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A Review on the Postharvest Quality and Composition of Small Fruit Crops Grown in Alabama and the Southeast U.S.A.

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Abstract

Globally, postharvest losses account for 25–50% of the total value of specialty crops. Postharvest physiology and technology of specialty crops aim to extend shelf-life, increase crop quality and mitigate losses. Rabbiteye blueberries, floricane blackberries and muscadines are among the most important small fruits for Alabama. These fruits are primarily marketed through local and regional outlets across the Southeast U.S. Yet, each of these small fruits exhibits distinct differences in shelf-life, optimal storage conditions, and susceptibility to postharvest degradation, which influence best handling practices and consumer satisfaction. To meet the demands of growers and consumers, new small fruit germplasm is constantly being developed. Many breeding programs have emphasized developing disease-resistant and heat-resilient genotypes with improved flavor and texture; however, postharvest suitability has been evaluated to a limited extent across newly developed germplasm. Understanding these crop-specific differences is essential for growers, distributors, and retailers aiming to maintain fruit quality and reduce postharvest losses throughout the supply chain. Shelf-life directly influences nutritional content, sensory attributes, and texture, all of which are critical to consumer acceptance. Texture degradation, particularly softening, greatly influences small fruit postharvest quality. Biochemical changes in cell structure can lead to a rapid decline in fruit firmness and overall acceptability. Given the perishability of small fruits, especially under high heat production and suboptimal storage conditions, postharvest research is urgently needed for Alabama to develop strategies that preserve quality and extend shelf-life. This includes screening new germplasm, refining storage protocols, and understanding textural and nutritional degradation. Postharvest research can identify key traits including firmness retention, color stability, water loss resistance, and flavor, thereby enhancing molecular knowledge to fast track the development of small fruit material with longer shelf-life and field heat resistance. Such efforts are essential for reducing small fruit loss, enhancing marketability, and supporting food security in Alabama and beyond.

Introduction and Importance of Postharvest Physiology

The world population is predicted to reach 9.1 billion people by 2050 (FAOSTAT 2009), with food security a global challenge to feed the increasing population (Godfray et al. 2010). A critical component of food security is postharvest physiology to extend shelf-life and quality. Direct outcomes of postharvest research include the establishment of the best storage conditions (e.g., temperature, relative humidity, atmosphere) or the use of hormone blockers to inhibit the action of plant ripening hormones like ethylene. The field of postharvest physiology is specifically focused on reducing food losses and preserving quality from harvest to consumption (Bisht and Singh 2024; Kitinoja et al. 2011). The major goals of postharvest physiology are to 1) identify cultivars with good flavor, nutritional quality and long postharvest shelf-life, 2) create integrated management systems that maximize yield without sacrificing quality and 3) advance optimal postharvest handling practices to maintain fruit (and vegetable) quality and reduce food losses (Kitinoja et al. 2011; Valenzuela 2023). Postharvest losses occur at multiple stages including on farm, during handling, packing and distribution and at the retail and consumer levels (Kitinoja et al. 2011). Worldwide, growers, distributors and retailers can lose between 25 to 50% of the total value of specialty crops (Blond 1984; Bisht and Singh 2024; Coulomb 2008; Tadesse 1991). While complete elimination of these losses may not be feasi-

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ble, reducing food waste is essential for global food security (Bisht and Singh 2024; Porat et al. 2018).

Over the past three decades, the introduction of sophisticated packing and cooling systems has transformed the small fruit industry and greatly improved shelf-life (Horvitz 2017). However, in states like Alabama, much of the small fruit production relies on smaller acreage growers (USDA NASS Accessed on 06-21-2025) where cold storage is minimal. Several systems can be implemented by postharvest physiology research programs to decrease postharvest loss and increase food security. These systems include screening improved genotypes for quality (Giongo et al. 2023), determining optimal temperature and humidity regimes immediately after harvest to preserve shelf-life (Kader 2005; 2010; Valenzuela 2023), evaluating edible coatings or packaging to reduce weight loss and slow senescence (Huynh et al. 2023; Tezotto-Uliana et al. 2014), and integrating physiological changes from genomics through phenomics phases (Zhao et al 2019).

Postharvest fruit texture and softening, which are products of ripening and senescence as well as postharvest handling practices, are among the most critical determinants of small fruit marketability and storage potential (Cappai et al. 2018; Giongo et al. 2013; Giongo et al. 2022; Giongo et al. 2023; Oh et al. 2024). In the southeastern U.S., high field temperatures further challenge fruit quality (Deltsidis et al. 2022), especially in crops that deteriorate rapidly when fully ripe and do not ripen properly if harvested early. In response, plant breeding strategies have largely focused on developing disease and heat-resistant genotypes, as well as improving textural characteristics to extend shelf-life (Blaker et al. 2014; Threlfall et al. 2016; Ru et al. 2024). Despite these efforts, the complex interplay of physical and biochemical processes underlying texture and the lack of reliable texture predictors continue to limit large-scale genotype screenings (Oh et al. 2024).

Small fruits such as blackberry, raspberry, muscadine, and blueberry have significant differences in shelf-life, optimal storage conditions, and susceptibility to textural and nutritional degradation. This review highlights critical gaps in small fruit postharvest research for Alabama and the southeast U.S. The gaps being discussed include limited postharvest data on newly released genotypes and advanced selections, as well as insufficient understanding of the mechanisms that drive fruit softening. Additionally, the effects of high production temperatures and postharvest storage conditions on nutritional degradation remain underexplored. We propose that tracking quality loss through firmness and texture (Trandel-Hayse et al. 2023), inner pulp composition (Trandel et al. 2021a; 2021b; Trandel-Hayse et al. 2025), and nutritional changes can guide breeding programs toward developing germplasm with improved consumer appeal and extended shelf-life.

Alabama Small Fruits and Postharvest Considerations

Small fruits are critically important to human health as blueberry, blackberry, raspberry and strawberry are rich in number of phytochemical compounds (Cordiero et al. 2021; Li et al. 2018; Maheshwari et al. 2022; Paparozzi et al. 2018). Improved production, availability, and fruit quality have led to consistent global increases in consumption (Scheerens 2001). A wide variety of small fruits, including rabbiteye and southern highbush blueberry, floricane-fruiting blackberry, golden kiwifruit, strawberry and muscadine are produced in Alabama (USDA NASS 2025). Alabama is unique in that its small fruits are marketed almost exclusively through local outlets. The state also lacks widespread access to sophisticated packing and cooling systems. These constraints present a valuable opportunity to position Alabama as a test location for evaluating and improving small fruit quality under resource-limited conditions. Thus, research focused on postharvest suitability and the development of shelf-life extension methods is critical to support expansion into regional and national markets.

Appearance, sensory qualities, nutritional content, and texture are factors that directly influence small fruit shelf-life (Gilbert et al. 2014; 2015). Developing accurate and precise methodologies for evaluating both visual and sensory shelf-life estimation is important for consumer acceptance (Giménez et al. 2012). Sensory perception plays a central role in marketing decisions, with flavor largely determined by the balance of sugars and acids, as well as volatile compounds and aromas (Potts et al. 2020). Sweetness arises from glucose, fructose, sucrose, sugar alcohols, and starch breakdown, while sourness is linked to organic acids such as malic, citric, tartaric, quinic, and succinic acids. Bitterness and astringency are produced by polyphenols such as phenolic acids (hydroxybenzoates and hydroxycinnamates) and flavonoids (Sánchez-Rodríguez et al. 2019).

After harvest, the rate of degradation in small fruits varies by species, occurring very rapidly in raspberries and blackberries (Huynh et al. 2023; Li et al. 2018) and more slowly in muscadine grapes and blueberries (Connor and MacLean 2019; Yan et al. 2023). Regardless of timing, degradation negatively impacts fruit appearance, texture, nutritional, and volatile and flavor profiles (Potts et al. 2020). Generally, extended storage leads to a loss of green or fresh notes and an increase in fruity, overripe or musty flavors which is deemed as “off flavors” by consumers (Potts et al. 2020). Soluble solids content (SSC), and titratable acidity (TA) content of small fruits tends to decrease with longer storage, reducing sweetness and increasing bland flavor. Currently, the number of days in storage is a key predictor used in handling and marketing decisions before noticeable changes in appearance and sensory quality occur (Torres-Sanchez et al. 2020).

Small fruits also undergo extensive fruit softening after harvest driven by biochemical processes that alter internal cell structure and texture (Sañudo-Barajas et al. 2019). These changes are influenced by hormonal activity (e.g., ethylene), water loss, shriveling, decay, cell size, and degradation of cell wall polysaccharides and the middle lamella (Allan-Wojtas et al. 2001; Konarska 2015). Understanding the specific drivers, including biochemical and molecular changes in postharvest softening can inform the development of new genotypes with firmer, more resilient small fruits (Sañudo-Barajas et al. 2019).

Caneberry Production and Postharvest Physiology

Blackberry. Blackberry is Alabama’s state fruit with 143 acres in production in 2020. A 136% increase in the number of operations engaged in blackberry production occurred between 2012 and 2017, suggesting increased consumer demand across the state (USDA NASS 2025). The harvest window for Alabama relies predominantly on floricane-fruiting blackberry cultivars, which are harvested from late May to mid-July. Primocane cultivars from the University of Arkansas breeding program produce fruit in both summer and fall offer advances in fruit quality, productivity and marketability (Clark et al 2005; Clark 2015; Clark and Barchenger, 2015). These types could greatly extend the marketing window for Alabama growers. One of the main challenges with primocane production is managing high summer and fall temperatures, which can reduce fruit bud development (Spiers and Neal 2024) and fruit quality from harvest through storage. To support blackberry cultivar selection and planning, Table 1 provides a list of suitable floricane- and primocane- fruiting cultivars for Alabama production.

Blackberries have a short shelf-life ranging from 2 to 18 days depending on harvest and storage conditions (Li et al. 2018). These berries lack a protective rind or cuticle, making them prone to bruising during harvest and transport, which can result in leakage, red drupelet reversion, and microbial growth (Chunghong et al. 2019). If mishandled, the fruit can have 100% loss of saleability within 48 hours of harvest (Samtani and Kushed 2015). Quality and composition have been widely

Table 1. Floricane- and primocane-fruiting blackberry culitvars for production in Alabama and the Southeast U.S.A.

Cultivar	Release Year	Fruiting Type	Thorn Type	Fruit size (g)	Soluble Solids (°Brix)	pH	Titratable Acid (%)	Chill Hours
Chester	1985	Floricane	Thornless	5				800
Navaho	1989	Floricane	Thornless	5	11.4			850
Arapaho	1993	Floricane	Thornless	5	9.6			450
Tripple Crown	1996	Floricane	Thornless	6-8				800
Kiowa	1996	Floricane	Thorny	9-14	10			300
Von	1998	Floricane	Thornless	6-7	9.4			500
Apache	1998	Floricane	Thornless	7-10	10			800
Ouachita	2003	Floricane	Thornless	5.5	9-10	3.43	0.66	500
Natchez	2007	Floricane	Thornless	10	9-14	3.17	1.03	400
Osage	2012	Floricane	Thornless	5	9-11.2	3.58	0.69	500
Sweetie Pie	2016	Floricane	Thornless	5	11			400
Caddo	2019	Floricane	Thornless	8-9	8-10	3.10	1.33	800
Ponca	2019	Floricane	Thornless	7	10-13	3.54	0.82	
Prime-Ark 45	2009	Primocane	Thorny	4-9	10-12	3.2	0.81	300
Prime-Ark Freedom	2014	Primocane	Thornless	9	10.4	3.20	0.92	500
Prime-Ark Traveler	2016	Primocane	Thornless	7-8	9-11	3.63	0.67	300-500
Stark Black Jim	2017	Primocane	Thornless	N/A	11-12			300-500

addressed on floricane-fruiting blackberries (Kim et al. 2015; Perkins-Veazie et al. 2007; Segantini et al. 2018). Some work has been conducted on the physiochemical and sensory attributes of primocane-fruiting blackberries (Threlfall et al. 2016).

The commercially acceptable range of physiochemical attributes for blackberries includes 8-11% for SSC (°Brix), 3.0-3.6 for pH, 0.7-1.5% for TA, 6-14 grams for berry weight, 50-150 for drupelets per fruit, and 51-115 for pyrenes per fruit (Threlfall et al. 2016). Typically, primocane fruits are larger than those from the floricanes (Clark 2015). Contradictory results have been reported when comparing floricane and primocane cultivars at harvest. A study by McCall-Thomas et al. (2007) reported primocane cultivars exhibited higher firmness and greater storability compared to floricane cultivars. Conversely, Threlfall et al. (2016) assessed three floricane cultivars ('Natchez', 'Osage', 'Ouachita') and two primocane cultivars at harvest ('Prime-Ark 45', 'Prime-Ark Traveler') indicating no consistent differences in physiochemical attributes. Most traditional cold storage studies have addressed early released floricane cultivars such as 'Natchez', 'Ouachita' 'Navaho', and 'Shawnee' (Kim et al. 2015; Perkins-Veazie, et al. 2007). University of Arkansas has assessed quality traits including red drupelet reversion, fruit size, textural change and color/appearance in both primocane and floricane-fruiting blackberries (Segantini et al. 2018; Chizk et al. 2023a; Chizk et al. 2023b).

North Carolina State University (NCSU) has a blackberry breeding program, which released its first thornless, floricane-fruiting cultivar, 'Von', in 2013. Postharvest research evaluated 'Von' for its fruit quality traits during cold storage (Fernandez et al. 2013). NCSU also evaluated many other floricane-fruiting blackberries including 'Shawnee', 'Navaho' and 'Arapaho' to further understand simulated retail storage effects on shelf-life (Perkins-Veazie et al. 2007). As well, NCSU evaluated nutritional content on organically grown 'Natchez', 'Ouachita' and 'Navaho' during cold storage for 13 days (Kim et al. 2016). The University of Florida has recently focused on enhanced breeding strategies for blackberry, emphasizing the development of thornless, disease-resistant and flavorful cultivars that can withstand Florida's hot/humid climate. Paudel et al. (2025) utilized genome assembly of primocane-fruiting blackberry to accelerate the development of new improved cultivars with enhanced horticultural and nutritional traits. Amidst the prevalent blackberry research in many southeastern states, minimal data is available on newly released floricane- and primocane-fruiting cultivars/advanced selections in Alabama, highlighting a critical gap in understanding the shelf-life potential.

Growing region and ambient climactic conditions are other considerations that can affect blackberry physiology and postharvest quality. The impact of production temperature and relative humidity on blackberry quality is critically important as blackberries prefer moderate production temperatures. High temperatures (>90 °F or 32 °C) can lead to reduced harvestable yields and fruit size as well as increased leakiness (Deltsidis et al. 2022), red drupelet reversion (Armour et al. 2021) softening and decay in blackberries. Firmness of primocane fruit has been noted to vary greatly depending on harvest temperatures and when harvest was done. Blackberries harvested in the peak summer tend to have shorter shelf-life compared to fall harvests when the temperatures have cooled (Strik and Thompson 2009). This is particularly relevant in the southeastern U.S., including Alabama, where diverse climatic zones from the Gulf Coast to the Appalachian foothills result in wide temperature (68 to 95 °F or 22 to 33 °C) and relative humidity (52 to 84%) ranges (USDA 2023). These environmental variations underscore the need for cultivar evaluations that account for regional differences in yield and quality. Postharvest research can play a pivotal role in identifying optimal harvest and handling practices to mitigate the effects of heat and humidity.

These insights support a more integrated approach to blackberry improvement, bridging breeding and postharvest research. The observed variability in fruit firmness, drupelet integrity, and shelf-life among floricane and primocane-fruit cultivars highlights the importance of selecting traits that enhance both field performance and postharvest durability. The development of primocane-fruiting cultivars with increased firmness and extended harvest windows presents promising opportunities for genetic advancement, particularly in the southeastern U.S. Further understanding production temperature and humidity on fruit decay, leakage, and red drupelet reversion will provide postharvest physiologists with a foundation for optimizing handling and storage protocols tailored to cultivar-specific responses.

Raspberry. In the U.S., raspberries (*Rubus idaeus*) are traditionally grown in more northern climates such as the Northeast, Midwest and Pacific Northwest (Molina-Bravo et al. 2011; Yao and Rosen 2011). Elevated production temperatures can adversely impact both flower development and fruit quality (Molina-Bravo et al. 2011; Spiers and Neal 2024). Many cultivars lack tolerance to heat and drought, making them poorly suited to the high summer temperatures of the south (Alabama Cooperative Extension 2023; Fernandez et al. 2016). Raspberry acreage in Alabama is limited with most production occurring in high, cool elevation zones (e.g., north Alabama) or sites that are partially shaded from intense sun irradiation (Alabama Cooperative Extension, 2023). Raspberry adaptation from best to worst for Alabama is floricane-fruiting black raspberry, floricane-fruiting purple raspberry and some floricane- and primocane- fruiting red raspberry (Alabama Cooperative Extension 2023). Alabama Cooperative Extension has released recommendations for the most suitable raspberry cultivars for local production, as outlined in Table 2. Auburn University is currently conducting a raspberry variety trial to assess the performance of 11 cultivars under both open-field and shaded production systems in Alabama's hot climate. This trial aims to introduce cultivars such as 'Himbo Top', 'Joan J', 'Mac Black', and 'Polka' to central and northern regions of the state, where they have not been widely grown.

Raspberries are highly perishable due to their delicate structure, high respiration rates and susceptibility to fungal pathogens (Huynh et al. 2023). They have a thin and fragile skin and are aggregates of drupelets attached to a receptacle. When picked the receptacle becomes completely detached, generating an internal cavity that accelerates quality deterioration, and further shortens shelf-life (Giongo et al. 2019). In current industry practices, raspberries are harvested and immediately cooled to near-freezing storage temperatures (0 to 2 °C) to attain a shelf-life of 10 days (do Nascimento Nunes et al. 2009; Nunes 2002). As most growers in Alabama lack cold storage, holding small fruits at ambient conditions or moderate cold storage (4.5 to 15 °C) decreases the shelf-life to 1 to 5 days (Huynh et al. 2023).

Raspberries at harvest range from 9.3 to 14.0% SSC (°Brix) and 1.39 to 2.61% TA with SSC increasing and TA showing no significant changes through 3 days of storage (Kruger et al. 2011). Much of the postharvest research on raspberries has been with refrigerated storage studies (Nunes 2002), application of edible coatings such as chitosan after harvest (Tezotto-Uliana et al. 2014), and passive and modified atmosphere packaging (Huynh et al. 2023). Many of these studies utilize raspberries harvested from climates with optimal temperature and production conditions. Field spray applications of chitosan might be useful in combating the hot and humid climate of the southeast. This work is being done on other tropical and subtropical crops to extend shelf-life (Wang et al. 2025), yet little is known about its efficacy on raspberry.

Southeastern states like North Carolina have had success in producing raspberries particularly in the mountain regions (Bradish et al. 2011). At harvest, research indicated red primocane-fruiting of 'Nantahala', 'Autumn Britten' and 'Caroline' will main-

Table 2. Floricane- and primocane-fruiting raspberry cultivars with suitability for production in Alabama and the Southeast U.S.A.

Cultivar	Release Year	Fruiting Type	Thorn Type	Fruit weight (g)	Fruit Color	Soluble Solids (°Brix)	Titratable Acid (%)	Chill Hours
Logan	1881	Floricane	Thorny	5.0	Purple			800
Bristol	1934	Floricane	Thorny	2.5	Black	7-7.5	1.6	>800
Blackhawk	1955	Floricane	Thorny	3.0	Black	9-11.5	1.5	>800
Allen	1957	Floricane	Thorny	2.5	Black	10.0	1.2-1.5	>800
Southland	1969	Floricane	Thorny	3.0	Red	10.0	1.0	800-900
Dorman Red	1972	Floricane	Thorny	3.0	Red	9.5	1.7	300-500
Jewel	1973	Floricane	Thorny	2.5	Black			>800
Bradywine	~1980	Floricane	Thorny	3.0	Purple	9.5	0.9	>800
Royalty	1993	Floricane	Thorny	5.0	Purple	9.5	0.9-1.1	200-300
Heritage	1969	Primocane	Thorny	4.5	Red	11.3	1.8	250
Caroline	1999	Primocane	Thornless	2.5	Red	9.7	1.5	200-300
Nantahala	2008	Primocane	Thorny	5.5	Red			800-1000

tain high nutritional quality when harvested from above-optimal production temperatures (>27 °C) (Bradish et al. 2011). Another study out of North Carolina assessed the same primocane-fruiting cultivars to determine the effect of warm production location (Mountain vs. Piedmont) and production systems (field vs. high tunnel) on anthocyanin, carotenoid and vitamin content. Cultivar differences were evident, but few differences were seen between production system and harvest location (Bradish et al. 2015). Despite the promising data from North Carolina, extended cold storage evaluations of raspberry cultivars grown under warm production conditions remain limited in other southeastern states, including Alabama, Georgia, and Florida.

To address this gap, identifying raspberry cultivars with greater heat tolerance, stable fruit quality, and adaptability to shaded or high-elevation systems provides a foundation for breeding efforts tailored to the southeastern U.S. In parallel, postharvest physiologists can use cultivar-specific data on respiration rates, shelf-life, and susceptibility to decay to refine cooling strategies, packaging technologies, and explore novel treatments such as field-applied chitosan. Together, these efforts can help overcome the climatic limitations of raspberry production in Alabama and similar regions.

Blueberry Production and Postharvest Challenges

Historically, the U.S. is one of the largest global fresh market blueberry producers with 310,800 MT harvested in 2022 (USDA NASS, Accessed on 06-21-2025). Alabama blueberry acreage (1,427 acres) predominantly relies on rabbiteye (RE) genotypes as they are easier to manage than southern highbush (SHB); RE is later flowering, tolerant to drought, has moderate disease resistance and produces high yields (Potter 2011). Unfortunately, acceptance of RE blueberry in the wholesale market remains a serious issue (Itle 2021), as fruit are considered to have poor quality and flavor compared to the highbush counterparts. The fruit are grittier, seedier and tougher compared to northern or southern highbush (Itle 2021). This perception has reduced the financial return to growers and can even cause exclusion of some RE varieties from the marketplace.

Due to these quality issues, breeding programs including University of Georgia and Auburn University have recently accelerated the development of RE blueberry germplasm (Coneva 2021). Consumers have made it clear they prefer fruits with both high-quality aroma and superior flavor (Sater et al. 2020). The premium consumers are willing to pay for more flavorful varieties justifies the development of new RE cultivars bred for flavor and aroma (Sater et al. 2020). Thus, recent emphasis on RE blueberry breeding is to generate fruit with high quality, increased firmness and consumer acceptance for fresh market (Ru S, personal communication). Moreover, increasing grower acceptance of SHB cultivars in Alabama is needed. Part of growers' concerns regarding SHB cultivars is that many bloom early, making them vulnerable to late-season frost damage. Without protected cultivation (e.g., high tunnels), Alabama growers view this as risky and have been less inclined

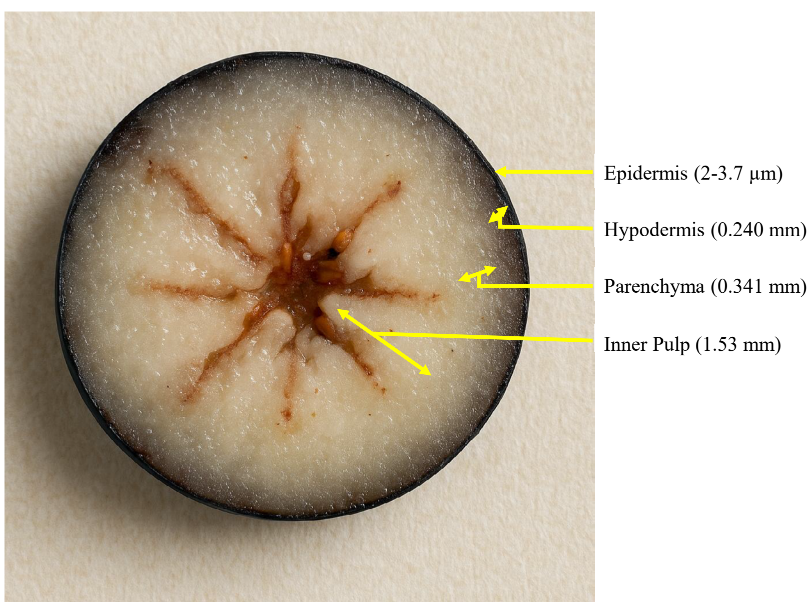

Figure 1. Morphology of blueberry fruit depicting the primary layers associated with texture and firmness.

to take on SHB. Postharvest studies comparing the composition, shelf-life, nutritional quality and flavor of RE and SHB cultivars can further elucidate fruit quality issues and target the needs of local growers.

Fruit texture of blueberry and postharvest gaps. Fruit texture is a crucial factor that influences consumer acceptance and informs the consumer about the fruit's overall quality and composition (Sañudo-Barajas et al. 2019). Ripening and harvest can trigger many biochemical processes associated with texture change and the postharvest period is critical for slowing the onset of undesirable texture attributes (Olmedo et al. 2021; Sañudo-Barajas et al. 2019). Blueberry firmness has become a key quality trait for blueberry breeding programs since firmness influences postharvest quality and consumer acceptance (Giongo et al. 2022). Giongo et al. (2013) defines blueberry firmness as "the force required to break or fracture the blueberry sample between molars". Phenotypically, blueberry fruit firmness is divided into three categories, crisp, firm, and soft, with firm cultivars considered the industry standard (Trandel-Hayse et al. 2023).

Blueberry cultivars and ecotypes display significant variation in fruit firmness (Olmedo et al. 2021; Trandel-Hayse et al. 2023). Older RE cultivars such as 'Tifblue', 'Woodard' and 'Climax' were firmer with undesirable texture traits including seediness and grittiness. In contrast, older SHB cultivars were considered softer with smaller seeds and higher quality (Silva et al 2005). The University of Florida breeding program has since improved fruit firmness in SHB blueberries, leading to the development of crisp-textured genotypes (Blaker and Olmstead 2014; Blaker and Olmstead 2015). Texture is a complex trait and understanding it requires rigorous phenotyping often employing various automatic texture-analyzing instruments (Oh et al. 2024) as well as assaying modifications of cell wall composition, cellular arrangement (shape, size) and middle lamella degradation (Blaker and Olmstead 2014; Blaker and Olmstead 2015; Chea et al. 2019; Olmedo et al. 2021; Sanhueza et al. 2024; Trandel-Hayse et al. 2023; Wan et al. 2024).

Blueberry fruit morphology plays a critical role in firmness and texture variability. Anatomically, blueberries consist of three primary layers: the epicarp or epidermis (skin), mesocarp (pulp) known as the largest tissue in the fruit, and endocarp (seed area) (Edwards et al. 1970; Wan et al. 2024). The epidermis, which is the outermost single layer of cells, is covered by a cuticle and a hydrophobic extracellular layer of wax offering protection against dehydration and external environmental stresses (Yeats and Rose, 2013). Below the epidermis, is a pigment-rich hypodermal layer surrounded by a ring of vascular bundles (Gough, 1994). The mesocarp exists after hypodermis, composed mainly of parenchyma cells and vascular bundle rings. These parenchymal cells and vascular bundles strengthen the flesh tissues in the pulp and contribute to the firmness of the fruit (Blaker and Olmstead 2014). The endocarp (inner pulp) encloses the seeds and is made up of 5 carpels, including 10 locules and highly lignified seed-containing placentae (Wan et al. 2024; Fig. 1).

While some cell wall work has been conducted on caneberries and muscadine, blueberry texture has been the focus of extensive research in recent years. Across the southeast, fruit firmness and texture have been extensively studied in SHB cultivars, with more limited data available for REs (Giongo et al. 2013; Giongo et al. 2022; Olmedo et al. 2021; Trandel-Hayse et al. 2023). Recent texture work conducted by Oh et al. (2024) assessed six established RE (soft and firm) and forty-one SHB cultivars (soft, firm and crisp) using a TA.XT2Plus texture analyzer (Stable Micro Systems, Hamilton, MA, USA) via 2 mm flat probe or 1.4 mm needle probe. The fruit were stored for 24 hrs, two, four or six weeks at 2 °C and 80 % RH with 21 total texture parameters evaluated. When all texture parameters were considered, no evident distinctions between SHB and RE cultivars were identified. Principal component analysis further indicated a high level of variation among the 21 texture parameters irrespective of the blueberry ecotype. Itle et al. (2024) evaluated firmness ratings over a 30-day shelf-life study in five RE and eight SHB cultivars using a TMS Pro Texture Analyzer (Food Technology Corporation, Sterling, VA, USA) to analyze Kramer Shear Press. The study was conducted over a two-year period with RE cultivars indicating a 26% increase in firmness in year 1 and 31% increase in year two after 30 days of storage, respectively. This increase in texture suggests that RE does not hold up as well during storage as SHB (Itle et al. 2024).

The type of texture analyzer used and probe shape offer distinctive roles in understanding blueberry texture. The TA.XT2Plus Flat probes are better suited for quantifying the overall softness of blueberry (Luby et al. 2023). While the needle probe penetration method offers a more targeted approach by quantifying texture as penetration force (N) from specific fruit layers, up to 3 mm depth. This includes layers such as the epidermis (2-3 µm), hypodermis (0.240 mm), parenchyma (0.341 mm), and inner pulp (1.53 mm), enabling a detailed analysis of how different fruit layers and tissue contribute to the overall texture (Oh et al. 2024; Fig. 1). Many studies on RE genotypes lack robust texture analysis or analyzed only small genetic populations (e.g., five to six cultivars). Moreover, these studies did not consider advanced selections which are being bred for increased quality and textural traits.

Blueberry Quality and Plant Cell Wall Polysaccharides. Fruit softening can strongly affect fruit quality and is a ripening process that has been strongly associated with plant cell wall polysaccharides (Zhang et al. 2019, Trandel et al. 2021a; Trandel-Hayse et al. 2023). Cell wall composition affects phenotypic firmness traits in blueberry and plant cell walls are highly complex in that they differ in relative amounts of cellulose, hemicellulose and pectic polysaccharides (Trandel-Hayse et al. 2023). Modification of cell wall polysaccharides can change blueberry firmness via depolymerization of matrix glycans, changes in neutral sugar composition, and loss of the middle lamella. Identification in the changes of cell wall constituents via cell wall sequential fraction extraction and characterization of neutral sugar components within the fractions can further elucidate quality changes in blueberry and other small fruit crops (Olmedo et al. 2021). Furthermore, the differences in composition levels, susceptibility to depolymerization, and enzymatic degradation of these polysaccharides in the cell wall are impacted during various postharvest stages. (Liu et al. 2021; Olmedo et al. 2021; Trandel-Hayse et al. 2023).

Previous research on blueberries has primarily focused on ripening and harvest related attributes, with relatively few studies examining changes during postharvest storage. Most investigations of cell wall composition have assessed only total sequential fractions, with limited work conducted on RE fruit (Deng et al. 2013). Most cell wall studies have been performed on SHB cultivars (Liu et al. 2019; Chea et al. 2019; Trandel-Hayse et al. 2025). Crude cell wall analysis of water-soluble, chelator soluble, sodium carbonate soluble, alkali soluble (hemicellulose) and cellulose fractions were followed through different ripening stages and at harvest (Vicente et al. 2007; Chea et al. 2019; Trandel-Hayse et al. 2025) with minimal data present on cold storage treatments (Deng et al. 2013; Chea et al. 2019; Liu et al. 2019) suggesting a critical gap in knowledge. While only one study to date has quantified neutral sugars, glycosidic linkages and polysaccharide classes in the peel and pulp of three SHB cultivars differing in firmness at harvest (Trandel-Hayse et al. 2023)

Generally, postharvest research on SHB fruit indicated the water-soluble fraction (pectic polysaccharides) increased while the sodium carbonate (covalently bound pectin), hemicellulose and cellulose decreased with both ripening stages and storage times (Deng et al. 2013; Chea et al. 2019). The displacement of the pectic fractions indicate structural modifications occur during fruit ripening and are related to fruit firmness (Chea et al. 2019). In addition to pectin, researchers have also linked blueberry firmness to hemicellulose. Specifically, Trandel-Hayse et al. (2023) found hemicellulosic polysaccharides to be the most abundant in both the peel and pulp of SHB blueberry fruit, however, the classes of hemicellulose differed between the tissue type and cultivars analyzed. Similarly, Vincente et al. (2007) observed reductions in hemicellulose content in two alkali-soluble fractions as highbush blueberries transitioned from green to fully blue, suggesting a strong association between hemicellulose degradation and fruit softening.

Despite these findings, research examining the total polysaccharide fractions, neutral sugar compositions of the fractions, cell wall modifying enzymes and tissue microstructure of whole berries have not fully explained the variation in firmness among blueberry cultivars. A significant gap remains in understanding the biochemical and structural differences between RE and SHB genotypes (Silva et al. 2005). While cell wall polysaccharide linkage analysis and quantitation have been performed on SHB cultivars at harvest (Trandel-Hayse et al. 2023), no comparable studies exist for RE blueberries. Characterizing biochemical differences at harvest and throughout extended storage in RE genotypes is essential for identifying key traits or molecular markers associated with improved textural quality.

Given the complexity of blueberry texture and its relationship to shelf-life, integrated approaches are needed to understand firmness and composition across cultivars and ecotypes. Anatomical, biochemical, and morphological contributors, such as tissue structure, cell wall composition, and probe-specific measurements, play critical roles in shaping postharvest performance and consumer appeal. Combining postharvest phenotyping with quantitative genetics enables the identification of molecular markers linked to texture stability and cell wall composition which will guide the development of improved cultivars. These findings emphasize the importance of standardized texture analysis methods and highlight how fruit morphology and cell wall dynamics influence storage outcomes. Together, this knowledge supports the advancement of genotypes that maintain desirable texture throughout the supply chain, ultimately reducing food loss and improving the quality and consistency of small fruit crops.

Muscadine Grape

In the U.S., grape cultivation dropped slightly from 113,6155 acres in 2017 to 110,8161 acres in 2022. In contrast, Alabama experienced a 38% increase in grape-growing acreage during this period (USDA NASS 2025), indicating a strong interest in grape production. Southeastern growers are eager to explore grape species such as *V. vinifera*, in addition to the traditionally grown muscadine grapes (*Muscadinia rotundifolia*) as a means of increasing profit. Unfortunately, a major danger to the *V. vinifera* grape industry is Pierce's Disease (PD). This disease is vectored by the glassy winged sharpshooter, which prefers the warm humid temperatures of the southeastern U.S. (Purcell 1997). Currently, only muscadine grapes with inherent resistance to the disease, as well as tolerant American and French-American hybrid bunch grapes can be grown in the southeast. The University of California Davis has released PD resistant *V. vinifera* cultivars including 'Camminare noir', 'Paseante noir' and 'Errante noir' (Riaz et al. 2018), but there is little postharvest information available on these cultivars.

Common fresh market muscadine cultivars with improved production habits (perfect flowered), flavor and texture characteristics, and seedlessness, have been released from public and private breeding programs in North Carolina, Arkansas, Mississippi, and Georgia (Clark and Barchenger 2015). Auburn University is currently conducting production assessments of standard (female flowered) cultivars compared to those with the improved production and quality characteristics. A list of cultivated muscadine for Alabama production can be seen in Table 3 (Coneva et al. 2024). Coneva et al. (2024) is also performing variety trial assessments for Alabama on muscadine advanced selections out of University of Georgia and University of Arkansas breeding programs.

Postharvest research on muscadine has been conducted on the physicochemical attributes of fruit firmness, composition of pH, soluble solids and titratable acidity, total organic acids and sensory analysis at the time of harvest (Felts et al. 2018). Older muscadine cultivars including 'Supreme' (industry standard) and 'Granny Val' typically have a shelf-life of 3 to 4 weeks (Perkins-Veazie et al. 2012). Newer cultivars of 'Ruby Crisp' and 'Hall' have increased firmness and have been shown to hold up in storage for up to 4 weeks (Connor and MacLean 2019).

Challenges with fresh market muscadine are the need for immediate removal of field heat to extend shelf-life as fruit ripen in the hottest part of the season (mean daily temperatures >30 °C). Other pertinent issues include weight loss and shrivel, softening, and decay, increasing peel toughness, and loss of flavor after extended storage (Himelrick et al. 2003; Habibi et al. 2024; Sarkhosh et al. 2024). Plantings of seedless muscadine cultivars and selections in Alabama have recently been added by Gardens Alive LLC. Performance of these seedless muscadines in Alabama and consumer acceptance is in early stages. Postharvest research is needed to address the above issues as well as cultivar suitability potential for extended storage. Postharvest research also needs to prioritize rapid cooling, shelf-life extension, and reducing issues like shrivel, peel toughness, and flavor loss. Data on storage performance and consumer response will also guide breeders in developing cultivars with improved texture, firmness, and postharvest resilience.

Table 3. Muscadine cultivars with suitability for Alabama production and the Southeast U.S.A.

Cultivar	Release Year	Flowering Type	Fruit weight (g)	Fruit Color	Soluble Solids (°Brix)	Titratable Acid (%)	Chill Hours
Granny Val	1983	Perfect	12	Bronze	15	0.3-0.9	200-600
Southern Home	1994	Perfect	7	Black	16.5	0.4-0.6	<500
Razzmatazz	2007	Perfect	0.5	Burgundy	17	0.4-0.6	<400
Lane	2012	Perfect	10	Dark purple	15.5	0.5	<500
Hall	2014	Perfect	10	Bronze	15.6		<500
Paulk	2017	Perfect	15.5	Purple	14-19	0.3-1.1	<500
Ruby Crisp	2019	Perfect	15	Dark red	17	0.3-0.5	200-600
Supreme	1988	Female	18	Dark purple	14-22		200-600

Nutritional Importance of Small Fruits and Gaps in Postharvest Physiology

Antioxidant activity, minerals, anthocyanins, phenolics/polyphenolics, chlorophyll, carotenoids, vitamins and volatile organic compounds are critical phytonutritional components of small fruits. Antioxidants encompass a number of molecules and act by decreasing free radical production during oxidative stress in the body and by decreasing anti-inflammatory responses (Jiménez-Aguilar and Grusak 2017). Phenolic compounds of flavanols, flavonoids, isoflavones and cinnamic acids are present in small fruits and have profound human effects on immunomodulatory, neuroprotection, anti-obesity, anti-diabetic, anti-microbial, and cardiovascular disease prevention properties (Silva et al. 2020). Anthocyanins are a group of polyphenolic compounds and represent one of the most important sub classes of pigmented flavonoids in the plant kingdom (Li et al. 2017). Chlorophyll and carotenoids are another class of natural pigments related to antioxidant activity, free radical scavenging, eye health and play a role in anticarcinogenic effects (Jiménez-Aguilar and Grusak 2017). While volatile organic compounds act as anti-inflammatory, anti-cancer, anti-obesity and anti-diabetic (Gu et al. 2022).

Anthocyanins are highly abundant in small fruits as accumulation generally increases during the ripening and peaks when fruit are fully ripe (Chung et al. 2016; Robinson et al. 2020). In storage, total anthocyanins in small fruits tend to be relatively stable due to the fruits' low pH. For example, a study conducted by Yan et al. (2023) performed a comprehensive anthocyanin and flavanol profiling on 20 blueberry genotypes at harvest and after 2 or 4 weeks of storage at 0.5 °C. The study indicated no significant loss of total anthocyanins occurred, while specific anthocyanins and flavanols varied greatly among genotypes with some increasing and others decreasing during storage (Yan et al. 2023). In red raspberry, an increase in total anthocyanins of 160 mg/L and phenolic activity of 275 mg/L was found after 3 d of storage at 3 °C followed by 1 d at 20 °C (Kruger et al. 2011). Similarly, Haffner et al. (2002) found total anthocyanins increased in 5 red raspberry cultivars after 7 d storage at 1.7 °C. In blackberries, anthocyanin levels remain stable during postharvest storage, with no significant increase or loss observed (Perkins-Veazie and Kalt 2002). Many studies have focused on total anthocyanin content during storage, but anthocyanins are diverse, with over 20 major derivatives in small fruits (Yan et al. 2023). Understanding how these compounds change during cold storage, especially in new cultivars and selections, is vital for Alabama. Given the state's limited cold storage capacity, studying anthocyanin stability under suboptimal conditions (>5 °C) can help determine the optimal timing for getting fruit to consumers at peak quality.

Although carotenoids are not highly abundant in several small fruits when fully ripe, they serve as important nutritional compounds to human health (Jiménez-Aguilar and Grusak 2017). Carotenoids can also contribute to aroma volatiles, specifically terpenes such as ionone or damascenone, which impart floral and fruity flavors in small fruits (Carvalho et al. 2013). Generally, in blueberries, raspberry, blackberries and muscadine many carotenoids decrease or are less evident as ripening persists (Beekwilder et al. 2008; Carvalho et al. 2013; Habibi et al. 2024; Li et al. 2024). When fully ripe, blueberries tend to have slightly higher content of total carotenoids (~21.40 μg/g) compared to blackberry which have been reported to range between 1.39 μg/g and 7.4 μg/g dry weight (Beekwilder et al. 2008; Toledo-Martin et al. 2018). While total carotenoids in red raspberry were found to be ~18 μg/g with the most abundant carotenoids being lutein/zeaxanthin and β-carotene (Bradish et al. 2015). Despite their low abundance in small fruits, there is limited understanding of how carotenoids degrade during storage. Most research has focused on carotenoid levels during ripening and at harvest, yet postharvest treatments and storage conditions may significantly influence their stability

Polyphenols (flavonoids, flavanols, and isoflavones) and volatile organic compounds are most notable in small fruits for their flavor and aroma attributes. There are thousands of phenolic compounds that exist in the plant kingdom, and they are classified based on structural similarities. In many small fruits phenolic acids, flavonoids and tannins are the most abundant (Craft et al. 2012; Robinson et al. 2020). Similarly, small fruits can contain hundreds of volatile organic compounds with esters, alcohols, terpenoids, aldehydes and ketones often the most abundant (Gu et al. 2022). The composition and content of these small compounds can vary greatly with small fruit species, cultivar and time of harvest (Robinson et al. 2020). For example, volatiles most associated with aroma in blueberry are hexanal, limonene, nerol, 1,8-cineole, 1-penten-1-ol, and terpineol (Sater 2020). In muscadine, 2-ethyl-1-hexanol, cinnamyl alcohol, Z-3-Hexenal, hexanal and propyl acetate are most associated with aroma and flavor. While Threlfall et al. (2020) assayed 10 blackberry genotypes for aroma volatile composition and identified 155 compounds with ethyl acetate, octanoic acid, D-limonene, and hexanal as the most abundant. As noted above, the diversity of volatiles is highly complex in small fruits, however their degradation during storage remains poorly understood. Moreover, limited information remains on analyzing larger genetic populations (established cultivars and advanced selections) of small fruit species. Additionally, the interaction between volatiles and polyphenols in shaping flavor and aroma remains largely unexplored (Bizzio et al. 2022; Lv et al. 2021). Research focusing on these gaps can lead to a greater understanding of flavor and consumer acceptance.

Summary

Small fruit crops grown in Alabama and the Southeastern U.S. face significant postharvest challenges that directly impact their marketability, textural changes, nutritional value, and consumer acceptance. Despite their rich phytonutrient profiles and increasing demand, blueberries, blackberries, raspberries and muscadines are highly perishable and prone to rapid quality degradation. This review highlights the critical need for targeted postharvest research to address cultivar-specific responses to storage, texture softening, and biochemical changes. While progress has been made in understanding fruit firmness and shelf-life, particularly in SHB blueberries, substantial gaps remain in understanding texture variability in RE blueberries. Diligent monitoring of postharvest performance of newly released cultivars and advanced selections is critical, particularly under the unique environmental conditions of the Southeast, to ensure suitability for extended storage and market expansion.

Postharvest physiology is also essential for evaluation, monitoring, and preserving the nutritional quality of small fruits. Although tremendous gains have been made in preventing postharvest decay, significant gaps remain in our understanding of how storage conditions affect the stability and degradation of key phytonutrients. The ability to screen and study multiple cultivars for responses to postharvest stress, and the biochemical interactions between volatiles and polyphenols that shape flavor and nutritional value remains challenging. Advancing postharvest physiology through integrated approaches such as combining biochemical, sensory, and structural analyses will be essential to support growers, reduce food loss, and enhance the competitiveness of small fruit industries in the Southeast.

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