) ratio, which is crucial for the fruit organoleptic properties and, consequently, the consumer's taste experience, varies significantly during the storage period [33]. During shorter storage times (up to 14 days), fruits from black and exclusion nets could be perceived as sweeter because of their higher S/A ratios, while after longer storage periods, black and red nets would probably be perceived as such. In practice, the suggested optimal storage length for cv. 'Bluecrop' is 14 days [23,34], which is supported by our results, since at that time point, the sugar content is the highest, with an intermediate S/A ratio.

Most of the work on blueberry storage shows a constant decrease in total soluble solids during storage [34], which was also confirmed in our results. However, the sugar content showed two periods: it increased during the first 14 days and then decreased. An increase in sugar content during the first hours of storage has already been proved in other short-term storage studies [35], and our data additionally demonstrates that this increase is

much longer. During storage, the respiration processes of the fruit continue, having simple sugars or organic acids as sources of energy, but due to the minimal content of starch in blueberries [36], it is difficult to explain the increase in simple sugar content through starch degradation. Although berries are considered non-climacteric fruits, as they do not ripen during storage, there have been some questions as to the accuracy of this statement [37]. Moreover, it was suggested that ethylene-dependent and ethylene-independent pathways coexist in fruits [38], blurring the clear distinction between climacteric and non-climacteric fruit. Our results in sugar content suggest that cv. 'Bluecrop' could have a metabolism more similar to climacteric fruit, with an initial decrease in respiration after harvest and a peak only after 14 days in storage. A similar performance during the first days of storage has also been observed in blueberry cv. 'O'Neal' and *Vaccinium ashei* [39,40]. However, it was stated that the climacteric nature of other fruit species can be cultivar-specific [41], which could explain the differences in fruit performance among blueberry cultivars [32,34]. It remains to determine the sources for the simple sugar increase. As the starch content in blueberry is minimal, other sources could be degrading and increasing simple sugars content, preferably those that also contribute to TSS, as it decreases during the first 14 days of storage. Potentially, one such source could be cellulose, which accounts for 3.5% of the total carbohydrate content in blueberry fruit [36]. Furthermore, additional metabolic pathway regulation could also be possible immediately after harvest, affecting the metabolite profile. Transcriptome analysis of *V. virgatum* blueberries during room temperature storage indicated that during the first 4 days up-regulation of genes prevails, while between 4 and 8 days, down-regulation takes over [42].

Plants accumulate phenolic compounds in order to protect their tissues from high solar and UV radiation [16]. This explains the differences between our treatments at harvest, as fruit from under black nets, which transmit higher levels of blue light compared to other nets [28], showed the highest content of phenolic compounds, especially anthocyanins [43]. Different light quality can affect the transcriptomic profile of the plant, particularly activating genes involved in the biosynthesis of flavonoids and flavonols [44] and, consequently, increasing their content [45], since these compounds have a protective function against UV radiation.

During the first week, storage time had a homogenizing effect on the fruit phenolic content, making phenolic content similar for all net colors, as it occurred with sugars. After that period, differences between nets were accentuated again, with fruits from the red net the ones with the highest phenolic content, especially anthocyanins and flavonols. Phenolics are highly susceptible to oxidative damage, and their fluctuations may be related to the efficiency of different antioxidant mechanisms [46]. Specifically, it has been proved that red light enhances different antioxidant enzyme activities, not necessarily related to phenolic compounds [47], reducing oxidative stress during storage of strawberries [48]. Under this premise, fruit from under the red net could initially have a higher pool of these antioxidant enzymes than fruit from under other net colors, which became relevant only after 14 days of storage, when oxidative processes became more notorious. Therefore, they could be more effective in protecting anthocyanins from oxidation than fruit from under other colored nets, leading to higher contents of these compounds. This could be the reason why fruit from under red nets showed the highest content of phenolic compounds at the end of storage despite not being the ones with the highest phenolic content at harvest [49].

Volatile organic compounds also contribute to the final fruit flavor. Although a decrease during storage was described before for other blueberry cultivars [50], our results showed that this may not always be the case. The total volatile content from fruit grown under different colored nets performed differently during storage, despite there were no differences at harvest between them. In line with the described performance of phenolic

compounds, two different periods were also detected during storage for the total volatile content. During the first 14 days of cold storage, fruit from all nets had similar values, while during the last 2 weeks, the content of total volatile compounds was higher in fruit from under black and red nets in comparison with yellow and exclusion, which corresponds with an increase in most volatile groups.

Different volatile groups showed different patterns and dynamics. During the first week of storage, only ketones content increased in fruit from under most net colors, while all other volatile groups decreased. These variations could be related to a regulation at the fatty acid metabolism level, since ketones are derived products of fatty acids and their derived long-chain aldehydes and alcohols, such as (*E*)-2-hexenal and 1-hexanol. Specifically, a decrease in the expression of lipoxygenase genes in *V. virgatum* blueberries during storage proved to be correlated with the decrease of C6 aldehydes and alcohols and the increase of ketones [42,51]. In fruit from under yellow nets, however, this does not seem to be the case, as ketones decrease also during the first weeks of storage, and it remains to be determined the reason for such a dynamic. During the last two weeks of storage, the presence of oxidative processes associated with respiration became evident in the increase of some groups that are usually oxidative products, such as alcohols and aldehydes. It has been shown in blueberries stored at room temperature that respiration-related pyruvate decarboxylase gene expression increased only after 6 days of storage [42], which would explain our results.

Considering individual volatiles, the most abundant compounds among aldehydes were (*E*)-2-Hexenal, with a green and cheesy aroma, and hexanal, which adds fruity tones [52]. They were the highest in fruit from the red net during the last 2 weeks of storage when the oxidation processes could be increased. In line with our results regarding phenolics, the antioxidant activity of the fruit from these treatments could prevent these compounds from further oxidation. As for the monoterpenes such as linalool, its content increased during the last two weeks of storage in fruit from the red and black nets, while in fruit from yellow and exclusion nets it was not detectable. This increase could be related to a gene up-regulation of linalool synthases that occurs in *V. virgatum* blueberries during room temperature storage, starting simultaneously with the respiration peak [42]. This suggests that linalool synthesis could be increased during blueberry storage, especially in fruit with a high antioxidant capacity that prevents its simultaneous degradation.

5. Conclusions

The metabolic analysis of blueberry performance during cold storage conducted in this research work highlighted the effect of pre-harvest conditions on storage performance. First, it showed that despite minimal observable changes at the morphological level, many metabolic processes differed distinctively between photoselective nets. Second, it showed that light quality during the growing season can affect fruit performance during storage significantly, with red and black nets the ones with the best performance regarding biochemical composition related to organoleptic properties. Third, results showed two distinctive metabolic periods during storage, with an inflection point at 14 days, after which oxidation processes could become more pronounced. Overall, our results suggest that this could be the optimal storage length, although fruit grown under red and black nets could maintain an acceptable quality longer. Specifically, the use of red nets could be promising, as the fruit showed the highest retention of secondary metabolites and the highest sugar/organic acid ratio, probably associated with a higher antioxidant capacity promoted by an increased red light proportion during the growth season. On the other hand, yellow nets seem to be less appropriate for blueberry management, as fruit produced under them showed the least favorable storage performance, as the light quality did not improve the metabolism

significantly. Further research should be conducted linking metabolic variability with tests of consumer acceptance.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/horticulturae11070713/s1, Figure S1: Average chromatograms of blueberries in (A) GC-MS and (B) HPLC-MS systems. Table S1: Individual volatile compounds contents (μg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net at harvest in 2023. Table S2: Individual volatile compounds contents (μg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 7 days in storage in 2023. Table S3: Individual volatile compounds contents (μg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 14 days in storage in 2023. Table S4: Individual volatile compounds contents (μg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 21 days in storage in 2023. Table S5: Individual volatile compounds contents (μg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 28 days in storage in 2023. Table S6: Individual phenolic compounds contents (mg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net at harvest in 2023. Table S7: Individual phenolic compounds contents (mg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 7 days in storage in 2023. Table S8: Individual phenolic compounds contents (mg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 14 days in storage in 2023. Table S9: Individual phenolic compounds contents (mg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 21 days in storage in 2023. Table S10: Individual phenolic compounds contents (mg/kg FW) in blueberry fruit from black, red, yellow and white exclusion net after 28 days in storage in 2023.

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