Cold Storage Performance and Postharvest Quality Evaluation of Four Blackberry Cultivars Commercially Grown in North Florida

Muneer Rehman and Nazneen Qureshi

Department of Energy, Environment and Climate Action (DEECA), Horticulture Production Sciences, Agriculture Victoria Research, Tatura SmartFarm, 255 Ferguson Road, Tatura, VIC 3616, Australia; and Horticultural Sciences Department, North Florida Research and Education Center, University of Florida/IFAS, Quincy, FL 32351, USA

Muhammad Nadeem

Horticultural Sciences Department, North Florida Research and Education Center, University of Florida/IFAS, Quincy, FL 32351, USA; and Institute of Food Science and Nutrition, University of Sargodha, Sargodha, 40100, Pakistan

Angelos Deltsidis

Department of Horticulture, University of Georgia-Tifton Campus, Tifton, GA 31793, USA

Mahmoud F. Seleiman

Department of Plant Production, College of Food and Agriculture Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Saudi Arabia

Muhammad Adnan Shahid

Horticultural Sciences Department, North Florida Research and Education Center, University of Florida/IFAS, Quincy, FL 32351, USA

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Abstract. The study focused on assessing the cold storage response of four blackberry cultivars, Osage, Traveler, Freedom, and Ponca, grown in North Florida. Blackberries are a highly perishable fruit, which limits postharvest life and creates economic difficulties for the growers. After harvesting, the fruits were stored at 1 °C with 85% to 90% relative humidity for durations of 7, 14, and 21 days. The assessment of postharvest quality involved multiple variables, including color metrics (L*, a*, H°, and total color), weight loss, firmness, respiration rate, soluble solids content (SSC), titratable acidity (TA), the ratio of SSC to TA, leakage, mycelium growth, red drupelet reversion (RDR), and marketability index (MI). Results showed significant differences among cultivars and storage times for all quality traits. Notably, 'Osage' maintained superior color, with the highest L* and lowest a* values, and exhibited lower respiration rates compared with the others. It also showed the highest firmness, SSC, and SSC/TA ratio, along with reduced leakage, mold growth, and RDR. Overall, 'Osage' was more effective at maintaining fruit color and quality during cold storage, demonstrating less weight loss, respiration, leakage, mold development, and RDR, while maintaining higher firmness, SSC, and SSC/TA ratios throughout all storage periods. These findings provide valuable guidance for growers and supply chain stakeholders in selecting blackberry cultivars with better postharvest performance, ultimately supporting longer shelf life, reduced losses, and improved marketability in North Florida's blackberry industry.

Blackberries (*Rubus* spp.), belonging to the Rosaceae family, are nutrient-dense fruits (Hummer et al. 2019). Their popularity has recently risen globally because of their distinct flavor, health benefits, and rich phytochemicals like anthocyanins, ellagic acid, and tannins (Beattie et al. 2005). Research suggests that blackberries may offer health benefits, including antioxidant activity, anti-inflammatory effects, and anti-ageing properties

(Gil-Martínez et al. 2023; Perkins-Veazie et al. 1999). Blackberries have become a significant berry crop worldwide, with cultivation expanding in North America, Europe, Asia, and South America (Strik et al. 2007). In the United States, blackberries are the fourth most important berry crop commercially. Primarily, most cultivation occurred in western states like California and Oregon (Strik et al. 2008) but expanding consumer demand has boosted

growth in southeastern regions. For example, blackberry farming in Florida grew from 64 acres in 2007 to 702 acres in 2022, especially in Central and North Florida. Because of their fragile skin, blackberries are highly perishable and are marketed both fresh and processed (Türkben et al. 2010). Their shelf life varies depending on the cultivar and genetic traits (Kim et al. 2015). Some cultivars can be stored at 5 °C for 12 to 15 d, while certain varieties can last up to 21 d at 2 °C (Perkins-Veazie et al. 1996, 1999). Generally, storing blackberries above 5 °C for more extended periods accelerates respiration, leading to faster spoilage and weight loss, which reduces shelf life (Joo et al. 2011; Perkins-Veazie et al. 1999).

Postharvest factors cause rapid changes in moisture and nutrients, which, as a result, encourage microbial entry and lead to decay. Consequently, most blackberries intended for fresh markets become unmarketable within 2 or 3 d (Hardenburg et al. 1986). Because blackberries are non-climacteric fruits, harvesting is recommended only when fully ripened (Benichou et al. 2018). Common physiological disorders that lead to rejection during commercialization include RDR, leakiness, and mycelium growth (Lawrence and Melgar 2018). Notably, RDR is a postharvest disorder occurring during cold storage and the supply chain, which diminishes the fruit's cosmetic appeal and reduces profit for growers. In addition, the breakdown of anthocyanins causes the berry color to change from black to red (McCoy et al. 2016; Perkins-Veazie et al. 1996). Transportation vibrations further influence color change and overall fruit integrity (Strik et al. 2007; Edgley et al. 2019). The reversion phenomenon is also more pronounced when fruits are harvested at warmer temperatures (McCoy et al. 2016). Fungal growth and leakage are other undesirable physiological issues. The thornless blackberry cultivar is susceptible to fungal diseases (Strik et al. 2007) and improper handling can cause the fruit to lose its marketability within 48 h of harvest (Samtani and Kushad 2015). Cold storage is a standard worldwide method for extending shelf life, but storing fruit at 0°C can still result in decay and leakage (Duan et al. 2020). Maintaining a blackberry shelf life remains a significant challenge for growers and marketers. Various postharvest strategies, such as bio-coatings, bio-containers, ozone treatment, and cold storage, have been used to improve shelf life (Bersaneti et al. 2021; Hadadinejad et al. 2018). Producers widely use cold storage to maintain quality, as low temperatures slow metabolism and inhibit fungal growth (Antunes et al. 2003; Perkins-Veazie et al. 1993). This approach helps growers stay competitive and enhance profitability (Basiouny 1995). Extending the shelf life of blackberries is an important industry goal due to their rapid postharvest deterioration. The present study does not test storage interventions directly; rather, it characterizes cultivar differences in key postharvest traits (weight loss, firmness, color, respiration, leakage, and decay) under cold storage. These

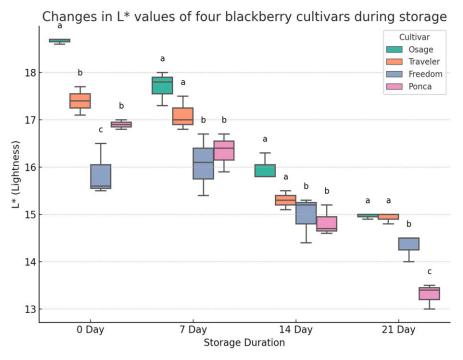


Fig. 1. Changes in L values of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above indicate mean separation by Fisher's least significant difference test (P ≤ 0.05). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.001. Mean percentage declines in L* from 0 to 21 d were 'Osage' −19.8%, 'Traveler' −14.2%, 'Freedom' −9.7%, and 'Ponca' −21.3%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.</p>

data provide a baseline to guide cultivar selection, breeding priorities, and practical shelf life extension strategies for blackberry production in North Florida.

In North Florida, cultivars such as Osage, Traveler, Freedom, and Ponca are commonly grown. Some cultivars reach harvest maturity at similar times during the growing season, yet growers often store their fruits in cold conditions before selling them. Despite this, many growers are unaware of how to prolong the shelf life of various blackberry cultivars in the region. Moreover, the cold storage responses of these cultivars have not been thoroughly studied elsewhere. To address this knowledge gap, we examined how four blackberry cultivars perform during cold storage at 1°C for durations of 7, 14, and 21 d. We hypothesized that postharvest quality attributes would vary significantly among the cultivars during cold storage, with some demonstrating greater resistance to deterioration over time. The objective of this study was to evaluate and compare the effects of cold storage on key quality parameters—including color, firmness, weight loss, respiration rate, SSC, TA, leakage,

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fungal growth, RDR, and marketability—across the four blackberry cultivars.

Materials and Methods

Site and orchard management. The study was conducted in a 3 year-old blackberry orchard located in Mayo, North Florida (30.0530°N, 83.1749°W). The cultivars used were Osage, Traveler, Freedom, and Ponca. All plants received uniform orchard management practices, including fertilization, irrigation, weed control, and pest management.

Harvest and sampling. Fifty fully ripe, blemish-free berries of uniform size and color were randomly harvested early in the morning (7:00-9:00 AM) when air temperature was 24–27 °C and relative humidity \sim 75%. Fruits were picked within 2 h, placed into 12-oz vented clamshells (5.68 \times 7.3 \times 1.88 inches; Cool Pak Packaging Solution, Oxnard, CA, USA) containing an absorbent pad, and transported in insulated coolers to the Fruit Physiology Laboratory at the North Florida Research and Education Center (Quincy, FL, USA). Fruit was stored at 1°C and 85% to 90% relative humidity for 7, 14, or 21 d. The experimental design was a completely randomized design with two factors (cultivar and storage duration), using three biological replicates (n = 3) per cultivar. Each clamshell (50 fruits) was considered an experimental unit.

Quality assessments. Fruit quality attributes were assessed at harvest (day 0) and after

each storage duration. Unless stated otherwise, 20 fruits per replicate were evaluated.

- Color: Surface color (L*, a*, b*) was measured using a chroma meter (CM-700d, Minolta, Ramsey, NJ, USA). Hue angle and total color difference (TCD) were calculated following McGuire (1992).
- Weight loss: Percent weight loss was determined by comparing clamshell weights at harvest and after storage, expressed as percentage loss relative to initial weight. The standard formula for calculating fruit weight loss during storage is as follows:

$$= \frac{\text{Weight loss (\%)}}{\text{(Initial weight)}} \times 100$$

- Firmness: Fruit firmness was measured using a texture profile analyzer (FirmTech Model FT7, BioWorks Inc., Wamego, KS, USA) designed for soft fruit. Measurements were taken after equilibration of the fruit to room temperature (21 ± 1°C) for 1 h. The system applies a standardized compression test by gently loading each berry against a flat plate and recording the maximum force required to cause deformation. Firmness was expressed in Newtons (N), and values for individual berries were averaged per replicate to obtain a representative firmness measurement.
- SSC: Determined using a digital refractometer (Atago-Palette PR 101, Atago Co. Ltd., Tokyo, Japan) in the juice and expressed as a percentage.
- TA: Measured by titration of juice with 0.1 N NaOH to pH 8.1 and expressed as % citric acid equivalents.
- Respiration rate: Respiration was assessed by placing 25 berries into 1 L airtight containers for 2 h. Following cold storage, fruit were equilibrated at room temperature (20 ± 1 °C) for 2 h before measurement, rather than being assessed directly at 1 °C. Headspace CO₂ concentration was then determined using a Bridge Analyzer (Model 900141, Bedford Heights, OH, USA). Respiration rate was calculated from the increase in CO₂ concentration, container volume, incubation time, and fruit weight, and expressed as mmol CO₂ kg⁻¹·s⁻¹.
- RDR: Berries with ≥3 red drupelets and no leakage were counted and expressed as a percentage of total fruit per replicate (Kim et al. 2015).

RDR (%)

 $= \frac{\text{(Number of RDR - positive fruits in a replication)}}{\text{(Total number of fruits in a replication)}}$

× 100

 Leakage and mycelium: Incidence of drupelet leakage and visible fungal growth were assessed on 50 berries per replicate and expressed as percentages.

M.S. is the corresponding author. E-mail: mshahid@ufl.edu.

Leakage (%) $= \frac{\text{(Number of leaking berries)}}{\text{(Total number of berries)}} \times 100$ $= \frac{\text{(Number of fruit with visible mold)}}{\text{(Total number of berries)}} \times 100$

• MI: Calculated as MI (%) = 100 – [(%RDR + % Leakage + % Mycelium)/3], with 85% as the minimum acceptable threshold (Clark and Perkins-Veazie 2011).

Cold storage quality index. The cold storage quality index (CSQI) was developed to integrate multiple postharvest traits into a single storability score. Each trait was normalized using min-max scaling to a 0-1 range. Positive quality traits (firmness, SSC, SSC/ TA ratio, MI) were expressed directly, whereas negative traits (weight loss, leakage, mycelium incidence, and RDR) were inverted so that higher values reflected better performance. Weighted contributions were applied, with greater emphasis given to firmness and MI (weight = 2.0) relative to other parameters (weight = 1.0), reflecting their higher commercial importance. The CSQI for each cultivar × storage duration was calculated as the weighted sum of normalized traits, yielding a composite score between 0 (poor quality) and 1 (excellent quality). For cultivar comparisons, mean CSQI values were standardized as Z-scores. Scores above 0 indicated above-average storability, whereas scores below 0 reflected below-average storability (Medina-Pastor et al. 2010).

Statistical analysis. Statistical analyses were carried out using Python v3.10 (Python Software Foundation, Wilmington, DE, USA 2021). Data were analyzed by two-way analysis of variance with cultivar and storage duration as fixed factors; interactions were also tested. When significant effects were detected $(P \le 0.05)$, means were separated using Fisher's least significant difference test. Percentage data (e.g., leakage, mycelium, RDR) were arcsine-transformed before analysis. Pearson's correlation coefficients (r) were calculated to evaluate relationships among quality parameters, and their significance was reported at $P \leq 0.05$. Principal component analysis (PCA) was performed using the scikit-learn package (v1.0, Python Software Foundation) to summarize multivariate trends, with variables having loadings > |0.4| considered significant contributors

Results

Color attributes change during storage

 L^* value. Changes in L* values during storage are presented in Fig. 1. Lightness declined progressively across all cultivars, with significant effects of cultivar (C), storage duration (SD), and their interaction (C \times SD; P < 0.001). At harvest (0 d), 'Osage' exhibited the highest L* (18.7), followed by 'Traveler' (17.4), 'Ponca' (16.9), and 'Freedom' (15.9).

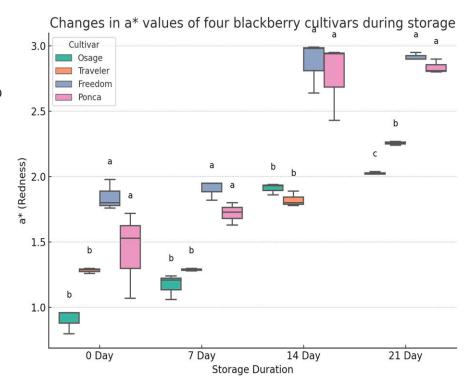


Fig. 2. Changes in a* values (redness) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes show interquartile range (IQR), horizontal lines indicate medians, and whiskers represent $1.5 \times IQR$. Letters above indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P = 0.004. Mean percentage increases in a* from 0 to 21 d were 'Osage' +123.5%, 'Traveler' +75.8%, 'Freedom' +57.9%, and 'Ponca' +97.0%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

Changes in Hue angle (h°) of four blackberry cultivars during storage

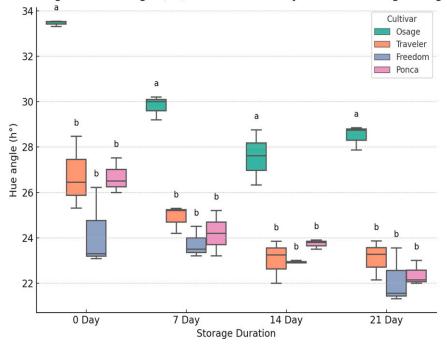


Fig. 3. Changes in hue angle (h°) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction ($C \times SD$) = P = 0.024. Mean percentage decreases in hue angle from 0 to 21 d were: 'Osage' –14.9%, 'Traveler' –13.7%, 'Freedom' –8.5%, and 'Ponca' –16.1%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

After 7 d, declines were modest, ranging from -3.2% in 'Freedom' to -6.1% in 'Ponca'. By 14 d, cultivar-specific differences became more pronounced: 'Osage' decreased to 16.5 (-11.8%), 'Ponca' to 14.9 (-11.8%), 'Traveler' to 15.5 (-10.9%), and 'Freedom' to 14.7 (-7.5%). At 21 d, all cultivars showed substantial darkening, with 'Osage' reduced to 15.0 (-19.8%), 'Ponca' to 13.3 (-21.3%), 'Traveler' to 14.9 (-14.2%), and 'Freedom' to 14.3 (-9.7%). Among cultivars, Ponca and Osage exhibited the steepest declines, whereas Freedom retained brightness for longer. These results demonstrate genotype-dependent darkening, consistent with differences in firmness and susceptibility to anthocyanin instability.

Redness a*. The redness index (a*) increased steadily during storage (Fig. 2) and was significantly affected by cultivar, storage duration, and their interaction (C, SD, C × SD; P < 0.001). At harvest, 'Osage' fruit had the lowest mean a* (0.91), whereas 'Freedom' had the highest (1.85), indicating greater initial redness. After 7 d, 'Osage' fruit showed a sharp increase to 1.45 (+59%), whereas 'Ponca' (2.08), 'Traveler' (1.70), and 'Freedom' (2.36) also rose, although more moderately (+13% to 28%). By 14 d, the progression intensified, with 'Osage' reaching 1.80 (+98%), 'Ponca' 2.50 (+48%), 'Traveler' 2.00 (+47%), and 'Freedom' 2.70 (+46%). At 21 d, 'Osage' increased further to 2.03 (+123.5%), 'Ponca' to 2.84 (+97.0%), 'Traveler' to 2.26 (+75.8%), and 'Freedom' to 2.92 (+57.9%). These results highlight that although 'Osage' fruit were initially the least red, they exhibited the greatest relative increase, whereas 'Freedom', despite being redder at harvest, changed more gradually. The acceleration of a* over storage closely paralleled the development of RDR.

Hue angle. Hue angle decreased significantly with storage (Fig. 3), reflecting a progressive shift from black toward red hues (C, SD, C \times SD; P < 0.05). At harvest, 'Osage' had the highest hue angle (33.5°), followed by 'Traveler' (26.7°), 'Ponca' (26.7°), and 'Freedom' (24.2°). After 7 d, reductions were modest (-3% to 6%), but cultivar differences remained. At 14 d, 'Osage' (30.1°) declined by -10%, 'Ponca' (24.3°) by -9%, 'Traveler' (24.5°) by -8%, and 'Freedom' (22.5°) by -7%. By 21 d, declines were greatest in 'Ponca' (22.4°, -16.1%) and 'Osage' (28.5°, -14.9%), whereas 'Traveler' (23.1°, -13.7%) and 'Freedom' (22.1°, -8.5%) retained relatively higher hue values. 'Osage' consistently maintained the highest hue angle, suggesting greater resistance to reddening, while 'Ponca' was most susceptible.

TCD. TCD values varied significantly with cultivar, storage duration, and their interaction (C, SD, C \times SD; P < 0.001; Fig. 4). At harvest, values were similar among cultivars, ranging from 4.2 (Ponca) to 4.6 (Osage). Over 21 d, 'Freedom' showed the largest reduction, declining to 3.87 (-10.8%). 'Osage' and 'Traveler' also declined, to 4.20 (-8.0%) and 4.23 (-4.5%), respectively. In contrast, 'Ponca' remained stable at 4.17 (0.0%). These findings indicate that although 'Freedom' was most unstable, 'Ponca' exhibited the greatest stability

Changes in Total Color Difference (TCD) of four blackberry cultivars during storage

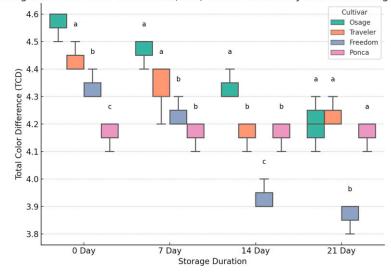


Fig. 4. Changes in total color difference (TCD) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above indicate mean separation by Fisher's least significant difference test (P ≤ 0.05). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.0001. Mean percentage changes in TCD from 0 to 21 d were 'Osage' ~8.0%, 'Traveler' ~4.5%, 'Freedom ~10.8%, and 'Ponca' 0.0%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.</p>

in overall color attributes, despite showing severe RDR development in parallel.

Fruit weight loss (%). Weight loss increased steadily across storage, with significant effects of cultivar, storage duration, and their interaction (C, SD, C \times SD; P < 0.05; Fig. 5). After 7 d, 'Ponca' and 'Osage' experienced the least weight loss (5.3% and 6.1%), with small interquartile ranges indicating consistent

moisture retention. Conversely, 'Freedom' had the highest loss at 9.2% and a larger IQR, reflecting more variability among samples. By 14 d, all cultivars suffered increased losses, with 'Freedom' (14.4%) and 'Traveler' (13.9%) showing the highest median losses and greater variability, whereas 'Ponca' maintained the lowest loss (11.9%) with more uniform results. After 21 d, the losses among all cultivars

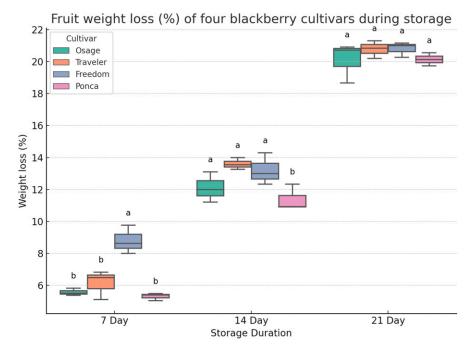


Fig. 5. Fruit weight loss (%) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C = P < 0.0001; storage duration (SD) = P < 0.0001; interaction ($C \times SD = P = 0.013$). Mean percentage increases in weight loss from 7 to 21 d were 'Osage' +255%, 'Traveler' +241%, 'Freedom' +150%, and 'Ponca' +288%. Data represent C = 0.0001) is biological replicates per cultivar, with 20 berries per replicate.

became similar, with medians between 19.7% and 20.5% and narrower IQRs, implying that long-term storage diminished differences based on genotype. Overall, the effects of cultivar were most noticeable between 7 and 14 d, but extended storage resulted in high water loss across all types.

Fruit firmness (N). Firmness decreased significantly during storage, with strong cultivar, duration, and interaction effects (C, SD, $C \times SD$; P < 0.001; Fig. 6). At harvest, 'Freedom' exhibited the highest firmness (1.4 N), followed by 'Ponca' (1.3 N), and 'Osage' and 'Traveler' were lowest (1.1 N). After 7 d, firmness remained stable in 'Osage' (1.1 N) and 'Traveler' (1.1 N), whereas 'Ponca' and 'Freedom' declined slightly to 1.2 and 1.1 N, respectively. By 14 d, cultivar differences became clearer: 'Freedom' dropped to 0.9 N (-36%), 'Ponca' to 0.7–0.8 N (-42%), and 'Osage' and 'Traveler' maintained ~1.0 N (-9%). At 21 d, firmness declined most sharply in 'Ponca', softening by -85% to 0.2 N, whereas 'Freedom' lost -50% (to 0.7 N). In contrast, 'Osage' and 'Traveler' showed only modest declines (-18%, both 0.9 N). These findings demonstrate that 'Osage' and 'Traveler' maintained greater structural integrity throughout storage, whereas 'Ponca' was most susceptible to rapid softening, and 'Freedom', despite being initially firmest, deteriorated progressively.

Respiration $(mL \cdot kg^{-1} \cdot s^{-1})$. Respiration rates varied significantly among cultivars and declined with storage (C, SD, C \times SD; P <0.001; Fig. 7). At harvest, the Freedom cultivar showed the highest median respiration rate (14.6 mL·kg⁻¹·s⁻¹) with moderate variability, indicating a higher metabolic activity. In comparison, 'Osage' (2.3 mL·kg $^{-1}$ ·s $^{-1}$), 'Traveler' (2.7 mL·kg $^{-1}$ ·s $^{-1}$), and 'Ponca' (4.0 mL·kg⁻¹·s⁻¹) had much lower and more consistent respiration rates. After 7 d, respiration decreased in all cultivars; Freedom remained the highest (9.0 mL·kg $^{-1}$ ·s $^{-1}$), whereas Osage dropped to \sim 1.6 mL·kg $^{-1}$ ·s $^{-1}$. The variability also decreased, suggesting a more uniform response during storage. By 14 d, respiration rates declined further, with Freedom at \sim 7.0 mL·kg⁻¹·s⁻¹ and the other cultivars ranging from \sim 2.0 to 2.7 mL·kg⁻¹·s⁻¹; Ponca showed slightly more variability. After 21 d, respiration rates across genotypes converged, ranging from roughly 0.6 to 2.5 mL kg^{-1} s⁻¹, with minimal variation. Overall, differences among cultivars were most pronounced at harvest and early storage, but extended cold storage led to low, uniform respiration levels across all cultivars.

SSC (%). SSC increased progressively during storage, with significant main and interaction effects (C, SD, C \times SD; P < 0.05; Fig. 8). At harvest, 'Osage' had the highest SSC, \sim 6.7%, with measurements consistently

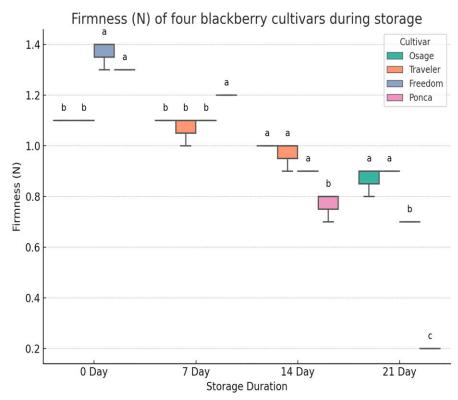


Fig. 6. Firmness (N) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Firmness was measured after berries were equilibrated to 20 °C for 1 h following removal from storage. Boxes represent the interquartile range (IQR), horizontal lines indicate medians, and whiskers show $1.5 \times IQR$. Letters above indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C = P < 0.0001; storage duration (SD) = P < 0.0001; interaction ($C \times SD = P < 0.0001$. Mean percentage declines in firmness from 0 to 21 d were 'Osage' -18%, 'Traveler' -18%, 'Freedom' -50%, and 'Ponca' -85%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

similar across replicates. In contrast, 'Traveler' and 'Ponca' showed lower SSC values, ~4.8% to 4.9%, with greater variability. The SSC of 'Freedom' was intermediate, at 5.9%. After 7 d of storage, SSC increased in all cultivars, with Osage and Freedom reaching \sim 7.2% and 7.1%, respectively, whereas Ponca exhibited more variation. By day 14, sugar content continued to rise, with 'Osage' remaining highest at 8.4%, followed by 'Freedom' at 7.5%, and 'Ponca' at 7.2%. 'Traveler' retained the lowest SSC at 6.7%. After 21 d, SSC increased across all cultivars, with Osage peaking near 8.5%, and the others stabilizing \sim 7.4% to 8.0%. Over the storage period, the interquartile ranges (IORs) decreased, indicating increased uniformity in sugar content. Overall, the cultivar differences persisted throughout storage, with Osage consistently showing higher sugar levels, reflecting ongoing ripening and sugar accumulation during storage.

TA (%). TA declined significantly with storage duration and its interaction with cultivar, although cultivar main effects were not significant (C = ns; SD, C \times SD; P < 0.01; Fig. 9). At harvest, 'Ponca' had the highest TA at 0.90%, followed by 'Osage' at 0.87%, whereas 'Traveler' and 'Freedom' exhibited lower levels at 0.79% and 0.78%, respectively. After 7 d, all cultivars showed a sharp decline, with values converging to $\sim 0.55\%$ to 0.62%. From day 14 onward, TA levels stabilized at low values (0.51% to 0.60%), indicating a metabolic balance of organic acids during cold storage. Boxplot analysis revealed smaller IQRs at days 14 and 21, reflecting decreased biological variability among samples. Although differences among cultivars were most evident at harvest, the duration of storage became the primary factor affecting TA after 7 d.

SSC/TA ratio. The SSC/TA ratio increased markedly across storage, with strong cultivar, duration, and interaction effects (C, SD, C × SD; P < 0.01; Fig. 10) At harvest, this ratio was generally low, with 'Osage' being the highest (7.6), whereas 'Ponca' (5.3), 'Freedom' (7.1), and 'Traveler' (6.1) had lower values. After 7 d, the ratio surged in all cultivars, reaching ~13.5 in Osage and 12.0 in Freedom, whereas Ponca and Traveler also increased to \sim 12.2 and 11.3, respectively. Further increases occurred by 14 d, with 'Osage' maintaining the highest ratio (15.0), whereas other cultivars ranged from 11.8 to 13.6. By 21 d, the values plateaued, with 'Osage' remaining at the top (15.5–16.0) and the other cultivars converging between 13.7 and 15.2. Boxplot analysis revealed broader IQRs at midstorage (7-14 d), indicating greater variability in ripening responses, which narrowed by 21 d, showing convergence in flavor development. Overall, the increasing SSC/TA ratio underscores the combined effects of rising sugar levels and decreasing acidity, resulting in increased sweetness and better palatability as storage time prolongs.

Leakage (%). Leakage developed progressively during storage, with significant effects of cultivar, storage duration, and their interaction (C, SD, C \times SD; P < 0.001; Fig. 11).

Respiration rate (ml CO₂ kg⁻¹ s⁻¹) of four blackberry cultivars during storage

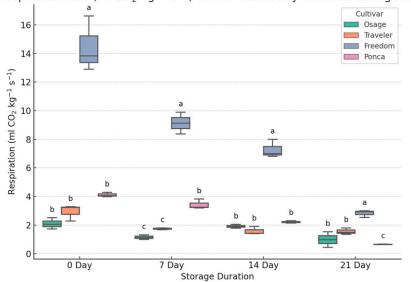


Fig. 7. Respiration rate (mL CO₂ kg⁻¹·s⁻¹) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above indicate mean separation by Fisher's least significant difference test (P ≤ 0.05). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.0001. Mean percentage declines in respiration from 0 to 21 d were 'Osage' -43%, 'Traveler' -46%, 'Freedom' -80%, and 'Ponca' -57%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.</p>

After 7 d, 'Freedom' had the highest leakage (29% to 31%), followed by 'Traveler' (17%), 'Osage' (15%), and 'Ponca' the lowest (11%). By 14 d, 'Ponca' showed a sharp increase to ~69%, whereas 'Osage' and 'Traveler' rose moderately to 38% to 40%. 'Freedom' remained high at 39% to 41%. At 21 d, 'Ponca' reached extreme levels (89%), 'Freedom' increased to 58%, 'Traveler' stabilized at

49%, and 'Osage' remained lowest at 43%. Relative to 7 d, 'Ponca' increased 8-fold, whereas 'Osage' and 'Traveler' tripled and 'Freedom' doubled. These results identify 'Ponca' as extremely leakage-prone, whereas 'Osage' displayed the highest resistance.

Mycelium growth (%). Fungal growth increased significantly with storage (C, SD, C \times SD; P < 0.001; Fig. 12). At 7 d,

Soluble solids concentration (SSC, %) of four blackberry cultivars during storage

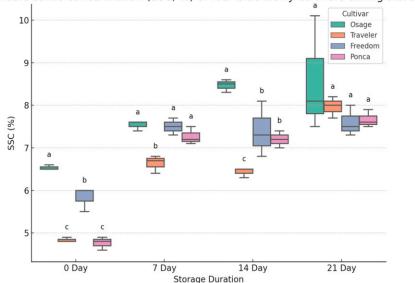


Fig. 8. Soluble solids concentration (SSC, %) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 $^{\circ}$ C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above boxes indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P = 0.015. Mean percentage increases in SSC from 0 to 21 d were 'Osage' +38%, 'Traveler' +63%, 'Freedom' +29%, and 'Ponca' +59%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

'Freedom' and 'Ponca' showed the highest early incidence (4% to 6%), whereas 'Osage' (0% to 2%) and 'Traveler' (0% to 2%) had minimal growth. By 14 d, 'Ponca' escalated to 12% to 14%, 'Freedom' increased moderately (8% to 10%), and 'Osage' and 'Traveler' remained lower (4% to 6%). At 21 d, differences widened: 'Ponca' recorded the highest incidence (22% to 24%), followed by 'Freedom' (15% to 20%) and 'Osage' (14% to 16%), whereas 'Traveler' was least affected (8% to 10%). Overall, 'Ponca' was most susceptible, 'Freedom' intermediate, 'Osage' moderate, and 'Traveler' consistently most resistant to fungal development under cold storage.

RDR (%). RDR incidence rose with storage, with significant cultivar, duration, and interaction effects (C, SD, C \times SD; P < 0.001; Fig. 13). At 7 d, 'Freedom' and 'Ponca' had the highest incidence (14% to 16%), 'Osage' was moderate (6%), and 'Traveler' lowest (1% to 2%). By 14 d, 'Freedom' doubled to 29% to 30%, 'Osage' increased to 9%, 'Traveler' to 5%, whereas 'Ponca' plateaued \sim 14% to 16%. At 21 d, 'Freedom' reached the highest RDR (44% to 45%), more than double the levels in other cultivars. 'Ponca' remained stable $(\sim 18\%)$, 'Osage' rose moderately (15% to 16%), and 'Traveler' stayed lowest (12%). These results show that 'Freedom' was most prone to RDR, whereas 'Traveler' had the strongest resistance, with 'Osage' and 'Ponca' displaying intermediate responses.

MI (%). MI declined significantly across storage, with strong cultivar, duration, and interaction effects (C, SD, C \times SD; P < 0.001; Fig. 14). At 7 d, 'Osage' and 'Traveler' maintained the highest MI (93%), followed by 'Ponca' (89%) and 'Freedom' (83%). By 14 d, 'Osage' and 'Traveler' retained 82% to 84%, whereas 'Freedom' dropped to 74% and 'Ponca' to 68%. At 21 d, 'Traveler' (77%) and 'Osage (75%) continued to outperform 'Freedom' (60%) and 'Ponca' (57%). Relative declines from 7 to 21 d were greatest in 'Ponca' (-36%), followed by 'Freedom' (-29%), 'Osage' (-19%), and 'Traveler (-17%). These results confirm 'Osage' and 'Traveler' as the best-performing cultivars under prolonged cold storage, whereas 'Freedom' and 'Ponca' lost commercial quality more rapidly.

Correlation among quality and physiological attributes. Analysis of stored blackberry fruit under cold conditions using Pearson's correlation revealed strong associations among color parameters, quality traits, physiological responses, and the MI (Fig. 15). Notably, MI was positively correlated with firmness (r = 0.96, P < 0.001) and lightness (L*, r = 0.93,), suggesting that maintaining firmness and surface brightness enhances marketability. In contrast, MI showed strong negative correlations with leakage (r = -0.98, P < 0.001), RDR (r = -0.97, P < 0.001), mycelium incidence (r = -0.96, P < 0.001), and weight loss (r = -0.95, P <0.001). These results demonstrate that disorder development was the strongest driver of marketability decline.

L* was negatively correlated with a* (r = -0.89, P < 0.001), confirming that darkening

Titratable acidity (TA, % citric acid equivalents) of four blackberry cultivars during storage

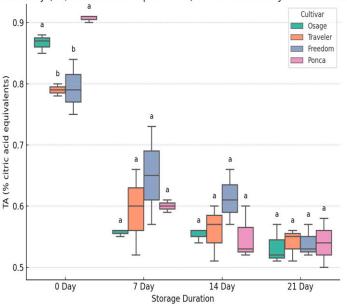


Fig. 9. Titratable acidity (TA, % citric acid equivalents) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above boxes indicate mean separation by Fisher's least significant difference test (*P* ≤ 0.05). Analysis of variance results: cultivar (C) = ns; storage duration (SD) = *P* < 0.0001; interaction (C × SD) = *P* = 0.007. Mean percentage declines in TA from 0 to 21 d were 'Osage' –39%, 'Traveler' –33%, 'Freedom' –31%, and 'Ponca' –43%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

during storage coincided with increased redness. Conversely, L* was positively associated with hue angle (r = 0.72, P < 0.001), suggesting that berries with higher lightness retained less red coloration. SSC correlated positively with SSC/TA ratio (r = 0.90, P < 0.001), reflecting the coupled accumulation

of sugars and decline in acids during storage. These results provide a mechanistic understanding of how fruit color, biochemical traits, and physiological disorders collectively shape commercial quality outcomes.

PCA. The PCA biplot and variance structure are shown in Fig. 16, with supporting

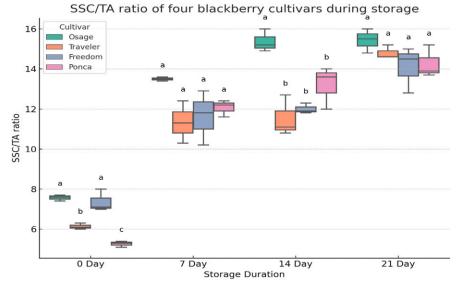


Fig. 10. Soluble solids concentration/titratable acidity (SSC/TA) ratio of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 0, 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show $1.5 \times IQR$. Letters above boxes indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P = 0.0028. Mean percentage increases in SSC/TA from 0 to 21 d were 'Osage' +110%, 'Traveler' +146%, 'Freedom' +89%, and 'Ponca' +171%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

eigenvalues and loadings provided in Supplemental Fig. 1 and Supplemental Table 1. Significant PCA loadings (|loading| > 0.4) are presented in Supplemental Table 2. The first two principal components explained 81.7% of the total variance (PC1 = 67.2%, PC2 = 14.5%). PC1 was strongly and positively associated with firmness, MI, and SSC, and negatively associated with leakage, mycelium, and RDR. Thus, PC1 primarily captured overall storability and resistance to postharvest disorders. PC2 was positively associated with respiration rate and negatively with hue angle and TCD (|loading| > 0.4), capturing variation in metabolic activity and color stability.

Cultivars separated clearly in the score plot. 'Osage' and 'Traveler' grouped on the positive side of PC1, characterized by higher firmness, superior MI, and lower disorder incidence. 'Freedom' and 'Ponca' grouped on the negative side of PC1, reflecting high leakage, elevated RDR, and faster softening. Along PC2, 'Freedom' aligned with higher respiration rates, whereas 'Ponca' associated with stronger declines in hue angle and color stability. The PCA therefore distinguished cultivar-specific physiological and quality responses, confirming 'Osage' and 'Traveler' as the most resilient cultivars under cold storage.

CSQI. The CSQI combines key quality features such as firmness, SSC, SSC/TA ratio, and the MI, along with physiological traits like weight loss, leakage, mycelium growth, and mycelium incidence (decay). It reveals differences among cultivars' storage performance at 1 °C (Fig. 17). 'Osage' had the highest CSQI (+0.95), demonstrating excellent firmness, marketability, and low leakage and RDR; 'Traveler' also performed well (+0.77), with good storage ability and minimal deterioration. Conversely, 'Freedom' (-0.74) and 'Ponca' (-0.98) scored negatively, indicating vulnerability to storage loss. 'Freedom' experienced sharp increases in leakage, mycelium, and RDR within 14 d, whereas 'Ponca' showed the worst results, with high leakage, mycelium, and rapid decline in marketability. Overall, CSQI effectively measures blackberry storage capacity, aligning with MI trends and highlighting postharvest differences. It identified 'Osage' and 'Traveler' as the most suitable for longterm storage, with 'Freedom' and 'Ponca' limited in potential.

Discussion

Blackberries are highly perishable because of their delicate fruit structure and rapid physiological changes after harvest. Storing them at 1 °C helps to prolong their shelf life by slowing metabolic processes. In this study, four blackberry cultivars from North Florida, Osage, Traveler, Freedom, and Ponca, were evaluated for their ability to retain quality over 0, 7, 14, and 21 d of cold storage.

Color retention and visual quality. Changes in the blackberry fruit surface color are the first sign of quality decline. Maintaining color during storage is crucial for keeping the fruit

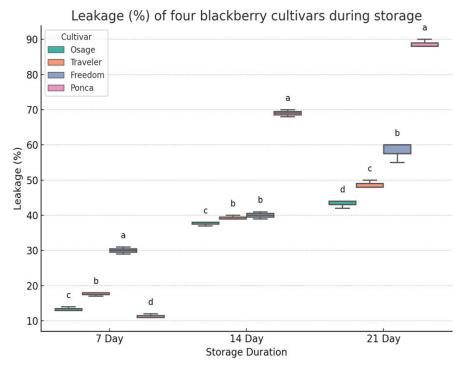


Fig. 11. Leakage (%) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above boxes indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.0001. At 21 d, mean leakage was 'Ponca' 89%, 'Freedom' 58%, 'Traveler' 49%, and 'Osage' 43%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

marketable. In our study, we observed significant shifts in berry surface color metrics, such as (L^*, a^*) , hue angle, and total color), during cold storage at $1\,^{\circ}$ C across four different cultivars. Specifically, the L^* value (Lightness) and

hue angle steadily decreased from 0 to 21 d of storage, indicating the fruit surface was darkening. Conversely, the a* value increased as storage progressed, suggesting a rise in red pigmentation, which is linked to RDR.

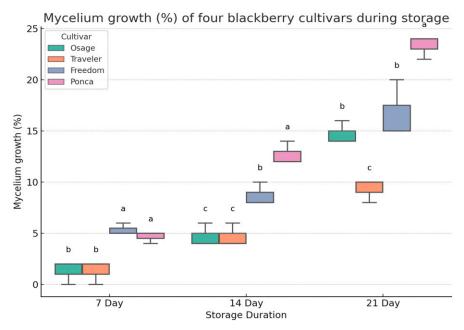


Fig. 12. Mycelium growth (%) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1°C for 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above boxes indicate mean separation by Fisher's least significant difference test (P ≤ 0.05). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.0001. At 21 d, mean mycelium incidence was 'Ponca' 23%, 'Freedom' 17%, 'Osage' 15%, and 'Traveler' 9%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.</p>

Among the cultivars, Osage maintained the highest visual quality with minimal RDR, whereas Freedom and Ponca were more prone to color loss and darkening.

These results are supported by previous studies on berry fruits, where Palonen and Weber (2019) observed similar patterns in raspberry genotypes, where cold storage led to decreased L* values and increased a*, particularly in the Heritage cultivar, which is high in anthocyanins. They emphasized that differences between genotypes affect how the fruit's color remains stable after harvest, regardless of ethylene presence. In addition, Horvitz et al. (2017) reported changes in the coloration of Andean blackberries during storage and ripening, associated with the buildup and breakdown of anthocyanins. Furthermore, Krüger et al. (2011) and Kalt et al. (1999) established that anthocyanin levels generally increase as the fruit ripens and may continue to do so during storage, although this growth slows near freezing temperatures. Particularly, Kalt et al. (1999) found that at temperatures between 10 and 20 °C, raspberries' antioxidant and anthocyanin content increased, whereas at 0 °C, these levels remained stable, accounting for the minimal pigment changes observed at 1 °C (Samaniego et al. 2020). In another study, Bordonaba et al. (2010) found that anthocyanin production in blackcurrants is highly influenced by temperature, with the most significant pigment increases observed between 5 and 12 °C. Although our storage temperature was lower, the observed decrease in L* and increase in a* still indicate metabolic changes in pigment composition, possibly due to postharvest enzymatic activity or cell membrane degradation. The occurrence of RDR, which involves the appearance of red coloration on black drupelets during storage, has been linked to the loss of anthocyanins, pH variations, and membrane damage. Furthermore, Edgley et al. (2020) reported higher RDR in cultivars with lower cellular integrity and firmness, consistent with our results. Cultivars like Freedom and Ponca with reduced firmness also had higher RDR and greater changes in a* and hue angle, indicating a physiological association. Overall, postharvest color changes vary by cultivar and are linked to traits like firmness, pigment makeup, and membrane stability. Choosing cultivars that retain more anthocyanins and have better structural integrity (e.g., Osage) can enhance visual appeal and consumer acceptance during cold storage.

Fruit firmness and weight loss. Fruit firmness is one of the most important post-harvest quality attributes in blackberries, directly influencing storage life, consumer acceptance, and market value. In this study, firmness declined significantly across all cultivars during 21 d of cold storage, except for Osage, which consistently retained higher firmness values throughout the storage period, whereas Freedom and Ponca softened more rapidly. This pattern of softening is typical of climacteric soft fruits. It is primarily attributed to the enzymatic degradation of cell wall components and the middle lamella, leading to reduced cell adhesion and tissue softening

Red drupelet reversion (RDR, %) of four blackberry cultivars during storage

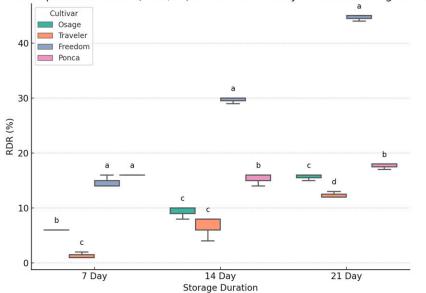


Fig. 13. Red drupelet reversion (RDR, %) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1°C for 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show 1.5 × IQR. Letters above boxes indicate mean separation by Fisher's least significant difference test (P ≤ 0.05). Analysis of variance results: cultivar (C) = P < 0.0001; storage duration (SD) = P < 0.0001; interaction (C × SD) = P < 0.0001. At 21 d, mean RDR incidence was 'Freedom' 45%, 'Ponca' 18%, 'Osage' 16%, and 'Traveler' 12%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.</p>

(Brummell 2006). Similar cultivar-dependent differences have been reported previously, with firmer genotypes showing superior post-harvest quality. For example, Strik et al. (2008) and Salgado and Clark (2016) highlighted the influence of genetic background on firmness,

and Perkins-Veazie et al. (1996) observed that cultivars such as Navaho maintained structural integrity better than softer types.

The loss of firmness in the present study was closely associated with weight loss over time. During the first 7 d of storage, weight loss

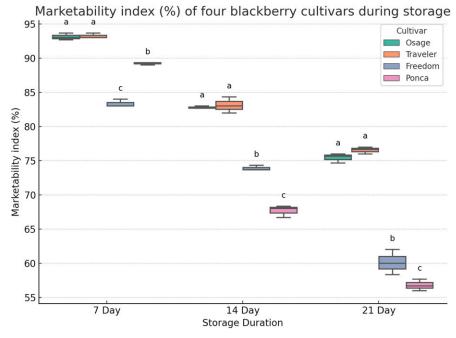


Fig. 14. Marketability index (MI, %) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) during storage at 1 °C for 7, 14, and 21 d. Boxes represent interquartile range (IQR), horizontal lines indicate medians, and whiskers show $1.5 \times \text{IQR}$. Letters above boxes indicate mean separation by Fisher's least significant difference test ($P \le 0.05$). Analysis of variance results: cultivar (C = P < 0.0001; storage duration (SD) = P < 0.0001; interaction ($C \times \text{SD}$) = P < 0.0001. Mean percentage declines in MI from 7 to 21 d were 'Osage' –19%, 'Traveler –17%, 'Freedom' –29%, and 'Ponca' –36%. Data represent n = 3 biological replicates per cultivar, with 20 berries per replicate.

was relatively low, but it increased markedly after 14 and 21 d, particularly in 'Freedom,' which also exhibited the lowest firmness. This supports earlier findings that softer cultivars tend to lose more water, likely due to greater cell membrane permeability and progressive cell wall breakdown, which accelerate dehydration (Segantini et al. 2017). These results are consistent with the work of Lawrence and Melgar (2018), who reported more weight loss with long storage duration. A practical consideration of the present results is the direct economic impact of weight loss during storage. Across cultivars, fruit lost \sim 13% of their initial weight between 7 and 14 d at 1 °C. In the United States, fresh-market blackberries are commonly sold in 6-oz (170 g) clamshells at retail prices of USD \$4.50-6.00 per package. At this price point, a 13% reduction in marketable weight corresponds to an estimated loss of 60-80 cents per clamshell. On a commercial scale, this equates to ~USD \$1,400-1,900 per metric tonne of fruit. The extent of shrinkage varied among cultivars: Ponca showed the greatest weight loss, translating into proportionally higher economic losses, whereas Osage retained the lowest weight loss and betterpreserved marketable yield. 'Traveler' and 'Freedom' displayed intermediate responses, with weight loss greater than 'Osage' but less severe than 'Ponca'. These differences reduce not only the saleable yield but also the visual quality and consumer acceptance, underscoring the importance of cultivar selection and improved postharvest handling practices to minimize shrinkage and preserve market value during storage. Collectively, the findings emphasize the importance of cultivar selection in postharvest management. Firmer cultivars such as Osage not only better maintain firmness but also show minimum water loss.

Respiration rate declined progressively during storage in all cultivars, reflecting the suppression of metabolic activity at low temperatures. Cold storage slows enzymatic reactions and reduces substrate utilization, thereby lowering CO₂ production (Kader 2002). Similar reductions in respiration have been documented in other soft fruits, including strawberries and blueberries, where near-freezing conditions limit energy demand and delay senescence (Perkins-Veazie and Collins 2002). The decline observed in this study may also reflect reduced availability of fermentable substrates as storage progressed, along with downregulation of key respiratory enzymes. Although this suppression can extend storability, it also signals a gradual transition toward senescence, which ultimately compromises fruit quality beyond 2 to 3 weeks of storage.

RDR. RDR is a postharvest disorder that negatively affects the cosmetic visual quality and marketability of blackberries. RDR incidence varied among cultivars and increased with storage time. 'Freedom' was most RDR susceptible, whereas 'Osage' had the lowest levels. Moreover, RDR roughly doubled from 7 to 21 d of storage across all cultivars. These results support previous studies showing a strong genetic influence on RDR and its negative

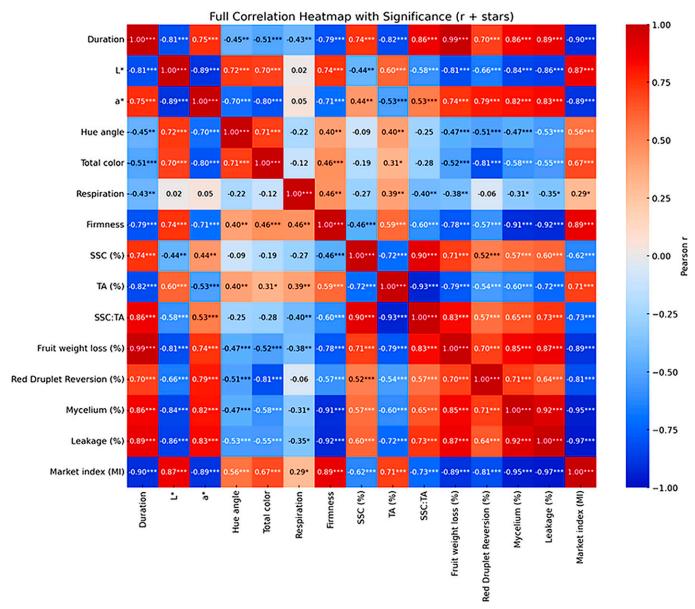


Fig. 15. Correlation heat map showing relationships among postharvest quality and physiological attributes of blackberry fruit stored at 1 °C for up to 21 d. Traits include color parameters (L*, a*, hue angle, total color difference), respiration rate, firmness, soluble solids concentration (SSC), titratable acidity (TA), SSC/TA ratio, fruit weight loss, leakage, mycelium growth, red drupelet reversion (RDR), and marketability index (MI). Pearson's correlation coefficients (r) are shown within cells, with the scale corrected to reflect the full range from −1 to +1. Significance is indicated as *P ≤ 0.05, **P ≤ 0.01, and ***P ≤ 0.001.

relation to fruit firmness (Armour et al. 2021; Perkins-Veazie et al. 1996).

Furthermore, multiple methods explain RDR, including anthocyanin degradation, cell wall breakdown, electrolyte leakage, and pH changes. Edgley et al. (2020) associated RDR with anthocyanin loss and cell damage in susceptible cultivars, corresponding with reduced firmness and increased leakage. In this study, results show cultivars with higher RDR also had higher leakage and lower firmness. 'Osage,' which maintained the firmest consistency, had the lowest RDR, suggesting cell wall integrity protects against pigment loss. Lawrence and Melgar (2018) observed lower RDR in 'Osage' and 'Traveler' compared with more susceptible 'Natchez' and 'Chester'. In addition, Armour et al. (2021) found a significant negative correlation between firmness and RDR over two seasons (r = -0.53 in 2018; r = -0.36 in 2019), supporting the role of tissue softening and membrane damage in RDR development.

Preharvest environmental stress, particularly high temperatures, and excessive ultraviolet radiation, has also been implicated in triggering RDR (Perkins-Veazie et al. 1999). In this study, however, storage was maintained at 1 °C under controlled conditions, suggesting that the observed differences were primarily attributable to inherent cultivar physiology and their postharvest responses, rather than external environmental factors.

SSC, TA, and SSC/TA ratio. The levels of SSC, TA, and their ratio SSC/TA are important indicators of blackberry flavor, influencing sweetness and tartness, and thus consumer preference and quality. Our study found that

cultivar type and storage duration significantly affected SSC and the SSC/TA ratio, whereas TA levels were primarily affected by duration of storage. The 'Osage' consistently showed the highest SSC and SSC/TA ratios, suggesting it maintains flavor better. An increase in SSC over storage time is associated with water loss and starch breakdown (Kim et al. 2015). Similar results by Kim et al. 2015 indicated SSC increased during storage, with TA mainly remaining stable. As TA decreased, the SSC/TA ratio increased, which is consistent with Oliveira et al. (2014), who observed that factors like temperature, genetics, and low oxygen conditions influence sugar and acid levels. Genetic differences also played a role; the higher SSC and lower TA in 'Osage' contributed to a more favorable balance between sweetness and acidity, aligning with

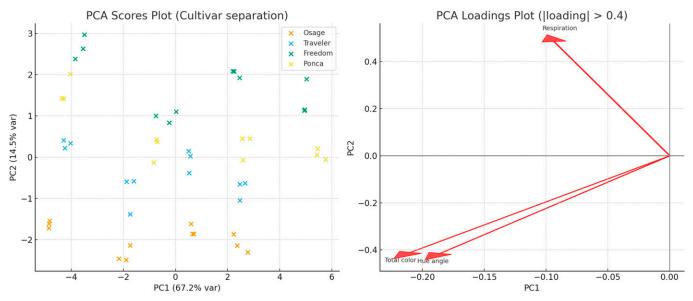
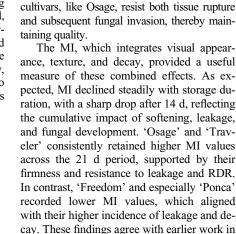


Fig. 16. Principal component analysis (PCA) of postharvest quality and physiological traits in four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) stored at 1 °C. (A) PCA scores plot (PC1 vs. PC2) showing cultivar × storage duration combinations. (B) PCA loadings plot displaying only variables with absolute loading values > |0.4| (respiration, hue angle, total color). PC1 and PC2 explained 67.2% and 14.5% of the variance, respectively (81.7% cumulative). A scree plot of variance explained per component (Supplemental Fig. 1) and a table of eigenvalues and loadings (Supplemental Tables 1 and 2) are provided.

previous research (Kim et al. 2015). Metabolic activities such as respiration cause changes in SSC and TA, with higher temperatures accelerating their decline (Ayala-Zavala et al. 2004). Cooler storage conditions slowed down this process, raising the SSC/TA ratio, especially in firmer varieties like 'Osage'. Conversely, softer varieties such as 'Freedom' experienced reductions in marketability due to microbial growth and leakage, despite having biochemical benefits.

Postharvest physiological disorders and marketability. Leakage and mycelium growth emerged as key indicators of postharvest deterioration in blackberries, with both factors strongly influenced by cultivar and storage duration. 'Ponca' consistently showed the highest levels of juice leakage and fungal development, whereas 'Osage' and 'Traveler' were far less affected. This reinforces the importance of cultivar choice for maintaining quality during storage. As storage advanced from 7 to 21 d, leakage and fungal incidence increased, particularly in softer cultivars such as Ponca and Freedom. This trend reflects the progressive breakdown of cell walls and cuticle integrity, which not only releases cell contents but also creates a humid microenvironment that favors



fungal proliferation. Similar associations among

leakage, tissue damage, and decay have been

reported in raspberries (Palonen and Weber

2019) and blackberries (Lawrence and Melgar

2018). The strong link between leakage and

fungal growth in our study suggests that firmer

storage.

Importantly, these cultivar differences were also captured in the CSQI, which integrates both quality and physiological traits into a composite measure of storability. 'Osage' and 'Traveler' achieved the highest CSQI scores, confirming their resilience under prolonged cold storage, whereas 'Ponca' and 'Freedom' ranked lowest, reflecting their susceptibility to leakage, fungal growth, and reduced firmness. The close alignment among MI, physiological disorders, and CSQI underscores that leakage and fungal development are not only critical markers of deterioration

blackberries (Armour et al. 2021; Lawrence and Melgar 2018), where genotypes with firmer textures and lower RDR were better able

to maintain commercial value over extended

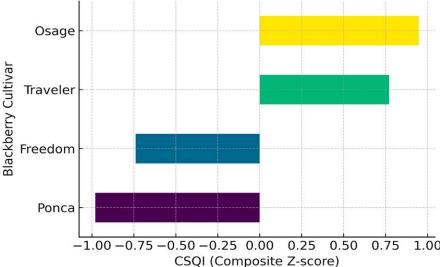


Fig. 17. Cold Storage Quality Index (CSQI) of four blackberry cultivars (Osage, Traveler, Freedom, and Ponca) stored at 1°C. Values represent composite Z-scores derived from normalized quality traits (firmness, soluble solids concentration [SSC], SSC/titratable acidity, marketability index) and physiological attributes (weight loss, leakage, mycelium incidence, and red drupelet reversion). Positive scores indicate superior storability, whereas negative scores reflect weaker performance under cold storage conditions.

but also reliable predictors of market value and overall storage potential.

Conclusion

This research evaluated the postharvest performance of four commercial blackberry varieties, 'Osage', 'Traveler', 'Freedom', and 'Ponca', grown in North Florida and stored at 1 °C for up to 21 d. Significant genetic differences were observed in berry surface color, firmness, weight loss, RDR, decay, and biochemical characteristics. 'Osage' demonstrated the best cold storage tolerance, maintained firmness, reduced leakage and RDR, and stable soluble solids up to 21 d. 'Traveler' also performed well, with less decay and acceptable firmness but moderate leakage restricted its optimal storage life to ~14-21 d. 'Freedom' showed faster firmness loss and higher leakage and mycelium development, limiting its commercial storage potential to \sim 14 d. Ponca was the least tolerant cultivar, with rapid quality deterioration driven by severe leakage, high RDR, and firmness decline, making it suitable for only 7-14 d of storage. The CSQI analysis supported these findings, ranking Osage and Traveler as superior cultivars for extended cold storage, whereas Freedom and Ponca were less suitable. These results provide cultivar-specific guidance for postharvest handling and underline the importance of selecting genotypes with stronger cold tolerance to maintain blackberry quality during storage.

Industry-focused recommendation

From a practical standpoint, these findings provide clear guidance for growers and supply chain managers. 'Osage' is well-suited for long-distance marketing and export, as it retains quality for up to 21 d at 1 °C. 'Traveler' can also support regional and some extended supply chains but should ideally be marketed within 14–21 d to avoid losses from leakage. 'Freedom' requires more careful handling and should be limited to domestic or short-chain distribution, with storage not exceeding 14 d. 'Ponca' is best suited for local markets where fruit can be sold within 7–14 d of harvest, as its susceptibility to leakage and RDR makes it unsuitable for long-term storage or export.

References Cited

- Antunes LEC, Duarte Filho J, Souza CMD. 2003. Conservação pós-colheita de frutos de amoreirapreta. Pesq Agropec Bras. 38(3):413–419. https:// doi.org/10.1590/S0100-204X2003000300011.
- Armour ME, Worthington M, Clark JR, Threlfall RT, Howard L. 2021. Effect of harvest time and fruit firmness on red drupelet reversion in blackberry. HortScience. 56(8):889–896. https://doi.org/10.21273/HORTSCI15853-21.
- Ayala-Zavala JF, Wang SY, Wang CY, González-Aguilar GA. 2004. Effect of storage temperatures on antioxidant capacity and aroma compounds in strawberry fruit. LWT Lebenson Wiss Technol. 37(7):687–695. https://doi.org/10.1016/j.lwt.2004.03.002.
- Basiouny FM. 1995. Ethylene evolution and quality of blackberry fruit as influenced by harvest time and storage intervals. Acta Hortic. 398:195–204. https://doi.org/10.17660/ActaHortic.1995.398.20.

- Beattie J, Crozier A, Duthie G. 2005. Potential health benefits of berries. CNF. 1:71–86. https://doi.org/ 10.2174/1573401052953294.
- Benichou M, Ayour J, Sagar M, Alahyane A, Elateri I, Aitoubahou A. 2018. Postharvest technologies for shelf life enhancement of temperate fruits, p 77–100. In: Mir SA, Shah MA, Mir MM (eds). Postharvest biology and technology of temperate fruits. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-76843-4_4.
- Bersaneti GT, Prudencio SH, Mali S, Pedrine Colabone Celligoi MA. 2021. Assessment of a new edible film biodegradable based on starchnystose to increase quality and the shelf life of blackberries IN THE U.S. Food Biosci. 42: 101173. https://doi.org/10.1016/j.fbio.2021.101173.
- Bordonaba GJ, Chope GA, Terry LA. 2010. Maximising blackcurrant anthocyanins: Temporal changes during ripening and storage in different genotypes. J Berry Res. 1(2):73–80. https://doi.org/10.3233/BR-2010-008.
- Brummell DA. 2006. Cell wall disassembly in ripening fruit. Funct Plant Biol. 33(2):103–119. https://doi.org/10.1071/FP05234.
- Clark JR, Perkins-Veazie P. 2011. 'APF-45' primocane-fruiting blackberry. HortScience. 46(4):670–673. https://doi.org/10.21273/HORTSCI. 46 4 670
- Duan Y, Wang G-B, Fawole OA, Verboven P, Zhang X-R, Wu D, Opara UL, Nicolai B, Chen K. 2020. Postharvest precooling of fruit and vegetables: A review. Trends Food Sci Technol. 100:278–291. https://doi.org/10.1016/ j.tifs.2020.04.027.
- Edgley M, Close DC, Measham PF, Nichols DS. 2019. Physiochemistry of blackberries (*Rubus* L. subgenus Rubus Watson) affected by red drupelet reversion. Postharvest Biol Technol. 153:183–190. https://doi.org/10.1016/j.postharvbio. 2019.04.012.
- Edgley M, Close DC, Measham PF. 2020. Red drupelet reversion in blackberries: A complex of genetic and environmental factors. Sci Hortic. 272:109555. https://doi.org/10.1016/j.scienta. 2020.109555.
- Gil-Martínez L, Mut-Salud N, Ruiz-García JA, Falcón-Piñeiro A, Maijó-Ferré M, Baños A, De la Torre-Ramírez JM, Guillamón E, Verardo V, Gómez-Caravaca AM. 2023. Phytochemicals determination, and antioxidant, antimicrobial, anti-inflammatory and anticancer activities of blackberry fruits. Foods. 12(7):1505. https:// doi.org/10.3390/foods12071505.
- Hadadinejad M, Ghasemi K, Mohammadi AA. 2018. Effect of storage temperature and packaging material on shelf life of thornless blackberry. Int J Hortic Sci Technol. 5(2):265–275. https://doi.org/10.22059/ijhst.2018.252144.218.
- Hardenburg RE, Watada AE, Wang CY, Service USAR. 1986. The commercial storage of fruits, vegetables, and florist and nursery stocks. US Department of Agriculture, Agricultural Research Service.
- Horvitz S, Chanaguano D, Arozarena I. 2017. Andean blackberries (*Rubus glaucus* Benth) quality as affected by harvest maturity and storage conditions. Sci Hortic. 226:293–301. https://doi.org/10.1016/j.scienta.2017.09.002.
- Hummer KE, Williams KA, Bushakra JM. 2019. North American crop wild relatives of temperate berries (*Fragaria* L., *Ribes* L., *Rubus* L., and *Vaccinium* L.), p 283–327. In: Greene SL, Williams KA, Khoury CK, Kantar MB, Marek LF (eds). North American crop wild relatives. Vol. 2. Springer International Publishing, Cham, Switzerland. https://doi.org/10.1007/978-3-319-97121-6 9.

- Joo M, Lewandowski N, Auras R, Harte J, Almenar E. 2011. Comparative shelf life study of blackberry fruit in bio-based and petroleum-based containers under retail storage conditions. Food Chem. 126(4):1734–1740. https://doi.org/10.1016/j. foodchem.2010.12.071.
- Kalt W, Forney CF, Martin A, Prior RL. 1999. Antioxidant capacity, vitamin C, phenolics, and anthocyanins after fresh storage of small fruits. J Agric Food Chem. 47(11):4638–4644. https:// doi.org/10.1021/jf990266t.
- Kim MJ, Perkins-Veazie P, Ma G, Fernandez G. 2015. Shelf life and changes in phenolic compounds of organically grown blackberries during refrigerated storage. Postharvest Biol Technol. 110:257–263. https://doi.org/10.1016/j.postharvbio. 2015.08.020.
- Krüger E, Dietrich H, Schöpplein E, Rasim S, Kürbel P. 2011. Cultivar, storage conditions and ripening effects on physical and chemical qualities of red raspberry fruit. Postharvest Biol Technol. 60(1):31–37. https://doi.org/10.1016/j. postharvbio.2010.12.001.
- Lawrence B, Melgar JC. 2018. Harvest, handling, and storage recommendations for improving postharvest quality of blackberry cultivars. HortTechnology. 28(5):578–583. https://doi.org/10.21273/ HORTTECH04062-18.
- McCoy JE, Clarke JR, Salgado AA, Jeemen A. 2016. Evaluation of harvest time/temperature and storage temperature on postharvest incidence of red drupelet reversion development and firmness of blackberry (*Rubus* L. subgenus Rubus Watson). Discovery, The Student Journal of Dale Bumpers College of Agricultural. Food Life Sci. 17(1):59–65.
- McGuire RG. 1992. Reporting of objective color measurements. HortScience. 27(12): 1254–1255. https://doi.org/10.21273/HORTSCI. 27.12.1254.
- Medina-Pastor P, Mezcua M, Rodríguez-Torreblanca C, Fernández-Alba AR. 2010. Laboratory assessment by combined z score values in proficiency tests: Experience gained through the European Union proficiency tests for pesticide residues in fruits and vegetables. Anal Bioanal Chem. 397(7):3061–3070. https://doi.org/10.1007/s00216-010-3877-3.
- Oliveira DM, Kwiatkowski A, Rosa CILF, Clemente E. 2014. Refrigeration and edible coatings in blackberry (*Rubus* spp.) conservation. J Food Sci Technol. 51(9):2120–2126. https://doi.org/10.1007/s13197-012-0702-3.
- Palonen P, Weber C. 2019. Fruit color stability, anthocyanin content, and shelf life were not correlated with ethylene production rate in five primocane raspberry genotypes. Sci Hortic. 247:9–16. https://doi.org/10.1016/j.scienta.2018. 11.088.
- Perkins-Veazie P, Collins JK, Clark JR. 1993. Changes in blackberry fruit quality during storage. Acta Hortic. 352:87–90. https://doi.org/10.17660/ActaHortic.1993.352.11.
- Perkins-Veazie P, Collins JK. 2002. Quality of erect-type blackberry fruit after short intervals of controlled atmosphere storage. Postharvest Biol Technol. 25(2):235–239. https://doi.org/10.1016/S0925-5214(02)00025-X.
- Perkins-Veazie P, Collins JK, Clark JR. 1996. Cultivar and maturity affect postharvest quality of fruit from erect blackberries. HortScience. 31(2):258–261. https://doi.org/10.21273/HORTSCI.31.2.258.
- Perkins-Veazie P, Collins JK, Clark JR. 1999. Shelf-life and quality of 'Navaho' and 'Shawnee' blackberry fruit stored under retail storage conditions. J Food Qual. 22(5):535–544. https://doi.org/10.1111/j.1745-4557.1999.tb00184.x.

- Salgado AA, Clark JR. 2016. "Crispy" blackberry genotypes: A breeding innovation of the University of Arkansas Blackberry Breeding Program. HortScience. 51(5):468–471. https://doi.org/10.21273/HORTSCI.51.5.468.
- Samaniego I, Brito B, Viera W, Cabrera A, Llerena W, Kannangara T, Vilcacundo R, Angós I, Carrillo W. 2020. Influence of the maturity stage on the phytochemical composition and the antioxidant activity of four andean blackberry cultivars (*Rubus glaucus* Benth) from Ecuador. Plants (Basel). 9(8):1027. https://doi.org/10.3390/plants9081027.
- Samtani JB, Kushad MM. 2015. A longer marketing life for blackberry and raspberry fruit. Virginia Cooperative Extension Publication 423–701. Virginia Tech, Blacksburg, VA, USA.
- Segantini DM, Threlfall R, Clark JR, Brownmiller CR, Howard LR, Lawless LJR. 2017. Changes in fresh-market and sensory attributes of blackberry genotypes after postharvest storage. JBR. 7(2):129–145. https://doi.org/10.3233/JBR-170153.
- Strik BC, Clark JR, Finn CE, Bañados MP. 2007. Worldwide blackberry production. HortTechnology.

- 17(2):205–213. https://doi.org/10.21273/HORTTECH. 17.2.205.
- Strik BC, Finn CE, Clark JR, Pilar Bañados M. 2008. Worldwide production of blackberries. Acta Hortic. 777:209–218. https://doi.org/ 10.17660/ActaHortic.2008.777.31.
- Türkben C, Sarıburun E, Demir C, Uylaşer V. 2010. Effect of freezing and frozen storage on phenolic compounds of raspberry and blackberry cultivars. Food Anal Methods. 3(3):144–153. https://doi.org/10.1007/s12161-009-9102-3.