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Seasonal Patterns of Soluble Carbohydrates in Spring- and Fall-Blooming Southern Highbush Blueberry Genotypes

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Abstract. **Temperature and daylength are key factors associated with soluble carbohydrates (SCs) partitioning in plant organs. Environmental cues and SC concentrations influence flower bud initiation (FBI) in fruit crops. Southern highbush blueberry (SHB, *Vaccinium corymbosum* interspecific hybrids) is a daylength-responsive crop. In most SHB genotypes, decreasing photoperiod and temperatures in the fall season trigger FBI, followed by bloom in the spring. Blueberry genotypes that bloom during the fall season have been identified in the University of Florida's SHB breeding germplasm. Off-season bloom suggests that FBI in those genotypes occurs under atypical environmental conditions. Drawing from these findings, we hypothesized that SC concentrations in fall-blooming genotypes differ from spring-blooming genotypes, especially in the period that precedes bloom. In this study, we quantified and compared SC concentrations of SHB genotypes with off-season and traditional spring-blooming phenology across 2 years. In addition, we recorded the developmental stages of each genotype at the SC sampling points. Our results indicate that SHB plants exhibit high SC concentrations during the winter before the traditional spring bloom, which agrees with prior studies in temperate fruit crops. However, no increase in SC concentrations was detected before fall bloom, indicating that this trait might be regulated by other endogenous factors. Further research on carbohydrate partitioning, metabolic pathways, and agricultural practices could support the investigation of off-season blooming in blueberry, contributing to the breeding of varieties with off-season production and the expansion of blueberry growing regions.**

Bloom time of economically important crops determines harvest season and yield. The transition from vegetative to reproductive growth is regulated by several mechanisms that integrate environmental and endogenous factors (Andrés and Coupland 2012). Daylength (short or long photoperiod) and temperature are key environmental cues that determine blooming time by modulating the reproductive development of several plant species (Samach and Coupland 2000). Short-day plants, like blueberry (*Vaccinium* spp.), initiate flower buds when days are short and temperatures are low (Bañados and Strik 2006; Spann et al. 2004). These same conditions lead to plant dormancy responses. Thus, short-day plants initiate flower buds from the moment conditions become inductive until defoliation (Williamson et al. 2002).

Decreasing temperatures and shortening photoperiod in the fall cue plants into endodormancy, which will be released by the accumulation of chilling hours during the winter as a survival strategy in woody perennial plants. While environmental conditions are unsuitable for resuming growth and development, plants enter ecodormancy, which will be overcome with the increasing temperatures in late winter and spring. Subsequently, favorable environmental conditions during the spring will promote growth, budbreak, and bloom (Melke 2015; Yang et al. 2021). This process has been described in several temperate fruit trees such as almonds (*Prunus dulcis*), peach (*Prunus persica* L.), pistachio (*Pistacia vera* L.), and grapes (*Vitis vinifera* L.) (Lebon et al. 2008; Sperling et al. 2019).

Considerable efforts have been made in the past decades to elucidate the influence of SCs on FBI as a tool for predicting the blooming time of important fruit crops (Bodson and Outlaw 1985; Heyer et al. 2004; Rolland et al. 2006; Sperling et al. 2019; Tixier et al. 2020; Yoon et al. 2021). Different SC concentrations (e.g., sucrose, glucose, and fructose) were reported in strawberry plants that were grown in flowering-inductive and noninductive conditions (Eshghi and Tafazoli 2006). In the work of Heyer et al. (2004) and Seo et al. (2011), carbohydrates were shown to have a significant impact on promoting flowering by rescuing the phenotype of mutant *Arabidopsis* plants, in which important flowering time genes such as *FLOWERING LOCUS T*, *LEAFY*, and *CONSTANS* were repressed. When carbohydrate translocation was interrupted by girdling in *Sinapis alba*, flowering was inhibited. This effect was reverted by exogenous sucrose application, thereby, suggesting its contribution to the flowering process (Havelange et al. 2000).

Blueberry is a woody perennial plant species that relies on short days and cool temperatures of the fall season for FBI and endodormancy (Melke 2015; Spann et al. 2004). SHB (*V. corymbosum* interspecific hybrids) exhibits a wide range of variability in plant size, morphology, fruit quality, and yield, including blooming time, which can also be altered by agricultural management practices (Fang et al. 2020). Pescie et al. (2011), Bañados and Strik (2006), and Spann et al. (2004) reported that short photoperiods combined with cool temperatures promoted FBI in blueberry, whereas long photoperiods and high temperatures significantly impaired FBI. In Florida, traditionally, the release of ecodormancy starts in late winter due to increasing temperatures. Thus, flower budbreak, bloom, and fruit set occur during early spring (Fang et al. 2020; Phillips et al. 2020). Recently, SHB genotypes that bloom in the fall have been identified in the University of Florida's SHB breeding germplasm (Silva et al. 2024). Fall-blooming genotypes exhibit day-neutral FBI (Benevenute et al. 2025). These genotypes could be used for off-season production, thus, expanding growing seasons and regions where SHB can be produced.

Because carbohydrate concentrations in the shoot apex have been shown to play a role in the regulation of the flowering process in many crop species, we investigated the SC concentrations in blueberry genotypes with contrasting blooming times. We hypothesized that SC concentrations in fall-blooming genotypes differ from the traditional spring-blooming genotypes, especially in the period that precedes bloom.

Materials and Methods

Sampling. During the fall season (September to November) and over 2 years (2019 and 2021), 536 genotypes of the University of Florida's SHB breeding population were visually evaluated weekly for off-season bloom capacity. Each genotype in the population was present as a block of ∼15 clonally propagated plants, totaling ∼8000 plants (Silva et al. 2024). Plants were grown in commercial field conditions according to Phillips et al. (2020) and Phillips and Williamson (2020) in Waldo, FL, USA (29° N, 82° W). Four genotypes with consistent bloom during the fall season were selected for SC quantification and phenology records. Four spring-blooming genotypes located immediately beside the fall-blooming ones were used for comparison (Table 1). Five plants of each genotype were sampled during 2021 and 2022.

SC extraction and quantification. The apical portion (10 cm) of two representative shoots from each plant were collected monthly,

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Table 1. Southern highbush blueberry genotypes used for soluble carbohydrate quantifications and phenology records.

Fall-blooming genotypes	Spring-blooming genotypes
‘FL 13-136’	‘FL 13-170’
‘FL 15-145’	‘FL 15-175’
‘FL 16-64’	‘FL 16-92’
‘FL 18-188’	‘FL 18-67’

except when plants had insufficient new growth after the summer hedging. Plants were hedged on May 31, 2021, and June 8, 2022. Samples were collected in mornings with clear skies, between 10:00 AM and 12:00 PM. Leaves, flower buds, flowers, and fruits were removed; therefore, only stems were considered for the extractions. Stems were oven dried at 65 °C to constant mass, ground by agitation (TissueLyzer II, QIAGEN, Venlo, The Netherlands) using stainless steel beads at a frequency of 30 Hz until reaching a fine powder state, and stored in paper bags at room temperature until further processing and extractions.

SC extraction and quantification was performed using the anthrone method adapted from Sperling et al. (2015, 2017). In summary, 30 mg of dried ground tissue was mixed with 1 mL of ethanol 80% vol/vol and incubated for 10 min in a water bath at 90 °C with continuous agitation. After centrifugation for 1 min at 4700 g_n, 50 μL of the supernatant was collected and diluted in 950 μL of deionized water. Then, 200 μL from the diluted solution was mixed with 600 μL of 0.1% (wt/vol) anthrone (Sigma-Aldrich, St. Louis, MO, USA) in concentrated sulfuric acid in a 96-well plate. The plate was heated to 100 °C for 10 min and then equilibrated to room temperature for 10 min. SC concentration, quantified as glucose (Glc) equivalents, was determined from colorimetric readings of absorbance at 620 nm using a standard curve (0, 0.05, 0.1, 0.15, 0.3, 0.45, and 0.65 mg·L^{-1} glucose) in a microplate reader (Synergy HT, Biotek Instruments, Inc., Winooski, VT, USA). Starch concentrations were not quantified.

SC concentrations were analyzed using a linear mixed-effects model fitted with the lme function from the nlme package in R (Pinheiro et al. 2025). Fixed effects included month, trait, their interaction, and year. To account for hierarchical sampling, we included random intercepts for traits (fall-blooming and spring-blooming), genotype nested within trait, and plant nested within genotype. Because repeated measurements were taken across months from the same plants, we modeled within-plant temporal autocorrelation using a first-order autoregressive correlation structure [AR(1)] with Month as the time covariate. The model was fitted using restricted maximum likelihood and effects were considered statistically significant at $P < 0.05$. Statistical analyses were performed using R (version 4.2.0; R Core Team 2022). Results were plotted using package ggplot2 (Wickham 2016), and image panels were created using Inkscape (version 1.2.2; Inkscape Project 2020).

Phenology and weather records. The phenology of all genotypes was recorded at the time of each sample collection, and the identification of developmental stages was based on MSU Extension’s article “Growing Stages” for northern highbush blueberry and Spiers (1978). Weather data were obtained from NASA’s “Prediction of Worldwide Energy Resources” (NASA/POWER n.d.) using the coordinates provided to the EnvRtype R package (Costa-Neto et al. 2021). Daylength data were obtained from the “Sunrise and Sunset” calculator (Time and Date AS). Growing degree days (GDDs) was calculated as GDD = (Tmax + Tmin)/2 − Tbase, where Tmax and Tmin represent the daily maximum and minimum air temperatures, and Tbase is the base temperature for blueberry (7.5 °C).

Results

Monthly phenology and SC concentrations. We identified nine developmental stages across our phenological records during 2021 and 2022 (Fig. 1, Supplemental Table 1). During the spring, all genotypes were in similar phenological stages (i.e., flower buds were breaking into full bloom, and fruits were ripening until the end of the production season). However, later in the year, spring-blooming and fall-blooming genotypes exhibited contrasting phenology (Fig. 1, Supplemental Table 1).

There was high variability in SC concentrations across all genotypes and months in both years. We found significant differences across months and years. However, there were no differences between traits (fall- and spring-blooming genotypes) in the months we were able to sample (Fig. 2, Table 2). The lowest SC concentrations occurred in the spring (March and April) and summer (August) (Table 2, Fig. 2C). During spring there is high reproductive sink activity due to fruit development, ripening, and new vegetative growth at a time of mild temperatures and increasing photoperiod (Fig. 3). SC concentrations increased in April and May with the end of the fruiting season. Following the summer hedging, SC concentrations remained stable. This corresponds to a period of high temperatures and long photoperiods, when new vegetative shoots (sinks) develop. Subsequently, SC increased peaking in November for both

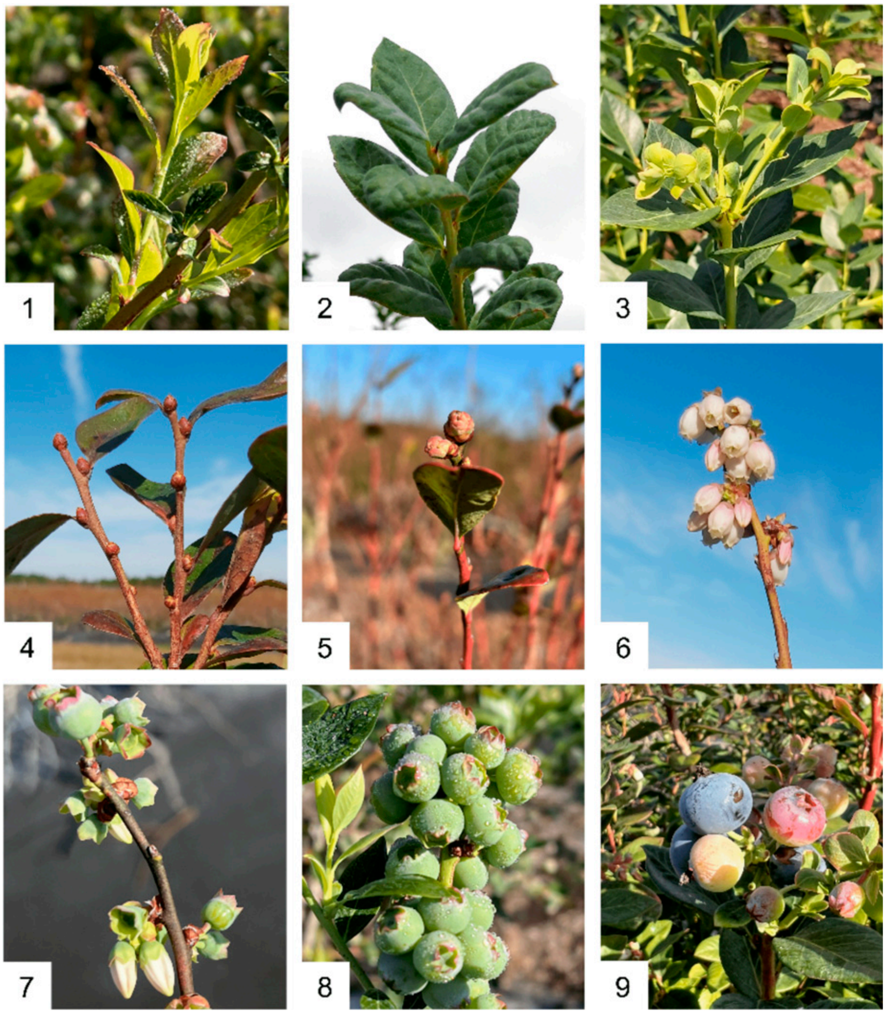

Fig. 1. Phenology of southern highbush blueberry genotypes of the University of Florida’s breeding population in Waldo, FL, USA, in 2021 and 2022. 1) Shoot expansion, 2) end of shoot growth, 3) apical curled leaf, 4) dormant flower bud, 5) flower budbreak, 6) late flower bud and bloom, 7) petal fall and fruit set, 8) green fruit, 9) ripe and ripening fruit.

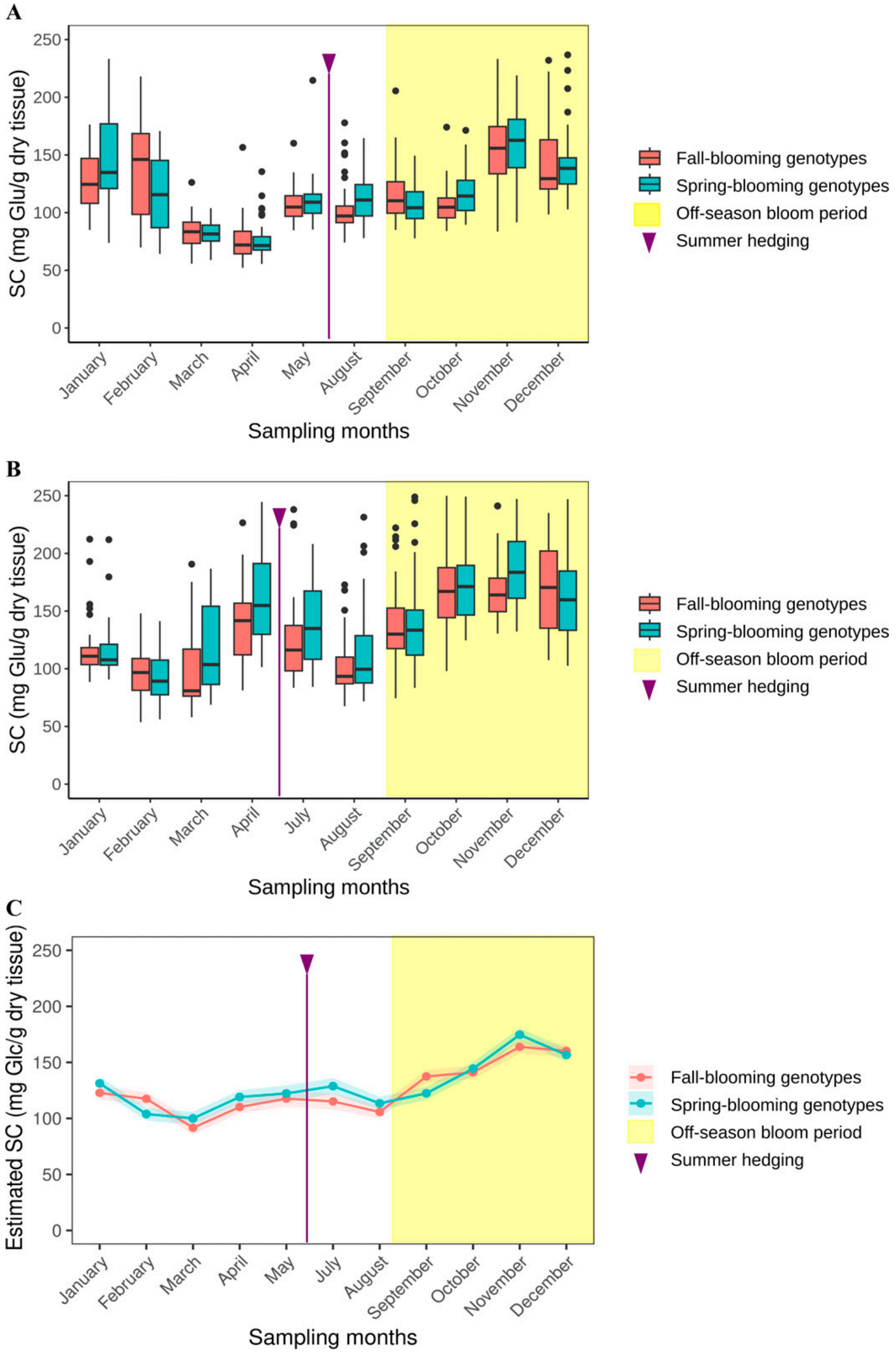

Fig. 2. Monthly soluble carbohydrate (SC) concentrations expressed as glucose equivalents (Glc/g dry tissue) in southern highbush blueberry genotypes in 2021 (**A**) and 2022 (**B**). SC estimates across years (2021, 2022), months, and traits (fall-blooming and spring-blooming) treated as fixed-effects using linear mixed-models ($P \leq 0.05$) (**C**).

spring- and fall-blooming genotypes. At this time, fall-blooming genotypes initiated reproductive growth while spring-blooming genotypes remained vegetative (Fig. 2, Supplemental Table 1).

In November and December, SC concentrations were the highest. This period is characterized by decreasing temperatures and shortening photoperiod (Fig. 3). FBI and defoliation were observed in all genotypes. Nevertheless, flower budbreak, bloom, and green fruits were also present in fall-blooming genotypes (Supplemental Table 1). Subsequently, SC concentrations decreased, which corresponds to the period when all genotypes were in full bloom and developing fruits. SC concentration patterns were similar in both years, except that SC and phenology were ~1 month earlier in 2022 compared with 2021 (Fig. 2C and 2D, Supplemental Table 1), likely due to higher GDD accumulation during the summer months in 2022 than in 2021 (Fig. 3).

The random-effects structure revealed substantial variation at the genotype and trait

Table 2. Standard errors (*SEs*) and *P* values of significant fixed effects on soluble carbohydrate (SC) estimates.

	Estimated SC (mg Glc/g dry tissue)	*SE*	*P* value
Month			
March	−31.141	5.745	0.000
April	−12.599	5.774	0.029
August	−17.06	5.754	0.003
September	14.646	5.757	0.011
October	18.287	5.775	0.002
November	41.066	5.775	0.000
December	37.476	5.782	0.000
Year			
2022	21.385	3.223	0.000

levels. The variance associated with genotypes (nested within trait) was 24.59 [standard deviation (*SD*) = 4.96], whereas variation at the trait level was smaller (11.84, *SD* = 3.44). In contrast, variance attributable to individual plants (nested within genotype) was negligible (6.9×10^{-6}, *SD* = 0.03). Residual variance was large (1317.37, *SD* = 36.30), indicating that most of the unexplained variability occurred at the within-plant level rather than among plants, genotypes, or trait (Table 3).

Discussion

Off-season bloom during the fall has been reported in hybrids of highbush (*V. corymbosum*) (Pescie et al. 2011; Wright 1993), lowbush (*Vaccinium angustifolium*) (Fear et al. 1985), rabbiteye (*Vaccinium virgatum*) (Omori et al. 2022) blueberry. Off-season bloom has also been reported in other crops including lychee (*Litchi chinensis* Sonn.) (Charoenkit et al. 2015), poplar (*Populus deltoides*) (Thapliyal et al. 2020), and mango (*Mangifera indica* L.) (Kaviarasu et al. 2017). This phenology is an opportunity to expand production regions and seasons, which can help growers target profitable market windows. Yet, literature on the mechanisms involved in this phenology is extremely limited.

We identified genotypes capable of blooming during the fall season in addition to the traditional spring season in Florida. The spring-blooming blueberry genotypes used as controls in this study initiated flower buds during late fall, a period with short days and low temperatures. This is the canonical blueberry response described by Kovaleski et al. (2015), Bañados and Strik (2006), Spann et al. (2003), and Darnell (1991). In contrast, our phenology records indicate that fall-blooming genotypes transitioned from vegetative to reproductive growth under high (and increasing) temperatures and daylength. This is consistent with day-neutral FBI, as proposed by Benevenute et al. (2025). This unusual blooming pattern resembles primocane bearing, a term used for raspberry and blackberry (*Rubus* spp.) in which flowers and fruits are produced on first-year canes (Clark et al. 2005). Yet, the term primocane is not entirely fitting because fall-blooming genotypes initiated flower buds on both old and new canes during the fall. Primocane bearing has been studied for decades regarding economic advantages (Clark 2008), inheritance (Lopez-Medina et al. 2000), development, and yield (Percival et al. 2001); however, it is unknown if any of these attributes are applicable to fall-blooming SHB.

Prior research has pinpointed a dual role for SCs, as energy supply and signaling molecules in the FBI process of *Arabidopsis thaliana* (Cho et al. 2018; Corbesier et al. 1998; Lebon et al. 2008; Moghaddam and Ende 2013). In horticultural crops, SC allocation has also been associated with bloom (Liu et al. 2021). In apical leaves of apple trees (*Malus domestica*), carbohydrate concentrations increased as flower buds developed. Glucose concentrations peaked in the middle of the FBI process, followed by a decrease at the end of it (Xing et al. 2015). In almonds, SC concentrations increased during winter, followed by a decline before bloom. The increase in SC during winter suggests that plants are breaking starch into SCs to maintain metabolism during dormancy. Subsequently, the drop in SC concentrations in late winter can be associated with increasing respiration rates due to warmer temperatures and increasing sink demands (Sperling et al. 2019; Tixier et al. 2019). Previous authors have linked SC and starch concentrations with FBI, dormancy onset, and release in deciduous woody perennials that bloom in the spring (Sperling et al. 2019; Xing et al. 2015). The interplay of temperature, phenology, and SC concentrations is well aligned with our observations in the spring-bloom period. On the other hand, we did not detect such trends in the fall-blooming genotypes,

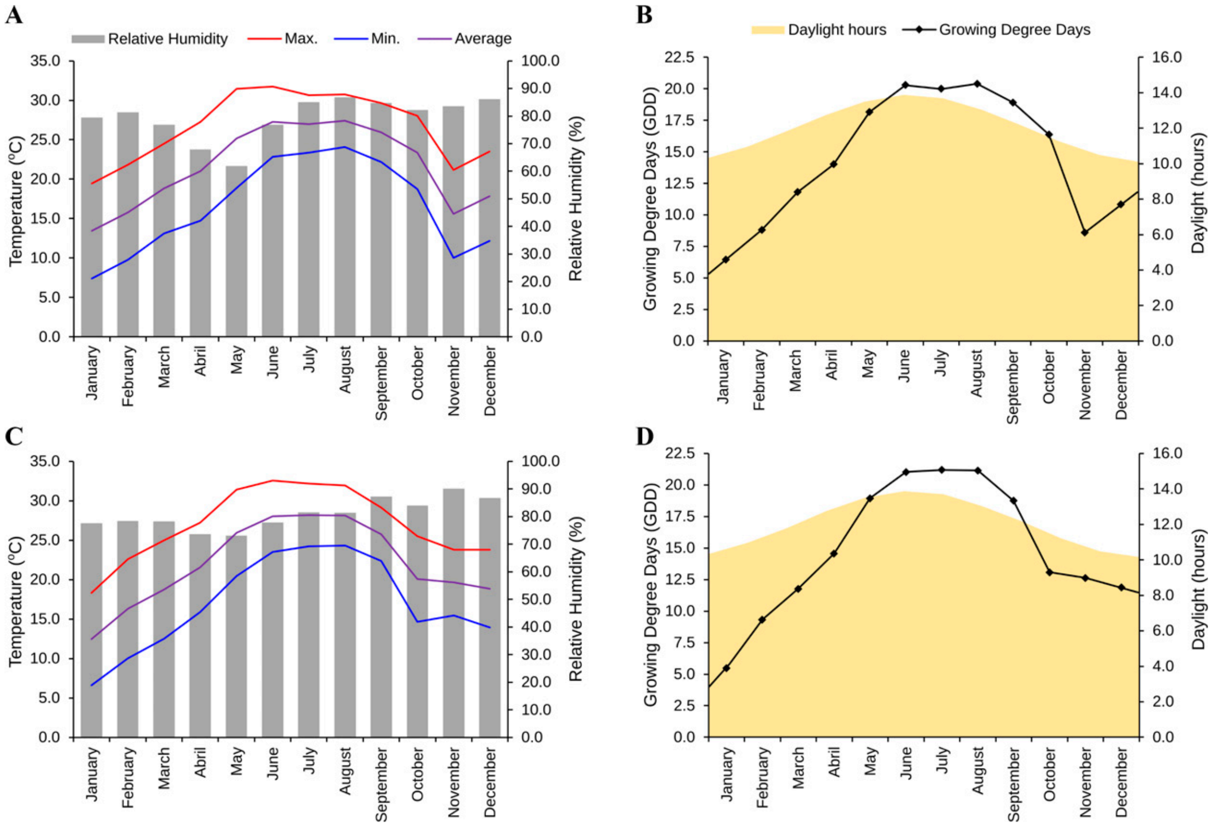

Fig. 3. Environmental conditions in the field where the southern highbush blueberry breeding germplasm in this study was located (Waldo, FL, USA). Temperature (left), daylength, and monthly growing degree days (right) in 2021 (**A** and **B**) and 2022 (**C** and **D**) are presented.

Table 3. Standard deviation (*SD*) and variance of random effects of the hierarchical mixed-effects model.

Random effects	Variance	*SD*
Trait	11.84	3.44
Genotype	24.59	4.96
Plant	6.9×10^{-6}	0.03
Residual	1317.37	36.3

suggesting that the off-season bloom is induced by distinct mechanisms (Sperling et al. 2019; Swain and Darnell 2001). In addition, it is possible that starch concentrations and not SC concentrations constitute the carbohydrate signal for FBI. Starch concentrations were not measured in this study. Thus, future research should address this knowledge gap.

In Florida, blueberry plants are conventionally pruned in the summer (at the end of May or first week in June). Fall bloom was observed in September. Therefore, the signals that lead to fall bloom should take place between the time of pruning and September. In this study, plants were not sampled in June and July in 2021 or May and June in 2022 because they did not have 10-cm apical shoots at those times. This approach might have limited our ability to detect SC concentration changes in the period preceding fall bloom. We also did not measure starch or standardize weather conditions, both of which can influence carbohydrate dynamics, reduce variability, and potentially shape the fall-bloom trait. Hence, additional trials are necessary, including the analysis of starch in nonpruned plants, and larger sample size to give us more accurate insights on the carbohydrate profile across the whole year.

In summary, flowering relies on a complex interplay of internal and external cues. Here we documented seasonal phenology and SC concentration patterns in spring- and fall-blooming SHB genotypes grown in Florida. Although SC concentrations were elevated before the conventional bloom season, they did not increase before the off-season bloom, indicating that SCs alone are unlikely to drive this trait. Uncovering the endogenous mechanisms behind off-season bloom is critical for breeding and managing blueberry and other perennial crops. Such knowledge may support the development of off-season blueberry production systems and help identify new suitable growing regions as global climate change shifts seasonal plant phenology and food production.

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