

High Soil Potassium Levels Do Not Increase Leaf Potassium Concentration in Rabbiteye or Southern Highbush Blueberry

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Abstract. In the coastal plains of Georgia, soils are sandy with low pH, low cation exchange capacity (CEC), and a high rate of K leaching. To manage crop nutrition effectively and preserve soil physicochemical properties, it is essential to adjust fertilizer applications to the physiological demands of the plants. This research project aimed to determine the relationship between K in the soil and leaves and its impact on yield of rabbiteye blueberry (*Vaccinium virgatum* Aiton) and southern highbush blueberry (a complex hybrid based largely on *Vaccinium corymbosum* L. and *Vaccinium darrowii* Camp.). Soil and leaf samples were collected on four commercial farms, including 384 soil samples and 252 leaf samples from Apr to Nov 2022 and 2023. Our results indicated no correlation between soil and leaf K concentrations. Still, soil K was positively correlated with P and Mn in the soil, and leaf K was positively correlated with P, Mn, S, and Na in the leaves. The highest-yielding farm did not have higher soil K concentrations than the other farms, but it did have plants with the highest level of K in the leaves. The results of this study show that soil K alone may not reliably indicate plant K or yield in blueberries. Leaf nutrient analysis is critical for effective nutrient management and better crop production.

Blueberry (*Vaccinium* sp.) production worldwide increased by 27% between 2020 and 2022. In 2023, the main blueberry-producing states in the southeast were Georgia (46,040 tons) and North Carolina (25,265 tons) (Brazelton 2023). Potassium is crucial in blueberry production, influencing various physiological processes essential for plant health and fruit quality. One percent to 10% of plant dry matter is composed of potassium. The role of potassium is to maintain electric potential gradients, activate enzymes, protein synthesis, regulate osmotic potential, and stress adaptation (Britto et al. 2021; Buchanan et al. 2015; Chérel et al. 2014; Epstein and Bloom 2004; Marschner 2011). Potassium also helps to maintain leaf relative water content and stomatal conductance, which are key factors for freeze tolerance, gas exchange, and evaporative cooling (Hasanuzzaman et al. 2018;

Lotfi et al. 2022; Wang et al. 2013). Plants absorb K^+ from soil solution through K channels located in the plasma membranes of cortical and epidermal root cells (Britto and Kronzucker 2008). Potassium delivery to the root surface is facilitated by transpiration-driven mass flow and local diffusion through the rhizosphere (Tinker and Nye 2000). In blueberries, available K^+ in the soil is one of the main factors determining the composition of microbial communities, shaping soil fungal composition, and promoting beneficial microbial associations in the roots, while the presence of mycorrhizal fungi can increase K uptake and its content in tissues (Che et al. 2022; Song et al. 2024; Tan et al. 2023).

Soil K concentration impacts plant root uptake of other nutrients. In barley (*Hordeum vulgare* L.), low soil K levels can increase NH_4^+ uptake, whereas high concentrations reduce NH_4^+ influx (Szczerba et al. 2008). In rice (*Oryza sativa* L.), the inhibitory effect between these two cations depends on the nutritional status of the plant. At high N and low plant K levels, the incorporation of K^+ in the media solution inhibited NH_4^+ uptake. However, at high K and low N, K^+ uptake increased in proportion to the concentration

of NH_4^+ in the media (Wang et al. 1996). When soil K levels are high in sugarcane (*Saccharum officinarum*), K^+ absorption can reduce the uptake of Ca^{2+} and Mg^{2+} (Rhodes et al. 2018). In wheat (*Triticum aestivum*), the accumulation of Na^+ in the soil solution can lead to a decrease in K^+ uptake, most probably by direct cation competition at absorption sites in the roots (Rubio et al. 1995). These intricate relationships could play a special role in cases in which N and K fertilizers are applied together, especially in the species that prefer the NH_4^+ form of N, like blueberries (Retamales and Hancock 2018).

Adequate leaf K levels in blueberry leaves range between 0.35% and 0.65% in southern highbush and between 0.30% and 0.60% in rabbiteye (RE) blueberries (Krewer and NeSmith 1999). According to Bañados et al. (2006), 25% to 32% of K accumulates in the crown and roots of all types of blueberries. Fruit K content rises sharply as fruit matures, averaging ~60 mg per berry at the ripened stage (Hart et al. 2006). The soils are sandy or sandy loam in the coastal plains of Georgia, where some blueberry species evolved (*Vaccinium myrsinites* and *Vaccinium hirsutum*) (Coleman 2017; Coville 1927; Krewer and NeSmith 2006). Potassium availability for plants is low in sandy soils, and the major proportion of the K is trapped in non-exchangeable sites (feldspar and micas). Furthermore, K^+ solubilized from exchangeable sites or that is supplied by fertilization is rapidly leached, especially in sandy soils with low organic matter (Rosolem and Steiner 2017; Sparks 1980). Northern highbush blueberries (NHB) (*V. corymbosum* L.) with K deficiency can be identified by dieback of the shoot tips and marginal scorching, cupping, curling, and necrosis in the leaves (Hanson 2016). In the leaves of northern and southern highbush blueberries (SHB), K deficiency can lead to an increase in the accumulation of Ca, whereas an excess of K decreases leaf Ca (Strik et al. 2019; Takahashi et al. 2021). It has been reported that Ca accumulation acts as a secondary messenger in response to K deficiency (Hafsi et al. 2014). There are mixed reports on how soil K can impact blueberry yield (Retamales and Hancock 2018; Strik et al. 2019). Leon-Chang et al. (2022) found no improvement in yield or fruit quality from K fertilization in NHB. In lowbush blueberry (*Vaccinium angustifolium* Aiton), applications of more than 30 kg-ha⁻¹ K reduced yield when combined with high N doses of more than 60 kg-ha⁻¹ N (Lafond 2020). The University of Georgia (UGA) established the K sufficiency levels for producing blueberries in the Georgia Coastal Plains soils between 80 and 135 kg-ha⁻¹ (35–60 mg·kg⁻¹) (Kissel and Plank 2011). In Georgia, there is a lack of information on potassium fertilization in blueberry production systems, and how K accumulates in the soil and leaf tissue. Furthermore, the established fertilization guidelines used by the blueberry industry in Georgia were developed more than a decade ago for blueberry cultivars that are no longer planted. The blueberry production area has increased in recent years, and new cultivars are

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being planted. Therefore, research on how K chemical fertilization affects the productivity of these new cultivars is key to the economic sustainability of the blueberry industry in Georgia and the southeast.

The objective of this study was to evaluate the impact of various fertilization practices on K and other nutrients in the soil and leaves at commercial farms of RE and SHB blueberry in Georgia, USA. Elucidating K accumulation during the production season will help update fertilization rates to more accurately meet crop needs and avoid possible overfertilization.

Materials and Methods

Location and experimental design. Experimental plots were established at four commercial blueberry farms located in South Georgia. The farms were selected because of their location in the most productive areas in the State of Georgia (Stubbs 2024). Farm 1 was in Brantley County (lat. 31°11'N, long. 82°01'W) and was planted with the RE 'Premier' in 2009 (RE-P). Farm 2 was located in Bacon County (lat. 31°32'N, long. 82°30'W) and was planted with 'Vernon' RE in 2013 (RE-V). Farm 3, located in Bacon County, was planted with 'Farthing' SHB in 2018 (SHB-F-Ba). Farm 4 was in Brantley County (lat. 31°06'N, long. 82°09'W) and planted with 'Farthing' SHB in 2014 (SHB-F-Br). A detailed description of the characteristics of each farm, such as plant density, irrigation periodicity, harvesting period, rate and

fertilizer practices applied during the first year and the production years, and the reported yield are shown in Table 1. Web Soil Survey indicates that Bacon County—farms 2 and 3—have loamy sand soil, farm 1 has loamy fine sand soil, and farm 4 has fine sand soil (NRCS 2023).

Each experimental plot consisted of three blocks of 10 plants, the blocks were located in the middle of the production area, avoiding edges, and the terrain did not present a gradient. Recently, fully expanded leaves were collected from five of the most vigorous plants in each block every month from Apr to Nov 2022, every 2 weeks from Apr to Aug 2023, and once per month from Sep to Nov 2023. In total, 252 leaf samples were collected over the 2 years from all the plots. Soil samples were also collected monthly from each block and divided into two depths (0–10 and 10–20 cm). In total, 384 soil samples were collected over the 2 years from all the plots. All samples were sent to the UGA Soil and Water Laboratory (Athens, GA, USA) for analysis.

Plant tissue analysis. The leaf samples were oven-dried at 65 °C for ~24 h, ground, sifted through a 20-mesh screen, and digested using Environmental Protection Agency (EPA) Method 3052 (USEPA 1996). This method involved weighing 0.5 g of each sample and adding 10 mL of concentrated HNO₃ to a fluorocarbon polymer microwave vessel. The vessels were then sealed and placed in a microwave digester at a temperature of 200 °C for 30 min. The resulting digest was

transferred to volumetric flasks and made up to a volume of 100 mL using deionized water. The solutions were then analyzed for various elements using EPA Method 200.8 using an inductively coupled plasma-optical emission spectroscopy (ICP-OES) instrument (Spectro Arcos FHS16, Kleve, Germany). Calibration standards were ensured, and independent laboratory performance checks were run with acceptable deviations for recoveries set at 100% ± 5%.

Soil analysis. Soil samples were analyzed for pH, P, K, Ca, Mg, and Mn. Nutrients like Ca, Mg, and Mn were chosen due to previously reported correlation with soil K in blueberry production (Leon-Chang et al. 2022; Strik et al. 2019). The soil samples were extracted using the Mehlich (1978) method. The samples were oven-dried at 40 °C, ground, and sieved through a 2-mm screen. Approximately 5 g of soil was weighed, and 20 mL of Mehlich I (0.025N H₂SO₄ + 0.05N HCl) extracting solution was added. Each sample was then placed on a high-speed shaker (250 oscillations/min) for 5 min, filtered through Whatman #1 paper, and analyzed for nutrients using ICP-OES (Spectro Arcos FHS16).

Statistical analysis. Leaf and soil nutrient data were analyzed using JMP v. 16 software (SAS Institute Inc., Cary, NC, USA). Partitioning modeling and multivariate correlation tools were used from JMP to establish correlations between nutrients during the productive season. Each sampling date had a corresponding result for leaf and soil nutrients

Table 1. Farm location, blueberry type, cultivar, year of establishment, plant spacing, irrigation management, harvesting period, reported yield, and fertilization management during the first year and the following production years¹ for the commercial farms sampled in Georgia, USA: Farm 1 'Premier' (RE-P), Farm 2 'Vernon' (RE-V), Farm 3 'Farthing' (SHB-F-B), and Farm 4 (SHB-F-Br).

Description	Farm 1 (RE-P)	Farm 2 (RE-V)	Farm 3 (SHB-F-B)	Farm 4 (SHB-F-Br)
Location	Brantley County	Bacon County	Bacon County	Brantley County
Blueberry type	Rabbiteye	Rabbiteye	Southern highbush	Southern highbush
Cultivar	Premier	Vernon	Farthing	Farthing
Established	2009	2013	2018	2014
Plant spacing (Between rows × Within plants)	3.7 × 0.91 m (3003 plants/ha)	3.4 × 1.22 m (2447 plants/ha)	3.4 × 0.76 m (3928 plants/ha)	3.7 × 0.91 m (3003 plants/ha)
Irrigation	Drip irrigated at 40% to 50% of management allowable depletion.	Drip irrigated 30 min, four times per day.	Drip irrigated for 30 min, four times per day.	Drip irrigated at 40% to 50% of management allowable depletion.
Harvest	Third week of June to second week of July.	The last week of May to the second week of June.	First and the second week of May.	Late May to the second week of June.
Fertilization (Year 1)	Granular fertilizer (10N–10P–10K); three applications per year: March, June, and August, at a rate of 33.6 kg·ha ⁻¹ each and a total of 10.1 kg·ha ⁻¹ K ₂ O.	Slow-release fertilizer (13N–6P–6K); five applications per year: March, April, May, June, and July, at a rate of 8.4 kg·ha ⁻¹ each and a total of 12.6 kg·ha ⁻¹ K ₂ O.	Slow-release fertilizer (13N–6P–6K); five applications per year: March, April, May, June, and July, at a rate of 11.2 kg·ha ⁻¹ each and a total of 16.8 kg·ha ⁻¹ K ₂ O.	Fertigation (10N–5P–5K); 33.6 kg·ha ⁻¹ per week (March to mid-June) and a total of 23.5 kg·ha ⁻¹ K ₂ O.
Fertilization (Production)	Granular fertilizer (10N–10P–10K); three applications, spring (during blooming), mid-August, fall (after harvest), at a rate of 33.6 kg·ha ⁻¹ each and a total of 100.8 kg·ha ⁻¹ K ₂ O per year.	Slow-release fertilizer (13N–6P–6K); two applications (March and June) applied in a 0.9-m-wide band across the bed at a rate of 33.6 kg·ha ⁻¹ each and a total of 40.3 kg·ha ⁻¹ K ₂ O per year.	Slow-release fertilizer (13N–6P–6K); two applications (March and June) applied in a 0.9-m-wide band across the bed at a rate of 50.5 kg·ha ⁻¹ each and a total of 60.6 kg·ha ⁻¹ K ₂ O per year.	Granular fertilizer (10N–10P–10K) twice per year (1 March and mid-June) at a rate of 168 kg·ha ⁻¹ each and a total of 33.6 kg·ha ⁻¹ K ₂ O per year. Fertigation (6N–6P–12K); 56 kg·ha ⁻¹ per week (March to mid-June) and a total of 94.1 kg·ha ⁻¹ K ₂ O per year.
Yield	3923 kg·ha ⁻¹	8967 kg·ha ⁻¹	9527 kg·ha ⁻¹	13,450 kg·ha ⁻¹

¹ At each farm, the plants were mechanically pruned after harvest every year.

used as an individual data point to develop the correlations. The Shapiro-Wilk test was run to evaluate the data's goodness of fit into a normal distribution. Data showed a Shapiro-Wilk level of significance below 0.05 and therefore was considered non-normally distributed. Thus, nonparametric comparisons for each pair were used to compare multiple means using the Wilcoxon method ($P < 0.05$).

Results and Discussion

Leaf and soil K levels during the production season. In RE blueberry, the concentration of K in leaves sampled 2 weeks after harvest was above the minimum recommended level at farm RE-P (Fig. 1), but it was lower at the RE-V farm (Fig. 2). In SHB, the harvest season lasted until the second week of May in farm SHB-F-B and the second week of June in farm SHB-F-Br. In both cases, leaf samples taken after harvest had K concentrations above the minimum recommended level (Figs. 3 and 4). For blueberries, the UGA recommends taking leaf samples the first two weeks after the end of harvest. Typically, this is when the plants have lower concentrations of nutrients, and nutrient levels are more stable, allowing for a comparison of these results with their nutrient sufficiency levels (Hart et al. 2006; Kissel and Sonon 2018).

In both years of study, soil K levels declined in June and September at each farm (Figs. 1–4). Soil K increased in July after fertilization but fell in September. The reductions in June and September may have been the result of additional plant uptake and an increase in leaf K concentrations in October. It has been reported that SHB blueberries have peaks of new root production

during July, August, and September, which can also explain increased uptake and decreased soil K levels (Steyn et al. 2024). Leaf K concentrations declined during spring and summer before increasing in October. Chuntanaparb and Cummings (1980) observed a similar trend in 'Jersey' NHB, and Strik and Vance (2015) observed an increase in leaf K at the end of September in several NHB cultivars. Furthermore, there is limited recent literature on potassium accumulation in blueberry leaves as the plants transition into dormancy during the fall.

Relationship between leaf and soil K and fruit yield. In both 2022 and 2023, average soil K levels were highest at farm 3 (SHB-F-B), as shown in Fig. 5A and B, even though this farm received the second lowest dose of K fertilizer, according to Table 1. In contrast, leaf potassium levels at farm 3 (SHB-F-B) were lower than those at the SHB farm in Brantley County (SHB-F-Br). However, the leaf potassium levels from the SHB-F-B farm were not significantly different compared with the two RE farms, including farm RE-P, which applied the highest dose of potassium fertilizer (Fig. 5C and D, Table 1). Consequently, there was no direct link between the quantity of fertilizer used and the concentrations of K in the soil and leaves. High rates of granular fertilizer applied at the RE-P farm in Brantley County did not result in higher K levels in the leaves but rather resulted in a higher accumulation of K^+ in the top layer of the soil (Fig. 6A and B). The other farms had a similar K^+ concentration in the two soil depths sampled (0–10 and 10–20 cm) (Fig. 6C–H). Accumulation of K^+ in surface soil layers increases the risk of losing fertilizer during rain events due to runoff and leaching, especially in sandy soils (Rosolem and Steiner

2017; Sparks 1980). In agricultural systems with high inputs of fertilizer, high K^+ leaching is linked to greater leaching of NO_3^-N , which increases the risk of water eutrophication (Brye and Norman 2004; Hubbard et al. 2004). In contrast, the RE-V farm in Bacon County received the lowest rate of K (Table 1) and was the only farm that experienced a significant decline in leaf K in the two years of the study (Fig. 5C and D) and had a leaf K below the minimum recommended level on the samples that were taken after harvest in July (Fig. 2). In addition, soil K concentration declined between the 2 years at this farm (Fig. 5A and B). The RE-V farm used slow-release fertilizer with a lower dose of K (13N–6P–6K) and only applied it twice per year, meanwhile, RE-P used regular fertilizer with a higher concentration of K (10N–10P–10K) and applied it three times per year (Table 1). Thus, RE-V plants received less fertilizer and did not have enough nutrients to accumulate in the leaf tissue.

Regardless of the rate, all farms that applied fertilizer in granular form had significantly less soil K in 2023 than in 2022. In SHB-F-Br, which was the only farm that used fertigation, the plants had high K concentrations in both soil and leaves (Fig. 5A–D). This suggests that the fertilization method is as important as the amount of fertilizer that is applied and corroborates that K fertigation is the best method to increase K in plants and fruit (Bryla and Orr 2017; Leon-Chang et al. 2022). Fertigation increases fertilizer use efficiency in mature plants because nutrient application can coincide with root growth and uptake.

The yield was unaffected by low K in leaves. Farm 1 (RE-P) had the lowest yield, even when leaf K and all the other leaf

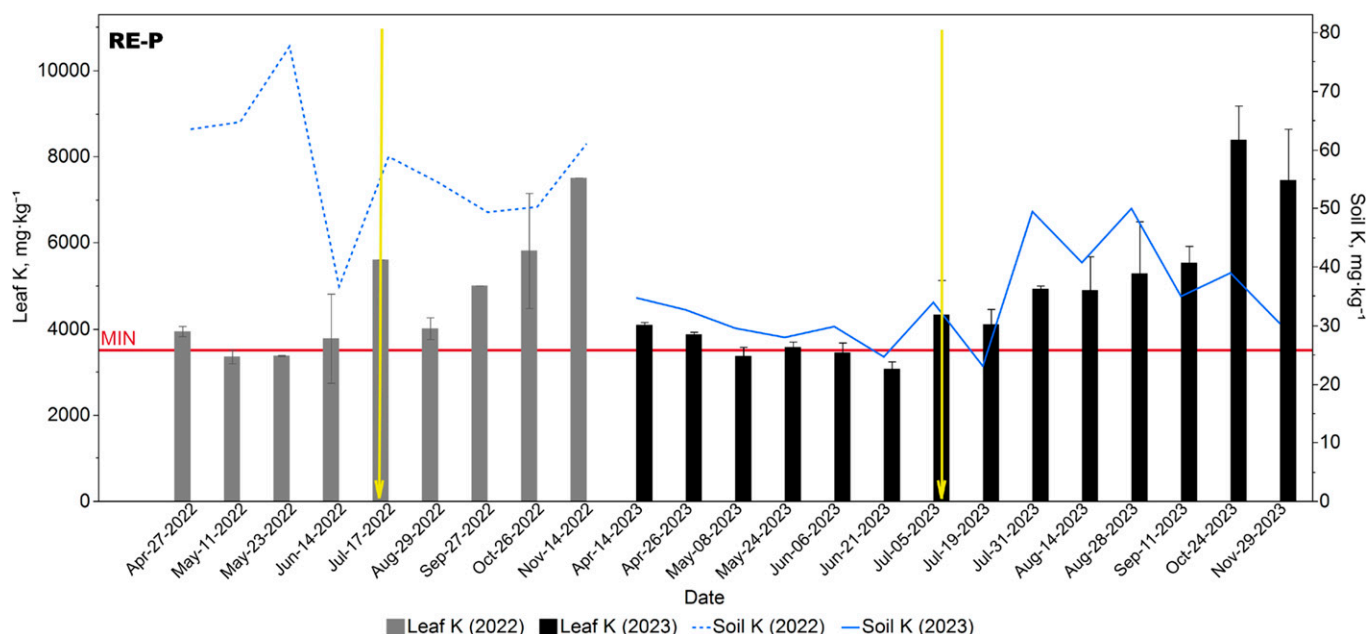


Fig. 1. Leaf and soil K concentrations from Apr to Nov 2022 and 2023 in rabbiteye blueberry commercial fields of 'Premier' (RE-P) farm located in Brantley County, GA, USA. Bars show the mean of three replicates, and error bars indicate the standard deviation. The red lines represent the minimum leaf K level (3500 mg kg^{-1}) recommended for blueberries in Georgia by Plank and Kissel (2024a, 2024b). Yellow lines indicate the date, 2 weeks after the end of harvest, which was used to compare with the sufficiency levels.

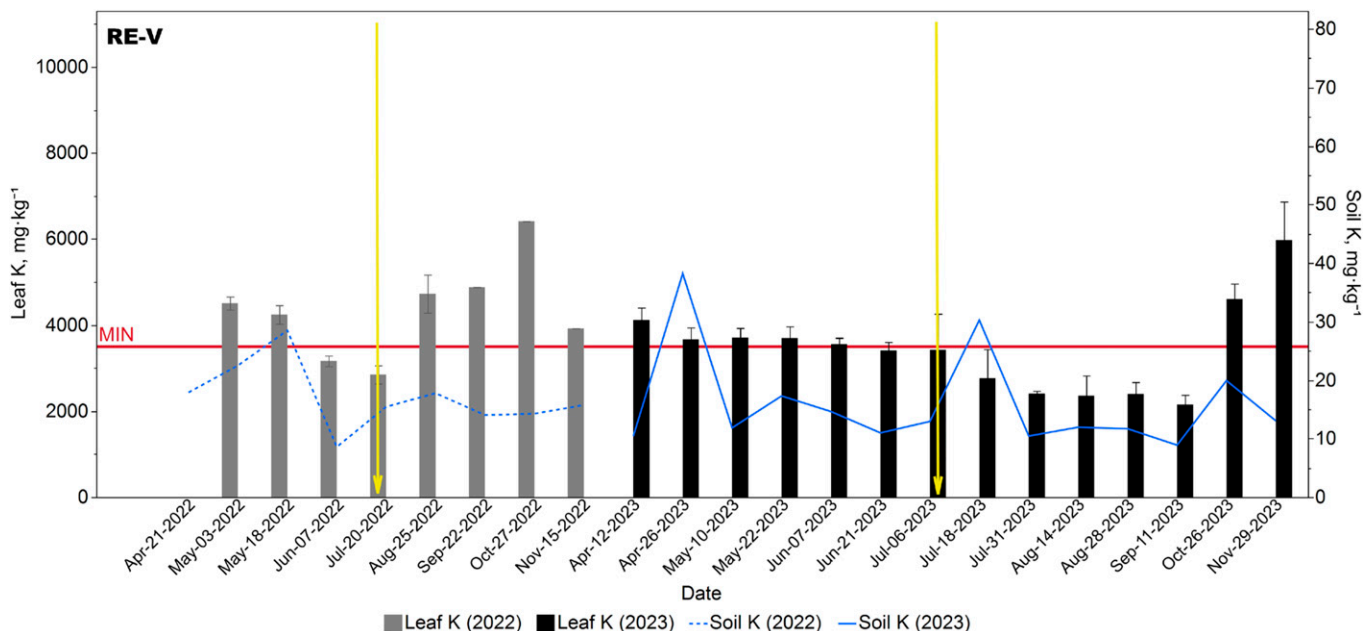


Fig. 2. Leaf and soil K concentrations from Apr to Nov 2022 and 2023 in rabbiteye blueberry commercial fields of ‘Vernon’ (RE-V) farm located in Bacon County, GA, USA. Bars show the mean of three replicates, and error bars indicate the standard deviation. The red lines represent the minimum leaf K level (3500 mg·kg⁻¹) recommended for blueberries in Georgia by Plank and Kissel (2024a, 2024b). Yellow lines indicate the date, 2 weeks after the end of harvest, which was used to compare with the sufficiency levels.

nutrient concentrations were above the minimum recommended range (Table 2). In contrast, the RE-V field had higher yields and lower leaf K concentrations in 2023 and all the other leaf nutrient concentrations were above the minimum levels (Tables 1 and 2). Both farms planted with RE had yields within the expected range for their cultivars, despite differing yields (Brazelton 2023). ‘Farthing’ SHB sampled in farms 3 and 4, presented leaf K levels in the sufficiency range and P

deficiency in leaf tissue, however, the two farms differed in yield per hectare. Farm 4 (SHB-F-Br), located in Brantley County, had the highest yield and the highest concentration of K in the leaves during both years of the study. In 2023, the leaf K in SHB-F-Br was above the recommended level, which could be a symptom of excessive fertilization. Farm 3, located in Bacon County (SHB-F-B), presented a deficiency in leaf N, which might contribute to its lower yields (Tables 1 and 2).

However, both farms are within the expected yield range per hectare for ‘Farthing’ (Brazelton 2023). The other reason for the differences in yield could be the age of the planting, the SHB-F-B farm is 4 years younger than the SHB-F-Br farm.

Fruit is an important sink for K (Hart et al. 2006). Thus, an increase in K levels might increase fruit yield. Nevertheless, K fertilization has varying effects on fruit yield in blueberries. Zhang et al. (2023) reported

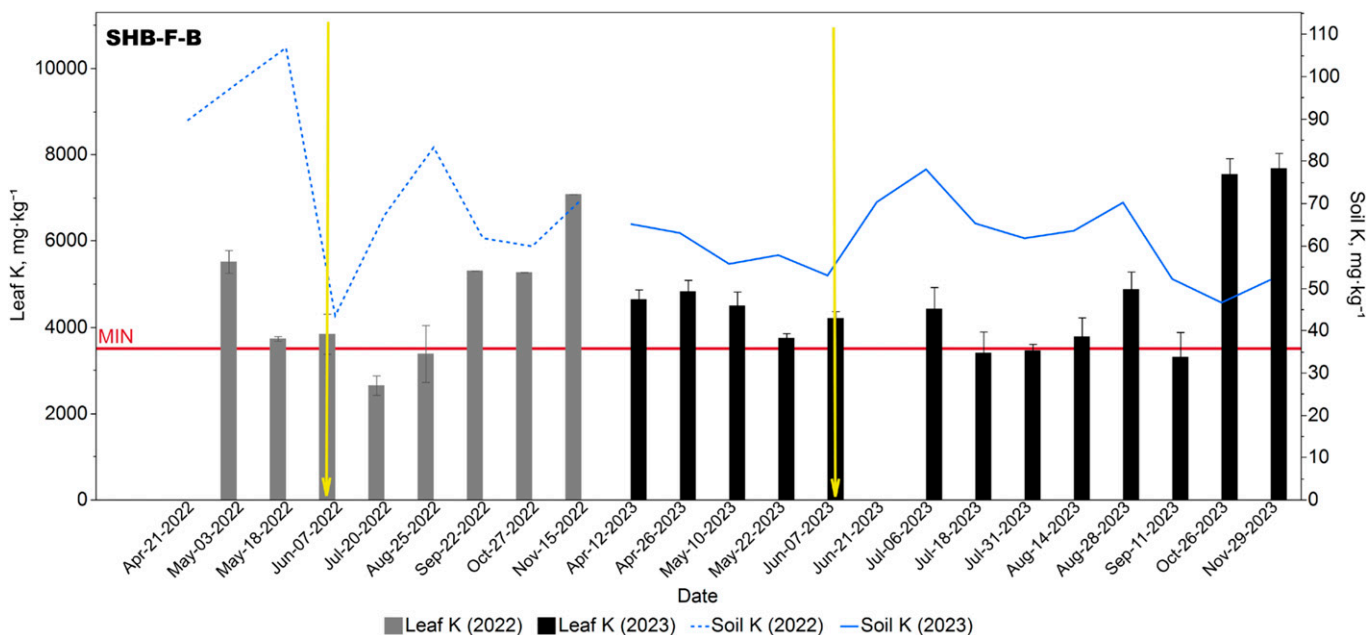


Fig. 3. Leaf and soil K concentrations from Apr to Nov 2022 and 2023 in southern highbush blueberry commercial fields of ‘Farthing’ (SHB-P-B) located in Bacon County, GA, USA. Bars show the mean of three replicates, and error bars indicate the standard deviation. The red lines represent the minimum leaf K level (3500 mg·kg⁻¹) recommended for blueberries in Georgia by Plank and Kissel (2024a, 2024b). Yellow lines indicate the date, 2 weeks after the end of harvest, which was used to compare with the sufficiency levels.

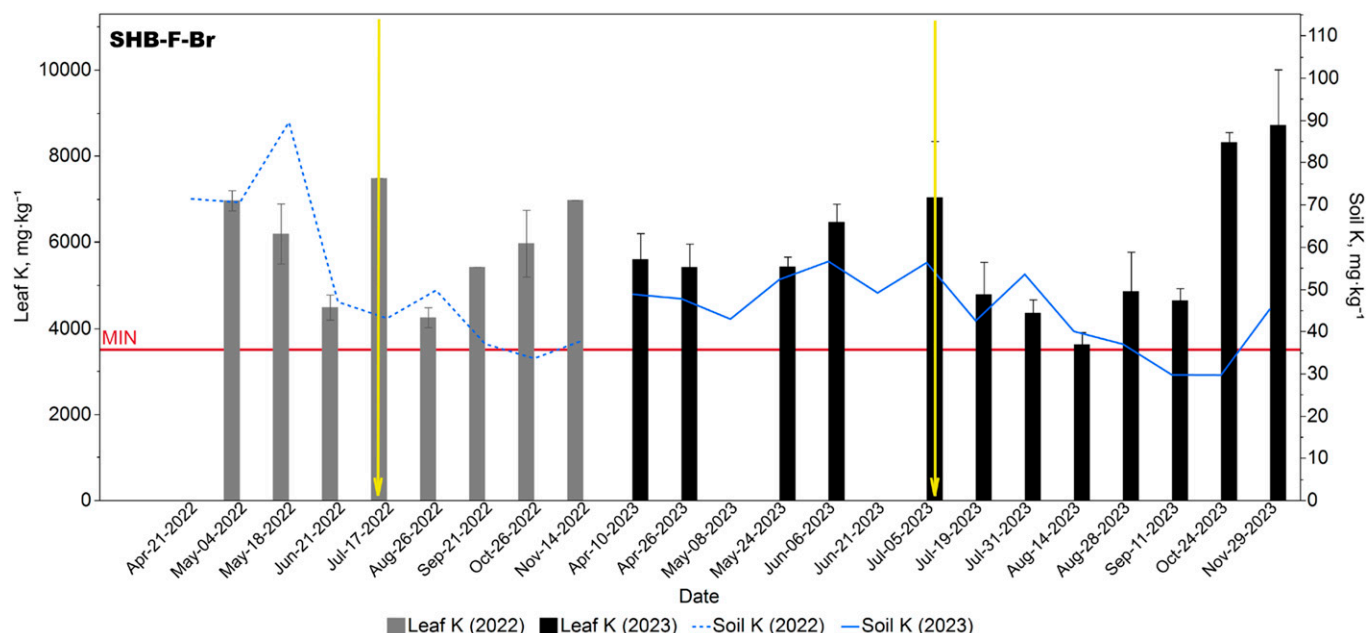


Fig. 4. Leaf and soil K concentrations from Apr to Nov 2022 and 2023 in southern highbush blueberry commercial fields of ‘Farthing’ (SHB-P-Br) located in Brantley County, GA, USA. Bars show the mean of three replicates, and error bars indicate the standard deviation. The red lines represent the minimum leaf K level ($3500 \text{ mg}\cdot\text{kg}^{-1}$) recommended for blueberries in Georgia by Plank and Kissel (2024a, 2024b). Yellow lines indicate the date, 2 weeks after the end of harvest, which was used to compare with the sufficiency levels.

that K fertilization was the main factor in increasing yield and fruit quality in ‘Brightwell’ RE blueberry. The rate tested in that study ($\sim 111 \text{ kg}\cdot\text{ha}^{-1} \text{ K}$) was higher than what was applied to all the farms. Eck (1983) found that on sandy soil in New Jersey, 20 to $40 \text{ kg}\cdot\text{ha}^{-1} \text{ K}$ increased yield in a 10-year-old NHB field but a higher rate of $80 \text{ kg}\cdot\text{ha}^{-1} \text{ K}$ did not increase yield. On the contrary, Lafond (2020) reported that a dose $>30 \text{ kg}\cdot\text{ha}^{-1} \text{ K}$ combined with a $>60 \text{ kg}\cdot\text{ha}^{-1} \text{ N}$ reduced yield. Strik et al. (2019) found that an increase in leaf K did not result in a higher yield when organic fertilizers were used in NHB blueberries. When the leaf K was 0.69% and 0.58% for ‘Duke’ and ‘Liberty’,

respectively, it decreased yield, even when the upper limit for sufficiency level was 0.70% (Strik and Davis 2023). Other studies found no effect of K fertilization on yield or fruit quality in blueberries (Bryla and Orr 2017; Stepień et al. 2014). The differences between fertilization rates, soil concentration, leaf concentration, and yield suggest that fertilization practices need to be customized to each specific location to ensure the economic and environmental sustainability of blueberry production. Thus, current fertilization guidelines need to be updated.

Correlations between K and other nutrients in the soil and leaves. Soil K data were not significantly correlated with leaf K or any

other leaf nutrients, nor was leaf K significantly correlated with soil nutrients (data not shown). Soil K showed positive correlations with many other soil nutrients such as P, Mg, Mn, and Ca (Table 3). Similarly, leaf K presented correlations with many leaf nutrients like P, Al, B, Cu, Mg, Mn, Na, S, and Zn (Table 4). Nevertheless, since the correlations between nutrients were not always present in all the farms, we chose to analyze the correlations that maintained similar trends and significance among at least three farms. Under this scenario, soil K showed positive correlations with soil P and Mn, meanwhile, leaf K had positive correlations with leaf P, Mn, S, and Na (Tables 3 and 4). The RE-V

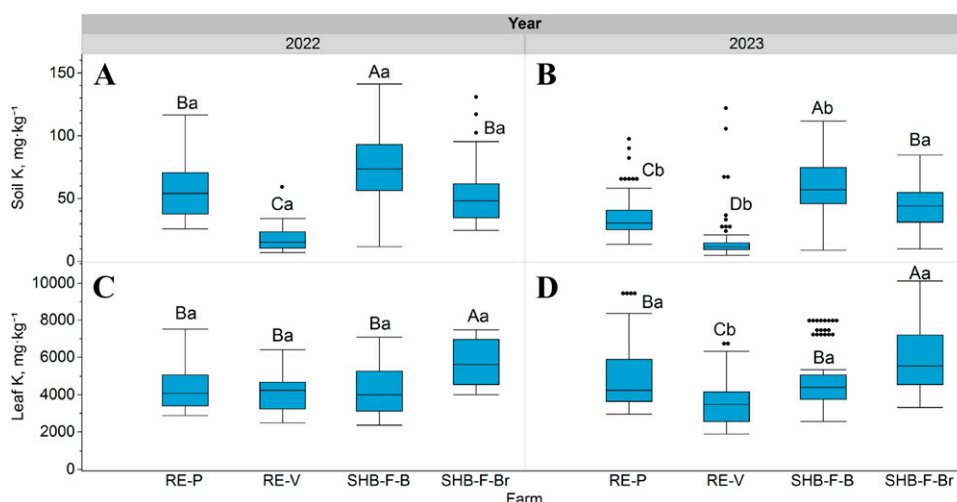


Fig. 5. Yearly mean of soil K (A, B) and leaf K (C, D) concentrations in commercial fields of ‘Premier’ (RE-P) and ‘Vernon’ (RE-V) rabbiteye blueberry and ‘Farthing’ southern highbush blueberry at farms located in Bacon (SHB-F-B) and Brantley Counties (SHB-F-Br), GA, USA. Different uppercase letters within a year represent a significant difference between the fields, while different lowercase letters represent a significance between years within each field ($P < 0.05$) (Wilcoxon test).

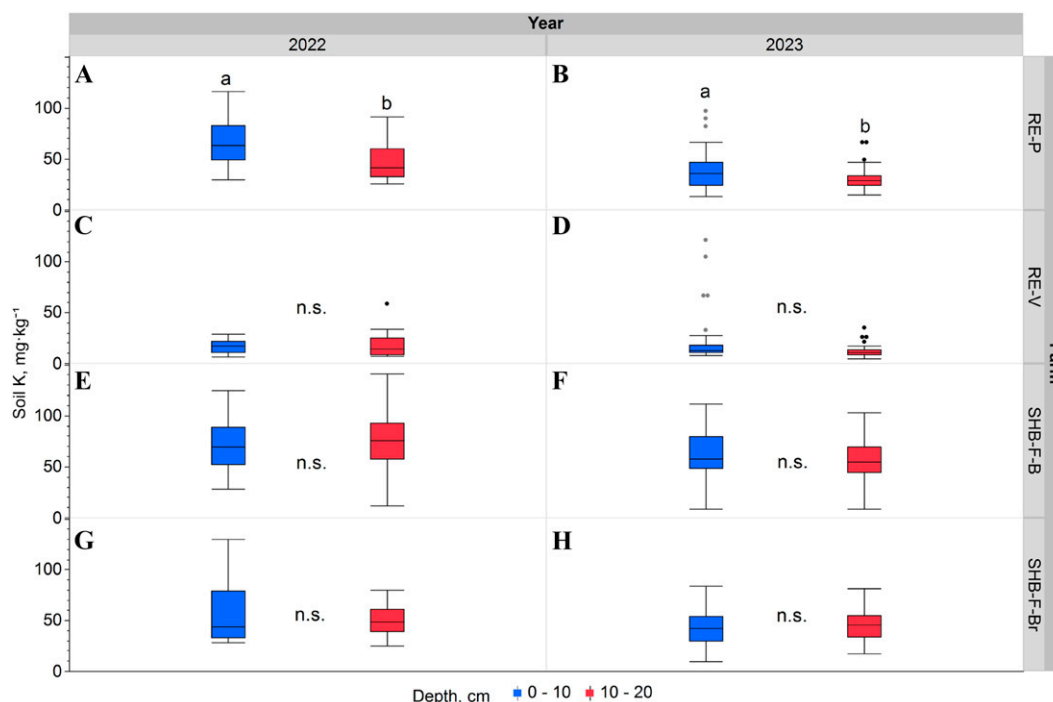


Fig. 6. Yearly mean of soil K concentrations at depths of 0 to 10 and 10 to 20 cm in commercial fields of 'Premier' (RE-P) (A, B) and 'Vernon' (RE-V) (C, D) rabbiteye blueberry, 'Farthing' southern highbush blueberry farms located in Bacon (SHB-F-B) (E, F) and Brantley (SHB-F-Br) (G, H) Counties, GA, USA. Means were separated at each farm at $P < 0.05$ (Wilcoxon test).

farm did not show a positive correlation between leaf K and S nor with leaf Na. This farm was the farm with the lowest fertilization rate and the lowest K soil concentration. The RE-V also had higher soil pH (a median of 5.0 in 2022 and 5.5 in 2023) when compared with the other farms (4.5 and 4.0) (data not shown). Furthermore, the Ca and Mg leaf concentrations from RE-V were above the sufficiency levels in 2023 (Table 2), even though Ca and Mg soil levels were similar to the other farms (data not shown). SHB blueberries cultivated under slightly alkaline soils (7.5) accumulate more Ca in the roots (Tamir et al. 2023). In the same manner, the SHB 'Emerald' fertigated with a high-pH solution had a higher Ca concentration in the roots under soilless cultivation (Schreiber and Nunez 2021). Thus, the higher Ca concentration in the leaf tissue of RE-V could be due to the higher pH of the soil. In 2023, the RE-V farm had a high positive correlation ($R^2 = 0.89$, $P < 0.0001$) between soil Ca and pH, but pH was not correlated to leaf Ca and soil Ca (data not shown). In addition, no Ca fertilizer was added to the RE-V farm, so it is probable that the increase in soil pH allowed Ca and Mg to be available to the plants, and therefore increased leaf Ca and Mg and changed the nutrient interaction in the plant. Strik et al. (2019) reported a negative correlation between Ca and K in NHB leaves. Probably this factor contributed to the lower concentrations of K that this farm had in 2023.

Correlation between K and P in soil. Soil P was the only nutrient consistently correlated to soil K at each farm during both years of the study (Table 3). The positive correlation can be explained by how both nutrients are applied at the same rate and at the same

time in mixed fertilizer formulas. The blueberry farms sampled in this study received 10N-10P-10K or 13N-6P-6K. In addition, P and K^+ soil interaction is influenced by the contrary charges of the ions. The presence of K^+ cations attracts P anions, decreasing the transportation of P particles during runoff and lowering the electric field around negative soil particles, which can repulse P anions in the soil solution (Chen et al. 2020), thus, helping maintain the P availability levels in the soil as long as K is present. In uncultivated land in Georgia's coastal plains, P tends to be low relative to K^+ . Low CEC facilitates the leaching of K^+ , which is slowly released from mica and K feldspars in sandy soils (Kolahchi and Jalali 2007; Mitchell and Huluka 2016; Sparks 1980). Therefore, blueberry producers are advised to apply P, but incorporating soil amendments tends to increase soil P concentration above recommended levels, causing leaching and impacting water quality (Gascho and Parker 2006; Novak and Watts 2004). For the production of SHB blueberry in the coastal plains of Georgia, soil K is considered low at levels $< 35 \text{ mg} \cdot \text{kg}^{-1}$, whereas P is considered limited at $< 15 \text{ mg} \cdot \text{kg}^{-1}$. The adequate ratio of K to P in the soil should be 2 to 1 (Kissel and Sonon 2018). However, the establishment of these soil nutrient requirements has not been updated. Indeed, further research is needed to understand how this ratio would impact root and shoot growth in blueberries.

Correlation between K and P in leaf. Potassium and P in leaves were positively correlated in all the farms. This correlation was observed almost every year, SHB-F-Br farm did not show a correlation in 2023 (Table 4). The correlation between K and P in leaves is

probably linked to the positive correlation between K and P in soil. There is little information on the relationship between P and K in blueberry leaves. In NHB, K and P in leaves follow the same trend, starting high during the spring and decreasing steadily until October (Strik and Vance 2015).

Correlation between soil K and leaf P. Even though soil P and K were positively correlated, and leaf P and K were also correlated, soil K did not influence leaf P or vice versa. Bhasin et al. (2021) found similar results, the application of organic fertilizer with high K did not increase leaf P in NHB blueberries. Meanwhile, Leon-Chang et al. (2022) determined that K fertilizer increased P in the crowns. In other crops, the interactions between these nutrients depend on the level of K^+ in the soil. In cowpeas (*Vigna unguiculata*), soil K deficiency causes a reduction in P uptake, even if P is available in the soil solution. This interaction occurs because there is a specific site for P absorption in the roots, which is only activated by K^+ (Adepetu and Akapa 1977). Conversely, it has been reported that high concentrations of K^+ in the soil solution can inhibit P uptake and impair P nutrition in *Arabidopsis* (Ródenas et al. 2019). Interactions between K and P are important in determining yield, root/shoot biomass, and cold hardiness in other species (Naciri et al. 2022; Reeves et al. 1970; Rietra et al. 2017).

Correlation between K and Mn. Potassium and Mn in the soil were positively correlated. This correlation was observed in the RE-V farm during both years of the study, and in 2022 at the RE-P and SHB-F-Br farms (Table 3). A constant application of K

Table 2. Average leaf nutrient levels sampled 2 weeks after harvest in milligrams per kilogram for 'Premier' (RE-P) and 'Vernon' (RE-V) rabbiteye blueberry and 'Farthing' southern highbush blueberry at farms located in Bacon (SHB-F-B) and Brantley (SHB-F-Br) Counties, GA, USA. The table shows the mean and the standard deviation (STD) values for total N, P, K, Ca, Mg, Zn, Mn, S, Cu, B, and Na in mg·kg⁻¹, and the sufficiency ranges for rabbiteye (RE) and southern highbush (SHB) blueberries in Georgia according to Plank and Kissel (2024a, 2024b). The numbers in red represent nutrient concentrations under the sufficiency range, and the numbers in blue represent concentrations above the sufficiency range.

Leaf nutrients	RE-P			RE-V			SHB-F-B			SHB-F-Br						
	Sufficient range RE			Mean ± STD (mg·kg ⁻¹)			Sufficient range SHB			Mean ± STD (mg·kg ⁻¹)						
	Min	Max		2022	2023		2022	2023		2022	2023		2022	2023		
Total N	12,000	17,000		14,500 ± 1,000	12,000 ± 500		19,000 ± 1,000	12,000 ± 500		18,000	21,000		15,000 ± 1,000	19,000 ± 0	18,100 ± 0	19,000 ± 2,000
P	800	2,000		898 ± 38	846 ± 40		861 ± 38	846 ± 40		1,200	4,000		896 ± 105	897 ± 20	1,157 ± 116	1,325 ± 207
K	3,500	6,000		4,606 ± 132	4,928 ± 62		2,848 ± 193	3,427 ± 759		3,500	6,500		3,838 ± 425	4,204 ± 144	4,804 ± 119	7,036 ± 1,193
Ca	2,500	7,000		5,025 ± 574	5,855 ± 604		6,837 ± 24	6,599 ± 487		4,000	8,000		5,025 ± 335	6,744 ± 117	5,397 ± 942	3,266 ± 112
Mg	1,400	2,000		1,927 ± 107	2,331 ± 240		2,516 ± 64	2,515 ± 182		1,200	2,500		2,310 ± 213	3,053 ± 147	2,244 ± 441	1,568 ± 93
Zn	10	25		35 ± 8	11 ± 1		17 ± 0	13 ± 0		8	30		18 ± 1	12 ± 1	14 ± 5	16 ± 2
Mn	25	100		144 ± 25	67 ± 2		59 ± 5	62 ± 9		50	350		67 ± 16	164 ± 47	59 ± 33	42 ± 6
S	1,100	2,500		1,885 ± 217	2,633 ± 408		2,759 ± 178	2,237 ± 225		1,200	2,000		1,450 ± 42	1,638 ± 53	1,700 ± 245	1,576 ± 189
Cu	4	10		52 ± 12	5 ± 1		22 ± 14	3 ± 1		4	20		7 ± 0	11 ± 1	4 ± 1	4 ± 1
B	12	35		104 ± 4	138 ± 53		52 ± 2	50 ± 4		30	70		29 ± 3	41 ± 4	62 ± 16	56 ± 9
Na				54 ± 8	168 ± 29		13 ± 2	221 ± 33					35 ± 10	110 ± 9	238 ± 29	220 ± 23

through drip irrigation increased Mn in the soil solution in mature NHB fields (Leon-Chang et al. 2022). An increase in potassium fertilization can enhance Mn availability in acidic soil conditions (pH ~4), particularly when phosphorus is also present in the soil solution. Potassium and phosphorus react under acidic soil conditions to form potassium dihydrogen phosphate, which extracts Mn from the soil and increases its solubility (Willard 1979).

It is likely that higher amounts of K and P in the soil increase Mn solubility and thereby increase the uptake of this nutrient (Leon-Chang et al. 2022; Spiers 1984; Townsend 1973). A positive interaction between leaf K and leaf Mn appeared at all the farms but only in the first year (Table 4). This interaction may be related to the correlation between soil potassium and soil manganese. Manganese is an essential micronutrient for plant development in blueberry, serving as a cofactor in enzymes and oxidation-reduction reactions. Nevertheless, it has been reported to cause toxicity in blueberries at levels as low as 476 ppm (Bañados et al. 2009). Manganese toxicity must be considered in Georgia blueberry production because pine bark contributes to the soil Mn quota (Smith et al. 2012). The average Mn levels in the surveyed farms were <300 ppm, but leaf Mn in the SHB-F in Bacon County increased during the second year.

Correlation between K and S. The interaction between K and S in plants was positive and significant during both years at every place except the RE-V in Bacon County. No direct interactions between K and S in leaves have been reported for blueberries, but the application of S to the soil can increase leaf K in 'Tiftblue' RE (Spiers and Braswell 1992). Granular K fertilizer significantly increased leaf S concentration in NHB when compared with plants that received no K (Leon-Chang et al. 2022). The RE-V farm had the lowest levels of K in the soil and leaves and higher pH than the other farms during both years of the study. In addition, leaf nutrient interactions were different from those at the other three farms. Both Bacon County farms had a negative correlation between soil K and pH (Table 2). The addition of S may cause a reduction in the soil pH, increasing the soil K availability, therefore explaining the positive correlation of S and K in leaves.

Correlation between K and Na in leaf. A positive interaction between leaf K and Na appeared in RE-P during both years and in the SHB-F-B and SHB-F-Br farms in 2022 and 2023, respectively (Table 4). In previous research reports, high Na concentrations of 88 mM applied to the soil increased leaf Na but decreased the K leaf level in RE blueberries. Lower Na concentrations of 22 mM did not affect leaf K (Spiers 1993). In 'Bluecrop' NHB, Na solution (20 mM) application significantly decreased K leaf levels (Muralitharan et al. 1992). According to Song et al. (2023), the maintenance of low levels of Na accumulation in blueberry leaves reflects the capacity of the cultivar to stand salinity stress

Table 3. Pearson correlation matrix between soil K and soil pH and other soil nutrients in commercial fields of 'Premier' and 'Vernon' rabbiteye blueberry and 'Farthing' southern highbush blueberry at farms in Brantley and Bacon Counties, GA, USA. Correlations were established using soil nutrient levels from samples from Apr to Nov 2022 and 2023. Green and red cells indicate significant correlation indexes ≥ 0.5 and ≤ -0.5 , respectively ($P < 0.05$).

Soil pH and other soil nutrients	Soil K							
	RE-P		RE-V		SHB-F-B		SHB-F-Br	
	2022	2023	2022	2023	2022	2023	2022	2023
pH	-0.1	0.0	-0.5	-0.2	-0.3	-0.5	0.2	-0.1
P	0.6	-0.1	0.8	0.9	0.6	0.6	0.8	0.5
Ca	0.3	0.2	0.3	0.0	0.1	-0.1	0.6	-0.2
Mg	0.4	0.4	-0.1	0.1	0.5	0.1	0.6	-0.1
Mn	0.7	0.1	0.7	0.7	0.2	0.4	0.6	0.0

Table 4. Pearson correlation matrix between leaf K and macro and micro leaf nutrients in commercial fields of 'Premier' and 'Vernon' rabbiteye blueberry and 'Farthing' southern highbush blueberry at farms in Brantley and Bacon Counties, GA, USA. Correlations were established using leaf nutrient levels from samples from Apr to Nov 2022 and 2023. Green and red cells indicate significant correlation indexes ≥ 0.5 and ≤ -0.5 , respectively ($P < 0.05$).

Macro and micro leaf nutrients	Leaf K							
	RE-P		RE-V		SHB-F-B		SHB-F-Br	
	2022	2023	2022	2023	2022	2023	2022	2023
P	0.5	0.8	0.6	0.8	0.8	0.8	0.2	0.5
Total N	0.2	-0.5	0.4	0.0	0.3	-0.1	0.2	-0.4
Al	0.0	0.4	-0.1	0.1	-0.3	0.0	0.6	0.6
B	0.1	0.4	-0.5	-0.1	-0.3	-0.1	0.5	0.7
Ca	0.4	0.4	-0.4	0.0	-0.3	0.2	0.6	0.5
Cu	-0.4	-0.4	-0.5	0.4	-0.3	-0.1	0.2	0.8
Fe	-0.2	0.1	-0.2	0.1	-0.2	0.2	0.5	0.5
Mg	0.1	0.5	-0.5	-0.2	-0.5	0.0	0.6	0.5
Mn	-0.2	0.7	0.2	0.7	0.4	0.6	0.7	0.3
Mo	-0.1	0.0	-0.3	0.1	0.1	0.0	-0.1	0.1
Na	0.7	0.6	0.1	0.1	0.8	0.4	0.4	0.7
Ni	-0.2	0.1	0.0	0.2	0.0	0.3	0.1	0.2
S	0.7	0.8	-0.2	0.1	0.6	0.7	0.5	0.9
Zn	0.3	0.5	0.1	0.5	0.2	0.5	0.1	0.7

and is correlated to the Na/K ratio. Susceptible cultivars like Sweetheart NHB exposed to high salinity soil or growing conditions had three times more leaf Na than the most resistant cultivar Duke. In contrast, the K leaf content decreased significantly and the Na/K ratio increased (Song et al. 2023). There is no current sufficiency level for leaf Na concentrations for blueberries in Georgia. Based on the Song et al. (2023) publication, NHB blueberry leaves presented Na content of $\sim 15,000 \text{ mg}\cdot\text{kg}^{-1}$ ('Sweetheart') and $\sim 5000 \text{ mg}\cdot\text{kg}^{-1}$ ('Duke') under soil saline conditions and were below $1000 \text{ mg}\cdot\text{kg}^{-1}$ for both cultivars under no saline conditions. For RE blueberries, leaf Na levels of $2900 \text{ mg}\cdot\text{kg}^{-1}$ under low Na fertilization levels (2.2 mM) were reported (Spiers 1993). In our results, none of the farms showed an average leaf Na above $250 \text{ mg}\cdot\text{kg}^{-1}$ (Table 2). So, it is possible that the negative correlation between Na and K only shows up when plants have accumulated higher levels of Na.

Conclusions

The absence of direct interactions between K in the leaves and soil indicates that further investigation is necessary to understand the mechanisms underlying nutrient interactions in blueberry plants. Farm 2 RE-V,

which applied the lowest dose of fertilizer and showed the lowest K levels in the soil, exhibited distinct nutrient interactions that were likely influenced by soil pH and fertility management. Furthermore, soil K was positively correlated with soil P and Mn in the study, suggesting complex interactions between soil nutrients influenced by soil characteristics and fertilization practices. Likewise, leaf K was positively correlated with leaf P, Mn, S, and Na. The data collected in this study suggest that the recommendation of leaf tissue sampling 2 weeks after harvest might need to be updated; we recommend that the leaf tissue be sampled in August because the nutrients were more stable.

Blueberry nutrient physiology is a complex interplay between environmental factors and management practices in a crop production system. Therefore, tailored management strategies are necessary to optimize plant health and productivity specific to different agroecosystems.

References Cited

- Adepetu JA, Akapa LK. 1977. Root-growth and nutrient-uptake characteristics of some cowpea varieties. *Agron J.* 69(6):940–943. <https://doi.org/10.2134/agronj1977.00021962006900060011x>.
- Bañados MP, Ibáñez F, Toso AM. 2009. Manganese toxicity induces abnormal shoot growth in

- 'O'Neal' blueberry. *Acta Hort.* 810:509–512. <https://doi.org/10.17660/ActaHortic.2009.810.67>.
- Bañados P, Bonomelli C, González J, Juillerat F. 2006. Dry matter, nitrogen, potassium and phosphorus partitioning in blueberry plants during winter. *Acta Hort.* 715:443–448. <https://doi.org/10.17660/ActaHortic.2006.715.67>.
- Bhasin A, Davenport J, Lukas S, Lu QW, Hoheisel G, DeVetter LW. 2021. Evaluating postharvest organic nitrogen fertilizer applications in early fruiting northern highbush blueberry. *HortScience*. 56(12):1565–1571. <https://doi.org/10.21273/HORTSCI16128-21>.
- Brazelton C. 2023. Global state of the blueberry industry report 2023. <https://www.internationalblueberry.org/2023-report/>. [accessed 24 Sep 2024].
- Britto DT, Coskun D, Kronzucker HJ. 2021. Potassium physiology from Archean to Holocene: A higher-plant perspective. *J Plant Physiol.* 262:153432. <https://doi.org/10.1016/j.jplph.2021.153432>.
- Britto DT, Kronzucker HJ. 2008. Cellular mechanisms of potassium transport in plants. *Physiol Plant.* 133(4):637–650. <https://doi.org/10.1111/j.1399-3054.2008.01067.x>.
- Brye KR, Norman JM. 2004. Land-use effects on anion-associated cation leaching in response to above-normal precipitation. *Acta Hydroch Hydrol.* 32(3):235–248. <https://doi.org/10.1002/ahch.200300534>.
- Bryla D, Orr S. 2017. Comparison between fertigation and granular application of potassium fertilizer on mineral nutrition, yield, and fruit quality in northern highbush blueberry. *HortScience*. 52(9):S247–S248.
- Buchanan B, Gruissem W, Jones R. 2015. Biochemistry and molecular biology of plants (2nd ed). Wiley Blackwell, Hoboken, NJ, USA.
- Che JL, Wu YQ, Yang H, Wang SY, Wu WL, Lyu L, Li WL. 2022. Long-term cultivation drives dynamic changes in the rhizosphere microbial community of blueberry. *Front Plant Sci.* 13:962759. <https://doi.org/10.3389/fpls.2022.962759>.
- Chen Y, Tian R, Li H. 2020. Phosphorus transportation in runoff as influenced by cationic non-classic polarization: A simulation study. *J Soils Sediments*. 20(1):308–319. <https://doi.org/10.1007/s11368-019-02380-w>.
- Chérel I, Lefoulon C, Boeglin M, Sentenac H. 2014. Molecular mechanisms involved in plant adaptation to low K availability. *J Exp Bot.* 65(3):833–848. <https://doi.org/10.1093/jxb/ert402>.
- Chuntanaparb N, Cummings G. 1980. Seasonal trends in concentration of nitrogen, phosphorus, potassium, calcium, and magnesium in leaf portions of apple, blueberry, grape, and peach. *J Am Soc Hortic Sci.* 105(6):933–935. <https://doi.org/10.21273/JASHS.105.6.933>.
- Coleman D. 2017. Soils. New Georgia encyclopedia. <https://www.georgiaencyclopedia.org/articles/geography-environment/soils/>. [accessed 18 Jun 2024].
- Coville F. 1927. Blueberry chromosomes. *Science*. 66(1719):565–566. <https://doi.org/10.1126/science.66.1719.565>.
- Eck P. 1983. Optimum potassium nutritional level for production of highbush blueberry. *J Am Soc Hortic Sci.* 108(4):520–522. <https://doi.org/10.21273/JASHS.108.4.520>.
- Epstein E, Bloom A. 2004. Mineral nutrition of plants: Principles and perspectives (2nd ed). Sinauer Associates-Oxford University Press, Sunderland, England.
- Gascho GJ, Parker MB. 2006. Nitrogen, phosphorus, and potassium fertilization of a coastal

- plain cotton-peanut rotation. *Commun Soil Sci Plan.* 37(9-10):1485-1499. <https://doi.org/10.1080/00103620600584347>.
- Hafsi C, Debez A, Abdelly C. 2014. Potassium deficiency in plants: Effects and signaling cascades. *Acta Physiol Plant.* 36(5):1055-1070. <https://doi.org/10.1007/s11738-014-1491-2>.
- Hanson E. 2016. Managing the nutrition of highbush blueberries. *MSU Ext Bull E2011*. <https://shorturl.at/bY3U6>. [accessed 8 Jul 2024].
- Hart J, Strik B, White L, Yang W. 2006. Nutrient management for blueberries in Oregon. *OSU Ext Serv Bull EM8918*.
- Hasanuzzaman M, Bhuyan M, Nahar K, Hossain M, Mahmud J, Hossen M, Masud A, Fujita M, Moumita. 2018. Potassium: A vital regulator of plant responses and tolerance to abiotic stresses. *Agronomy.* 8(3):31. <https://doi.org/10.3390/agronomy8030031>.
- Hubbard RK, Sheridan JM, Lowrance R, Bosch DD, Vellidis G. 2004. Fate of nitrogen from agriculture in the southeastern coastal plain. *59(2):72-86*.
- Kissel D, Plank O. 2011. Soil test handbook for Georgia. *UGA Ext Bull.* 62.
- Kissel D, Sonon L. 2018. Blueberries-southern highbush in soil or amended soil. <https://aesl.ces.uga.edu/publications/soil/cropsheets/133.pdf>. [accessed 15 Mar 2024].
- Kolahchi Z, Jalali M. 2007. Effect of water quality on the leaching of potassium from sandy soil. *J Arid Environ.* 68(4):624-639. <https://doi.org/10.1016/j.jaridenv.2006.06.010>.
- Krewer G, NeSmith DS. 1999. Blueberry fertilization in soil. *UGA Ext. Fruit Pub 01-1*.
- Krewer G, NeSmith DS. 2006. Blueberry cultivars for Georgia. https://smallfruits.org/files/2019/06/06bbcvproc_Nov0206.pdf. [accessed 16 Jul 2024].
- Lafond J. 2020. Nitrogen, phosphate and potassium fertilization in the production of wild lowbush blueberries. *Can J Soil Sci.* 100(2):99-108. <https://doi.org/10.1139/cjss-2019-0087>.
- Leon-Chang DP, Bryla DR, Scagel CF, Strik BC. 2022. Influence of fertigation and granular applications of potassium fertilizer on soil pH and availability of potassium and other nutrients in a mature planting of northern highbush blueberry. *HortScience.* 57(11):1377-1386. <https://doi.org/10.21273/HORTSCI16747-22>.
- Lotfi R, Abbasi A, Kalaji HM, Eskandari I, Sedghieh V, Khorsandi H, Sadeghian N, Yadav S, Rastogi A. 2022. The role of potassium on drought resistance of winter wheat cultivars under cold dryland conditions: Probed by chlorophyll a fluorescence. *Plant Physiol Biochem.* 182:45-54. <https://doi.org/10.1016/j.plaphy.2022.04.010>.
- Marschner H. 2011. *Marschner's mineral nutrition of higher plants* (3rd ed). Academic Press, London, England.
- Mehlich A. 1978. New extractant for soil test evaluation of phosphorus, potassium, magnesium, calcium, sodium, manganese and zinc. *Commun Soil Sci Plan.* 9(6):477-492. <https://doi.org/10.1080/00103627809366824>.
- Mitchell CC, Huluka G. 2016. Potassium dynamics in US coastal plain soils. *Commun Soil Sci Plan.* 47(sup1):54-63. <https://doi.org/10.1080/00103624.2016.1232096>.
- Muralitharan MS, Chandler S, Van SR. 1992. Effects of NaCl and Na₂SO₄ on growth and solute composition of highbush blueberry (*Vaccinium corymbosum*). *Funct Plant Biol.* 19(2):155-164. <https://doi.org/10.1071/PP9920155>.
- Naciri R, Rajib W, Chtouki M, Zeroual Y, Ouksarroum A. 2022. Potassium and phosphorus content ratio in hydroponic culture affects tomato plant growth and nutrient uptake. *Physiol Mol Biol Plants.* 28(4):763-774. <https://doi.org/10.1007/s12298-022-01178-4>.
- Novak JM, Watts DW. 2004. Increasing the phosphorus sorption capacity of southeastern coastal plain soils using water treatment residuals. *Soil Sci.* 169(3):206-214. <https://doi.org/10.1097/01.ss.0000012252.03492.30>.
- NRCS. 2023. Web soil survey. <https://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>. [accessed 18 Mar 2024].
- Plank O, Kissel DE. 2024a. Blueberry, rabbiteye. In: *Plant analysis handbook for Georgia*. University of Georgia. <https://aesl.ces.uga.edu/publications/plant/Blueberry.html>. [accessed 2 Dec 2024].
- Plank O, Kissel DE. 2024b. Blueberry, southern highbush in pine bark. In: *Plant analysis handbook for Georgia*. University of Georgia. <https://aesl.ces.uga.edu/publications/plant/Blueberry Pine.html>. [accessed 2 Dec 2024].
- Reeves SA, McBee GG, Bloodworth ME. 1970. Effect of N, P, and K tissue levels and late fall fertilization on cold hardiness of Tifgreen bermudagrass (*Cynodon dactylon* × *C. transvaalensis*). *Agron J.* 62(5):659-662. <https://doi.org/10.2134/agronj1970.00021962006200050034x>.
- Retamales J, Hancock J. 2018. *Blueberries* (2nd ed). CABI, Boston, MA, USA.
- Rhodes R, Miles N, Hughes JC. 2018. Interactions between potassium, calcium and magnesium in sugarcane grown on two contrasting soils in South Africa. *Field Crop Res.* 225:180. <https://doi.org/10.1016/j.fcr.2018.07.004>.
- Rietra R, Heinen M, Dimkpa CO, Bindraban PS. 2017. Effects of nutrient antagonism and synergism on yield and fertilizer use efficiency. *Commun Soil Sci Plan.* 48(16):1895-1920. <https://doi.org/10.1080/00103624.2017.1407429>.
- Ródenas R, Martínez V, Nieves-Cordones M, Rubio F. 2019. High external K⁺ concentrations impair pi nutrition, induce the phosphate starvation response, and reduce arsenic toxicity in arabidopsis plants. *Int J Mol Sci.* 20(9). <https://doi.org/10.3390/ijms20092237>.
- Rosolem CA, Steiner F. 2017. Effects of soil texture and rates of K input on potassium balance in tropical soil. *European J Soil Sci.* 68(5):658-666. <https://doi.org/10.1111/ejss.12460>.
- Rubio F, Gassmann W, Schroeder JI. 1995. Sodium-driven potassium uptake by the plant potassium transporter HKT1 and mutations conferring salt tolerance. *Science.* 270(5242):1660-1663. <https://doi.org/10.1126/science.270.5242.1660>.
- Schreiber MJ, Nunez GH. 2021. Calcium carbonate can be used to manage soilless substrate pH for blueberry production. *Horticulturae.* 7(4):74. <https://doi.org/10.3390/horticulturae7040074>.
- Smith E, Krewer G, Ruter J. 2012. Fertilizing blueberries in pine bark beds. https://secure.caes.uga.edu/extension/publications/files/pdf/B%201291_3.PDF. [accessed 17 Jun 2024].
- Song HF, Cao YB, Zhao XY, Zhang LY. 2023. Na⁺-preferential ion transporter HKT1;1 mediates salt tolerance in blueberry. *Plant Physiol.* 194(1):511-529. <https://doi.org/10.1093/plphys/kiad510>.
- Song ZJ, Xiao LH, Guo XL, Zhu YZ, An XL, Tan Y, Zhang XY, Wang DL. 2024. Effects of inoculating different mycorrhizal fungi on rhizosphere soil fungi and nutrient uptake of blueberry. *Hortic Environ Biotechnol.* 65(1):29-41. <https://doi.org/10.1007/s13580-023-00527-w>.
- Sparks DL. 1980. Chemistry of soil potassium in Atlantic coastal-plain soils - a review. *Commun Soil Sci Plan.* 11(5):435-449. <https://doi.org/10.1080/00103628009367051>.
- Spiers JM. 1984. Elemental leaf content and deficiency symptoms in rabbiteye blueberries: 3. Phosphorus and potassium. *J Plant Nutr.* 7(11):1567-1581. <https://doi.org/10.1080/01904168409363303>.
- Spiers JM. 1993. Calcium, magnesium, and sodium uptake in rabbiteye blueberries. *J Plant Nutr.* 16(5):825-833. <https://doi.org/10.1080/01904169309364577>.
- Spiers JM, Braswell JH. 1992. Soil-applied sulfur affects elemental leaf content and growth of 'Tifblue' rabbiteye blueberry. *J Am Soc Hortic Sci.* 117(2):230-233. <https://doi.org/10.21273/JASHS.117.2.230>.
- Stepień W, Stepień T, Koziński B, Smolarz K. 2014. Effect of diverse long-term mineral fertilization on fruit yield and mineral content in the leaves of highbush blueberry plants. *Acta Hortic.* 1017:205-208. <https://doi.org/10.17660/ActaHortic.2014.1017.25>.
- Steyn J, Hoffman EW, Lötze E. 2024. Root growth dynamics of two southern highbush blueberry (*V. corymbosum* L. interspecific hybrids) cultivars in the western cape, South Africa. *Sci Hortic.* 336:113344. <https://doi.org/10.1016/j.scienta.2024.113344>.
- Strik BC, Davis AJ. 2023. Lessons learned from long-term research on organic production systems of northern highbush blueberry. *Acta Hortic.* 1357:27-34. <https://doi.org/10.17660/ActaHortic.2023.1357.5>.
- Strik BC, Vance A. 2015. Seasonal variation in leaf nutrient concentration of northern highbush blueberry cultivars grown in conventional and organic production systems. *HortScience.* 50(10):1453-1466. <https://doi.org/10.21273/HORTSCI.50.10.1453>.
- Strik BC, Vance A, Bryla DR, Sullivan DM. 2019. Organic production systems in northern highbush blueberry: II. Impact of planting method, cultivar, fertilizer, and mulch on leaf and soil nutrient concentrations and relationships with yield from planting through maturity. *HortScience.* 54(10):1777-1794. <https://doi.org/10.21273/HORTSCI14197-19>.
- Stubbs K. 2024. Georgia farm gate value report 2022. <https://caed.uga.edu/content/dam/caes-subsite/caed/publications/annual-reports-farm-gate-value-reports/2022%20Farm%20Gate%20Value%20Report.pdf>. [accessed 8 Jul 2024].
- Szczerba MW, Britto DT, Balkos KD, Kronzucker HJ. 2008. Alleviation of rapid, futile ammonium cycling at the plasma membrane by potassium reveals K⁺-sensitive and -insensitive components of NH₄⁺ transport. *J Exp Bot.* 59(2):303-313. <https://doi.org/10.1093/jxb/ern309>.
- Takahashi S, Che JG, Horiuchi N, Cho HY, Onwona-Agyeman S, Kojima K, Yamada M, Ogiwara I. 2021. Production of low-potassium fruit of potted and fertigated southern highbush blueberry (*Vaccinium corymbosum* L. interspecific hybrid). *Hortic J.* 90(2):161-171. <https://doi.org/10.2503/hortj.UTD-238>.
- Tamir G, Zeng QL, Eli D, Zilkah S, Bar-Tal A, Dai NR. 2023. Combined effects of alkaline pH and high Ca concentration on root morphology, cell-wall polysaccharide concentrations and blueberry plant performance. *Front Agron.* 5:1121448. <https://doi.org/10.3389/fagro.2023.1121448>.
- Tan YL, Wang J, He YG, Yu XM, Chen SJ, Penttinen P, Liu SL, Yang Y, Zhao K, Zou LK. 2023. Organic fertilizers shape soil microbial

- communities and increase soil amino acid metabolites content in a blueberry orchard. *Microb Ecol.* 85(1):232–246. <https://doi.org/10.1007/s00248-022-01960-7>.
- Tinker PB, Nye P. 2000. Solute transport in the soil near root surfaces, p 130–155. In: Tinker PB, Nye P (eds). *Solute movement in the rhizosphere*. Oxford University Press, New York, NY, USA. <https://doi.org/10.1093/oso/9780195124927.003.0010>.
- Townsend LR. 1973. Effects of N, P, K, and Mg on the growth and productivity of the highbush blueberry. *Can J Plant Sci.* 53(1):161–168. <https://doi.org/10.4141/cjps73-029>.
- USEPA. 1996. Microwave assisted acid digestion of siliceous and organically based matrices. Method 3052, 20.
- Wang M, Zheng QS, Shen QR, Guo SW. 2013. The critical role of potassium in plant stress response. *Int J Mol Sci.* 14(4):7370–7390. <https://doi.org/10.3390/ijms14047370>.
- Wang MY, Siddiqi MY, Glass ADM. 1996. Interactions between K^+ and NH_4^+ : Effects on ion uptake by rice roots. *Plant Cell Environ.* 19(9):1037–1046. <https://doi.org/10.1111/j.1365-3040.1996.tb00210.x>.
- Willard L. 1979. *Chemical equilibria in soils*. John Wiley and Sons, New York, NY, USA.
- Zhang XY, Li SS, An XL, Song ZJ, Zhu YZ, Tan Y, Guo XL, Wang DL. 2023. Effects of nitrogen, phosphorus and potassium formula fertilization on the yield and berry quality of blueberry. *PLoS One.* 18(3): e0283137. <https://doi.org/10.1371/journal.pone.0283137>.