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Global Challenges in Blueberry Cultivation: Emphasis on Mineral Nutrition and Substrate Management—A review

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Review Article

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ABSTRACT

Blueberry, scientifically known as *Vaccinium* L., is a small berry with high nutritional and economic value. Owing to its recognized health benefits, the demand for blueberry consumption is increasing worldwide. However, due to varying soil and climatic conditions around the world and the sensitivity of blueberries, cultivating this plant presents more limitations for growers compared to other fruit trees, creating challenges for expanding production in different regions. The goal of this research is to investigate on the challenges and solutions in the blueberry production process, including soil characteristics, climate change, the relationship between element status and plant physiological conditions and the properties of specialized cultivation substrates. We have found that the challenges within the blueberry industry can be effectively addressed by optimizing pH levels, ensuring nutrient balance and utilizing appropriate substrates. Fertilizer requirements exhibit significant fluctuations throughout the successive years of a shrub's life cycle. Research indicates that blueberry cultivation in areas and soils exposed to heavy metals results in minimal fruit contamination, with the majority of heavy metals accumulating in the vegetative organs. Given the shallow root system of blueberries, cultivation substrate with high moisture retention capacity have proven to be well-suited. This article combines the results of a research roundtable on the challenges of blueberry production among researchers in these fields and provides insights into the importance of expanding blueberry production globally to meet the increasing demand for blueberries, while also identifying research gaps and directions for future studies.

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1. Introduction

Blueberry, scientifically known as Vaccinium L., is part of the Ericaceae family, which includes over 450 species primarily found in the Northern Hemisphere, as well as in parts of Asia, Central and South America. Southeast Asia houses nearly 40% of these species (Song and Sink 2006). The three major products of the Vaccinium genus include blueberry, cranberry and lingonberry, all of which were domesticated in the 20th century. Species from the Vaccinium genus that have been most commonly used in the production of today's commercial varieties include Cyanococcus, Vitis-idaea, Myrtillus, Vaccinium and Oxycoccus (Prodorutti et al. 2007). Blueberry varieties are primarily divided into three types: highbush blueberry, rabbiteye blueberry and lowbush blueberry (Figure 1). Among these, the highbush blueberry can be further categorized into northern highbush, half-high and southern highbush based on different chilling requirements (Xu et al. 2020). In recent years, the main breeding objectives for blueberries have focused on fruit size, firmness, flavor, shelf life, adaptability and high yield, considering the remarkable global climate changes (Gasic et al. 2019).

Figure 1: Major Groups of Blueberry Cultivar Classifications

Blueberries have a high antioxidant capacity and are rich in anthocyanins, vitamins, amino acids, phenolic acids and other nutrients. Blueberry is a small berry with high nutritional and economic value (Krishna et al. 2023). The high concentration of anthocyanins found in blueberries is associated with antioxidant activity in mammalian cells, including humans (Bornsek et al. 2012). Lowbush cultivars have a higher concentration of anthocyanins and total phenolics compared to highbush cultivars (Giongo et al. 2006). Furthermore, blueberry anthocyanins serve as an important and safe natural food coloring compared to artificial colors, making them valuable as natural additives in various food products (Liu et al. 2025). Consequently, global blueberry production has grown due to high market prices. Demand for blueberries has also increased as more consumers recognize their health benefits (Asensio et al. 2025). According to statistics published in 2024, global blueberry production in 2023 was approximately 1,302,000 tons and blueberry cultivation worldwide continues to rise annually. The Americas is the largest producer of blueberries. The area under cultivation and production of blueberries in various regions of the world, including Asia, has seen significant jumps, with China recognized as the main driver of this production surge. Additionally, the area under cultivation in the Middle East is increasing, but the region remains one of the top three importers of blueberries in the world (IBO 2024).

Calcareous soils, as a limiting factor for blueberry cultivation, naturally occur in arid and semi-arid regions, covering over 500 million hectares of soil worldwide. The pH of these soils is typically above 7. In some soils, $CaCO_3$ can exist as an impermeable layer (Morad Wahba et al. 2019; Soufi et al., 2025). Limited access to phosphorus and certain micronutrients such as iron, zinc and copper in these soils is a limiting factor for plant growth (Taalab et al. 2019). It is well established that blueberries thrive best in acidic soil environments (optimal pH between 4.0 to 5.5) with high organic matter content and good drainage. High soil pH is a major abiotic stress factor for blueberry production (Yang et al. 2022). Conversely, low and acidic pH can also create problems such as toxicity from micronutrients and non-essential elements, which are harmful to production and consumer health (Klavins et al. 2021). Despite this, global warming has emerged as a common issue worldwide. Climate changes, including rising temperatures and reduced rainfall, have altered patterns that fruit crops have faced in recent years. Food security in the coming decades will be significantly impacted by severe changes in agricultural yields. Climate change will alter growth patterns and flowering and fruiting capabilities of many perennial and annual horticultural plants (Ali et al. 2022). Our objective is to investigate challenges, gather information and identify solutions. A significant strategy to mitigate the adverse effects of global warming is balanced fertilization and nutrient management in agricultural production (Raza et al. 2019). Furthermore, greenhouse cultivation presents a promising solution. While traditional soil-based greenhouse cultivation has limitations, such as requiring extensive land, high nutrient concentrations, increased pesticide use, hydroponic cultivation using specialized substrates offers superior quality (Farvardin et al. 2024). Consequently, hydroponic systems are gaining traction in regions with similar climatic conditions to improve fertilization efficiency and, notably, reduce water consumption, thereby bolstering food security (Ebenehi Enemaku and Bamidele Ogunlade 2020). In hydroponic systems, nutrient deficiencies are rapidly detectable, underscoring the necessity for ongoing research to establish optimal nutrient solutions for specific crops (Khaleghi et al. 2024).

2. Environmental Factors

2.1. Soil Quality

Globally, the extent of saline-alkaline soils is nearly 1 billion hectares, accounting for approximately 33.3% of the total land area of the world (Shang et al. 2021). Alarmingly, these soils are rapidly expanding, with nearly 12 million hectares added each year (Li et al. 2025). Blueberry plants grow best when soil pH is between 4.2 and 5.5, and an EC above 1.5 dS/m leads to reduced productivity. Extremely high or low pH levels in water or soil negatively affect the natural growth, physiological processes and biological performance of blueberries. Blueberry growth is significantly associated with soil organic matter, soil enzyme activity and soil microbial communities (Zhou et al. 2022). Blueberry bushes, characterized by their shallow root systems, exhibit a reduction in fruit yield when subjected to moderate water stress. Drip irrigation has become the predominant method for watering blueberry plants in recent years. Research indicates that young blueberry plants receiving drip irrigation yield more fruit with less water consumption during their crucial establishment phase (Messiga et al. 2018).

Nutrient accessibility in soil is dependent on pH, which has become a problem for alkaline soils. Generally, all micronutrients except for Mo are biologically available at acidic to neutral soil pH levels. Therefore, alkaline soils pose limitations for sustainable agriculture (Riaz et al. 2020). Acidic pH can also create issues. Soil acidity encompasses a range of factors, including nutrient deficiencies and toxicity, low activity of beneficial microorganisms and reduced root growth, which limits the uptake of nutrients and water. Soil acidity is a serious problem in high-rainfall areas and can lead to reduced or complete crop failure. The leaching of cations in the soil is the primary factor increasing soil acidity, which has adverse effects on the environment and can threaten human health as well as the safety and quality of food (Ameyu, 2019). While soil acidity is suitable for blueberries, a pH of less than 4 can also be problematic for blueberry plants (Li et al. 2024).

2.2. Climate Change

Today, climate change exerts a profound influence on blueberry performance, with rising temperatures and reduced rainfall potentially diminishing productivity. Over time, these climatic shifts are expected to impose multiple adverse effects on the growth, reproduction, and yield of blueberries. Effectively addressing these changes will be crucial for advancing conservation initiatives and ensuring the sustainable management of blueberry habitats (Negrușier et al. 2024). The optimal temperature range varies among blueberry varieties, and those recently developed from wild subtropical species may exhibit greater tolerance to higher temperatures (Moon et al. 1987). One study found that the use of regulated deficit irrigation did not negatively affect the fruit quality of certain varieties studied, and even improved firmness. Additionally, blueberries grown under plastic tunnels had lower acidity and higher soluble solids content compared to those grown in open fields (Ordóñez-Díaz et al. 2020). Changing rainfall patterns may induce water stress due to increased drought frequency or flooding from excessive rainfall, both of which negatively affect plant health (Zeppel et al. 2014).

The temperature is higher than optimal, which may reduce photosynthesis by disrupting the structure of chloroplasts, damaging the function of photosystem II and suppressing the activation status of Rubisco (Zheng et al. 2017). Additionally, high temperatures increase plant respiration, which can reduce plant growth and increased oxidative stress (Crous et al. 2011; Tang et al. 2020). Furthermore, rising temperatures can expand the range and life cycle of pests and diseases, increasing vulnerability and necessitating greater pesticide use (Subedi et al. 2023). These climatic changes also affect fruit quality, altering the sugar-acid balance and potentially changing the taste of the fruit (Jiang et al. 2020). Phenological changes may disrupt the timing of flowering and fruiting, leading to a mismatch with pollinator activity and reduced fruit set (Figure 2) (Gérard et al. 2020). Successful pollination in blueberries requires the help of insect pollinators, but among varieties, the morphology of inflorescences and nectar availability varies, which primarily affects honeybees and bumblebees based on nectar volume and flower density (Cromie et al. 2024). Since this plant often grows in cooler, humid climates and has a long-term symbiosis with bees, greenhouse blueberries rely on pollination by bees for fruit set; thus, pollination is a key stage in blueberry production, with honeybees providing the best pollination for blueberries (Sun et al. 2021). Generally, the quality and quantity of pollen required for maximizing the reproduction of various plants differ, and variations in pollen volume may impact reproductive efficiency. Such differences may lead to changes in fruit set, and the number of seeds in the fruit can significantly affect the timing of ripening and fruit quality (Sampson and Spiers 2002). Hydroponic systems in greenhouses not only create a controllable climatic ecosystem but also effectively control the uniform distribution of nutrients and water. This ecosystem, combined with standard growing substrates, optimizes the efficiency of nutrient use and water utilization (Sharma et al. 2024).

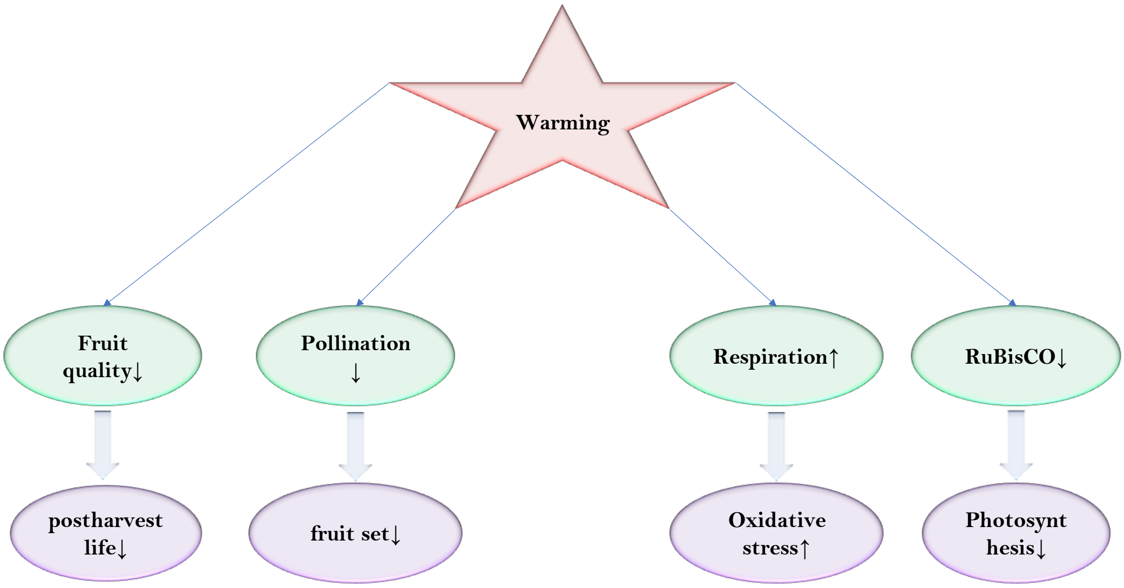

Figure 2 Physiological traits of blueberries affected by global warming

2.3. Environmental Factors and Nutritional Value of Blueberries

Human-induced climate change poses a significant threat to the nutritional quality of blueberries, a crop of considerable health and economic importance. Warming has been linked to declines in fruit quality. As temperatures increase, concentrations of total soluble solids, fructose, total soluble sugars, and total soluble protein decrease, whereas levels of anthocyanins, total flavonoids, and phenols remain unchanged. Future global warming may further diminish the nutritional value and marketability of blueberries. These findings underscore the need for effective strategies to mitigate the impacts of climate change and highlight the importance of improved water and nutrient management to preserve the high nutritional quality of blueberries (Alaba et al. 2024). Blueberries, being one of the best sources of anthocyanins, have been linked to numerous health benefits. Various environmental factors, including temperature, light, oxygen and pH can significantly affect the stability of anthocyanins (Herrera-Balandrano et al. 2021). Hence, the hydroponic cultivation system plays an important role because it allows for precise control of plant nutrition. Since fertilization is one of the principles of productivity in agriculture, this method is one of the most effective pre-harvest methods to improve the quality and nutritional value of agricultural products for the consumer (Golestani et al. 2024). Generally, fresh blueberries consist of water (84%), carbohydrates (9.7%), protein (0.6%) and fat (0.4%). Blueberries are also a good source of fiber, constituting 3 to 3.5 percent of the fruit weight. In addition to flavor, the main interest in this fruit is due to its vitamin C content (Michalska and Łysiak 2015). As indicated in (Table 1), Anthocyanin flavonoids account for up to 60% of the total polyphenols present in ripe blueberries. Thus, anthocyanins play a significant role in the health benefits of blueberries. The polyphenolic compounds in blueberries include various flavonoid and non-flavonoid types. Other flavonoid categories present in blueberries include proanthocyanidins and flavanols. The abundant non-flavonoid polyphenolic compounds in blueberries are hydroxycinnamic acid esters (particularly chlorogenic acid) (Kalt et al. 2020).

Table 1 Nutritional value and bioactive compounds in blueberry fruit.

Nutritional Composition			(mg/100 g)	References
Vitamins	Vitamin C		3.4–9.5	(Krishna et al. 2023)
	Vitamin B complex	Vitamin B1	19.6–26.7	
		Vitamin B2	38.0–70.2	
		Vitamin B3	1.0–1.7	
		Vitamin B6	0.052	
	Vitamin E		0.57	
	Vitamin K		56.1–79.9	
	Vitamin A		5.0–83.1	
Macro elements	Nitrogen		74.4–103.1	(Karlsons et al. 2018)
	Calcium		6.6–15.2	
	Magnesium		4.5–10.1	
	Potassium		66.2–98.0	
	Phosphorus		6.8–20.3	
	Sulphur		10.1–25.4	
Micro elements	Iron		0.15–0.57	(Krishna et al. 2023)
	Manganese		0.14–1.52	(Karlsons et al. 2018)
	Copper		0.01–0.09	
	Boron		0.08–0.14	(Krishna et al. 2023)
	Molybdenum		0.003–0.012	(Karlsons et al. 2018)
	Zinc		0.06–0.13	(Krishna et al. 2023)
Total Phenolic Content			393 ± 52	(Krishna et al. 2023)
Total Flavonoids			2.5–387.48	
Anthocyanidins (mg/kg FW)			134	(Miller et al. 2019)
Anthocyanins			233 ± 34	(Krishna et al. 2023)
	Malvidins		22–33%	
	Delphinidins		27–40%	
	Petunidins		19–26%	
	Cyanidins		5.7–14%	
	Peonidins		1.4–4.5%	
Flavonols (mg/kg FW)			38–46	(Miller et al. 2019)
Quercetin			24	(Krishna et al. 2023)
Myricetin			26	
Flavanols (mg/kg FW)			1.1	(Miller et al. 2019)

3. nutrient elements

3.1. Macronutrients

Currently, only a limited number of specialized fertilization formulas are available to enhance blueberry productivity. This limitation arises because the recommended dosage varies annually relative to the previous year (Makarov et al. 2024). Additionally, the mineral content in different parts of the branches, leaves and rhizosphere of blueberries is not uniform at various growth stages, as the peaks of growth and development for each part do not occur at the same time (J. Li et al. 2024).

Blueberries require fewer nutrients compared to many horticultural crops and grow in acidic soils with limited access to essential nutrients such as nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). However, despite the plant ability to survive with low or no fertilization, a good fertilization program is crucial for rapid plant growth and high-quality fruit production (Phillips and Williamson 2020; Bryla and Strik, 2015).

Protons react with anions present in organic residues, and these carbon cycle reactions contribute to increasing pH. On the other hand, involved nitrogen cycle reactions may lead to either an increase or decrease in pH, as ammonification and nitrate uptake in the rhizosphere can raise pH, while nitrification and ammonium uptake tend to lower pH (Butterly et al. 2013). Reports indicate that nitrogen uptake by blueberries correlates with plant growth rate, with the highest nitrogen uptake occurring during the active growth period between late flowering and fruit maturation (Throop and Hanson 1997). Nitrogen is a key factor affecting plant growth, yield and fruit quality. Phosphorus aids in performance through its role in metabolism, while potassium enhances fruit quality and stress tolerance (Li et al. 2009). The application of the three main elements N, P and K increases the soluble solid content and anthocyanin concentration in blueberries (Albert et al. 2011). For blueberries grown in substrates, all essential nutrients must be provided in the nutrient solution. Improper water and nutrient management can lead to significant leaching. In cases of high salinity, substrates should be leached with large volumes of acidified water to remove excess salts. The timing and method of fertilizer application enable growers to influence the nutrient status of the root zone (Bryla et al. 2010; Parks et al. 2023).

Blueberries differ from other fruits in their absorption, utilization and transport of nutrients. Since blueberries require less fertilization, over-fertilization can lead to adverse effects (Zhang et al. 2023). A longitudinal study on blueberry plants revealed that, in the years following fertilization treatments, including controls that received no fertilization, achieved higher yields in the sixth year. Therefore (Table 2), blueberries are sensitive to high fertilizer amounts and require less fertilizer compared to other fruit trees and berries (Townsend 1973; Ben Hadj; Daoud et al. 2024).

Table 2 Comparison of Blueberry Nutrient Solution Formulations to Strawberry and Raspberry Solutions

Variable	Berry			
	Blueberry	Blueberry	strawberry	raspberry
References	(Voogt et al. 2014)	(Ben Hadj Daoud et al. 2024)		
Macronutrients ($mmoI.L^{-1}$)				
NH_4^+	1.75	3.00	0.50	1.00
NO_3^-	1.50	4.50	10.00	11.50
P	0.50	0.50	1.00	1.00
K	1.50	1.50	4.00	3.00
SO_4^{2-}	2.50	2.50	1.25	2.00
Ca	1.12	2.00	3.50	4.50
Mg	0.75	1.00	1.25	1.75
Micronutrients ($\mu moI.L^{-1}$)				
Fe	15.00	20.00	20.00	20.00
Mn	5.00	10.00	15.00	15.00
Zn	3.00	7.00	7.00	7.00
Cu	0.50	0.50	0.50	0.50
B	5.00	10.00	10.00	10.00
Mo	0.50	0.50	0.50	0.50

Currently, there are several different strategies for blueberry cultivation and the fertilization regimen and amount should be adjusted based on the plant growth stages and commercial practices. Clark and Zheng (2020) (Clark and Zheng 2020) found that excessive fertilization can be detrimental to plant growth and fruit production. According to Kingston et al. (2017) (Kingston et al. 2017), fertilizers should be applied continuously to prevent the risk of nutrient absorption reduction.

Nutrient deficiencies can be determined through leaf nutrient analysis based on the plant phenology; leaf tissue analysis is a useful method for monitoring nutrient needs. All elements used in blueberries, including phosphorus, potassium, calcium, magnesium, sulfur (S), iron (Fe), boron (B), copper (Cu) and zinc (Zn), must be supplied through irrigation fertilizers to achieve a balanced formulation (Zhang et al. 2023). In blueberry nutrition, the response of cultivars to fertilization rates varies. The optimal rates of mineral nutrients, especially the optimal nitrogen (N) rate, depend on the specific cultivar (Wilber and Williamson 2008).

3.1.1. Nitrogen

Nitrogen is the most important nutrient supplied to blueberries and must be applied annually. Unlike many other crops, blueberries preferentially utilize ammonium (NH_4^+) rather than nitrate (NO_3^-), owing to the inherently low nitrate reductase activity in their roots and leaves(Peterson1 et al. 1988). Nitrate uptake increases rhizosphere pH through the release of hydroxide ions, which consequently reduces micronutrient availability. In contrast, ammonium uptake promotes rhizosphere acidification, thereby enhancing micronutrient availability(Soufi et al. 2025). Under nitrogen deficiency, plants exhibit reduced above-ground growth, with leaves turning pale green or yellow (chlorotic) and often developing a reddish hue(Hirzel et al. 2024). Chlorophyll index is dependent on the concentration of nitrogen and magnesium in blueberry leaves (Pinzón-Sandoval et al. 2023). Nitrogen is the most critical mineral element for plant growth, often limiting growth and development in both natural and managed ecosystems (Cassman and Dobermann 2022).

Plants utilize different strategies to acquire nitrogen, including symbiotic relationships with fungi or bacteria and the uptake of amino acids from organic soils. However, the primary mode of nitrogen uptake for most plants involves the absorption of mineral ions, particularly NH_4^+ and NO_3^-, through the roots from the soil solution (Arias et al. 2024). A 50:50 ammonium to nitrate ratio is beneficial for shoot growth and the accumulation of beneficial mineral elements, resulting in increased flower bud formation and fruit set speed. In contrast, a 75:25 ammonium to nitrate ratio can bring blueberries to full bloom earlier and accelerate the growth process from flower to fruit (Anwar et al. 2024). Plants exhibit different responses to specific mineral N sources, affecting their growth, biomass production and performance. For example, blueberries are believed to prefer NH_4^+ over NO_3^- forms of mineral N, which impacts their physiological responses, especially in branch tissues (Britto and Kronzucker, 2013). The increase in yield from additional nitrogen is only observed in the first year, and high nitrogen levels can reduce the accumulation of calcium, magnesium and copper in blueberries(Jayasinghege et al. 2024).

3.1.2. Phosphorus

The amount of phosphorus available in plants is limited and easily absorbable. Most phosphorus found in soil becomes unavailable to plants due to its insolubility. The phosphorus that is used often transforms into less accessible forms due to soil characteristics, organic matter content and fertilizer application. Approximately 30 to 65 percent of total phosphorus exists in organic forms, which are not readily available for plant absorption (El Attar et al. 2022; Lu et al. 2020; Sharma et al. 2013).

Soil type and depth significantly affect phosphorus levels, with unstable phosphorus accumulation more prevalent in shallower layers, particularly in Kuroboku (0-30 cm, 30-60 cm), Brown Forest soils (0-30 cm, 30-60 cm) and Fluvic soils (0-30 cm). This indicates a strong capacity for phosphorus fixation. The correlation between the C/N ratio and phosphorus at 0-30 cm suggests microbial involvement in the phosphorus cycle. Notably, NaOH-Po plays a critical role in converting unstable phosphorus to stable phosphorus in the 0-30 cm soil layer, primarily through its interactions with electrical conductivity (EC) and pH. Meanwhile, in the 30-60 cm layer, NaOH-Po and $NaHCO_3$-Po are key modifiers of this process (Lu et al. 2024). Southern highbush blueberries respond to phosphorus deficiency by remobilizing phosphorus from older to younger organs, especially in older plants. Phosphorus-deficient Southern highbush blueberries exhibit lower root volumes and longer root lengths compared to control plants, most species also increased acid phosphatase activity and root carbon secretion. Phosphorus deficiency can lead to reduced carbon uptake, increased respiration rates and enhanced root exudation (Retana-Cordero and Nunez 2025).

Species within the Vaccinium genus are characterized by shallow, fine roots, making them inefficient at directly absorbing phosphorus from the soil. To overcome such limitations, these plants establish mutualistic relationships with ericoid mycorrhizal fungi (ERM), which play a pivotal role in enhancing phosphorus availability, particularly in acidic or nutrient-poor soils. This specialized symbiosis not only alleviates phosphorus constraints but also contributes directly to plant productivity and the resilience of the surrounding ecosystem(Lu et al. 2025). Additionally, bacteria can produce growth hormones, particularly cytokinins and promote plant growth through nitrogen fixation (Kämpfer et al. 2005). Proteobacteria exhibit a positive correlation with soil nitrogen content. Studies have shown that Acidobacteria can enhance soil organic matter by decomposing animal and plant materials, suggesting that Proteobacteria may be linked to Acidobacteria and can increase soil nutrients through plant nitrogen fixation (Yang et al. 2014).

3.1.3. Potassium

Factors contributing to K deficiency include poor soil drainage, drought, low soil pH (<4) and heavy crop yields. Symptoms of K deficiency often resemble drought damage in blueberries and include leaf drop and burned leaf margins (Polashock et al. 2007). Potassium fertilizer has an immediate effect on soil pH and the availability of other nutrients in the soil solution, consequently influencing the concentration of nutrients in various plant tissues, including Mg, S, B, Cu and Mn in young leaves; Mn and Zn in vascular tissues; and P, S and Mn in the tree crown, as well as Ca, Mg and B in the fruit (Leon-Chang et al. 2022). In addition to environmental factors that play a significant role in the biosynthesis of anthocyanins, potassium is also an essential nutrient for blueberry growth and can act as an enzyme activator. Potassium treatment significantly increases the activity of key enzymes, including F3H, F3'5'H and UFGT, in the anthocyanin synthesis pathway in blueberries (Yan et al. 2025).

3.1.4. Calcium

Blueberries are described as plants with higher efficiency in the absorption and utilization of Ca^{2+}. The homeostasis of Ca^{2+} in blueberries, like other fruit trees, can show symptoms of deficiency in other organs, such as fruit, even when high concentrations of Ca^{2+} are present in the leaves (Dayod M et al. 2010). Calcium enters the soil through mass flow to the roots and subsequently enters the apoplastic space within the roots, where it can be stored in root cells or transported to the xylem (Tamai 2003).

The transport and distribution of Ca^{2+} to organs such as fruit are primarily dependent on the xylem and transpiration. Ca^{2+} likely plays an important role in regulating fruit quality at harvest and during post-harvest storage. Therefore, the role of fruit transpiration, xylem function and transporter activity are crucial in determining the entry and distribution of Ca^{2+} to blueberries (Doyle et al. 2021). Calcium is more abundant in older leaves, while deficiency is observed in younger leaves and fruit. The presence of calcium helps maintain firmness, cellular turgor, prevents enzymatic degradation, reduces disease incidence and prevents physiological disorders (Jaime-Guerrero et al. 2024). Calcium is absorbed by plants as the divalent cation Ca^{2+}. Soil factors such as calcium deficiency, very low pH, excessive presence of other cations, especially Mg^{2+}, NH_4^+, K^+ and Na^+, affect Ca^{2+} absorption and can lead to deficiency. Cation exchange capacity (CEC) contributes to the apoplastic space in roots and influences the movement and distribution of cations such as Ca^{2+}. Calcium can form cross-links through ionic interactions with carboxyl groups of pectic substances such as homogalacturonans, significantly affecting the apoplastic transport of free Ca^{2+}(Doyle et al. 2021).

3.1.5. Sulfur

Blueberries are acid-loving plants, with an optimal pH range for growth between 4/8 and 5/3 (Jiang et al. 2019). As illustrated in Figure 3, the availability of nutrients for blueberries is emphasized at a pH of 4.5-5.5, highlighting this as an ideal range. Blueberries inherently require significantly fewer nutrients than other fruit trees, which means they have a certain limitation in macro-nutrient absorption and a risk of toxicity from excessive micro-nutrient uptake (Ortiz-Delvasto and Carvajal 2025). Soil pH for blueberry cultivation must be acidic. While various methods can be used to regulate soil pH, the application of S is a conventional approach for blueberries. Following treatment with SO_2, soil pH was reduced to 5.9 after planting, indicating that sulfur can be used effectively for rapid soil pH reduction post-planting, proving more effective than using SO_2 before planting (Almutairi et al. 2017).

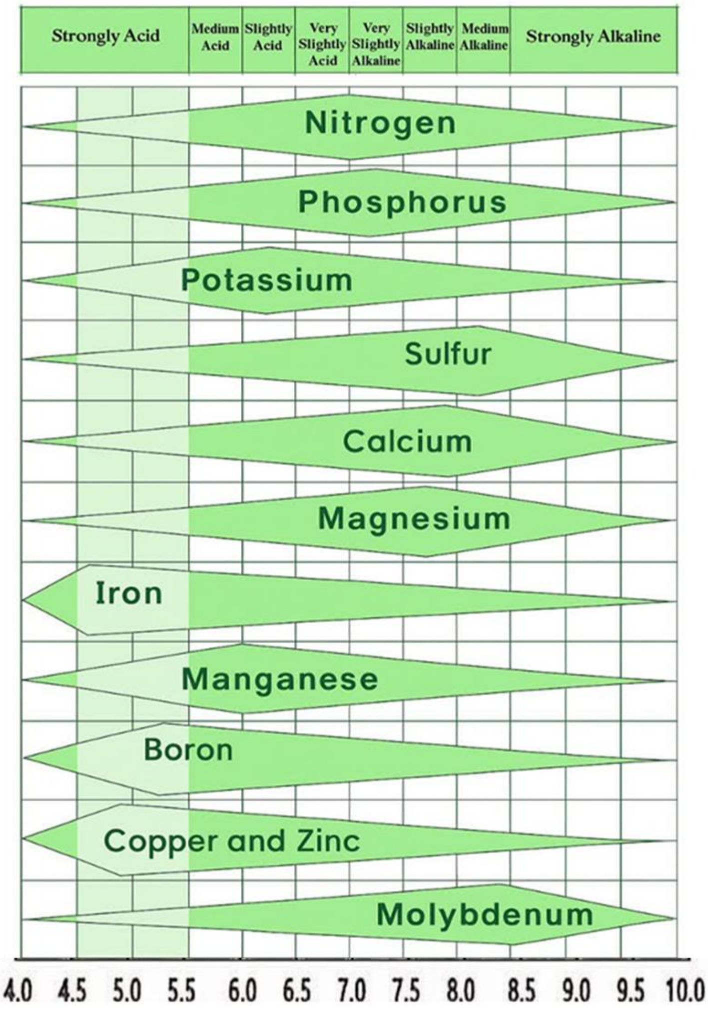

Figure 3: Nutrient Availability within the Optimal pH Range for Blueberry

Peat moss, elemental sulfur and sulfur-oxidizing bacteria (Thiobacillus) contribute to lowering soil pH. When peat moss is added to the soil, an increase in the peat moss mixing ratio results in a decrease in pH and an increase in organic matter content. Furthermore, the use of elemental sulfur reduces soil pH, and combining elemental sulfur with sulfur-oxidizing bacteria accelerates the pH reduction compared to using elemental sulfur alone. The application of elemental sulfur alone also impacts pH, reducing it after 40 days and showing better effectiveness than peat moss alone. Treatments with sulfur-oxidizing bacteria are not essential for blueberry cultivation or have minimal effect (Lee et al. 2021). The density of sulfur-oxidizing bacteria in farm soil is low, microbial activity can be significantly suppressed or limited depending on conditions. When sulfur and sulfur-oxidizing bacteria are added to calcareous soils, the solubility of phosphorus, zinc, iron and other nutrients significantly increases with the reduction of soil pH, although electrical conductivity (EC) also increases (Lee et al. 2021; Corwin and Yemoto 2020). Research indicates that granular forms of sulfur are more suitable than powdered forms for regulating soil pH, especially in fields where blueberries have already been planted. This is due to the avoidance of high surface levels of sulfur and unnecessary electrical conductivity, providing a longer-lasting effect and reduced leaching (Karlsons et al. 2019).

3.2. Micronutrients

Blueberries are generally acid-loving plants that thrive in low pH conditions. Consequently, controlling pH reduces the problem of micronutrient deficiencies compared to other fruit trees, as most micronutrients are readily absorbed in acidic environments. This control helps alleviate chlorosis symptoms caused by micronutrient deficiencies, particularly iron, in blueberry leaves. Therefore, the optimal pH, which varies for different Vaccinium cultivars, can positively or negatively affect photosynthesis and chlorophyll levels (Jiang et al. 2019). Research indicates that the use of Fe-EDDHA increases anthocyanin concentrations, as well as certain hydroxybenzoic acids, hydroxycinnamic acids, flavanols and flavonoids. These results demonstrate that iron nutrition is crucial for yield and quality in blueberries (Michel et al. 2019). Iron homeostasis can be maintained in a soluble, non-toxic and bioavailable form through the application of ferritin nanoparticles, which positively influence the stability of anthocyanins against unfavorable pH conditions and temperature fluctuations (Huang et al. 2023). Ferritin is an important iron-storage protein that plays a role in regulating iron metabolism balance in organisms. It contains a large amount of irregular mineral iron cores composed of iron hydroxide and phosphate (Arosio et al. 2009).

Manganese acts as an activator and cofactor for hundreds of metalloenzymes in plants. It plays a critical role in a wide range of enzymatically catalyzed reactions, including redox reactions, phosphorylation, decarboxylation and hydrolysis (Schmidt and Husted 2019). Manganese deficiency often occurs in soils with high pH and calcareous conditions. However, in acidic soils, its excess and toxicity can become problematic, as the absorption and availability of manganese ions are exacerbated under acidic conditions (Rahim et al. 2024). High concentrations of manganese stress induce physiological and biochemical reactions, particularly strong toxicity in leaves. Elevated Mn levels cause changes in the content of photosynthetic pigments, malondialdehyde, manganese accumulation, ascorbate (AsA) and reduced glutathione (GSH), leading to oxidative damage in blueberry leaves as a result of higher manganese fertilizer application (Dong et al. 2020). Studies indicate that excess manganese negatively and variably affects the physiological and biochemical traits of different cultivars. The Vaccinium corymbosum cultivars, such as Legacy and Brigitta, are resistant to manganese, while Bluegold is sensitive. Excess manganese adversely impacts plant growth, photochemical efficiency, CO_2 uptake, biochemical traits and photosynthesis in corymbosum cultivars, although they maintain their vegetative growth. Conversely, Brigitta preserves photosynthesis and growth despite reduced stomatal conductance. Oxalate and citrate are the most important organic acid anions in Legacy and Brigitta, with their concentrations gradually increasing with higher manganese doses (Millaleo et al. 2020).

The availability of boron, in the form of boric acid (H_3BO_3) or the borate anion [$B(OH)_4^-$], is directly related to soil pH. Both boron toxicity and deficiency exhibit similar symptoms, including reduced photosynthesis and photochemical efficiency of photosystem II, lower transpiration rates, decreased stomatal conductance, altered antioxidant enzyme activity and increased lipid peroxidation (Reyes-Díaz et al. 2024). Boron deficiency has been associated with disruptions in cell wall structure, reduced growth rate, particularly in shoots, nutrient imbalances, disruptions in water relations and changes in antioxidant activity. Conversely, boron toxicity is linked to reduced plant growth and increased oxidative stress, evident through heightened lipid peroxidation, along with the activity of antioxidant compounds, indicating oxidative damage due to excessive production of reactive oxygen species (ROS). Both boron deficiency and excess lead to increased concentrations of phenols and H_2O_2. Boron toxicity has also been associated with interveinal chlorosis and burned leaf margins. Boron-rich soils are much rarer than boron-deficient soils. Boron deficiency in plants often occurs in acidic soils in temperate climates, characterized by high rainfall and significant leaching losses (Liu et al. 2014; Meriño-Gergichevich et al. 2017).

Selenium enrichment in blueberries through foliar application of Se has been effective and can improve Se concentration and the quality of blueberries. Selenium is an essential micronutrient for humans and is non-essential but beneficial for plants. Selenium primarily accumulates in blueberry fruit pomace; therefore, consuming blueberry juice as a source of Se has a lesser impact compared to directly consuming blueberries (Li et al. 2018). Many regions with Se-rich soils have been identified, indicating that blueberries have a high capacity for Se enrichment (Wu et al. 2024).

4. Toxicity of Essential and Non-Essential Elements

An assessment conducted on the accumulation and transfer of heavy metals in blueberries grown in contaminated soils indicated that the concentrations of heavy elements within the berries remained below the established safety standards (Yang et al. 2023). It was also found in another study all mixed concentrations of copper, lead and zinc pose minimal risk for human consumption. The accumulation of heavy metals in the fruits showed that the order of accumulation in blueberries is Zn > Cu > Pb, with zinc having the highest accumulation among the studied metals. The concentration of lead in the fruit was lower than that of the control sample, indicating that, despite high concentrations, the capacity for heavy metal absorption in the soil decreases, which may be linked to protective mechanisms in plants, resulting in low bioconcentration of metals in the fruits. However, metal accumulation may have occurred in other vegetative parts (Nițu et al. 2022).

Plant tissues can absorb and accumulate both essential micronutrients for plant growth (such as Co, Fe, manganese, molybdenum, nickel, zinc and copper) and non-essential metals (such as lead, cadmium, arsenic, chromium and mercury). While micronutrients are essential for plant performance in small amounts, non-essential metals can negatively impact plant productivity and food quality, even at low concentrations. In particular, the presence of heavy metals can alter root structure and change the plant's accumulation capacity (Gajić et al. 2018; Kandziora-Ciupa et al. 2022). Significantly higher concentrations of cadmium, lead, zinc and iron were found in V. myrtillus and V. vitis-idaea growing in the most contaminated locations compared to cleaner areas. High bioconcentration of these metals was found in blueberry organs. Furthermore, blueberries demonstrated a strong ability to accumulate manganese (Kandziora-Ciupa et al. 2017).

4.1. Chlorine

Blueberries are recognized as a chlorine-sensitive plant, primarily accumulating chlorine in their leaves and stems. Ma et al. (2025) (Ma et al. 2025) evaluated the chlorine tolerance of five blueberry cultivars by determining 10 indices, including plant morphology, osmotic regulators and antioxidant enzyme activity under chlorine stress. They reported that soluble proteins, chlorophylls and proline are closely related to chlorine stress and can serve as key indicators for assessing chlorine tolerance in blueberries. The tolerance levels of the five blueberry cultivars, in descending order, were as follows: 'Duke' > 'Bonnie' > 'Reka' > 'PL19' > 'Northland'. Among these, 'Duke', a cultivar with relatively high resistance to chlorine, is recognized as suitable for use in more saline soils.

4.2. Cadmium and Zinc

Cadmium (Cd^{2+}) stress significantly inhibits the growth of blueberry plants. The activity of antioxidant enzymes and phenolic compounds plays a crucial role in the response of blueberries to cadmium stress. Cultivation experiments have shown that Cd^{2+} at certain concentrations (5–15 $mg \cdot kg^{-1}$) contributes to the accumulation of biomass in rabbit-eye blueberry and also increases the activities of catalase (CAT) and peroxidase (POD) (Song et al. 2023). In this context, numerous studies have demonstrated that a toxic element like Cd alters root length, surface area and root hair length, thereby changing root structure. Some micronutrients, particularly zinc, can be classified as both essential and hazardous elements depending on their availability in the soil and concentration in plant biomass. Additionally, high concentrations of zinc lead to significant changes in cell structure, root tips and organelles (Nin et al. 2025).

Cadmium stress not only impacts the yield and quality of crops but also leads to the accumulation of cadmium in animals and humans through the food chain, ultimately posing a serious threat to human health and food safety. Cadmium stress accelerates the accumulation of reactive oxygen species (ROS) in tissues and lipid peroxidation, suppresses chlorophyll synthesis, disrupts photosynthesis and antioxidant systems and hinders the absorption and transport of nutrients, thereby inhibiting plant growth and reducing fruit quality. Furthermore, as the concentration of cadmium in the cultivation substrate increases, the cadmium content in each plant organ also rises, with roots exhibiting the highest capacity as a defense mechanism in cadmium enrichment. Cadmium accumulates sequentially in the stems, leaves and fruits (Yang et al. 2024).

The presence of Cd^{2+} increases malondialdehyde (MDA) content and leads to changes in phenolic compounds. The main phenolic compound in blueberries is chlorogenic acid, which increases in abundance with rising Cd^{2+} concentrations. Blueberry seedlings produce phenolic compounds with reducing capacity as a selective mechanism induced by high Cd^{2+} activity. The production of MDA and accumulation of H_2O_2 are indicators of oxidative damage caused by cadmium (Manquián-Cerda et al. 2016). Additionally, cadmium-induced stress alters anthocyanin levels in blueberry leaves, negatively affecting antioxidant defense mechanisms and inhibiting plant growth. In contrast, ericoid mycorrhizal fungi (ERM) form a specialized symbiotic association with blueberry plants, improving nutrient acquisition and enhancing tolerance to environmental stresses. Elucidating the interplay among Cd stress, anthocyanin accumulation in blueberries, and ERM-mediated mitigation is essential for developing effective strategies to strengthen plant defenses, improve fruit quality, and increase resilience against metal-induced stresses(Chen et al. 2024).

4.3. Aluminum

Overall, the effects of aluminum on plant growth and productivity are considered a significant threat to achieving global food security. Acidic soils have been a major concern and a primary subject of scientific research worldwide. Acidic soils include Oxisols or Ultisols, with a pH below 5(Kochian et al. 2015). The benefits of aluminum are often observed in plants adapted to acidic soils, native species and aluminum hyperaccumulators (Sun et al. 2020). Hyperaccumulator plants are indifferent to the concentration and duration of aluminum exposure, showing no toxic effects even at higher doses (Rehmus et al. 2014). Exposure of plants to Al and Cd increases the contents of malondialdehyde (MDA) and H_2O_2. In contrast, high superoxide dismutase (SOD) activity leads to a significant increase in phenolic compounds, with chlorogenic acid being the main component. Phenolic compounds play an important role in the response to reactive oxygen species (ROS) (Manquián-Cerda et al. 2018). Research has identified root growth inhibition as the most prominent symptom of Al toxicity (Wang et al. 2016). As soil acidifies, toxic aluminum ions (Al^{3+}) are released into the soil solution, negatively affecting plant growth, yield and product quality. The primary accumulation site of Al^{3+} in plants appears to be the root elongation zone, indicating that Al^{3+} interacts with dividing and expanding cells, thereby inhibiting root cell growth. Although Al^{3+} cannot catalyze redox reactions, lipid peroxidation (LP) and the production of reactive oxygen species (ROS) are common and early signs of Al toxicity in plants, leading to alterations in plasma membrane integrity throughout LP. These active oxygen species and LP can result in nutritional and metabolic disorders (Reyes-Díaz et al. 2010).

Trivalent Al is a significant factor limiting plant growth in acidic soils (pH < 5.0). It can interact with cellular membrane components and increase lipid peroxidation. Additionally, Al^{3+}can bind to DNA and various enzymes, altering the normal functioning of diverse metabolic and physiological processes (Silva 2012). Various studies have indicated that Al^{3+}induces the production of reactive oxygen species (ROS) due to its binding to the plasma membrane and the consequent increase in calcium levels in the cytoplasm. Plants implement two main strategies to detoxify Al, Al-Tolerance: This mechanism involves the transport of Al^{3+} ions to less sensitive cells or into vacuoles through specific transporters and pumps located in the plasma membrane and tonoplast. Al-Exclusion: In this strategy, plants secrete organic molecules from their roots that limit Al^{3+} in the rhizosphere and convert it into non-toxic complexes, along with selective transporters that prevent its uptake into root cells (Ofoe et al. 2023).

Antioxidant activity is correlated with photosynthetic performance and total phenol concentration in leaves exposed to Al^{3+}, indicating increased resistance. Some improved cultivars can exude more organic acids than conventional ones, allowing them to chelate Al in the rhizosphere (Cárcamo et al. 2019). The cultivars Brigitta and Legacy are considered the best for use in acidic soils with Al toxicity, while Bluegold is highly sensitive to Al stress (Reyes-Diaz et al. 2009).

One way to reduce oxidative damage caused by Al is through foliar application of ascorbate (ASC). The use of ASC improves growth and regulates physiological responses in the Al-sensitive blueberry cultivar Star under Al stress conditions. Additionally, ASC application can have a direct relationship with organic acid secretion, highlighting its importance in mechanisms of Al resistance and as a practical strategy to enhance plant resilience under stress (Cárcamo-Fincheira et al. 2025). Soil amendment with gypsum has been shown to be somewhat effective in fully recovering from the toxic effects of Al in Al-resistant cultivars and it may also be a good source of nutrients such as Ca and S (Reyes-Díaz et al. 2011). The application of methyl jasmonate (MeJA) also reduces Al uptake and stimulates antioxidant pathways, which may counteract the toxic effects of Al and protect the photosynthetic apparatus (Ulloa-Inostroza et al. 2019).

4.4. Nickel

Nickel reduces biomass in underground organs such as rhizomes and roots. Anthocyanins in aerial shoots decrease with nickel accumulation in the roots, but they do not play a role in osmotic regulation under nickel stress (Tahkokorpi et al. 2010). The accumulation pattern of copper and nickel in different tissues is as follows: root > stem > leaf > fruit. The root tissue serves as the primary site for the accumulation of these metals when environmental levels of copper and nickel are high. The highest concentrations of copper and nickel are found in galls, indicating that gall tissues act as a strong physiological reservoir for micronutrients (Bagatto and Shorthouse 1991).

5. Cultivation Substrate

Blueberries typically prefer light, acidic soils with high organic matter content and good water retention capacity. To amend clay soils and enhance porosity and moisture retention, materials such as peat, sawdust, animal manure and green manure are commonly used (Caspersen et al. 2016). Today, fruit trees are primarily irrigated using drip irrigation systems, which only wet a portion of the soil, allowing roots to concentrate in this moist area. Consequently, most nitrogen applied during fertilization is added directly in this zone. As a result, less nitrogen is required for feeding blueberries and decomposing organic matter, which also applies to other nutrients (Bryla and Strik 2015). Most roots are very fine (40-75 micrometers in diameter) and are often colonized by mycorrhizal fungi (Valenzuela-Estrada et al. 2008). The roots do not penetrate very deeply and are usually restricted to the upper 12-18 inches of most soils (Bryla and Strik 2007).

Considering that the costs of acidifying high pH soils can be substantial and may not be sustainable in the long term, cultivating blueberries in specialized substrates to reduce pH is an effective method to mitigate this issue. These substrates typically consist of a mix of organic materials such as peat, which has a low pH, and sawdust or pine bark that generally maintains a pH of around 4.0–4.2, with an electrical conductivity (EC) below 0.5 dS/m. This makes them suitable substrates for growing blueberries in pots (Kingston et al. 2017). The production of Vaccinium species is limited to acidic soils with high organic matter content. Research indicates that pine bark is recognized as a superior cultivation substrate compared to peat moss (Schmid et al. 2009). These plants can thrive in organic-rich soils, such as peat, sawdust and deciduous tree bark, or a mixture of these materials (Braha and Kullaj 2024). Powdered sulfur and phosphate urea rapidly acidify the studied soils, achieving the highest levels of acidity, while the least acidification occurs with sulfuric acid solutions. The concentration of salts is reduced under the influence of sulfur and phosphate urea. Among the substrates, loamy sand exhibits the greatest sensitivity to salinity, whereas peat shows the least sensitivity. Additionally, it has been demonstrated that phosphate urea has a stimulatory effect on soil enzyme activity (Ochmian et al. 2021).

Based on research, the use of hydroponic systems has proven successful in preventing soil contamination from pathogens and physiological disorders. In hydroponics, crops are grown in nutrient solutions and soil-less substrates, leading to a 90% reduction in water and soil usage while also decreasing greenhouse gas emissions. This makes hydroponics a sustainable alternative to conventional agriculture (Chopra et al. 2024). However, in hydroponic systems, trees and shrubs like blueberries require a solid substrate for support and weight tolerance, making it impractical to cultivate them solely in liquid growing environments (Atherton and Li 2023).

In most cases, the addition of perlite to the cultivation substrate has resulted in reduced growth in Highbush Blueberries. However, perlite has shown little impact on the nutrient composition of the substrate or the uptake of nutritional elements by the plant. In contrast, peat has been found to enhance plant growth, likely due to its effects on plant nutrition and salinity. Peat contained lower salt levels and improved the uptake of nutrients such as N, P, Mg and S (Kingston et al. 2020). Another report indicated that cocoa husk substrate had the highest levels of N and Zn, along with a higher pH. Conversely, sawdust substrate exhibited the lowest salinity but the highest levels of Mn and Cu, along with the least Cd. Peat showed the highest salinity and the lowest pH. This study demonstrated the feasibility of cultivating highbush blueberries in alkaline clay soils, provided that the plants grow in channels filled with peat or sawdust and are irrigated with acidic water (Ochmian et al. 2009). The use of cocoa husk substrate increases the N, P, K content in leaves and berries, as well as Mn levels in the leaves. Blueberries grown in sawdust substrate exhibit the highest levels of Cd, Mg, Zn and Fe in the leaves, along with Cu in both leaves and berries. Berries cultivated in sawdust also show higher levels of soluble solids, titratable acidity and antioxidant capacity. Additionally, berries grown in peat had the highest amounts of Ca and Mg (Ochmian et al. 2009). It is noteworthy that the use of endophytic mycorrhizal fungi has a positive impact on plant growth, enhancing the uptake of P and N from the substrate and promoting early fruiting (Vohník et al. 2012).

Blue peat is an innovative cultivation substrate recognized for its exceptional properties for blueberry cultivation, characterized by a lightweight structure, adequate drainage and a pH range of 4.8. Blue peat is a product of pine bark and contains a lot of lignin, which is why it is very resistant to decomposition. It is identified as an acidic and specialized substrate for blueberries in Iran (Figure 4) (Hasankhah 2021). Although limited research has been conducted on this substrate, empirical evidence supports its effectiveness. One study compared blue peat with peat moss, revealing that blueberries grown in blue peat produced more flowers, leaves, leaf area, crown diameter and spring buds than those in peat moss (Sabetifar et al. 2023). This substrate could play a significant role in the future of the blueberry industry.

Figure 4 View of the blue peat substrate

Ortiz-delvasto et al. (2023) (Ortiz-Delvasto et al. 2023) reported that blueberry shrubs established in a 100% cocopeat substrate exhibited a greater capacity for nutrient retention and produced higher yields compared to those grown in a cocopeat–peat mixture. This yield improvement may be attributed to enhanced moisture retention. In that study, leaves from plants grown in 100% cocopeat contained higher P levels, whereas leaves from the cocopeat + peat treatment had higher Ca and Mg concentrations. Additionally, greater stomatal conductivity was observed in the cocopeat + peat substrate, while the highest stomatal density (number of stomata per mm^2) occurred in plants grown in 100% cocopeat. Moreover, the 100% cocopeat substrate had a higher available water content, which was associated with lower stomatal conductivity; however, the increased stomatal density may compensate for this limitation in water transport. These findings suggest that blueberries cultivated entirely in cocopeat exhibit greater resilience, owing to their ability to regulate water uptake and transport through a higher number of stomata. In contrast, plants grown in rockwool, despite their smaller size and lower berry weight, produced more berries than those grown in peat–perlite mixtures. Conversely, blueberries cultivated in peat–perlite substrates generated approximately six times more biomass than those grown in either rockwool or peat alone (Schwab and Williams 2017).

Conclusion

A review of prior research indicates that blueberries are acid-loving plants, highly sensitive to hot and arid conditions. Many global climates exhibit these characteristics and a significant, widespread challenge stems from the fact that most agricultural soils worldwide are calcareous. These two factors present the foremost obstacles to the global expansion of the blueberry industry. Furthermore, formulating a consistent and effective fertilizer program for blueberries proves difficult, given the dynamic nature of optimal nutrient dosage requirements. This plant thrives in various temperate climate regions and is globally recognized as a nutritious and highly sought-after food source. From an economic perspective, the blueberry market is experiencing significant growth, with expanding applications in the nutrition and pharmaceutical industries.

Blueberries prefer the NH_4^+ form of nitrogen over NO_3^- for absorption. Potassium plays a crucial role in anthocyanin biosynthesis in blueberries due to its function as an enzyme activator. Notably, blueberries cannot grow and develop at high pH levels due to limited mineral absorption. The use of sulfur is a common and effective method for lowering pH for blueberries. Reducing pH increases the solubility of elements such as phosphorus and micronutrients.

However, excessive acidification or very low pH can lead to increased absorption of micronutrients and non-essential elements (heavy metals), resulting in toxicity in blueberry bushes. Typically, berries exhibit lower toxicity, with the accumulation pattern of these metals being root, trunk and branches, leaf and finally berry. Therefore, the highest accumulation occurs in the roots, causing structural disorders and leading to the production of reactive oxygen species (ROS), H_2O_2 and other harmful compounds in the leaves, ultimately affecting yield and product quality. Our review found that the Legacy, Dake and Brigitta varieties were the most resistant to element toxicity.

Recent research indicates that managing pH and nutritional balance via specialized substrates within hydroponic systems, coupled with precisely formulated nutrient solutions, can effectively prevent damage caused by essential nutrient deficiencies or excesses, while also restricting root access to non-essential elements. This approach further allows for optimal fertilization management and enhanced water conservation. Our analysis also concluded that coco peat should comprise at least 50% of the cultivation substrate for blueberries, owing to its superior water and nutrient retention capabilities.

We anticipate that future research, focusing on the development of suitable fertilizer formulations and specialized blueberry substrates like blue peat, alongside the introduction of new varieties adapted to diverse environmental conditions, will facilitate blueberry production across various global regions.

Conflict of Interest

The authors declare that they have no conflicts of interest.

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