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# Delayed Harvest Reduces Postharvest Quality and Storability of Southern Highbush cv. Meadowlark and Rabbiteye Blueberry cv. Brightwell

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***Abstract.*** **Blueberries are produced worldwide due to their high demand and antioxidant benefits. Berry quality, including texture, flavor, and antioxidant properties, influence consumer preferences and marketability. Harvesting blueberries at shorter intervals is essential for maintaining fruit quality, including firmness and flavor, while also minimizing postharvest losses. This study investigated the effects of delayed harvests on the postharvest quality of 'Meadowlark', a highbush blueberry, and 'Brightwell', a rabbiteye blueberry, harvested from two different locations in South Georgia in 2022 and 2023. The treatments consisted of harvest dates, with two harvests in 2022 and three harvests in 2023, followed by three storage-duration treatments (7, 14, and 21 days of storage) to evaluate postharvest quality. Fruit firmness, berry diameter, color, total soluble solids, titratable acidity, berry damage (%), and anthocyanin concentration were assessed at harvest and following storage days. In both cultivars, harvest 1 showed higher fruit firmness and storability compared with harvests 2 and 3 in 2023. During storage, the decline in firmness was higher in harvests 2 and 3 compared with harvest 1. Fruit from the delayed harvests exhibited the highest percentage of berry damage both at harvest and after 21 days of storage. Anthocyanin concentration varied across cultivars and years, with berries from harvest 2 having a higher anthocyanin concentration at harvest in 2022 and 2023 in the Brightwell cultivar. Overall, this study highlights the importance of optimizing harvest dates to maintain the postharvest quality and shelf life of blueberries.**

Over the past decade, global blueberry production has more than doubled, making blueberries the second most widely cultivated berry crop in the United States (Kramer 2020; Protzman 2021). In 2023, Georgia produced a total of 29,900 tons of blueberries, with a farm gate value of $449.4 million, making blueberries the state's most valuable horticulture fruit commodity (University of Georgia 2022; US Department of Agriculture 2021). Blueberry fruit quality encompasses several parameters: color and firmness, as well as the concentrations of sugars, organic acids, aroma volatiles, and phenolic compounds (Gilbert et al. 2014; Molina et al. 2008). Firmness is a critical factor in consumer acceptance of fresh blueberries, directly affecting texture and postharvest quality (Blaker et al. 2014; Chiabrando et al. 2009; Giongo et al. 2013). Blueberry postharvest quality can be influenced by several factors such as climatic conditions, temperature, fruit maturity or ripeness, and harvest interval (Bergqvist et al. 2001; Di Vittori et al. 2018). All these parameters can affect the overall quality, thus affecting consumer acceptability and repeat purchasing of blueberries (Gilbert et al. 2014; Qu et al. 2017).

Blueberry color is a major factor influencing consumer choice (Gilbert et al. 2014; Saftner et al. 2008), cuticular wax contributes to the surface color by giving a lighter blue appearance, generally preferred by consumers (Chu et al. 2018; Yan et al. 2023). This wax layer plays a critical role in reducing water loss, delaying decay, and maintaining the sensory and nutritional quality of the fruit, which collectively extends its shelf life (Chu et al. 2018). However, the wax layer is susceptible to damage or removal during harvesting, packaging, and transport, which can diminish the fruit's visual appeal (Mukhtar et al. 2014). Furthermore, blueberry peel color is the primary index used to indicate fruit maturity and harvestability (Kalt et al. 1995; Lobos et al. 2014). Blueberry growers determine the optimal picking date, with 100% blue color being the most widely used criterion to facilitate commercial harvesting operations (Leiva-Valenzuela et al. 2013; Ribera-Fonseca et al. 2016). Nevertheless, blueberries can be visually identical (100% blue) but at different degrees of physiological maturity, because surface color is no longer a reliable indicator of physiological maturity once berries reach the full blue stage (Lobos et al. 2018). Thus, it is common that some blueberries are ripe while others may be overripe within a cluster. In this sense, several harvests with short intervals are needed to optimize fruit quality (Moggia et al. 2017; Lobos et al. 2018).

A major challenge in blueberry harvesting is that individual berries within the same plant and fruit cluster ripen asynchronously (Vander Kloet and Cabilio 2010). Variations in blueberry maturity at harvest can affect their postharvest quality and storage potential, with overripe berries being more prone to softening and decay during storage. On the contrary, berries that are underripe at harvest may not have the desired flavor or texture (Lobos et al. 2018). Therefore, to accomplish optimal blueberry quality and to maintain storage potential, it has traditionally been recommended that harvest intervals remain shorter, about every 3 to 5 d between successive harvests on a single plant to enhance shelf life (Lobos et al. 2018; Strik 2019). This strategy aims to preserve fruit quality throughout the supply chain.

Blueberry hand harvesting requires a high number of personnel, resulting in high expenditure for blueberry growers. Currently, the blueberry industry is facing labor shortages and high labor costs, leading to increased use of machine harvesters for the fresh market (Gallardo et al. 2018). The shift to mechanical harvesting has led blueberry growers to experiment with longer harvest intervals to avoid fruit yield losses. As a result, harvests

Table 1. Harvest schedule and frequency for 'Meadowlark' and 'Brightwell' blueberries in 2022 and 2023.

| | | | Harvest dates | | |
|---|---|---|---|---|---|
| No. | Cultivar | Year | Harvest 1[i] | Harvest 2[ii] | Harvest 3[iii] |
| 1 | Meadowlark | 2022 | 17 May | 24 May | No harvest |
| 3 | Brightwell | 2022 | 2 Jun | 9 Jun | No harvest |
| 4 | Meadowlark | 2023 | 18 Apr | 25 Apr | 1 May |
| 6 | Brightwell | 2023 | 2 Jun | 9 Jun | 16 Jun |

[i] Harvest 1 is the commercial harvest. It represents the initial harvest, conducted when the blueberries reach their peak commercial readiness.
[ii] Harvest 2 is the 7-d delayed harvest, which occurs 1 week after the commercial harvest.
[iii] Harvest 3 is the 14-d delayed harvest, which is conducted 2 weeks after the commercial harvest.

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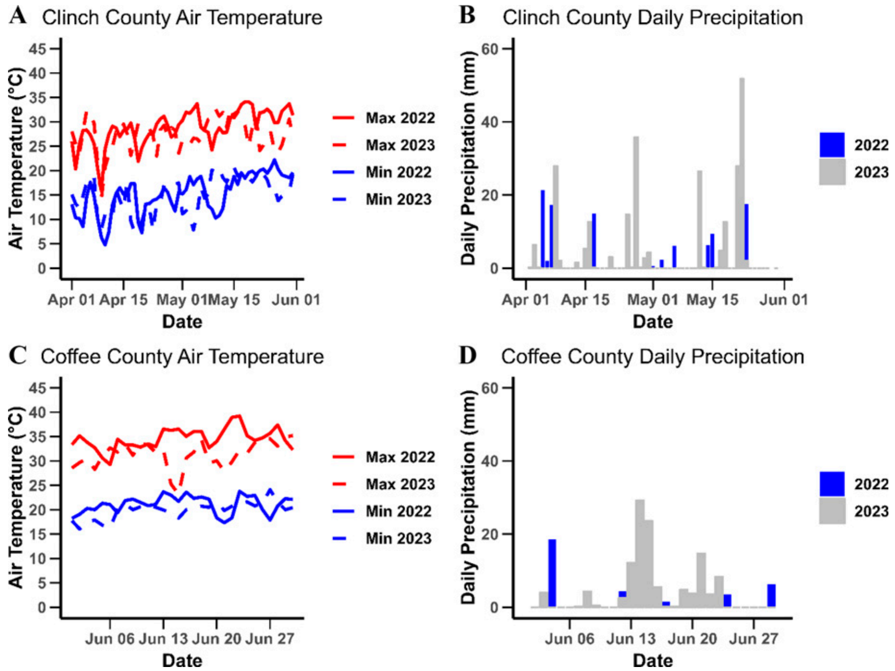


Fig. 1. Maximum and minimum daily air temperature (**A**) and daily precipitation (**B**) in 2022 and 2023 from 1 Apr to 31 May in Clinch County (Meadowlark cultivar), and maximum and minimum daily air temperature (**C**) and daily precipitation (**D**) from 1 Jun to 30 Jun in Coffee County (Brightwell cultivar). Weather data are from the University of Georgia Weather Network.

are performed in less-than-optimal intervals, which leads to a greater percentage of overly ripe fruit being harvested (Lobos et al. 2018; Olmstead and Finn 2014). This can negatively affect the quality of the packed fruit, especially when it is stored for extended periods (Strik 2019). In Georgia, quality issues such as leaking, splitting, wet stem scar, and tearing have been reported by growers in recent years (Ames ZR, personal communication). These fruit quality issues are characterized by rapid fruit softening and the subsequent leakage of juice from the stem wet scar at harvest, which increases the susceptibility of berries to postharvest decay, rendering them unfit for fresh market sales.

As a result, substantial financial losses due to rejected loads are often encountered in the local blueberry industry. The cause of these quality issues has not been previously investigated in Georgia. Therefore, this study aimed to investigate the effects of different harvest dates on the postharvest quality of southern highbush and rabbiteye blueberry cultivars with the hypothesis that delayed harvests are responsible for reduced berry quality and storability. The findings will provide valuable insights into the effects of harvest timing on the postharvest quality of blueberries, facilitating more efficient harvesting practices. Ultimately, this research will contribute to enhancing the economic sustainability of the blueberry industry by reducing postharvest losses and improving fruit marketability.

## Materials and Methods

*Experimental setup.* The research trial was conducted on two different commercial farms located in Georgia, using the cultivar Meadowlark in Clinch County (lat. 30°57′21.5″N, long. 82°40′50.7″W) and the cultivar Brightwell in Coffee County (lat. 31°30′31.7″N, long. 82°42′12.4″W) (Table 1). In 2022, two harvests ($n = 2$) were conducted, whereas in 2023, three harvests ($n = 3$) were carried out for both cultivars. The harvest dates were considered as treatments: harvest 1 (H1) was conducted on the date determined by the commercial producer for both cultivars. Harvest 2 (H2) took place 7 d after H1, using a set of plants that were left unharvested. Harvest 3 (H3), which was only conducted in 2023, occurred 14 d after H1. The experiment was conducted using a randomized complete block design with five blocks. Each block contained 30 plants, with 10 plants assigned to each treatment within the block. The treatments (harvest dates) were randomly assigned within each block to minimize variability and ensure robust statistical analysis. Fruit were hand-harvested in the morning and stored at 19 °C during transportation to the Vidalia Onion Research Laboratory (postharvest laboratory) in Tifton, GA. Upon arrival at the laboratory, after 1:00 PM, fruit were hand-sorted, packed into vented 170.1-g clamshells (one dry pint; Terra Box Florida LLC, Lakeland, FL), and stored at 1 °C and 85% relative humidity for up to 21 d. Fruit evaluations were done at harvest and subsequently after 7, 14, and 21 d ($n = 3$) following harvest (storage). Three clamshells per replication were evaluated at harvest and after 7, 14, and 21 d of cold storage, resulting in a total of 12 clamshells per replication per harvest. Overall, we had five total replications, resulting in 60 clamshells per harvest.

*Postharvest laboratory analysis.* The external color of the berry was measured using 25 berries per replication from the equatorial side perched with a colorimeter (CR-400 Chroma Meter; Minolta, Tokyo, Japan) calibrated with a white tile. The results were expressed as International Commission on Illumination (CIE) color space ($L^*C^*h$). The values of $L^*$ (lightness), $C^*$ (Chroma), and $h$ (hue angle) were used to report the color. A digital fruit firmness machine (FruitFirm® 500; CVM Inc., Pleasanton, CA) was used to assess firmness and berry diameter using the same 25 berries used for color measurements.

Berries with symptoms of splitting and juice efflux from the wet stem scar (pedicel scar) and splitting/peel tearing were visually assessed using 100 fruit samples per replicate. The collective damage from these symptoms was determined as a percentage and was calculated as follows:

$$\text{Berry damage (\%)}: \frac{\text{Number of oozing and splitting fruit}}{\text{Total number of tested fruit}} \times 100$$

Total soluble solids (TSS) concentration, titratable acidity (TA), and total anthocyanin concentration were measured using an aliquot of 100 g of berries blended with a tissue

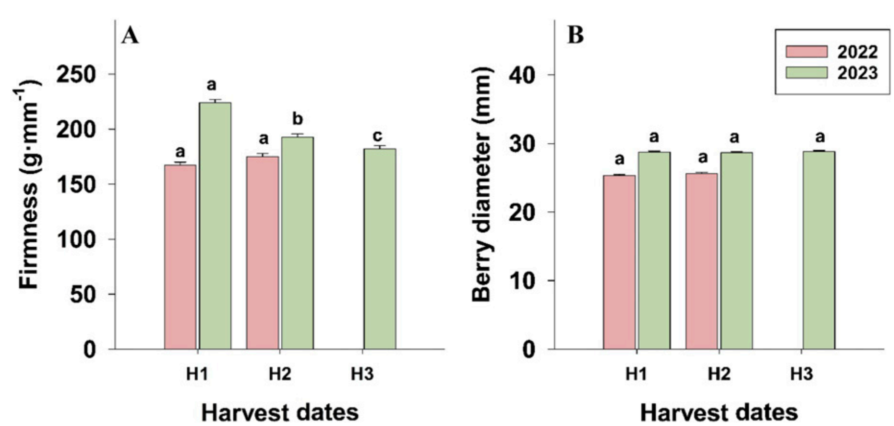


Fig. 2. Effect of different harvest dates on fruit firmness (**A**) and berry diameter (**B**) of 'Meadowlark' southern highbush blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

Table 2. Effects of harvest date on fruit quality of 'Meadowlark' southern highbush blueberry at each storage duration.

| Year | Harvest date[i] | Storage days | Firmness ($g·mm^{-1}$) | Berry diam (mm) | Color ($L^*$)[ii] | Chroma ($C^*$)[iii] | Hue ($h°$)[iv] | Total soluble solids (%) | Titratable acidity (%)[v] | Berry damage (%)[vi] | Anthocyanin concn ($mg·L^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2022 | H1 | 7 | 191 ± 2.9 a | 24.9 ± 0.2 b | 29.4 ± 0.3 a | 3 ± 0.2 a | 280.2 ± 2.4 a | 13.4 ± 0.3 b | 0.4 ± 0.1 a | 18.6 ± 1.9 b | 325.2 ± 25.5 a |
| | H2 | 7 | 147.1 ± 2.9 b | 25.9 ± 0.2 a | 29.9 ± 0.3 a | 2.5 ± 0.2 b | 279.7 ± 2.4 a | 14.5 ± 0.3 a | 0.3 ± 0.1 b | 35.8 ± 1.9 a | 401 ± 25.5 a |
| | H1 | 14 | 180.4 ± 2.8 a | 27 ± 0.2 a | 30.1 ± 0.3 a | 3.4 ± 0.2 a | 276.8 ± 0.8 b | 14.2 ± 0.3 a | 0.4 ± 0.1 a | 14.6 ± 1.6 b | 279.9 ± 23.6 b |
| | H2 | 14 | 141.4 ± 2.8 b | 26.2 ± 0.2 b | 30 ± 0.3 a | 3 ± 0.2 b | 281.4 ± 0.8 a | 15 ± 0.3 a | 0.3 ± 0.1 b | 31.4 ± 1.6 a | 383 ± 23.6 a |
| | H1 | 21 | 167.2 ± 2.9 a | 25.4 ± 0.2 b | 29.8 ± 0.3 a | 3.2 ± 0.2 a | 277.4 ± 1.1 a | 14 ± 0.3 b | 0.5 ± 0.1 a | 40.4 ± 1.9 b | 296.3 ± 23.5 a |
| | H2 | 21 | 136.1 ± 2.9 b | 25.8 ± 0.2 a | 30.1 ± 0.3 a | 3.1 ± 0.2 a | 279.9 ± 1.1 a | 15.1 ± 0.3 a | 0.4 ± 0.1 a | 48.2 ± 1.9 a | 328.1 ± 23.5 a |
| 2023 | H1 | 7 | 210.1 ± 2.9 a | 28.6 ± 0.2 b | 33.2 ± 0.3 a | 5.3 ± 0.2 a | 275.7 ± 0.9 a | 10.5 ± 0.2 c | 1.2 ± 0.1 a | 4 ± 2 c | 211.7 ± 20.8 a |
| | H2 | 7 | 183.9 ± 2.9 b | 29.3 ± 0.2 a | 32.4 ± 0.3 b | 5 ± 0.2 ab | 275.6 ± 0.9 a | 11.2 ± 0.2 b | 0.5 ± 0.1 b | 18.6 ± 2 b | 191.4 ± 20.8 a |
| | H3 | 7 | 176.2 ± 2.9 b | 28.7 ± 0.2 b | 32.3 ± 0.3 b | 4.9 ± 0.2 b | 277.7 ± 0.9 a | 12.3 ± 0.2 a | 0.4 ± 0.1 b | 57.6 ± 2 a | 218 ± 20.8 a |
| | H1 | 14 | 197.2 ± 3 a | 28.9 ± 0.2 ab | 33.1 ± 0.3 a | 5.3 ± 0.2 a | 274.2 ± 0.6 b | 10.6 ± 0.2 b | 0.9 ± 0.1 a | 6.4 ± 1.9 c | 215.3 ± 17.9 a |
| | H2 | 14 | 185.2 ± 3 b | 29 ± 0.2 a | 32 ± 0.3 b | 4.8 ± 0.2 b | 275.6 ± 0.6 ab | 12 ± 0.2 a | 0.5 ± 0.1 b | 19.2 ± 1.9 b | 226.3 ± 17.9 a |
| | H3 | 14 | 175.8 ± 3 c | 28.5 ± 0.2 b | 33 ± 0.3 a | 5.2 ± 0.2 a | 276.5 ± 0.6 a | 12 ± 0.2 a | 0.4 ± 0.1 b | 72.2 ± 1.9 a | 176 ± 17.9 a |
| | H1 | 21 | 193 ± 2.8 a | 28.8 ± 0.2 a | 32.4 ± 0.3 a | 5 ± 0.2 a | 275.3 ± 0.8 b | 10.4 ± 0.2 b | 0.8 ± 0.1 a | 5.8 ± 0.7 c | 184.4 ± 38.4 b |
| | H2 | 21 | 173.1 ± 2.8 b | 28.5 ± 0.2 a | 32.8 ± 0.3 a | 5.2 ± 0.2 a | 273.9 ± 0.8 b | 12.2 ± 0.2 a | 0.5 ± 0.1 b | 23.4 ± 0.7 b | 304.9 ± 38.4 a |
| | H3 | 21 | 156.9 ± 2.8 c | 28.7 ± 0.2 a | 32.6 ± 0.3 a | 5 ± 0.2 a | 278.7 ± 0.8 a | 12.2 ± 0.2 a | 0.5 ± 0.1 b | 74.4 ± 0.7 a | 205.1 ± 38.4 ab |

[i] The first harvest (H1) was conducted as the scheduled first harvest of the season by the grower, followed by two delayed harvests: one after 7 d (H2) and another after 14 d (H3).

[ii] The lightness parameter represents the brightness of a color, with 0 being black and 100 being white.

[iii] The chroma parameter indicates color intensity or saturation, with higher values for vivid colors.

[iv] The hue parameter represents the hue angle, describing the type of color (e.g., red, green, blue) on a 0 to 360° scale.

[v] Titratable acidity is expressed as the percent citric acid equivalent.

[vi] From each replication, 100 berries were evaluated.

The table shows the effects of harvest date on fruit quality of 'Meadowlark' at each storage duration (7, 14, and 21 d) in 2022 and 2023. Fruit were stored at 1 °C and 85% relative humidity. Parameters measured include firmness ($g·mm^{-1}$), berry diameter (mm), color ($L^*$, $C^*$, $h°$), berry damage (%), titratable acidity (%), total soluble solids (%), and anthocyanin concentration ($mg·L^{-1}$). The values are presented as means ± standard error for each parameter. Comparisons are made between harvest dates in 2022 (H1 and H2) and 2023 (H1, H2, and H3) within each storage duration, and means followed by different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

homogenizer (PowerGen 500; Fisher Scientific, Schwerte, Germany). The slurry was then centrifuged at 4 °C and 9000 rpm (Sorvall X4R Pro-MD; Thermo Scientific, Osterode, Germany). Subsequently, the supernatant was filtered using cheesecloth, stored in plastic vials, and frozen at −20 °C until analysis. TA was measured by titrating 6 mL of blueberry juice mixed in 50 ml of deionized water to pH 8.2 with 0.1 $mol·L^{-1}$ NaOH using a titrator (916 Ti-Touch; Metrohm AG, Herisau, Switzerland). TA results were expressed as percent citric acid equivalents. TSS was determined by placing an aliquot of blueberry juice on a digital refractometer (PAL-1, model 3810; ATAGO, Tokyo, Japan) while expressing results as a percentage.

Anthocyanin concentrations were measured using the pH differential method as described by Giusti and Wrolstad (2001). Blueberry juice was mixed separately with two buffers: potassium chloride (KCl) at a concentration of 0.025 M and a pH of 1.0 and sodium acetate ($CH_3COONa$) at a concentration of 0.4 M and a pH of 4.5. A microplate spectrophotometer (BioTek Epoch 2; Agilent Technologies, Winooski, VT, USA) was used to measure the absorbance of anthocyanins at 520- and 700-nm wavelengths using a blank cell filled with deionized water as a reference. The concentrations of total monomeric anthocyanins were calculated as follows:

$$\text{Total anthocyanin concentration } \left(\text{mg}\cdot\text{L}^{-1}\right): \frac{A \times \text{MW} \times \text{DF} \times 1000}{\varepsilon \times l}$$

where $A = (A_{520\,\text{nm}} - A_{700\,\text{nm}})_{\text{pH}\,1.0} - (A_{520\,\text{nm}} - A_{700\,\text{nm}})_{\text{pH}\,4.5}$, the molecular weight (MW) is 449.2 (cyanidin-3-glucoside), the dilution factor (DF) is 10, the molar absorptivity (0190) is 26,900, and the path length ($l$) is 1 cm).

*Statistical analyses.* All statistical analyses were conducted using JMP Pro 17 software (SAS Institute, Cary, NC). Two harvests were conducted in 2022 and three harvests were conducted in 2023 for both cultivars. For the comparative analysis, harvest dates (H1, H2, and H3) were treated as treatments, and a one-way analysis of variance was conducted, where the harvest date was modeled as a fixed effect, and replications were modeled as random effects. The analyses were conducted separately by year for measurements recorded at harvest and for each storage duration (7, 14, and 21 d) to assess the effect of harvest dates at each evaluated period. For 2022, only two harvest dates (H1 and H2) were analyzed, whereas for 2023, three harvest dates (H1, H2, and H3) were analyzed. The Fisher's least significant difference test was used for mean separation at a significance level of $\alpha = 0.05$.

A full factorial model (harvest date × storage duration) was used to analyze the interactions between harvest dates and storage periods. For post hoc comparisons, Tukey's honestly significant difference test was used. Statistical differences were indicated by different letters, with significance set at $\alpha = 0.05$, and the data from

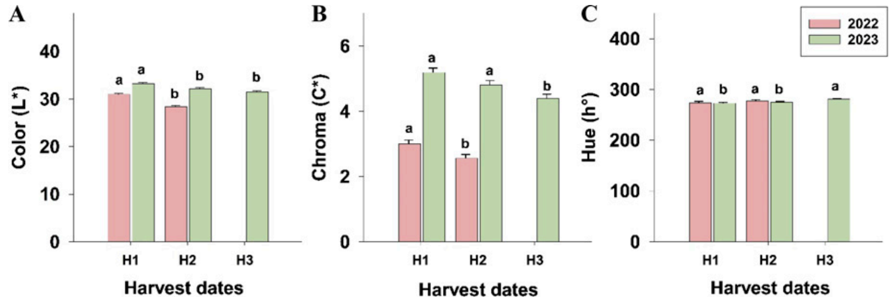


Fig. 3. Effect of different harvest dates on color parameters: $L^*$ (**A**), chroma ($C^*$) (**B**), and hue ($h°$) (**C**) of 'Meadowlark' southern highbush blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

this analysis are presented in the Supplemental Tables 1 and 2. Graphical representations of the results were generated using SigmaPlot 15.0 (Systat Software Inc., San Jose, CA, USA).

## Results

### Weather data from both locations

The average maximum air temperatures in Clinch County from early April to late May were higher in 2022 (26.7 and 31 °C, respectively) compared with 2023 (26.5 and 28.3 °C, respectively), indicating a warmer season (Fig. 1A). Precipitation was higher in Apr 2023 (4 mm) compared with Apr 2022 (1 mm), whereas May rainfall was similar in both years at 4 mm (Fig. 1B). In Coffee County, the maximum and minimum air temperature in June was also higher in 2022 (34.5 and 21.1 °C, respectively) compared with 2023 (31.4 and 20 °C, respectively) (Fig. 1C). Similarly, the precipitation data indicate that 2023 experienced more rainfall compared with 2022 (2.3 and 4 mm, respectively) (Fig. 1D). These observations highlight significant year-to-year variations in temperature and rainfall, which are crucial for understanding regional climate patterns.

### Changes in 'Meadowlark' berries with delayed harvest

*Berry firmness, diameter, and color.* 'Meadowlark' berries show a strong change in firmness with the harvest date, and generally, all berries decrease in firmness with storage (Supplemental Table 1). In 2022, the firmness of berries harvested at H1 was not significantly different compared with H2. In 2023, berries from H1 were significantly firmer at harvest compared with H2 and H3 (Fig. 2A). A similar result was obtained across all storage durations (7, 14, and 21 d), in which berries from H2 and H3 had significantly lower firmness (Table 2). The decline in berry firmness was more pronounced in H2 and H3 after 21 of storage (Supplemental Table 1). Berry diameter at harvest was not significantly affected by harvest dates in 2022 and 2023. However, during storage in 2022, H2 berries had a larger diameter compared with H1 berries after 21 d of storage (Fig. 2B). In 2023, H2 berries had a larger diameter compared with H1 berries after 7 d of storage, whereas no significant differences were found between harvest dates after 21 d of storage (Table 2).

In 2022, H1 berries had higher $L^*$ values compared with H2 berries at harvest (Fig. 3A). A significant difference in $L^*$ values was found during the storage duration (7, 14, and 21 d) (Table 2). In 2023, H1 berries had the highest $L^*$ values at harvest and during storage (after 7 and 14 d) compared with H2 and H3 (Fig. 3A and Table 2). Chroma ($C^*$) was significantly affected by harvest date; berries from H2 in 2022 and H3 in 2023 had significantly lower chroma values at harvest (Fig. 3B). During storage (after 7 and 14 d), berries from H1 had higher chroma values in 2022 and 2023, and chroma was not significantly different after 21 d of storage (Table 2). Hue angle ($h°$) was not significantly affected by the harvest date in 2022, but after 14 d of storage, H1 berries had a lower hue value (Fig. 3C and Table 2). In 2023, the hue was significantly higher in berries from H3 at harvest and after 21 d of storage (Fig. 3C and Table 2).

*Fruit composition.* Total soluble solids (%) were not significantly affected at harvest in 2022. In 2023, berries from H2 and H3 had significantly higher TSS values of 11.5% and 12% compared with 10.4% for H1 (Fig. 4A). During storage in 2022, H2 berries had higher total soluble solids after 7 and 21 d of storage, whereas there was no difference after 14 d of storage (Table 2). In 2023, H3 berries had higher TSSs compared with H1 after 21 d of storage (Table 2). TA was not significantly affected by the harvest date in 2022. In 2023, berries harvested at H1 exhibited the highest TA value of 1.3% at harvest, compared with 0.57% for H2 and 0.41% for H3 (Fig. 4B). During storage, H1 berries had higher titratable acidity compared with H2 after 7 and 14 d in 2022 (Table 2). In 2023, H1 berries also had higher TA compared with H2 and H3 throughout the storage duration (Table 2).

In 2022, the percentage of berry damage at harvest was significantly higher in H2 compared with H1 (Fig. 4C). In 2023, H3 berries had the highest percentage of damage, followed by H2 at harvest (Fig. 4C). The percentage of berry damage was consistently higher in H2 compared with H1 across all storage durations in 2022 (Table 2). In 2023,

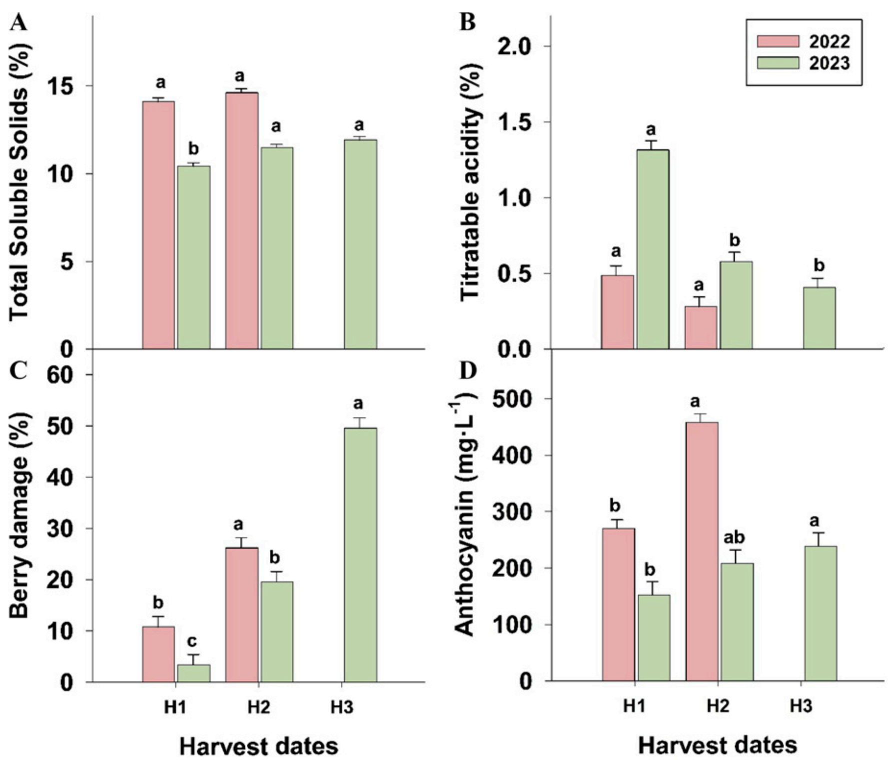


Fig. 4. Effect of different harvest dates on fruit quality parameters: total soluble solids (**A**), titratable acidity (**B**), berry damage (**C**), and anthocyanin concentration (**D**) of 'Meadowlark' southern highbush blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

berries from the H3 had the highest percentage of damage throughout the storage duration (Table 2). The berry damage significantly increased to 48.2% for H2 in 2022 and 23.1% and 74.4% for H2 and H3 in 2023 after 21 d of storage (Supplemental Table 1).

Total anthocyanin varied with harvest date and year. Anthocyanin concentration at harvest was significantly increased from 280 to 450 $mg{\cdot}L^{-1}$ between H1 and H2. In 2023, total anthocyanin was lower, at 180 $mg{\cdot}L^{-1}$, and increased slightly by H3 to 280 $mg{\cdot}L^{-1}$ (Fig. 4D). In 2022, H2 berries had higher anthocyanin concentrations compared with H1 after 14 d of storage. In 2023, berries from H1 had a significantly lower anthocyanin concentration compared with H2 after 21 d of storage (Table 2).

### Changes in 'Brightwell' berries with delayed harvest

*Berry firmness, diameter, and color.* In 2022 and 2023, berries harvested from H1 had significantly higher firmness at harvest compared with H2 and H3 (Fig. 5A). In 2022, H1 berries had significantly higher firmness compared with H2 throughout the storage duration. In 2023, berries from H3 had the lowest firmness throughout storage compared with H1 (Table 3). The firmness decline was more pronounced in H3 after 21 d of storage in 2023 (Supplemental Table 2). Berry diameter at harvest was not significantly affected in 2022. In 2023, H2 berries had a smaller diameter compared with H1 and H3 (Fig. 5B). In 2022, berries from H2 had a larger diameter throughout the storage duration. In 2023, berries from H3 showed a significant decline in diameter after 14 d of storage, whereas there were mixed results for the rest of the harvests during storage (Table 3).

In 2022, H2 berries had a higher $L^*$ value compared with H1 at harvest and after 7 d of storage (Fig. 6A and Table 3). In 2023, H3 berries had the highest $L^*$ values at harvest, compared with H2 and H1 (Fig. 6A). In 2023, H3 berries had the highest $L^*$ values compared with H1 and H2 throughout storage (Table 3). In 2022, the chroma value at harvest was not significantly different. In 2023, the chroma value was significantly lower for berries from H1 compared with H2 and H3 at harvest and after 14 and 21 d of storage (Fig. 6B and Table 3). In 2022, hue was significantly higher at harvest and after 14 d of storage in berries from H1 (Fig. 6C and Table 3). In 2023, berries from H1 had a higher hue value compared with H2 and H3 after 14 and 21 d of storage (Table 3).

*Fruit composition.* Total soluble solids (%) was significantly higher at harvest with 15.2% in berries from H1 in 2022. In 2023, TSS was not significantly affected by the harvest date (Fig. 7A). In 2022, H1 berries had higher TSS after 7 d of storage, whereas TSS did not change after 14 and 21 d of storage (Table 2). In 2023, H2 berries had higher TSS throughout the storage duration (Table 3). In 2022, TA declined from 1.5% to 1.2% at H2 (Fig. 7B). TA in 2023 was not significantly affected by the harvest date. In 2022, H1 berries had higher titratable acidity compared with H2 throughout storage. In 2023, H3 berries had higher TA after 7 d of storage, whereas H2 berries had higher TA compared with H3 after 14 d of storage (Table 3).

The berry damage was 7.2% higher in H2 compared with H1 at harvest in 2022 (Fig. 7C). In 2023, berries from H3 and H2 had a significantly higher percentage of damage with 21% and 25% berry damage at harvest compared with H1 (Fig. 7C). In 2023, berries from H3 and berries from H2 in 2022 showed the highest percentage of damage after 21 d of storage compared with H1 (Table 3).

In 2022 and 2023, anthocyanin concentration was significantly higher in berries from H2 (248 and 379 $mg{\cdot}L^{-1}$) compared with H1 and H3 (Fig. 7D). Anthocyanin concentration did not show any change during storage and was not significant in 2022. In 2023, H2 berries had significantly higher anthocyanin concentrations after 7 d of storage, and no significant difference was found after 14 and 21 d of storage (Table 3).

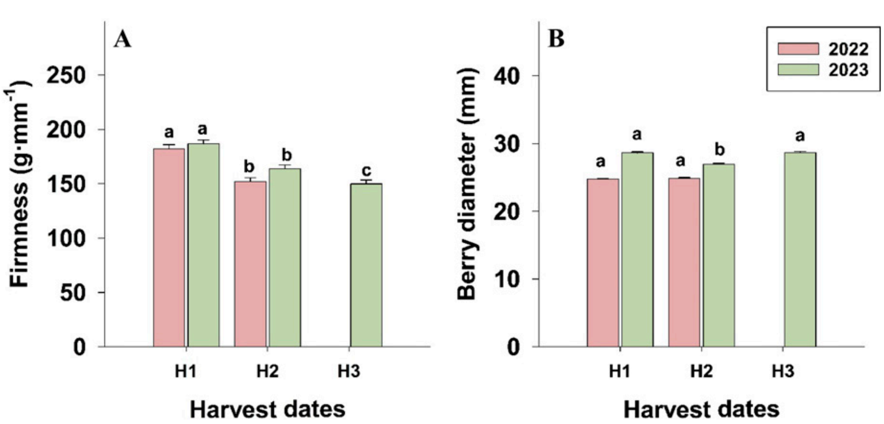


Fig. 5. Effect of different harvest dates on fruit firmness (**A**) and berry diameter (**B**) of 'Brightwell' rabbiteye blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

## Discussion

In the present study, three harvests were performed at 1-week intervals to evaluate the berry quality at harvest and the storage potential of blueberries collected at each harvest date. The findings aide preharvest decision-making as well as general postharvest handling recommendations for southern highbush cv. Meadowlark and rabbiteye cv. Brightwell blueberry growers in the southeastern United States. The importance of harvest timing and optimal maturity in blueberries relies on the rapid changes in fruit cell wall components due to increased enzymatic activity during ripening leading to changes in fruit texture (Chen et al. 2015; Giongo et al. 2013: Vicente et al. 2007). Higher berry firmness has been associated with denser harvest intervals, suggesting that overmature berries are softer both at harvest and during storage. This means that harvesting berries 3 to 6 d after reaching the 100% blue stage results in lower firmness (Sargent et al. 2006; Lobos et al. 2018; Strik 2019; Moggia et al. 2022). Delaying harvests reduced firmness in 'Meadowlark' and 'Brightwell', negatively affecting shelf life, as fruit firmness is an essential economic trait for long-distance shipping and extended shelf life. Strik (2019) reported a similar result in which a delayed harvest of 8 and 12 d resulted in a firmness decline in Aurora, Bluecorp, and Duke cultivars of blueberry. Harvesting blueberries at the appropriate maturity stage ensures fruit of higher quality with a longer shelf life (Rivera et al. 2022; Varaldo et al. 2022). The firmness of blueberries may vary significantly depending on the cultivar, as different genetic characteristics influence the texture and structural integrity of the fruit (Lobos et al. 2014). For instance, the storage life of the Elliott cultivar was negatively affected by berry maturity, whereas the Aurora and Liberty cultivars were not significantly affected by crop ripeness (Lobos et al. 2014). Harvesting blueberries at the appropriate maturity stage ensures fruit of higher quality with a longer shelf life (Rivera et al. 2022; Varaldo et al. 2022). Berry diameter results were inconsistent at harvest in 2023, likely due to high rainfall. However, during storage, berries from H2 in 2022 and berries from H3 in 2023 showed a larger diameter compared with H1 in the Brightwell cultivar. This observation aligns with stage III of the double sigmoid growth model, during which significant fruit volume expansion occurs, resulting in berries that were not only larger at harvest but also maintained a greater size after 21 d of storage (Godoy et al. 2008).

The color of blueberry fruit transitions from green to dark blue due to the accumulation of anthocyanins in the skin and pulp (Chung et al. 2016; Lin et al. 2018). In the CIE color space, $L^*$ represents the lightness of the color, with values ranging from 0 (black) to 100 (white), indicating how light or dark the color appears. Chroma ($C^*$) describes the intensity or saturation of the color, where higher values denote more vivid and saturated colors. Hue ($h°$) refers to the type of color on the color wheel, such as red,

Table 3. Effects of harvest date on fruit quality of ‘Brightwell’ rabbiteye blueberry at each storage duration.

| Year | Harvest date[i] | Storage days | Firmness ($g \cdot mm^{-1}$) | Berry diam (mm) | Color ($L^*$)[ii] | Chroma ($C^*$)[iii] | Hue ($h°$)[iv] | Total soluble solids (%) | Titratable acidity (%)[v] | Berry damage (%)[vi] | Anthocyanin concn ($mg \cdot L^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2022 | H1 | 7 | 176.7 ± 3.9 a | 23.9 ± 0.2 b | 28.1 ± 0.3 b | 2.7 ± 0.2 a | 264.8 ± 5.8 a | 15.2 ± 0.3 a | 1.4 ± 0.1 a | 29.4 ± 1.3 a | 287.4 ± 19.8 a |
| | H2 | 7 | 143.7 ± 3.9 b | 24.9 ± 0.2 a | 29.9 ± 0.3 a | 2.9 ± 0.2 a | 279.7 ± 5.8 a | 14.4 ± 0.3 b | 1.2 ± 0.1 b | 28 ± 1.3 a | 303.5 ± 19.8 a |
| | H1 | 14 | 180.2 ± 3.6 a | 23.9 ± 0.2 b | 29.1 ± 0.3 a | 2.6 ± 0.2 a | 295.8 ± 2 a | 14.5 ± 0.4 a | 1.3 ± 0.1 a | 26.4 ± 2.2 a | 233.5 ± 16.1 a |
| | H2 | 14 | 128.6 ± 3.6 b | 24.7 ± 0.2 a | 29.1 ± 0.3 a | 2.4 ± 0.2 a | 283.6 ± 2 b | 14.4 ± 0.4 a | 0.9 ± 0.1 b | 27.4 ± 2.2 a | 267.6 ± 16.1 a |
| | H1 | 21 | 185.9 ± 3.4 a | 23.8 ± 0.2 b | 29.1 ± 0.3 a | 2.4 ± 0.1 a | 278 ± 4.2 a | 14.4 ± 0.3 a | 1.2 ± 0.1 a | 35.2 ± 2.1 b | 230.6 ± 27.2 a |
| | H2 | 21 | 125.4 ± 3.4 b | 24.5 ± 0.2 a | 28.7 ± 0.3 a | 2.4 ± 0.1 a | 282.4 ± 4.2 a | 14.2 ± 0.3 a | 0.9 ± 0.1 b | 45.6 ± 2.1 a | 239.9 ± 27.2 a |
| 2023 | H1 | 7 | 159.9 ± 3.6 a | 26.7 ± 0.2 b | 28.3 ± 0.3 b | 2.8 ± 0.2 a | 283.4 ± 2.6 a | 12.9 ± 0.3 b | 1.2 ± 0.2 b | 24.4 ± 2.5 a | 198.7 ± 26.7 b |
| | H2 | 7 | 151.6 ± 3.6 a | 28 ± 0.2 a | 28.3 ± 0.3 b | 2.9 ± 0.2 a | 284.7 ± 2.6 a | 14.3 ± 0.3 a | 1 ± 0.2 b | 22.8 ± 2.5 a | 293.7 ± 26.7 a |
| | H3 | 7 | 135.8 ± 3.6 b | 9.9 ± 0.2 c | 30.6 ± 0.3 a | 3 ± 0.2 a | 269.9 ± 2.6 b | 13.1 ± 0.3 b | 1.7 ± 0.2 a | 17.8 ± 2.5 a | 181.6 ± 26.7 b |
| | H1 | 14 | 158.2 ± 3.6 a | 27.3 ± 0.2 a | 27.2 ± 0.3 c | 2.5 ± 0.2 b | 283.7 ± 3.2 a | 13 ± 0.3 b | 1.2 ± 0.2 ab | 24 ± 2.7 a | 287 ± 42 a |
| | H2 | 14 | 143.3 ± 3.6 b | 9.9 ± 0.2 c | 30.5 ± 0.3 b | 3.8 ± 0.2 a | 272.1 ± 3.2 b | 14.7 ± 0.3 a | 1.7 ± 0.2 a | 18.2 ± 2.7 a | 203 ± 42 a |
| | H3 | 14 | 120.99 ± 3.6 c | 14.1 ± 0.2 b | 32.5 ± 0.3 a | 3.8 ± 0.2 a | 271.3 ± 3.2 b | 13.1 ± 0.3 b | 1.1 ± 0.2 b | 24.8 ± 2.7 a | 198.9 ± 42 a |
| | H1 | 21 | 150.4 ± 3.6 a | 9.9 ± 0.2 c | 28.7 ± 0.3 c | 2.9 ± 0.2 b | 278 ± 1 a | 13.1 ± 0.3 b | 1.2 ± 0.3 a | 19.2 ± 2.1 b | 213.2 ± 34.5 a |
| | H2 | 21 | 160 ± 3.6 a | 12.6 ± 0.2 b | 30.8 ± 0.3 b | 4.2 ± 0.2 a | 275 ± 1 b | 14.7 ± 0.3 a | 1.7 ± 0.3 a | 21 ± 2.1 ab | 196.7 ± 34.5 a |
| | H3 | 21 | 127 ± 3.6 b | 14.6 ± 0.2 a | 31.6 ± 0.3 a | 3.9 ± 0.2 a | 274.7 ± 1 b | 13.7 ± 0.3 b | 1.2 ± 0.3 a | 25.8 ± 2.1 a | 281.3 ± 34.5 a |

[i] The first harvest (H1) was conducted as the scheduled first harvest of the season by the grower, followed by two delayed harvests: one after 7 d (H2) and another after 14 d (H3).

[ii] The lightness parameter represents the brightness of a color, with 0 being black and 100 being white.

[iii] The chroma parameter indicates color intensity or saturation, with higher values for vivid colors.

[iv] The hue parameter represents the hue angle, describing the type of color (e.g., red, green, blue) on a 0 to 360° scale.

[v] Titratable acidity is expressed as the percent citric acid equivalent.

[vi] From each replication, 100 berries were evaluated.

The table shows the effects of harvest date on fruit quality of ‘Brightwell’ at each storage duration (7, 14, and 21 d) in 2022 and 2023. Fruit were stored at 1 °C and 85% relative humidity. The parameters measured include firmness ($g \cdot mm^{-1}$), berry diameter (mm), color ($L^*$, $C^*$, $h°$), berry damage (%), titratable acidity (%), total soluble solids (%), and anthocyanin concentration ($mg \cdot L^{-1}$). The values are presented as means ± standard error for each parameter. Comparisons are made between harvest dates in 2022 (H1 and H2) and 2023 (H1, H2, and H3) within each storage duration, and means followed by different letters are significantly different at $P \leq 0.05$ based on the Fisher’s least significant difference test.

yellow, green, or blue, and is measured as an angle. The ripening and harvesting periods of southern highbush (‘Meadowlark’) and rabbiteye (‘Brightwell’) blueberries differ significantly in Georgia, reflecting variations in their genetic makeup and environmental requirements, with ‘Meadowlark’ typically harvested in April and May and ‘Brightwell’ typically harvested in June. ‘Brightwell’ berries exhibited higher lightness and chroma in delayed harvests (H2 and H3). On the other hand, higher hue values were observed in H1 berries, this indicates a shift toward a more vivid and bluish tone in the delayed harvests (H2 and H3). This change can likely be attributed to an increased wax deposition at maturity and the gradual wearing of the wax in overly mature fruits giving the different color values. Yan et al. (2023) reported that wax-removed treatment had lower lightness ($L^*$) and higher glossiness compared with berries with wax-covered treatment. On the other hand, berries from the cultivar Meadowlark showed a gradual decline in chroma values observed during delayed harvests (H2 and H3), which may be attributed to the increased deposition of epicuticular waxes, as indicated by previous studies (Chu et al. 2018; Konarska 2015; Saftner et al. 2008). The accumulation of cuticular wax (or fruit bloom) in blueberries increases throughout fruit development, resulting in a thicker cuticle at maturity, contributing to a less vibrant skin color (Chu et al. 2018; Trivedi et al. 2019). The decrease in $L^*$ values observed during this period likely reflects anthocyanin accumulation, aligning with findings reported in other blueberry cultivars (Chung et al. 2016; Matiacevich et al. 2013; Smrke et al. 2023; Spinardi et al. 2019). These findings underscore the importance of considering postharvest storage conditions and harvest timing to maintain the desired color qualities of blueberries, which are crucial for consumer acceptance and market value.

Blueberries undergo significant changes during maturation and ripening; biochemical changes occur as total soluble solids increase and titratable acidity decreases (Hassan et al. 2022; Li et al. 2020; Liu et al. 2019; Moggia et al. 2018). It has been found that harvesting ‘Duke’ blueberries 5 to 7 d after reaching 100% blue results in a higher accumulation of TSSs, with levels reaching 16.5% compared with 13.8% at the 100% blue stage (Moggia et al. 2016). This aligned with our present work, for ‘Meadowlark’ and ‘Brightwell’ in 2022 and 2023, when the TSS content was highest in berries from H2 and H3 at harvest and during storage. Similar results were reported by Strik (2019), who found that harvest intervals longer than 12 d resulted in 12% increased TSS content and 46% decreased TA content. In the present work, TA was higher in H1 berries and declined with delayed harvests (H2 and H3), consistent with results reported by other authors (Lobos et al. 2014; Moggia et al. 2018; Strik 2019). The inverse trajectories of sugars and organic acids in ripening fruit are a general phenomenon across fruit crops (Fawole

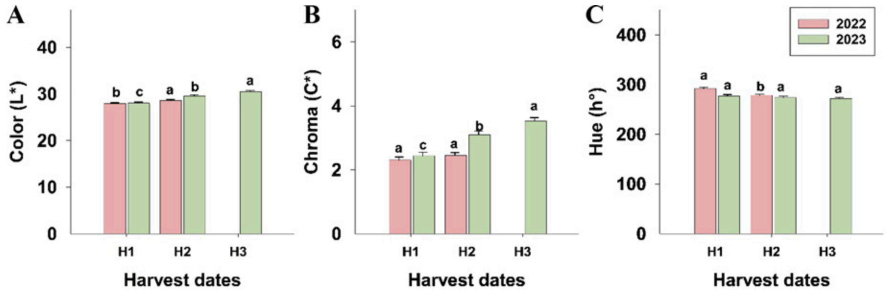


Fig. 6. Effect of different harvest intervals on color parameters: $L^*$ (**A**), chroma ($C^*$) (**B**), and hue ($h°$) (**C**) of 'Brightwell' rabbiteye blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

and Opara 2013; Strik 2019; Teka 2013). Overall, our study confirmed that the physicochemical properties of blueberry fruit vary significantly between commercial harvest stages and overripe berries.

The percentage of berry damage was also significantly higher in delayed harvests of H2 and H3 in the Brightwell and Meadowlark cultivars in both years. This increase is likely attributed to the accumulation of overripe fruit resulting from the extended harvest dates, because overripe berries typically exhibit lower firmness at harvest and throughout storage, making them more susceptible to damage compared with those harvested at optimal maturity (Lobos et al. 2018). This is supported by another study stating that fruit from the advanced maturity stage (delayed harvests) have higher decay incidence (Miller et al. 1988). Furthermore, the variation in anthocyanin concentration based on harvest time and storage duration observed in our study was aligned with findings by Mallik and Hamilton (2017), who investigated the effect of harvest date and storage conditions on the quality and health-related chemistry of wild blueberries native to NW Ontario, Canada, and found that late harvest and low-temperature storage significantly increased the total phenol and anthocyanin contents for most genotypes. This observation is consistent with the present work, in which berries from H2 in 2022 and 2023 and H3 berries from the Meadowlark cultivar had higher anthocyanin concentrations. Kalt et al. (2003) found that total anthocyanin concentration was substantially higher in the fruit of advanced maturity stages, whereas the phenolic content and antioxidant capacity were lower in overmature fruit. The blueberry cultivars Brigitta and Nelson resulted in decreased anthocyanin from the 100% blue stage to the fully ripe stage. This suggests that the concentration of anthocyanin, along with other beneficial compounds, might increase during fruit maturation. However, the concentrations of anthocyanin and phenolic content can subsequently decrease when the fruit is overmature (Kalt et al. 2003).

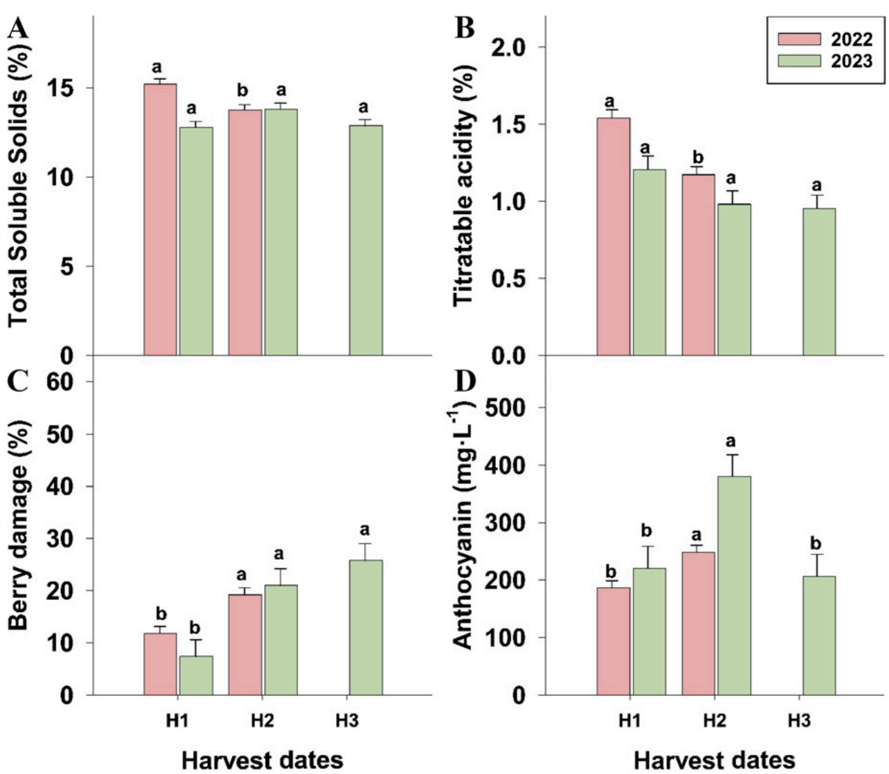


Fig. 7. Effect of different harvest dates on fruit quality parameters: total soluble solids (**A**), titratable acidity (**B**), berry damage (**C**), and anthocyanin concentration (**D**) of 'Brightwell' rabbiteye blueberry in 2022 (pink) and 2023 (green) at harvest. The fruit were harvested on different dates (first commercial harvest: H1; two delayed harvest treatments: H2 and H3). The means followed by the different letters are significantly different at $P \leq 0.05$ based on the Fisher's least significant difference test.

## Conclusions

Based on our 2-year study, delayed harvests influenced the postharvest quality of southern highbush cv. Meadowlark and rabbiteye cv. Brightwell blueberries. Delayed harvests resulted in greater TSS accumulation in 'Meadowlark' berries in 2023, which may be beneficial for flavor. However, delayed harvests decreased fruit firmness initially and during storage for both cultivars. In particular, firmness declined more significantly in delayed harvests after a 21-d storage period. Additionally, the percentage of berry damage was significantly higher in delayed harvests (H2 and H3). Maintaining shorter harvest intervals for blueberries cultivated in warm and humid environments, in conjunction with optimized storage conditions, is essential for preserving the postharvest quality and extending the shelf life. Future studies should focus on implementing harvest intervals shorter than 7 d to better preserve the postharvest quality of fresh-market blueberries.

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