A Review of Rabbiteye Blueberry Breeding: From Historical Foundations to Future Opportunities

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Abstract. **Among cultivated blueberry types, rabbiteye blueberry (*Vaccinium ashei* Reade) is a native hexaploid species valued for its exceptional vigor, adaptability to diverse soils, tolerance to abiotic and biotic stresses, and longevity. Despite these advantages and its continued importance to small-scale and mid-scale growers, rabbiteye breeding has progressed more slowly than southern highbush blueberry breeding. The lack of breeding effort leaves key production challenges in rabbiteye blueberry unaddressed, thus weakening the competitive edge of rabbiteye cultivars and resulting in drastically reduced planting acreage in recent years. These issues, including low fruit quality, late harvest timing, and pollination dependence, highlight important gaps in rabbiteye improvement. Therefore, this review summarizes the origin, biology, commercial history, and global production of rabbiteye blueberry. It also traces the development and status of public and private breeding programs and evaluates the performance of existing cultivars with regard to productivity, stress tolerance, disease resistance, phenology, and fruit quality. We further examined progress made through interspecific hybridization and highlighted persistent challenges, including a narrow genetic base, limited genomic resources, and insufficient breeding investment. Finally, we outlined key priorities for future rabbiteye improvement and emphasized enhanced fruit quality and shelf life, mechanical harvestability, parthenocarpy, optimized phenological development, and the integration of modern genomic and phenomic tools. Renewed and coordinated breeding efforts that leverage both traditional and modern approaches are essential to restoring market confidence in rabbiteye blueberries and supporting a more sustainable and resilient blueberry production system.**

Introduction

The numerous health benefits and improved quality of blueberries (Rodriguez-Mateos et al. 2016) have spurred a rapid expansion of the blueberry industry over the past two decades (Food and Agriculture Organization Corporate Statistical Database 2024). As the world's second largest producer of blueberry, the United States accounts for 32% of global production and generates an annual crop value exceeding $1 billion (US Department of Agriculture, Economics Statistics and Market Information System). The southeastern United States is a major production region, contributing 28% of the US fresh market value by producing the earliest and most profitable blueberries in the country (US Department of Agriculture, National Agricultural Statistics Service 2022). Cultivated blueberries belong to the Ericaceae family (genus *Vaccinium*, section *Cyanococcus*) (Camp 1945). Among major species of cultivated blueberries, the rabbiteye (*V. ashei* Reade; $2n = 6x = 72$) and southern highbush blueberry (*V. corymbosum* L. interspecific hybrids; $2n = 4x = 48$) are mainly grown in the southeastern United States, with mild winters. In contrast, northern highbush (*V. corymbosum* L.; $2n = 4x = 48$) and low bush blueberries (*V. angustifolium* Aiton; $2n = 4x = 48$) are cultivated in northern regions of the United States, where longer chilling requirements and greater cold hardiness are essential (Retamales and Hancock 2018; Vander Kloet 1980).

The genus *Vaccinium*, section *Cyanococcus*, encompasses nine diploid, 12 tetraploid, and three hexaploid species (Camp 1945). Rabbiteye blueberry as a category was originally considered to comprise three distinct hexaploid species, *V. amoenum* Aiton, *V. ashei* Reade, and *V. virgatum* Aiton, which are all native to the southeastern and southcentral regions of United States. Among these three species, *V. virgatum* was initially erroneously identified as tetraploid (Camp 1945). Subsequent studies suggested that these three species may be best considered a single and highly variable hexaploid species consolidated under the name *V. virgatum* based on their uniform ploidy level and continuous morphological variation across natural populations (Ballington 2006). However, recent molecular evidence,

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supported by morphological data, have shown that *V. ashei* and *V. virgatum* are distinct species (Fritsch et al. 2024; Weakley et al. 2024). Phylogenetic analyses based on DNA sequence data place *V. virgatum* and *V. ashei* in separate clades, with *V. virgatum* allied with "highbush" species (e.g., *V. corymbosum* L. and *V. formosum* H.C. Andrews), whereas *V. ashei* is more closely allied with a clade containing *V. darrowii* Camp and *V. tenellum* Aiton (Weakley et al. 2024). In addition, Weakley et al. (2024) identified morphological characteristics that distinguish *V. ashei* from *V. virgatum*, including differences in the size, shape, and distribution of trichomes, as well as variations in leaves, flowers, and fruits. Proceeding from these taxonomic studies, the descriptors for *V. ashei* Reade are clearly the taxonomy representative of commercial rabbiteye cultivars; therefore, this is the terminology that we use hereafter.

As a native species of the southeastern United States, rabbiteye blueberries have been commercially cultivated in this region and other parts of the United States and the world for more than a century. Rabbiteye blueberries are valued for their excellent stress tolerance, adaptability to diverse soils, high vigor, yield, and longevity (Erb, 1993; Hancock et al. 2008; Lyrene 1987, 2006; Retamales and Hancock 2012; Scherm and Krewer 2008; Smigell et al. 2012). Currently, rabbiteye is the preferred choice for many small growers. In the Southeast, more than half of the blueberry farms are small operations that rely on rabbiteye cultivars (US Department of Agriculture, National Agricultural Statistics Service), despite the prevalence of southern highbush on large-scale farms in Georgia, Florida, and North Carolina. However, rabbiteye breeding has significantly lagged behind highbush breeding as driven by the needs of large-scale producers. To fully capitalize on the favorable traits of rabbiteye blueberries and better support small to mid-sized growers, this review describes the history of rabbiteye breeding, highlights recent progress and remaining challenges, and outlines future directions for cultivar improvement.

Origination and Biology

The rabbiteye blueberry is native to the southeastern United States (Camp 1945). Wild populations were mainly found in northern Florida, southern Georgia and Alabama, southern Mississippi, and other parts of the Southeast, where they often thrived in river valleys, swamps, open woods, or abandoned farmland (Camp 1945; Lyrene 1987). In the wild, rabbiteye plants typically range between 1.5 and 7 m in height (Lyrene 1987). Like other cultivated blueberries, rabbiteye exhibits a deciduous growth habit with simple leaves arranged alternately along the stem (Eck 1966; Lyrene 1987). Their leaves have minutely stalked glands on the abaxial surfaces, whereas leaves of both lowbush and highbush blueberry are nonglandular. Under warm winter conditions, some cultivars may retain their leaves and exhibit a semi-evergreen habit (Eck 1966; Lyrene 1987).

Compared with highbush cultivars that have undergone more intensive breeding, rabbiteye cultivars are typically only three to four generations from their wild ancestors. Rabbiteye cultivars tend to preserve greater vigor, higher productivity, and broader tolerance to diverse soil types and environmental stresses compared with southern highbush (Abdolshahi et al. 2025; Lyrene 1987). Unlike highbush blueberries, which are autotetraploid, rabbiteye blueberries are hexaploid (Lyrene and Ballington 1986). It remains unclear whether rabbiteye are autohexaploid, allohexaploid, or autoallohexaploid (Lyrene 1987). This unique ploidy level creates reproductive barriers between rabbiteye and other *Vaccinium* species, limiting allele introgression and genome diversity.

The growth cycle of rabbiteye in the southern region is like that of southern highbush. Based on a model for northcentral Florida, flower buds are initiated primarily between October and December, when daylength falls below 12 h (Darnell et al. 1992). Plants typically enter dormancy during winter and remain dormant until midspring; thereafter, blooming and fruit development occur. Vegetative growth tends to peak both before and after the harvest. A brief period of root growth may occur soon after fruit harvest, with the most significant root growth following the last wave of late-season shoot growth (Darnell et al. 1992).

Commercial Production

The first commercial production of rabbiteye began on a farm in northeast Florida in 1887 and expanded to approximately 1000 ha by the 1930s (Camp 1945; Lyrene 1987). This early commercial venture ultimately failed, primarily because of the lack of market competitiveness (Lyrene 1987). At that time, highly variable wild plants were transplanted to the commercial fields, resulting in inconsistent fruit quality. However, northern highbush clonal plantations produced high-quality fruits and overtook the market. Later, public breeding programs were initiated in the Southeast to revitalize the commercial production of rabbiteye. The development of rabbiteye cultivars with consistent performance and improved fruit quality enabled the resurgence of rabbiteye blueberry production. As a result, rabbiteye blueberry became the dominant type in the Southeast from the 1970 to 1990s. At the peak of rabbiteye planting history, this species was planted in more than half of Florida's blueberry acreage and more than 90% of Georgia's (Scherm and Krewer 2003; Williamson et al. 2019). So far, rabbiteye blueberries have been commercially produced in 10 states in the southeastern United States, including Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, and Texas (Darnell et al. 1992), primarily between latitudes of 30 °N and 37 °N. Additionally, small-scale rabbiteye cultivation has been reported in other states in the United States, such as Illinois, Kentucky, Maryland, and western states like California (Darnell et al. 1992) and parts of Oregon (Finn et al. 2014). Outside the United States, rabbiteye blueberries have been commercially produced in countries such as Australia (Wright), China (Jiang et al. 2019), Chile (France et al. 2017), New Zealand (Buck et al. 2012), Japan (Miyashita et al. 2012), and Latvia (Ripa and Audriņa 2009).

Competition from Southern Highbush and New Opportunities for Rabbiteye

In recent years, the prominence of rabbiteye blueberries has declined with the increasing popularity of southern highbush cultivars. Extensive breeding efforts for southern highbush have led to significant improvements in fruit quality, early maturity, and overall performance, thus making them the preferred type among large-scale producers (Lyrene 2002; Williamson et al. 2019). A recent survey reported that rabbiteye acreage has decreased to less than 40% in Georgia (Chu and Williams 2024), and only minimal rabbiteye acreage remains in small U-pick operations in

Florida. This sharp decline has been exacerbated by negative perceptions of rabbiteye fruit, including its thick skin and seedy and gritty texture (Itle et al. 2025), which are associated with large seed size, high seed number, and high stone cell content (Wan et al. 2024). Additionally, rabbiteye quality is challenged by postharvest fruit rot issues (Itle et al. 2025; Smith et al. 1996).

Although southern highbush blueberries dominate the acreage in southeastern United States growing regions, they require intensive management practices, including spring frost protection, soil amendments, and disease control (Scherm et al. 2001), which are often cost-prohibitive for small growers. In contrast, rabbiteye blueberries offer advantages such as reduced production costs and high productivity because of their resilience and vigorous growth (Makus et al. 1996). Additionally, market demand for late-maturing blueberries in the southeastern United States continues to increase. The US fresh blueberry imports have increased rapidly over the past 15 years, filling the seasonal gap from fall to early spring (Kramer 2020). This influx of imports has reduced the premium price for southern highbush blueberries in early spring. Consequently, southeastern growers are seeking late-season cultivars to extend their production period. Rabbiteye blueberries, which ripen 1 to 2 months later than southern highbush, have regained interest as a viable option. To meet this growing demand, new rabbiteye cultivars with improved fruit quality, higher yields, and an extended harvest window need be developed.

History and Status of Rabbiteye Breeding

Rabbiteye blueberry breeding was initiated in the early 20th century by the US Department of Agriculture (USDA), Agricultural Research Service (ARS) and Georgia Coastal Plains Experiment Station in Tifton, GA, USA (Lyrene 1987). The facility is now part of the University of Georgia (UGA), Tifton campus. Subsequently, more breeding programs were established in other parts of the Southeast to improve rabbiteye cultivars, including those at North Carolina State University (NCSU) in the 1930s, University of Florida (UF) in the 1940s, and USDA-ARS in Poplarville, MS, USA, in the 1970s (Hancock 2006; Lyrene 2006; Suszkiw 2008). Between 1925 and 1943, intensive evaluations of wild rabbiteye collections at the USDA-ARS station in Tifton, GA, USA, identified superior selections such as 'Black Giant', 'Clara', 'Ethel', and 'Myers' (Krewer and Nesmith, 2002; Lyrene 1987), which later served as founders for many cultivars. The first rabbiteye cultivars, Callaway and Coastal, were released in 1949 through collaboration between the UGA and the USDA-ARS. Since then, more than 64 rabbiteye cultivars have been released by eight public and private breeding programs worldwide (Fig. 1, Table 1). Early breeding efforts led to commercial adoption of rabbiteye cultivars beginning in the 1960s (Hancock 2006; Stringer et al. 2023) and subsequently established rabbiteye blueberries as the dominant type in the Southeast until 1990s (Scherm and Krewer, 2003; Williamson et al. 2019). However, with the development of southern highbush cultivars, which offer earlier ripening, superior fruit quality, and higher profitability, Florida and Georgia growers shifted toward southern highbush production beginning in the 1980s, prompting public breeding programs to focus on southern highbush breeding to better meet industry demands (Dr. Patricio Munoz and Dr. Hudson Ashrafi, personal communications).

Both public and private breeding programs have been instrumental in rabbiteye cultivar development across the Southeast and beyond. The UGA blueberry breeding program, active since the 1940s, remains a leader in rabbiteye breeding. This program has released 21 cultivars (Fig. 1, Table 1), including widely adopted cultivars such as Brightwell, Alapaha, and Titan (Nesmith, 2009). Current UGA efforts focus on enhancing rabbiteye for large fruit size, extended fruiting window, desirable fruit quality, and machine harvestability. Historically, the blueberry breeding programs at NCSU and UF have made significant contributions to rabbiteye improvement, releasing 10 cultivars each. Cultivars such as Powderblue, Premier, and Columbus from NCSU and Beckyblue and Bonita from UF and are still widely grown (Table 1). However, both programs have shifted the focus primarily to southern highbush because of evolving industry demands. The blueberry

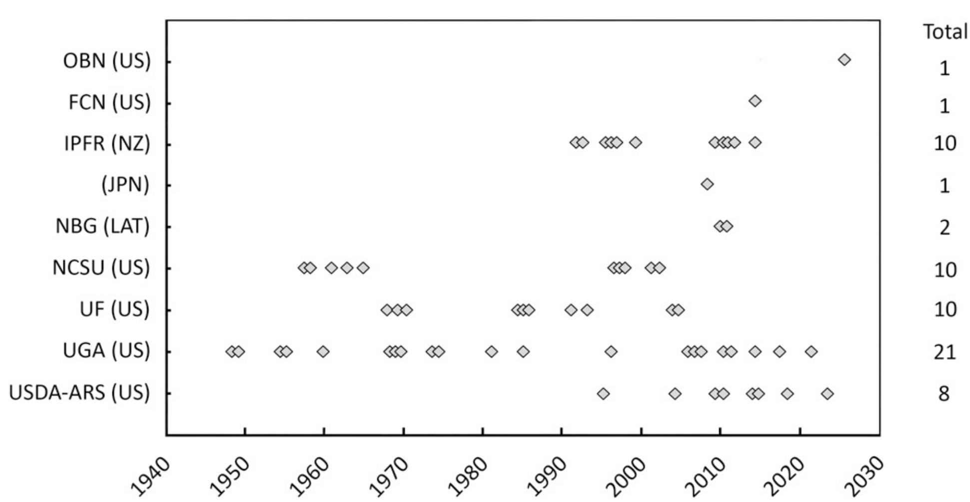

Fig. 1. Timeline of rabbiteye (RE) cultivars released by public and private breeding programs. The y-axis presents the year of cultivar releases. Breeding programs (from bottom to top) are as follows: US Department of Agriculture, Agricultural Research Service (USDA-ARS; USA); University of Georgia (UGA; USA); University of Florida (UF; USA); North Carolina State University (NCSU; USA); National Botanic Garden (NBG; Latvia); Japan (JPN; program name unknown); Institute for Plant and Food Research (IPFR; New Zealand); Fall Creek Nursery (FC; USA); and Oregon Blueberry Nursery (OBN; USA). The number of RE cultivars released by each program is listed on the right.

Table 1. Rabbiteye cultivars released by multiple breeding programs (adapted from Abdolshahi et al. 2025). The number of cultivars released by each program is listed in parentheses.

Breeding program	Cultivar name	Female/male parents	Year of release	Estimated chilling hours[i]	References
Fall Creek Nursery (USA) (1)	Overtime	Centurion/Powderblue	2014		Brazelton and Wagner 2012
Oregon Blueberry Nursery (USA) (1)	Raptor (OBG-16252)	Titan (T-959)/Summer Sunset (T-885)	2026		Wagner and NeSmith 2026
Institute for Plant and Food Research (New Zealand) (10)	Maru	Premier/OP	1992		Okie 2002
	Rahi	Premier/OP	1992		Okie 2002
	Tasty Blue (Ono)	Premier/OP	1996		Finn and Clark 2012
	Blue Magic (Whitu)	Premier/OP	1996		Finn and Clark 2012
	Takahe	Premier/OP	1999		Finn and Clark 2012
	Centra Blue	Centurion/Rahi	2009		Patel 2008; Scalzo et al. 2009
	Sky Blue	Centurion/Rahi	2010		Patel 2009b
	Dolce Blue	Centurion/Rahi	2011		'Dolce Blue' NZ PVR3185
	Ocean Blue	Centurion/Rahi	2011		Patel 2009a
	Velluto Blue	Maru/Briteblue	2014		Scalzo 2013
Japan (1)	Fuku-berry	Woodard/Tifblue	2008		Gasic and Preece 2014
National Botanic Garden (Latvia) (2)	Lielogu	Delite/Woodard	2010		Gasic and Preece 2014
	Salaspils Izturiga	Tifblue/OP	2010		Gasic and Preece 2014
NCSU (USA) (*joint with USDA-ARS) (10)	Garden Blue*	Myers/Clara	1958		USDA National Plant Germplasm System (PI 657217)
	Menditoo*	Myers/Black Giant	1958		Okie 2004
	Centurion*	W-4/Callaway	1961	550–650	USDA National Plant Germplasm System (PI 554715)
	Powderblue*	Tifblue/Menditoo	1963	550–600	USDA National Plant Germplasm System (PI 554721)
	Premier*	Tifblue/Homebell	1965	500–550	USDA National Plant Germplasm System (PI 554717)
	Montgomery	NC763/Premier	1997	550	USDA National Plant Germplasm System (PI 657151)
	Yadkin	Premier/Centurion	1997	500–600	USDA National Plant Germplasm System (PI 657153)
	Ira	Centurion/NC911	1997	600	USDA National Plant Germplasm System (PI 657152)
	Onslow	Premier/Centurion	2001	500–600	USDA National Plant Germplasm System (PI 657154)
	Columbus	NC758/NC911	2002	600	Okie 2004
UF (USA) (10)	Beckyblue	FL6-138/E96	1968	300–400	Lyrene and Sherman 1979
	Aliceblue	Beckyblue/OP	1970	300–400	Lyrene and Sherman 1979
	Bluegem	Tifton31/OP	1970	350–400	USDA National Plant Germplasm System (PI 554718)
	Bonita	Beckyblue/OP	1985	350–400	Lyrene et al. 1985a
	Chaucer	Beckyblue/OP	1985	350–400	Lyrene et al. 1985b
	Choice	Tifton31/OP	1985	550	USDA National Plant Germplasm System (PI 554720)

(*Continued on next page*)

Table 1. (*Continued*)

Breeding program	Cultivar name	Female/male parents	Year of release	Estimated chilling hours[i]	References
	Snowflake	Florida-K/NC1830	1991	400–500	Lyrene 1991
	Windy	FL79-19/FL79-27	1993	300	Lyrene 1991
	Savory	Unknown selection OP	2004	300–400	Lyrene 2024
	Florida Rose	FL94-88/FL94-81	2004		Lyrene 2002
UGA (USA) (*joint with USDA-ARS) (21)	Callaway	Myers/Black Giant	1949		Brightwell 1950
	Coastal	Myers/Black Giant	1949		USDA National Plant Germplasm System. Coastal (PI 554705)
	Tifblue*	Ethel/Clara	1955	600–700	Brooks and Olmo 1972
	Homebell*	Myers/Black Giant	1955		Brightwell 1962
	Woodard*	Ethel/Callaway	1960	350–400	Brooks and Olmo 1972
	Briteblue*	Ethel/Callaway	1969	600	Brightwell 1969
	Delite*	Bluebelle/T-15	1969	500	Brightwell 1969
	Southland*	Garden Blue/Ethel	1969		Brightwell 1969
	Bluebelle*	Callaway/Ethel	1974	450–500	Brooks and Olmo 1974
	Climax*	Callaway/Ethel	1974	400–450	Brooks and Olmo 1974
	Brightwell*	Tifblue/Menditoo	1981	350–400	Austin and Draper 1983
	Baldwin*	Tifblue/Homebell	1985	550–650	Austin and Draper 1985
	Austin*	T-110/T-99	1996	450–500	Hall and Draper 1997
	Ochlockonee*	Tifblue/Menditoo	2006	650–700	NeSmith et al. 2002
	Alapaha*	T-65/T-99	2006	450–550	NeSmith and Draper 2004
	Vernon*	T-23/T-260	2007	500–550	NeSmith et al. 2005
	Summer Sunset[ii]*	Climax/US-1056	2010		NeSmith and Ehlenfeldt 2011
	Titan (T-959)	T-460/FL80-11	2011	500–550	NeSmith 2014
	Krewer (T-1101)	Vernon/OP	2014	400–450	NeSmith 2018
	T-460 (Frostberry Delight™)	T-223/T-258	2017	500–550	Karp and Gasic 2022
	TO-3097 (Pink Cosmo™)	T-459/T-743	2021	400–450	NeSmith 2022
USDA-ARS Southern Horticultural Research Unit (Mississippi, USA) and USDA-ARS (Beltsville/ Chatsworth, NJ, USA) (8)	Little Giant[ii]	*V. constablaei*/T-65	1995		Murrell 1995
	De Soto	T 110/T 107	2004	600–650	Stringer et al. 2006
	Prince	MS 598/FL80-11	2009	300–400	Stringer et al. 2010
	ARS 96-138, Pink Lemonade[ii]	Delite/NJ 89-158-1	2010		Clark and Finn 2010
	Bluesfest	T 142/Powderblue	2014	500–600	Stringer et al. 2015
	Nocturne[ii]	US 874/Premier	2014		Ehlenfeldt et al. 2015
	Muffin Man	T 366/Brightwell	2018	400–500	Babiker et al. 2018
	USDA-Spiers	MS 167/MS 536	2023	400	Stringer et al. 2023

[i] Estimated chilling hours based on cultivar release information, mostly calculated based on temperature between 0 and 7 °C.
[ii] Hexaploid interspecific hybrids.
NCSU = North Carolina State University; OP = open pollination; UF = University of Florida; UGA = University of Georgia; USDA-ARS = US Department of Agriculture, Agricultural Research Service.

breeding program at the USDA-ARS Southern Horticultural Research Unit in Poplarville, MS, USA, was initiated in 1971, targeting both southern highbush and rabbiteye blueberries. Together with the USDA-ARS blueberry breeding program in Beltsville/Chatsworth, NJ, the two USDA programs have released eight rabbiteye cultivars, including the most recent release, 'USDA-Spiers', in 2023 (Stringer et al. 2023). Auburn University launched its small fruit breeding program in 2021 to address the needs of small to mid-sized producers in the Southeast. Similar to UGA, Auburn University rabbiteye breeding targets include improved fruit quality, extended shelf life, early maturity, and enhanced disease and stress tolerance.

In the private sector, Fall Creek Farm & Nursery (www.fallcreeknursery.com) and Oregon Blueberry Nursery (www.oblueberry.com) have each released one rabbiteye cultivar, Overtime from Fall Creek Farm & Nursery and Raptor from Oregon Blueberry Nursery; however, their primary emphasis is highbush blueberries. International breeding programs have also contributed to the rabbiteye cultivar pool. The New Zealand Institute for Plant and Food Research released 10 cultivars between 1992 and 2024 (Abdolshahi et al. 2025) (Table 1). The National Botanic Garden of Latvia introduced two cultivars and Japan released 'Fuku-berry', but details about its developer are limited (Gasic and Preece 2014) (Table 1).

Interspecific Hybridization

Rabbiteye cultivars primarily originated from wild *V. ashei* selections; however, interspecific hybridization using species other than *V. ashei* did result in the release of several hexaploid cultivars with 50% or more rabbiteye in their genome. The other hexaploid wild blueberry species native to the southern Appalachian Mountains, *V. constablaei* A. Gray, was commonly used in interspecific hybridization with *V. ashei*. The relatively high cold hardiness and short ripening intervals of *V. constablaei* (Ehlenfeldt et al., 2007) are desirable traits for rabbiteye breeding because they provide tolerance to winter coldness, evasion of spring freeze damage, and advancement of the harvest season. Additionally, it was found that *V. constablaei* contributed to favorable fruit volatiles (Ehlenfeldt et al. 2015). The earliest report of using *V. constablaei* in breeding was reported by Brightwell et al. (1949); in that report, an F_1 breeding population from *V. constablaei* × rabbiteye cultivar 'Pecan' produced progenies with early maturity and small dry stem scars. However, most of the lines were weak and produced small berries with black skin. In a separate interspecific crossing experiment, cold hardy and vigorous F_1 progenies were created from rabbiteye and *V. constablaei* crosses (Darrow et al. 1952). More extensive study of the hexaploid *Vaccinium* hybrids from F_1, $F_1 \times F_2$, BC_1, BC_1 intercross, and $BC_1 \times F_2$ crosses between rabbiteye and *V. constablaei* produced highly variable progenies in both phenological development and fruit quality (Ballington et al., 1986). A few selections from these crosses produced high-quality fruits. Therefore, it appears the outcome of interspecific progenies is highly dependent on the parental line combinations (Ballington and Isenberg 1986), and interspecific hybridization broadens the phenotypic diversity of rabbiteye blueberries.

An impactful interspecific hybrid cultivar Little Giant was selected by Dr. Draper from a *V. constablaei* × *V. ashei* cross (Murrell 1995). 'Little Giant' had small and dark fruits amenable to food processing while exhibiting concentrated ripening, extraordinary cold hardiness, and superior flavor (Ehlenfeldt et al. 2012). The concentrated ripening is desirable for mechanical harvesting (Zapien-Macias et al. 2025), while cold hardiness is useful for extending the planting zone of rabbiteye to the northern United States regions. Besides 'Little Giant', another set of rabbiteye cultivars with *V. constablaei* in their pedigree and unique fruit colors were released (Fig. 2). These cultivars were derived from a USDA program that evaluated the possibility of Northern-adapted rabbiteye cultivars for late-season northern production. These cultivars, including Pink Lemonade (tested as ARS 96-138) (Ehlenfeldt and Finn 2007), Nocturne (Ehlenfeldt et al. 2015), and Summer Sunset (NeSmith and Ehlenfeldt 2011), were products of a complex interspecific breeding pathway. This pathway involved tetraploid northern highbush, hexaploid rabbiteye, and several diploid species including *V. tenellum*, *V. corymbosum*,

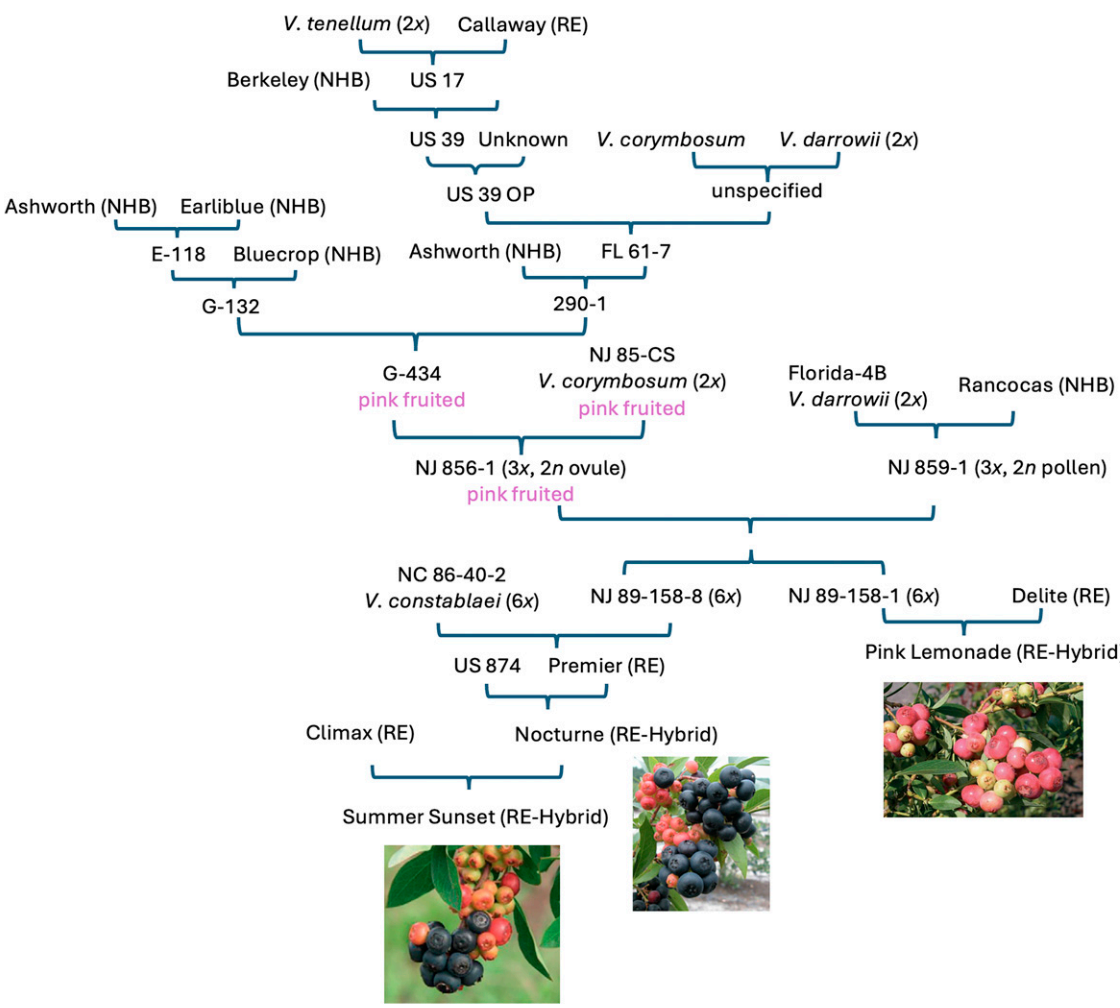

Fig. 2. Interspecific introgression leads to unique colored fruits in rabbiteye cultivars. Adapted from Ehlenfeldt and Finn (2007), NeSmith and Ehlenfeldt (2011), and Ehlenfeldt et al. (2015). RE-HYB = rabbiteye hybrid.

and *V. darrowii*. These cultivars with colorful fruits are attractive for the edible ornamental market. It is worth noting that interspecific hybridization is not the only source of unique fruit colors in rabbiteye. For example, two pink-fruited rabbiteye cultivars, Florida Rose (Lyrene 2004) and Pink Cosmo (NeSmith 2022), were selected from progenies from a cross with *V. ashei* parents.

By crossing with highbush blueberries, rabbiteye contributed to the development of pentaploid cultivars Heintooga (Ballington and Bland 2016), Pearl River (Spiers et al. 1997), and Roberson (Ballington and Rooks 2009), which have a relatively low seed number because of their pentaploid nature. Two pentaploid hybrids from rabbiteye and highbush crosses [hybrid HoSp-S65G-14 from the cross 'Homebell' (rabbiteye) × 'Spartan' (northern highbush) and hybrid ElTi-S65G-14 from the cross 'Elliott' (northern highbush) × 'Tifblue' (rabbiteye)] were found to produce parthenocarpic fruits that were suitable for cluster harvesting because of the synchronized fruit maturation within clusters (Miyashita et al. 2019). Additionally, rabbiteye, reciprocally, was found to make 5% to 15% of the genetic contribution to 24 surveyed southern highbush cultivars (Brevis et al. 2008).

Performance of Existing Rabbiteye Cultivars

Rabbiteye blueberries provide distinct advantages that contribute to sustainability and lower production costs for growers with their excellent soil adaptability and stress tolerance (Erb 1993; Lyrene 1987; Retamales and Hancock 2012; Scherm and Krewer 2008). The tough, stress-resistant nature of rabbiteye blueberries also allows them to remain healthy and productive for more than 30 years compared with just 8 to 10 years for southern highbush under southeastern United States conditions (Fig. 3) (Lyrene 2006). Longevity of rabbiteye cultivars minimize the need for frequent replanting, thus reducing production costs (Smigell et al. 2012). Rabbiteye cultivars also possess several challenging characteristics, such as late ripening, dependence on cross-pollination, and generally less desirable fruit quality than that of southern highbush (Fig. 3), which can create challenges in both production and marketing. We examined the major production and fruit quality traits of rabbiteye blueberries by comparing them with highbush.

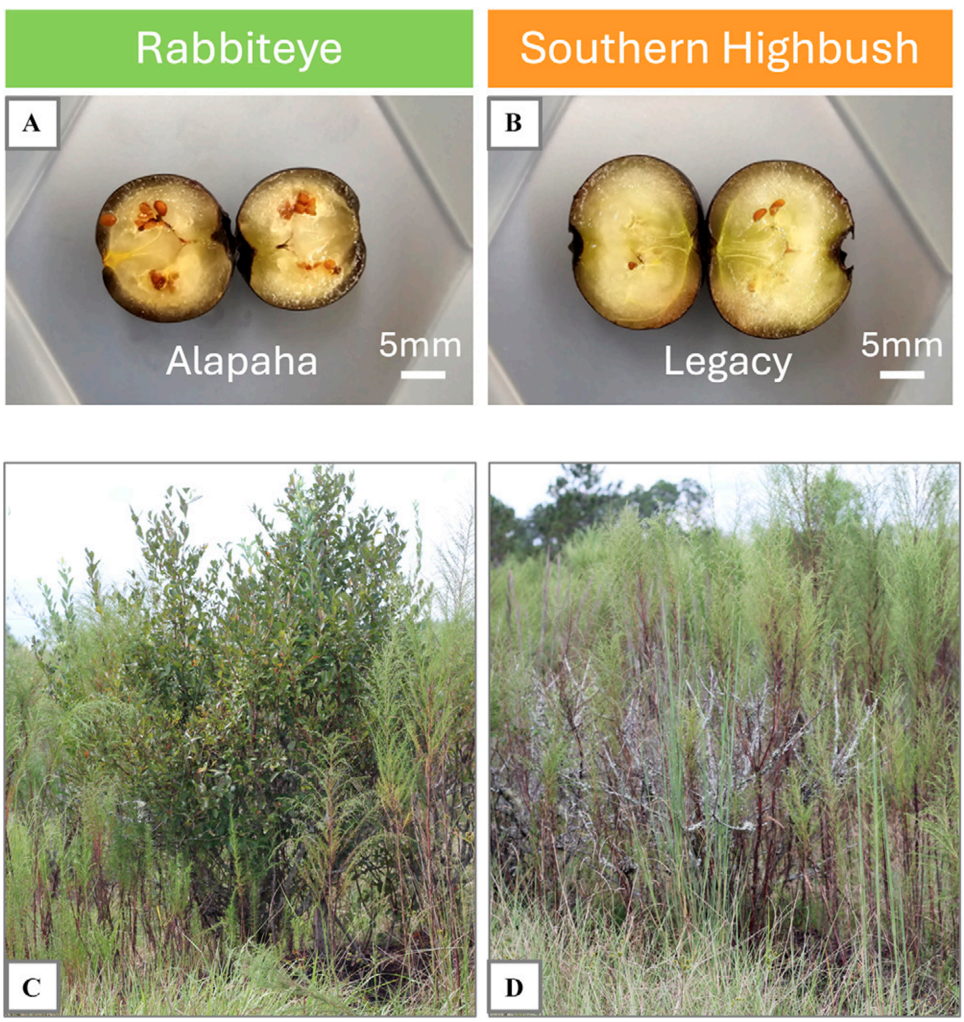

Fig. 3. Comparison of southern highbush and rabbiteye blueberry traits. (**A** and **B**) Variations in fruit size and seediness. Rabbiteye cultivar Alapaha (**A**) produced smaller berries with larger and more seeds compared with southern highbush cultivar Legacy (**B**). (**C** and **D**) Plant resilience after 2 years without maintenance in an abandoned field at the University of Georgia Blueberry Research Farm. Rabbiteye plants remained vigorous and healthy (**C**), whereas southern highbush plants vanished (**D**).

Root distribution and soil adaptability

Blueberries have a characteristically weak root system that is shallow, fibrous, and lacking root hairs (Coville 1910). Most roots of highbush blueberries are thread-like, with diameters less than 1 mm (Gough 1980). In mature northern highbush blueberry plants grown with sawdust mulch and drip irrigation, more than 95% of the roots can be found within the top 60 cm of soil (Gough 1980). Similarly, roots of southern highbush plants tend to confine to the top pine bark bed zone and do not penetrate deeper soil layers (Phillips and Williamson, 2022). Although rabbiteye blueberries generally develop a stronger root system than that of highbush types, they are still considered shallow-rooted compared with other fruit crops (Eck 1966). Austin, 1982 reported that 96% of the roots of rabbiteye cultivars Ethel, Climax, and Tifblue were concentrated in the top 80 cm of sandy-loam soil, and 60% concentrated in the top 80 cm of loamy sand soil (Austin 1986). Spiers (1986) examined the effects of cultivation practices on rabbiteye root distribution and found that mulching and irrigation confined roots of 'Tifblue' to the upper 15 cm of soil, whereas using peatmoss in combination with irrigation resulted in a more uniform root distribution from 0 to 60 cm.

The weak root systems of blueberries also underpin their strict requirements for soil type and pH. Highbush plants prefer sandy to sandy-loam soils enriched with organic matter and maintain optimal growth at a soil pH of 4.5 to 5.5 (Korcak 1986). Their sensitivity to higher pH is associated with a strong preference for ammonium (NH_4^+) as the primary nitrogen form because ammonium availability declines sharply when soil pH increases to 6.0 or above (Darnell et al. 2015). Elevated soil pH also reduces iron solubility, predisposing blueberries to iron-deficiency chlorosis (Darnell et al. 2015). Although rabbiteye blueberries also thrive in acidic well-drained soils rich in organic matter, they are known for greater tolerance of higher pH and a wider range of soil conditions (Erb 1993; Lyrene 1987; Retamales and Hancock 2012; Scherm and Krewer 2008). When used as rootstocks for northern highbush cultivars, rabbiteye roots substantially improved plant survival on soils where highbush seedlings had previously failed, enhancing survival by up to 60% while also increasing plant vigor and yield (Galletta and Fish 1971). Korcak (1986) studied the adaptation of blueberry seedlings to various soil types and found that offspring with a higher proportion of exotic species and rabbiteye background in contrast to a highbush ancestry exhibited greater plant volume even in clay-loam and sandy clay-loam soils with no amendments. In another study, Korcak (1992) evaluated the performance of two northern highbush cultivars (Collins and Spartan) and two rabbiteye cultivars (Woodard and Bluegem) in eight soil types. Rabbiteye was found to produce significantly higher shoot to root ratios than those of highbush blueberries, indicating higher efficiency in nutrient acquisition (Korcak 1992).

Plant growth habit

Rabbiteye blueberry clones have a highly contrasting plant architecture and growth habit. Most of the rabbiteye cultivars have a normal plant height of 1.5 to 2 m (Andersen et al. 2009). Some rabbiteye plants can reach heights of 3 to 4 m, whereas other rabbiteye clones, such as 'Ethel' and wild selections MS134 and FL78-66, have a short and compact dwarf structure (Garvey and Lyrene 1987; Noffsinger et al. 2000). Excessive height of the bush presents a challenge to both machine and hand harvesting. Dwarfism in rabbiteye could be useful for reducing labor costs of rabbiteye berry production (Noffsinger et al. 2000). Studies of F_1 seedling populations from crosses between a dwarf and normal statured rabbiteye plant exhibited highly variable growth habit, indicating partial dominant inheritance of dwarfism in rabbiteye (Garvey and Lyrene 1987). A different study suggested a recessive inheritance model based on the segregation of dwarf phenotypes from a hexaploidy × pentaploid cross {'Montgomery' (rabbiteye) × US 1771 [highbush × (rabbiteye × V. constablaei)]} (Ehlenfeldt 2021). In the modern era, 'DeSoto', a semi-dwarf rabbiteye cultivar with high growth vigor and a plant height of 2 m, was released from the USDA-ARS Poplarville, MS, USA program (Stringer et al. 2006). Continued breeding and selection for normal to short rabbiteye plants will facilitate effective plant management and harvesting.

Plant suckering is another unique problem of rabbiteye architecture. Rabbiteye plants tend to produce new shoots from the rhizomes around the root crown (Lyrene 1987). Although these new shoots are essential for renewing the plant structure, excessive suckering requires additional management effort to remove these suckering shoots. Several modern rabbiteye cultivars, such as Centurion, Delite, Montgomery, and Premier, have considerably lower degrees of suckering (Dr. Mark Ehlenfeldt, personal observations). These cultivars form a valuable resource in breeding for this trait.

Drought tolerance

Blueberries are prone to drought stress because of their weak root systems and the absence of root hairs, which limit their capacity for water uptake under water deficit conditions (Coville 1910). Consequently, drought often triggers rapid stomatal closure, reduced photosynthesis, and slowed plant growth, which further lead to negative impacts on yield, berry number, and berry size (Ru et al. 2024). One of the few earlier studies by Davies and Johnson (1982) reported that moderate and severe water stress reduced leaf area and stem and leaf dry weights in 1-year-old rabbiteye plants. Root dry weight remained unchanged under moderate stress, but it declined significantly under severe drought. Rabbiteye cultivars are generally considered more drought-tolerant than highbush cultivars for their stronger root systems (Hancock et al. 2008). This is supported by empirical observations that many rabbiteye plants can survive and stay productive without irrigation. For instance, in Alabama, although 90% of farmland lacks irrigation access (Zhang et al. 2022), numerous farms have successfully grown rabbiteye blueberries for years by solely relying on rainfall. Beyond the empirical observations, controlled experiments that directly compare drought tolerance between rabbiteye and southern highbush cultivars are limited (Ru et al. 2024). Most studies have focused on short-term physiological responses rather than comprehensive assessments of drought impacts on plant health, productivity, and fruit quality (Ru et al. 2024).

Disease tolerance

Phytophthora root rot disease. Blueberry *Phytophthora root rot* disease is caused by the soilborne oomycete pathogen *Phytophthora cinnamomi* (Hardham 2005; Smith 2008), which attacks the young feeder roots and causes considerable damage to the root system. *Phytophthora root rot* disease is exacerbated by high soil moisture content (Scherm and Krewer 2003); therefore, in areas with poor soil drainage, heavy soil type, drip irrigation, and flooding from large rainfall events, *Phytophthora root rot* disease prevails among susceptible genotypes. Advancement of *Phytophthora root rot* reduces plant vigor and decreases the productive life span of blueberries (Milholland 1975). Ensuring adequate drainage through proper site selection, raised beds, and fungicide applications is critical for reducing infections, but these methods alone are rarely sufficient. Host tolerance or resistance to *Phytophthora root rot* is highly desirable. Tolerance of rabbiteye to *Phytophthora root rot* was demonstrated in a hydroponic growing system (Erb et al. 1987) and pathogen-infected field (Smith 2008).

Mummy berry disease. Mummy berry disease caused by fungal pathogen *Monilinia vaccinii-corymbosi* (Reade) Honey (*Mvc*) is another economically important disease that reduces blueberry production. In the North American blueberry production regions, mummy berry disease is ranked the most important disease by the blueberry industry because of the complete rejection of mummified berries by commercial packing facilities (Gallardo et al. 2018). Infection of blueberries with *Mvc* occurs at two blueberry developmental stages, including shoot emergence and flowering (Ehlenfeldt et al. 2010). In the first stage, *Myc* produces ascospores and infects young shoot and flowers to cause infected tissue to become blighted in early spring. In the second stage, *Myc* conidia are deposited on the stigma of open flowers by pollinators and germinate to produce fungal hyphal (Ngugi and Scherm 2004). The fungal hyphal germ tube extends along the pollen tube pathway and colonizes blueberry ovary, causing fruit to blight. Fungal-infected berries have a normal appearance until harvest. The infected berries turn salmon or a creamy color, shrivel, and drop off from the bushes (Ehlenfeldt et al. 2010). A range of host response to shoot blight from *Myc* was reported among 26 rabbiteye cultivars, with Coastal, Delite, Centurion, Walker, Callaway, and Garden Blue demonstrating lower levels of mummy berry blight infection compared with other cultivars evaluated (Ehlenfeldt and Stretch 2000). Enhancement of mummy berry resistance would be of significant economic value and practical value and significant blight resistance could largely break the pathogen infection cycle.

Other diseases. In addition to tolerance to *Phytophthora root rot* and mummy berry, rabbiteye blueberry has demonstrated tolerance to several other important diseases, including blueberry leaf scorch caused by the bacterium *Xylella fastidiosa* (Hancock et al. 2008; Scherm and Krewer 2008; Sicard et al. 2018) and bacterial wilt caused by *Ralstonia solanacearum* (Genin and Denny 2012). Disease tolerance of rabbiteye blueberries can substantially reduce management costs by decreasing the need for chemical applications and replanting. In blueberry leaf scorch, pathogenic *X. fastidiosa* bacterium vectored by sharpshooters infects and blocks the xylem vessel of the blueberry plant (Horton et al. 2022). Infected plants have reduced water and nutrient transportation, which could lead to plant death within 1 or 2 years upon infection. In terms of bacterial wilt caused by *Ralstonia solanacearum* (Genin and Denny 2012), resistance was reported in rabbiteye cultivars (Conner et al. 2022). In particular, the bacterial pathogen failed to colonize the plant tissue in 'Ochlocknee', indicating qualitative resistance or effector-triggered immunity (Conner et al. 2022). Although disease tolerance to multiple pathogens was identified in rabbiteye, the molecular mechanism of the disease tolerance is not known. Further studies that identify the genetic control of disease tolerance in rabbiteye will enhance the development of disease-resistant blueberry cultivars.

Pollination requirement and timing of flowering and harvesting

Cross-pollination is generally preferred in blueberries, and its importance is especially pronounced in rabbiteye compared with highbush types. Gupton and Spiers (1994) reported that selfing in several rabbiteye cultivars (Tifblue, Brightwell, Beckyblue, Bonita, Climax, Briteblue, and Baldwin) reduced fruit set to 40% compared with 68% under cross-pollination. Sources of self-fertility, however, do appear to be present in rabbiteye blueberry. Meader and Darrow (1944) reported self-fertility in rabbiteye cultivar Blue-toy. Similarly, it was reported that 'Brightwell' was more self-fertile (fruit set of 62%) than 'Tifblue' (fruit set of 23%) when self-pollination was conducted on day 2 after anthesis in a growth chamber condition (Brevis et al. 2006). A low pollen-to-ovule ratio in rabbiteye (402 ± 35) compared with that in other outcrossing species (5859 ± 937) was suggested to be one of the factors leading to low fruit set in rabbiteye (Brevis 2005). Self-pollination also extended the fruit development period by 14 d (from 81 to 95 d) (Gupton and Spiers 1994). In contrast, highbush blueberries ('Sharpblue', 'Avonblue', 'Georgiagem', 'Gulfcoast', 'Cape Fear', 'O'Neal', and 'Blue Ridge') showed a minor decline in fruit set, from 71% (cross-pollination) to 68% (self-pollination). The fruit development period increased by 10 d, from 55 d (cross-pollination) to 65 d (self-pollination). The lower self-fertility rate and greater dependence on cross-pollination in rabbiteye necessitate deliberate field design to pair compatible cultivars and supplement of pollinators during flowering season (Ehlenfeldt and Kramer 2012; Spiers et al. 1985), which not only increase production cost but also contribute to yield instability because pollination efficiency is strongly influenced by weather conditions and pollinator activities. From a breeding perspective, proper selective inbreeding may enable selection for greater self-fertility.

Parthenocarpy is the capability of producing seedless fruit without fertilization, which has been investigated mainly in southern highbush blueberries as a strategy to achieve more reliable yields and reduce pollination cost (Cullen et al. 2024). An evaluation of 13 highbush genotypes including 'Farthing', 'Indigocrisp', 'Raven', and advanced selections from the blueberry breeding program at UF showed that some genotypes such as FL15-80 and FL14-72 had a high level of parthenocarpy and were able to produce marketable fruit without pollination. In contrast, parthenocarpy in rabbiteye blueberries has been reported only under greenhouse conditions in a few cultivars such as Baldwin and Premier (Ehlenfeldt 2012). The overall understanding of parthenocarpy in rabbiteye remains limited, and large-scale germplasm evaluations for this trait are lacking.

In addition to the limitations associated with pollination, rabbiteye cultivars generally bloom later than most southern highbush cultivars and require a longer interval between flowering and harvest (Lyrene 2006), collectively contributing to a later harvest window compared with that of southern highbush blueberries. Darnell et al. (1992) reported that the fruit development period ranged from 60 to 135 d for rabbiteye blueberries as compared with 42 to 90 d for highbush; however, evaluation of modern cultivars will be valuable to update these values in both rabbiteye and southern highbush. The later bloom time of rabbiteye blueberries can provide advantages such as reduced risk of spring frost damage (Lyrene 2006), making them a more practical option for growers without frost protection. However, the extended fruit development period exposes fruit to additional environmental stresses such as heat, drought, and storms. Incidences of fruit split, anthracnose infection, and other fruit rot diseases increase in late harvest seasons because of the combination of high temperature and humidity. Subsequently, the late harvesting window may result in low fruit quality and low market prices relative to early-season production.

Fruit quality

Despite many desirable features, rabbiteye blueberry cultivars have struggled to gain traction in the wholesale market because of less favorable fruit quality. This challenge is primarily attributed to the smaller berry size of early cultivars and their less appealing texture, often described by consumers as seedier, grittier, and having thicker skins compared with southern highbush cultivars (Gündüz et al. 2015; Scherm and Krewer 2003). Consequently, many wholesale brokers preferentially accept only highbush cultivars (Clinard JC, Chief Operating Officer of Wish Farms, Plant City, FL, USA, personal communication).

However, improvements in some fruit quality traits have been demonstrated in newly released rabbiteye cultivars. One critical improvement is berry size. Historically, rabbiteye fruit was characterized by smaller berries compared with southern highbush (Scherm and Krewer 2003), as seen in early cultivars such as Tifblue (released in 1955), Woodard (1960), and Climax (1974) (Scherm and Krewer 2003). New cultivars, including Titan (2010) and Krewer (2002), are recognized for larger berry size (weight, >3 g per berry; diameter, >20 mm), improved firmness, and smaller dry stem scars compared with older cultivars (NeSmith 2017). Comparisons of other fruit quality traits of rabbiteye and southern highbush are described in the following sections.

Fruit firmness and texture

Fruit firmness and texture in southern highbush blueberry cultivars have been extensively studied, with more limited data available for rabbiteye (Cappai et al. 2020; Giongo et al. 2013, 2022; Olmedo et al. 2021; Trandel-Hayse et al. 2023). Previous research has shown that southern highbush cultivars exhibited lower tissue firmness compared with rabbiteye blueberries (Itle and NeSmith 2017; Silva et al. 2005). For example, a consumer sensory and firmness study by Silva et al. (2005) reported that rabbiteye blueberries had an average firmness of 6.50 N and skin toughness of 1.48 N. In comparison, southern highbush cultivars exhibited lower values, with an average firmness of 3.96 N and skin toughness of 0.81 N. These findings reflect characteristics of earlier southern highbush and rabbiteye cultivars. Since then, the UF breeding program aimed to improve fruit firmness in southern highbush blueberries, leading to the development of crisp-textured genotypes (Blaker et al. 2014). Cappai et al. (2018) provided a comprehensive review of the physiological and genetic factors underlying blueberry fruit firmness. Their review also highlighted a consistent increase in fruit firmness in both southern highbush and northern highbush cultivars over time, reflecting the success of targeted breeding efforts. The improvement in firmness has been particularly evident in southern highbush blueberries. In contrast, gains in fruit firmness among rabbiteye cultivars have been less apparent, which may be attributable to the relatively limited number of new rabbiteye cultivars released in recent years compared with highbush types or the scarcity of published firmness data for newly developed rabbiteye cultivars.

Recent texture work conducted by Oh et al. (2024) assessed six rabbiteye (soft and firm) and 41 southern highbush cultivars (soft, firm, and crisp) using a TA.XT2 Plus texture analyzer via a 2-mm flat probe or 1.4-mm needle probe. The fruit were stored for 24 h, with 2, 4, or 6 weeks at 2 °C and 80% relative humidity, and 21 total texture parameters evaluated. When all texture parameters were considered, no evident distinctions between southern highbush and rabbiteye cultivars were identified in the fruit 24 h after harvest. A principal component analysis also indicated a high level of variation among the 21 texture parameters irrespective of the blueberry ecotype.

Oh et al. (2024) further correlated TA.XT2 Plus with FirmTech II data. Specifically, the slope maximum force and young modulus burst strain test measured using the TA.XT2 Plus was most representative of FirmTech II readings. Interestingly, when considering only the slope maximum force, southern highbush had higher texture values than that of rabbiteye. Cultivar differences in firmness and shelf life were also evident. For example, 'Titan' (rabbiteye) was comparable to 'Indigocrisp' (southern highbush) as both measured greater than 240 g·mm^{-1} at harvest, with 'Titan' losing minimal firmness during storage. While northern highbush cultivar Draper and southern highbush cultivars Misty, Vireo, Keecrisp, Meadowlark, Southmoon, Prince, Pinnacle, Sweetheart, and Millennia lost significant firmness through storage.

Itle et al. (2024) evaluated visual and firmness ratings over a 30-d shelf life study in five rabbiteye cultivars (Alapaha, Austin, Brightwell, Powderblue, and Vernon) and eight southern highbush cultivars (Camellia, Farthing, Keecrisp, Legacy, Meadowlark, Star, and Suziblue). The study was conducted over a 2-year period, with significant differences between the years. In the first year, rabbiteye cultivars demonstrated a 26% increase in firmness after 30 d of storage. In year 2, both southern highbush and rabbiteye increased in firmness at 25% and 31%, respectively. Itle et al. (2024) suggested southern highbush cultivars have better quality retention during storage because the cultivars experienced less change in firmness. However, future research incorporating more detailed texture analyses may help characterize variations in texture and firmness throughout storage. Additionally, including advanced selections in future studies will help evaluate texture improvement in newly developed materials.

Composition and flavor

Flavor attributes such as sweetness and sourness, often measured as the soluble solid content (SSC; °Brix) and titratable acidity (TA; %), respectively, were initially considered the main drivers of consumer acceptance and willingness to buy blueberries (Brazelton et al. 2023; Canales et al. 2024). Beaudry (1992) suggested blueberries must contain a SSC greater than 10 °Brix and TA between 0.3% and 1.3% for optimal flavor. Fruit with SSC greater than 14 °Brix is generally considered high in SSC and often associated with increased perceived sweetness (Beaudry 1992; Xiong et al. 2026).

Saftner et al. (2008) conducted a quality characteristic analysis consisting of two rabbiteye cultivars (Coastal and Montgomery) and 10 northern highbush blueberry cultivars (Chanticleer, Berkeley, Bluecrop, Bluegold, Coville, Duke, Elliott, Hannah's Choice, Lateblue, and Weymouth). When considering the SSC between the two types, no discernable differences were found. The SSC content differed by 2.6% among all cultivars ranging from 10.8 to 13.2 °Brix; however, differences in TA were large, with some cultivars having TA that was two-times to four-times higher. The two rabbiteye cultivars, Coastal and Montgomery, had lower TA between 0.35% and 0.58%, and northern highbush had TA that ranged between 0.44% and 1.27%.

Another study examined general composition at harvest in two rabbiteye cultivars (Premier and Gardenblue) and three southern highbush cultivars (Misty, O'Neal, and Bluerain) (Cheng et al. 2020). Although rabbiteye cultivars Premier and Garden Blue tended to have higher SSC compared with the southern highbush cultivars, differences in SSC and TA were not significant. Cheng et al. (2020) and other studies also suggested that the overall eating experience cannot be explained by general composition alone. Rather, consumer perception is also influenced by other traits, such as organic acid composition (e.g., citric, malic, and quinic acids), soluble sugar composition (sucrose, fructose, and glucose), texture, juiciness, bitterness, aroma, and volatile organic compounds (Babiker et al. 2023; Cheng et al. 2020; Ferrão et al., 2022; Gilbert et al., 2015; Wang et al. 2019).

Soluble sugars are water-soluble carbohydrates that are key determinants of fruit quality. Blueberry fruit contains three dominant soluble sugars of glucose, fructose, and sucrose, which differentially contribute to flavor depending on their relative abundance (Zhang et al. 2020). In both rabbiteye and southern highbush blueberries, glucose and fructose are the predominant sugars, which typically range between 15.0 and 22.5 $mg·g^{-1}$, whereas sucrose is often present at lower concentrations between 0.03 to 3.0 $mg·g^{-1}$ (Babiker et al. 2023; Itle and NeSmith 2017). Rabbiteye cultivars often accumulate greater total soluble sugars and can exhibit a higher proportion of fructose, which contributes to increased perceived sweetness (Babiker et al. 2023; Cheng et al. 2020; Ferrao et al. 2022). This trend is supported by Itle and NeSmith (2017), who evaluated seven southern highbush cultivars (Camelia, Emerald, Farthing, Legacy, Meadowlark, Rebel, and Star) and seven rabbiteye cultivars (Alapaha, Brightwell, Ocklockonee, Powderblue, Premiere, Tifblue, and Vernon). The study reported higher total sugar concentrations in rabbiteye fruit (40.5 $mg·g^{-1}$) compared with southern highbush (32.7 $mg·g^{-1}$), along with a substantially greater sucrose content in rabbiteye (2.54 $mg·g^{-1}$ vs. 0.12 $mg·g^{-1}$). In contrast, southern highbush blueberries tend to exhibit more variable sugar profiles depending on the genotype and growing conditions, with some cultivars showing more balanced glucose-to-fructose ratios (Babiker et al. 2023).

Blueberries contain different organic acids, including citric, quinic, malic, and succinic acids, that also contribute to their unique flavor (Ehlenfeldt et al. 1994; Wang et al. 2019). Citric and malic acids are generally the dominant acids in both rabbiteye and southern highbush fruit, and quinic acid also contributes to total acidity. Southern highbush cultivars tend to exhibit a greater proportion of citric acid compared with rabbiteye, which often contains lower overall acid concentrations (Ehlenfeldt et al. 1994; Saftner et al. 2008; Wang et al. 2019). A study conducted by Ehlenfeldt et al. (1994) assessed six southern highbush cultivars, five rabbiteye cultivars, and three rabbiteye selections. Southern highbush cultivars had significantly higher citric acid concentrations (9.37 $mg·g^{-1}$) compared with their rabbiteye counterparts (1.74 $mg·g^{-1}$). Conversely, rabbiteye cultivars contained higher concentrations of malic (5.02 vs. 0.48 $mg·g^{-1}$) and quinic acids (0.82 vs. 0.51 $mg·g^{-1}$) compared with southern highbush cultivars (Ehlenfeldt et al. 1994), resulting in softer, less sharp acidity (Cheng et al. 2020; Yan et al. 2025).

These sugar and acid interactions ultimately influence sweetness perception and flavor balance, thus helping to explain why rabbiteye blueberries are often described as milder and sweeter, whereas southern highbush types are characterized by brighter, more acidic flavor profiles.

Aroma contributes much of the diversity of flavors in the consumer's tasting experience (Ferrao et al. 2022). Volatile organic compounds (VOCs) are specific to the olfactory system and create the sensation of aroma (Klee 2010). The VOCs isolated from southern highbush fruit at harvest typically include esters, terpenoids, aldehydes, and alcohols (Blaker et al. 2014; Ferrao et al. 2022). However, a volatile assessment of rabbiteye blueberries has been conducted only during three ripening stages and when fruit were fully ripe on a few cultivars (Cheng et al. 2020; Horvat and Senter 1985). A study by Beaulieu et al. (2014) analyzed VOCs in green, blue-red, and fully ripe fruit of 'Premier', 'Powderblue', 'Climax', 'Brightwell', and 'Tifblue'. A total of 53 VOCs were found among the rabbiteye cultivars, with terpenes, aldehydes, and esters in highest abundance. Similarly, esters, especially ethyl acetate, which impart a pineapple and fruity flavor/aroma, were especially high in two rabbiteye cultivars compared with southern highbush (Cheng et al. 2020; Xu et al. 2007). Linalool and geraniol, which are also VOCs, were considered to be the major aroma-active terpenoids during fruit ripening and in fully ripe rabbiteye fruit in many studies (Beaulieu et al. 2014; Cheng et al. 2020; Horvat and Senter 1985; Xu et al. 2007). These compounds are known for their fruity and floral flavor, which is typically preferred by consumers (Cheng et al. 2020).

Nutritional compounds

Rabbiteye blueberry fruit has a unique nutritional matrix beneficial for human health. The fruit is rich in water, sugars (glucose, fructose), organic acids (citric, ascorbic acids), minerals (phosphorus, potassium, and magnesium), and fiber (pectin) (Dróżdż et al. 2018; Zhang et al. 2020). Rabbiteye fruit also has a variety of phenolic compounds that provide numerous health-promoting benefits such as antioxidant, antimutagenic, antitumoral, anti-inflammatory, immunomodulatory, neuroprotection, antiobesity, antidiabetic, antimicrobial, and cardiovascular disease prevention properties (Seeram and Burton-Freeman 2018; Silva et al. 2020; Toyama et al. 2023). Furthermore, antioxidants and flavonoids in rabbiteye reduce the oxidative stress of the body by decreasing free radical production and creating an anti-inflammatory effect, whereas the polyphenols present in blueberries have been correlated with cardioprotective effects (Martínez et al. 2024; McLeay et al. 2012).

In terms of phytonutrient composition, rabbiteye blueberries are known to be high in phenolic compounds, specifically anthocyanins, compared with southern highbush (Shibata et al. 2021). Although southern highbush blueberries tend to exhibit earlier eluting peaks for delphinidin, petunidin, and malvidin, suggesting these as major anthocyanins present in the fruit, rabbiteye blueberries have a higher total anthocyanin content than that in southern highbush. A study conducted by Lohachoompol et al. (2008) found that rabbiteye cultivar Climax had the highest total anthocyanin content at 13.7 $g·kg^{-1}$ cyanidin 3-glucoside equivalents dry weight, followed by Powderblue (11.9 $g·kg^{-1}$) and Brightwell (10.1 $g·kg^{-1}$). In comparison, southern highbush cultivars such as Crunchie, Sharpblue (also referred to as Sharpe), and Star recorded lower values at 7.9, 9.6, and 5.8 $g·kg^{-1}$, respectively. More recently, Ma et al. 2022 quantified anthocyanin profiles and reported that rabbiteye cultivars Brightwell and Gardenblue had higher anthocyanin levels compared with southern highbush cultivars Legacy and Misty. These findings are also consistent with a study conducted by Cheng et al. (2020), who indicated that rabbiteye blueberries were consistently higher in total anthocyanin content.

Another important phenolic compound is chlorogenic acid. This compound has been related to decreases in metabolic diseases, obesity, and the onset of cardiovascular diseases (Yousef et al. 2016). A study by Perkins-Veazie et al. (2024) analyzed the chlorogenic acid (CGA) content in 50 blueberry cultivars and revealed that rabbiteye blueberries had a higher mean CGA content of 401.61 mg·100 g^{-1} dry weight, whereas that of southern highbush cultivars was 270.33 mg·100 g^{-1} dry weight. Consistent with these findings, Yousef et al. (2016) reported that the mean CGA concentration in southern highbush cultivars was 49 mg·100 g^{-1} g fresh weight, whereas that in rabbiteye blueberries was 102 mg·100 g^{-1} g. These compositional differences not only highlight the unique quality of rabbiteye blueberries but also allude to their importance as a functional food for human health.

Challenges in Improving Rabbiteye Genetics

Developing competitive rabbiteye cultivars is a key strategy for addressing challenges in rabbiteye production and marketing. However, breeding progress for rabbiteye blueberries has been constrained by a narrow genetic base, limited technological resources and tools tailored for rabbiteye, and limited industry support.

Narrow genetic base

Genetic diversity is the foundation of plant breeding because it enables the creation of new genotypes and the selection of traits important to growers and consumers (Cooper et al. 2001; Swarup et al. 2021). Early rabbiteye breeding heavily relied on the following five wild selections: ‘Ethel’, ‘Clara’, ‘Myers’, ‘Black Giant’, and ‘W-4’ (Abdolshahi et al. 2025; Lyrene 1987). As suggested by a pedigree analysis of 180 rabbiteye accessions, these five founders collectively contribute more than 73% of the genetic composition of rabbiteye cultivars (Abdolshahi et al. 2025). Repeated use of common parents has resulted in a rapid increase in inbreeding coefficients, from an average of less than 0.0002 in cultivars released before 1980 to an average of 0.014 in cultivars released after 2000 (Abdolshai et al. 2025). Because rabbiteye blueberries are sensitive to inbreeding depression (Hancock and Siefker 1982; Lyrene, 1983), this narrow genetic diversity can hinder genetic gain and jeopardize a crop’s ability to adapt to new environmental stressors or market demands. Therefore, broadening the genetic base for rabbiteye is crucial for effective and sustainable crop improvement in the long term.

Limited genetic molecular tools

Traditional blueberry breeding encompasses two main processes: cultivar development and population improvement. Cultivar development focuses on generating biparental crosses and selecting superior seedlings for cultivar release, whereas population improvement aims to increase the frequency of favorable alleles within the breeding germplasm through recurrent selection and introgression of wild germplasm (Ferrão et al. 2021). Integration of DNA marker information into breeding can enhance the efficiency of both processes through marker-assisted selection (MAS) and genomic selection (GS). Although MAS is most suitable for traits with simple genetic architectures controlled by major effect trait loci, GS is designed for the selection of complex quantitative traits by predicting genomic estimated breeding values using genome-wide markers (Bernardo 2014; Jannink et al. 2010). Compared with conventional phenotypic selection, genomic selection enables earlier selection of both offspring and parents, thereby potentially shortening breeding cycles, reducing selection costs, and increasing genetic gains per unit time and investment (Fig. 4) (Ferrao et al. 2021; Jannink et al. 2010). Both MAS and GS have been successfully integrated into southern highbush breeding programs, most notably UF, where molecular information was applied at multiple stages of selection (Ferrao et al. 2021). In contrast, the application of MAS and GS in rabbiteye blueberry breeding has been rarely documented.

The more advanced breeding strategies available for highbush blueberries are largely driven by extensive genomic resources and associated research findings. To date, highbush blueberry genome assemblies dominate the public database (https://www.vaccinium.org/). There are two well-annotated blueberry reference

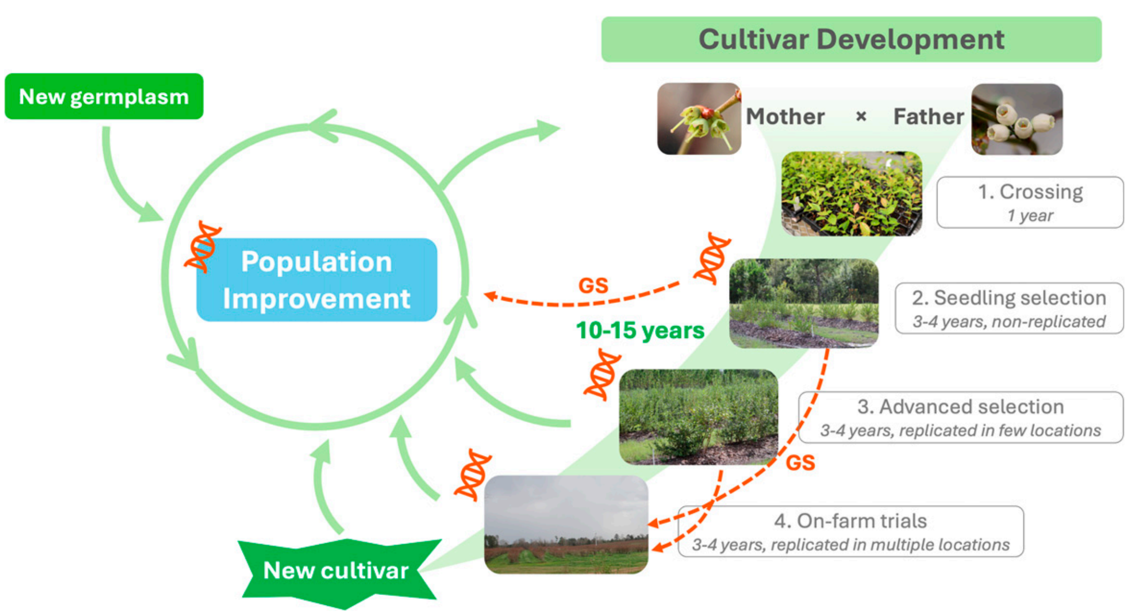

Fig. 4. Genomic selection (GS) can be applied to improve the efficiency of both blueberry cultivar development and population improvement. The GS can be applied in the various selection stages to save 3 years or more for cultivar development. The GS can also select parents at an early stage to accelerate the breeding cycle while preserving genetic diversity.

genomes. One is a diploid genome from W85-20, which is a diploid *Vaccinium corymbosum* accession (Edger et al. 2022), and the other is a tetraploid genome from Draper, which is a northern highbush cultivar (Colle et al. 2019). Similarly, the first blueberry pangenome was constructed using southern and northern highbush accessions (Yocca et al. 2023). Combined with the availability of multiple genotyping platforms for *Vaccinium* (Clare et al. 2024), these resources have enabled the identification of numerous quantitative trait loci in highbush blueberry, including loci associated with fruit firmness (Cappai et al. 2020), organic acid composition (Oh et al. 2025), and volatile compounds (Ferrão et al. 2020). In contrast, genomic resources and reported quantitative trait loci for rabbiteye blueberry are extremely limited, thus substantially constraining the utilization of genomic tools in rabbiteye breeding.

Limited breeding investments

Less competitive rabbiteye cultivars can be largely attributed to inadequate breeding efforts (Lyrene 2006). Among the five public breeding programs in the Southeast, only a few are actively pursuing rabbiteye breeding; most programs have shifted to mainly focus on southern highbush breeding. This lack of investment has resulted in slower progress and development compared with those associated with southern highbush blueberries (Lyrene 2002). To date, less than 70 rabbiteye cultivars have been released, in contrast to 182 northern highbush and 242 southern highbush cultivars (Fruit and Nut Cultivar Database 2024). Many rabbiteye cultivars are only three to four generations away from their wild ancestors, indicating significant potential for genetic improvement.

Future Strategies to Improve Rabbiteye

To regain market acceptance and restore acreage of rabbiteye blueberries, breeding efforts must become more focused and efficient to close the performance gap between rabbiteye and highbush blueberries. Several traits should be prioritized in future breeding programs. The highest priority is improving overall fruit quality and extending shelf life to enhance consumer acceptance because inferior fruit quality has been the principal limitation of rabbiteye blueberries, particularly in wholesale markets. Surveys involving highbush blueberries indicated that overall flavor, including sweetness, acidity, and their balance, as well as texture are the key factors that influence consumers' willingness to pay (Canales et al. 2024). Among these traits, texture represents the most pronounced weakness of rabbiteye cultivars, particularly issues related to seediness and thick skin. Therefore, reducing fruit grittiness through selection for thinner skins and fewer seeds should be a major breeding priority. Concurrently, selection for high sweetness and a balanced sweetness–acidity profile is essential. In addition, extended shelf life is a critical target to ensure that fruit quality is maintained during transportation through wholesale supply chains.

With regard to productivity, key traits such as strong root systems, tolerance to abiotic and biotic stresses, disease resistance, and good plant vigor should be preserved. Particular emphasis should be placed on traits related to mechanical harvestability, including upright growth habit, high fruit firmness, and low fruit detachment force, to help address labor shortages and reduce production costs (Gallardo et al. 2018). Additionally, parthenocarpy is an important trait to select for because it can enhance production reliability by eliminating the need for compatible cultivars and supplemental pollination. From the phenological perspective, shorter flower-to-harvest intervals could advance harvest windows to increase profitability through earlier season production. Moreover, reduced fruit development time may limit exposure to environmental stresses during fruit formation, thereby reducing fruit loss while improving fruit quality.

Achieving these breeding goals will require a coordinated and efficient approach to accelerate genetic gains in rabbiteye blueberries. Improvements in breeding efficiency can be achieved through the integration of modern breeding tools, including genomic and marker-assisted selection, complemented by enhanced data collection and high-throughput phenotyping. Consequently, additional research is needed to develop genomic and phenomic resources for rabbiteye blueberries, such as high-quality reference genomes, robust genotype–phenotype associations, and modern genotyping, phenotyping, and biotechnological platforms.

To ensure the long-term sustainability of rabbiteye improvement, efforts should also focus on broadening the genetic base through deliberate parent selection informed by pedigree and molecular data as well as targeted interspecific hybridization. Historically, interspecific hybridization within *Vaccinium* has expanded fruit color diversity, modified phenological development, and introduced cold tolerance to rabbiteye cultivars. Continued introgression of favorable alleles is needed to further improve fruit quality and other traits while broadening the genetic base. Conversely, the use of rabbiteye germplasm to enhance soil adaptability, stress tolerance, vigor, and longevity in highbush blueberries through interspecific hybridization is promising for improving the sustainability of the blueberry industry.

Sustained breeding progress will require continued investment and coordinated support from the public and private sectors. With increased emphasis on rabbiteye blueberry breeding, there is strong potential to develop new cultivars with improved consumer perception, restore market confidence, and expand production opportunities. Ultimately, these advances will benefit both large-scale and small-scale producers by reducing production costs and environmental impacts, thereby promoting a more sustainable blueberry production system.

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