Journal of Medicinal Plants for Economic Development
ISSN: (Online) 2616-4809, (Print) 2519-559X

Blueberry cultivation under different nitrogen sources: A review

Check for updates

Authors:
Asemahle Mshweshwe[1]
Nonkululeko Mfeka[1]
Francis B. Lewu[1]
Mbappe Tanga[1]

Affiliations:
[1]Department of Agriculture, Faculty of Applied Sciences, Cape Peninsula University of Technology, Cape Town, South Africa

Corresponding author:
Nonkululeko Mfeka,
mfekan@cput.ac.za

Dates:
Received: 05 June 2025
Accepted: 23 Aug. 2025
Published: 09 Dec. 2025

How to cite this article:
Mshweshwe, A., Mfeka, N., Lewu, F.B. & Tanga, M., 2025, 'Blueberry cultivation under different nitrogen sources: A review', Journal of Medicinal Plants for Economic Development 9(1), a293. https://doi.org/10.4102/jomped.v9i1.293

Background: Global blueberry production has proliferated in recent years, driven by the increasing consumer awareness of its nutritional benefits. Blueberry is considered a rich source of antioxidants, believed to contribute to several health benefits, including maintaining heart health and protecting against cellular damage.

Aim: This review critically evaluated the existing literature on blueberry cultivation using different nitrogen sources and identified research gaps needing further investigation.

Setting: This review provides an overview of blueberry cultivation under different nitrogen sources.

Methods: A literature search for existing information on blueberry cultivation under different nitrogen sources was conducted using online databases via the Cape Peninsula University of Technology (CPUT) library website database.

Results: Findings suggest that nitrogen sources significantly affect the productivity of blueberries, with ammonium producing better results than nitrate. There is a noticeable gap in the literature on how different nitrogen sources influence the biosynthesis of secondary metabolites in blueberries.

Conclusion: The review revealed that there are few research studies on blueberry cultivation under different nitrogen sources. Given the nutritional and antioxidant significance of blueberry secondary metabolites, further research is critical.

Contribution: Information gained can aid in understanding different nitrogen sources of nutrition in blueberries. Insights from this research can inform nitrogen management strategies in blueberry cultivation. This is important for sustaining production trends and ensuring the economic viability of the industry.

Keywords: blueberry; nitrogen sources; fertiliser; phenolic compounds; ammonium.

Introduction

Global blueberry (*Vaccinium* spp.) production has proliferated in recent years, owing to consumers' increased demand for this nutritious fruit (Osorio, Cáceres & Covarrubias 2020). Driven by increasing consumer awareness of nutritional benefits, the worldwide blueberry cultivation area increased significantly from 151 000 tonnes in 2001 to over 1.5 million tonnes in 2021 (Pienaar et al. 2022).

Blueberries are famous for delaying human ageing while providing various health benefits. The antioxidant properties of blueberries protect human health by neutralising free radicals that cause ageing and various diseases, including cancer and cardiovascular disease, as well as immune system deterioration, brain dysfunction and cataracts (Tarkanyi et al. 2019). Nitrogen (N) fertilisation has been shown to influence the accumulation of bioactive compounds, such as phenolics, carotenoids and glucosinolates, in crops, which determines the nutritional value and health benefits of the fruit (Kishorekumar et al. 2020).

Nitrogen is an essential nutrient for plant growth and development, accounting for approximately 50% of yield performance. It is a key component of various metabolic processes in plant physiology involving shoot biomass, root development and N use efficiency (NUE) (Li et al. 2021). N in blueberry production promotes vegetative growth; as a result, it is important for the production of strong leaves, stems, branches and flower bud differentiation (Leitzke et al. 2015). Yuan-Yuan et al. (2021) indicated that optimal N levels increase the photosynthetic rate of blueberry plants by serving as an essential constituent of chlorophyll pigment, which captures light energy and contributes to fruit development by improving the seed setting rate for the quality and yield of fruits.

Blueberry plants obtain N through ammonium ion (NH_4^+) and nitrate ion (NO_3^-) absorption, which leads to specific genetic and metabolic responses in plants (Peterson, Stang & Dana 2022). Blueberries show a preference for NH_4^+ as their N source, while most plants prefer NO_3^-, although NH_4^+ is less available in soil than NO_3^- (Yuan-Yuan et al. 2021). Plant growth responses to different N sources are influenced by NH_4^+ or NO_3^- uptake and environmental factors such as temperature, soil pH and nutrient availability (Ye, Tian & Jin 2022). This makes the selection of N sources a critical aspect in blueberry production, which influences plant growth, yield and physiology. N has been noted to be essential for many physiological processes, including biomass production, root development and enzymatic activity (Alt, Doyle & Malladi 2017; Osorio et al. 2020). However, the effect of N on the complex synthesis of phenolic compounds, which are important for blueberry antioxidant properties, nutritional value and health benefits, remains under-investigated.

Nitrogen is one of the growth-limiting nutrients in plants. In blueberries, different sources of N stimulate vegetative growth; however, this is usually at the expense of secondary metabolite synthesis (González, Rugeles & Magnitskiy 2018). Because of increasing global demand for high-quality blueberries and their unique preference for nitrogen sources, a comprehensive understanding of how different nitrogen sources affect blueberry growth, yield and secondary metabolites is essential. Studies on the preferred N sources for blueberry plants will assist in enhancing production while using low N fertiliser rates, which will reduce production costs and environmental impacts. This review explores the role of various N sources in blueberry growth, yield and physiology. It further suggests areas for future research for sustainable N application in blueberry production.

Research methods and design

The search was conducted for relevant literature using various platforms to ensure all the sources were reliable. The Cape Peninsula University of Technology (CPUT) library database, where we accessed this information, includes ProQuest Agriculture Journals, ScienceDirect, Springer Nature Link, Scopus, Wiley and Google Scholar. Frontiers, ResearchGate and Artificial Intelligence (AI) tools like Connected Papers and Lit maps were used to find relevant articles linked to the information of interest. The review employed an extensive search using a combination of the following keywords: (1) blueberry, (2) nitrogen sources, (3) fertiliser and (4) phenolic compounds. Boolean operators were applied to refine searches in the databases accessed. The search covered published literature from 2014 to 2024, and only articles published in English were selected. Grammarly was used to correct grammar to improve readability, Turnitin for the similarity index and Mendeley as a reference management tool. Proper attribution to all original authors and sources was maintained throughout the review process, and findings were reported transparently.

Ethical considerations

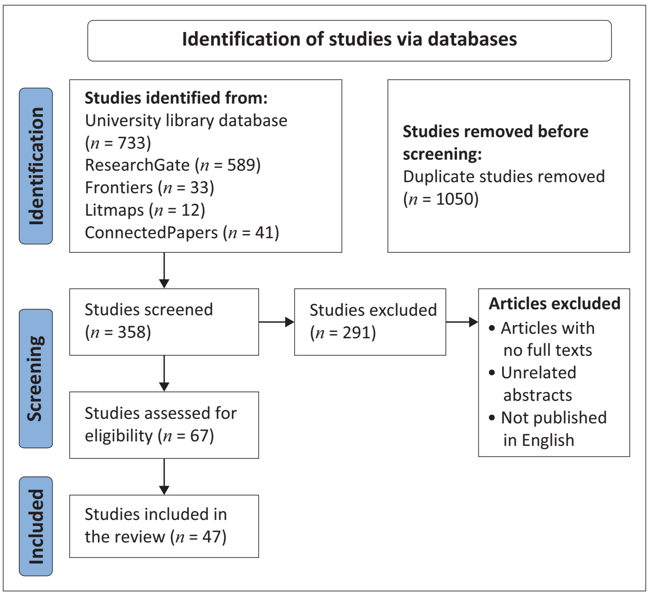
Ethical clearance to conduct this study was obtained from the Cape Peninsula University of Technology Faculty of Applied Sciences Research Ethics Committee on 19 April 2024. The ethical clearance number is 230407862/04/2024.

Results

The flowchart with the number of selected and excluded criteria in each stage was built using Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Figure 1). The initial search produced 1408 articles from the five databases; 1050 duplicates were excluded, and thereafter, 291 articles were excluded after reading the titles and abstracts. 67 articles were imported into the reference manager software (Mendeley) for further eligibility; finally, 47 studies were included in this review.

Nitrogen sources and overview

Plants primarily rely on two N forms, NH_4^+ and NO_3^-, which are derived from various soil processes such as mineralisation and nitrification (Zhang, Cai & Müller 2018). Nitrogen is available in the atmosphere, primarily in its gaseous form (N_2), which constitutes about 78% of the Earth's atmosphere (Glass & Rousk 2024). Nitrogen fixation occurs through a symbiotic relationship between root nodule-dwelling N-fixing bacteria (rhizobia) and plants, where the plant provides the bacteria with carbohydrates while the bacteria



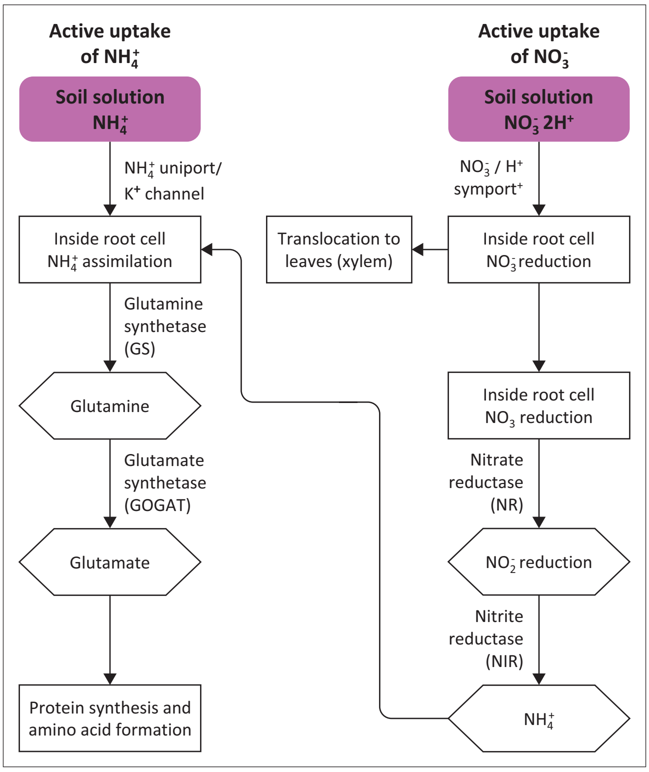
Source: Adapted with slight modifications from Helm, M., Alaba, T., Klimis-Zacas, D., Izuora, K. & Basu, A., 2023, 'Effect of dietary berry supplementation on antioxidant biomarkers in adults with cardiometabolic risks: A systematic review of clinical trials', *Antioxidants* 12(6), 1182. https://doi.org/10.3390/antiox12061182. Please see article's full reference list, https://doi.org/10.4102/jomped.v9i1.293

FIGURE 1: PRISMA flow diagram illustrating the process of searching and selecting studies based on the established inclusion and exclusion criteria, adapted with slight modifications from Helm et al. (2023).

fix N_2 into a form that the plant can use (Ahmadi 2023). Another way that some plants may obtain nitrogen for their nutrition is through nitrite (NO_2^-) from the atmosphere (Bashir et al. 2024). NO_2^- is a significant air pollutant produced in the soil when N-containing substances break down under low oxygen conditions (Ye et al. 2022). However, most of it is produced through the combustion of fossil fuels (vehicles, power plants and industrial processes). In soil, NO_2^- availability is generally low, and at high concentrations, it becomes toxic to plants (Bashir et al. 2024).

Ammonium (NH_4^+) as a nitrogen source

Ammonium N (NH_4^+) is present in soils through mineralisation of soil organic N and applied as a product of urea hydrolysis. NH_4^+ uptake is mediated by both high- and low-affinity transport systems, possibly via an NH_4^+ uniport or K^+ channel (Jose et al. 2023). NH_4^+ is the preferred form of N uptake when plants grow under N deficiency; it is rapidly assimilated into amino acids within the roots via the glutamine synthetase and glutamate synthase (GS/GOGAT) pathway (Figure 2), which requires less energy than NO_3^- assimilation (Zhang et al. 2018). Because of its positive charge, NH_4^+ is adsorbed by negatively charged soil colloids (clay and organic matter) and thus is less prone to leaching. Uptake of NH_4^+ causes rhizosphere acidification because of H^+ exchange (Imler, Arzola & Nunez 2019). The most used single N (NH_4^+) is ammonium sulphate, containing 21% N and 24% sulphur (S).



Source: Adapted from Imler et al. (2019), Muratore et al. (2021), and Jose et al. (2023) available in this article's full reference list, https://doi.org/10.4102/jomped.v9i1.293

FIGURE 2: Assimilation pathways of ammonium (NH_4^+) and nitrate (NO_3^-). Ammonium is incorporated into amino acids via the glutamine synthetase and glutamate synthase (GS and GOGAT) pathways, while nitrate is reduced to nitrite and then ammonium through nitrate reductase (NR) and nitrite reductase (NiR).

Nitrate (NO_3^-) as a nitrogen source

Most agricultural soils allow plant roots to absorb N mainly through NO_3^- even though NH_4^+ might be more accessible in certain soil types. This is mainly because of the higher concentration of NO_3^- in soils as compared to NO_2^- and NH_4^+. Additionally, because of its (NO_3^-) negative charge, it remains in the soil solution rather than binding to negatively charged soil particles, allowing for high mobility and plant uptake (Pinheiro et al. 2020). NO_3^- is absorbed via an NO_3^-/H^+ symport (Figure 2), involving three transport systems (Muratore, Espen & Prinsi 2021), and the uptake of NO_3^- leads to rhizosphere alkalinisation (Imler et al. 2019).

The conversion of NO_3^- to NH_4^+ and amino acid synthesis for protein synthesis depends on nitrate reductase enzyme activity, which is inefficient in blueberries (Kishorekumar et al. 2020). Blueberry plants demonstrate N form and concentration sensitivity in acidic NH_4^+-dominant soils; however, they thrive best at pH 4.0 to 5.5, which supports acidic soil conditions that favour NH_4^+ uptake as their preferred N source (Yang et al. 2022). Sensitivity of young blueberry plants to high ammonium sulphate applications may be because of ammonium toxicity, which is linked to increased electrical conductivity (EC) in the soil solution, with growth suppression observed at EC levels above 1.5 dS·m^{-1} (Machado, Bryla & Vargas 2014).

Table 1 shows that N form and soil acidity are important, with most studies indicating a preference for NH_4^+ over NO_3^- as an N source.

TABLE 1: A summary of the effect of nitrogen sources on blueberry species' pH levels.

Blueberry species	Nitrogen forms	pH	Key findings	References
'Northblue' (*V. corymbosum* and *V. angustifolium*)	NH_4^+, NO_3^- NH_4NO_3	4.5 and 6.5	More vegetative growth at pH 4.5 vs. 6.5, regardless of N form. No effect of N form at the given pH.	Rosen et al. (2019)
'Climax' and 'Chaoyue No. 1' (*V. corymbosum* L.)	NH_4^+ vs. NO_3^-	4.5, 5.3 and 6	Low pH (4.5) enhanced growth, yield, photosynthesis and micronutrient uptake; high pH (6.0) reduced growth and fruit quality. NH_4^+ alleviated high pH stress more effectively than NO_3^-	Jiang et al. (2019)
Andean blueberry (*V. meridionale Swartz*)	100% NH_4^+, 100% NO_3^- 50% NH_4^+: 50% NO_3^-	6.0	NH_4^+ fertilisation led to higher dry matter accumulation, shoots and leaves. NO_3^- fertilisation increased anthocyanin production because of stress from N deficiency and low chlorophyll synthesis.	Gonzalez et al. (2018)
'Tifblue' rabbiteye (*V. ashei* Reade)	NH_4^+ vs. NO_3^-	3.5–7.5	Higher fruit yield, greater shoot growth and higher leaf nutrient concentration with NH_4^+ compared to NO_3^-	Spiers (2022)
'Emerald' (*V. corymbosum*)	NH_4^+ vs. NO_3^-	5 and 75	Plants grew better at pH 5.0 than pH 7.5, and the plant growth was the best with NH_4^+:NO_3^- ratio of 2:1 at pH 5.0	Xu et al. (2021)

Source: Adapted from González et al. (2018), Jiang et al. (2019), Rosen et al. (2019), Xu et al. (2021), Spiers (2022) available in this article's full reference list, https://doi.org/10.4102/jomped.v9i1.293

TABLE 2: A summary of nitrogen sources indicating the effect of nitrogen on blueberry species' growth and yield.

Study or source	Nitrogen source	Blueberry cultivar or species	Growth or yield response	Key observations
Rosen et al. (2019)	NH_4^+	'Northblue'	Shoot length ↑ from 38.4 cm to 127.3 cm (pH 4.5)	Significant shoot elongation under NH_4^+
Osorio et al. (2020)	NH_4^+ vs. NO_3^-	'Emerald'	Leaf dry mass: NH_4^+ (24.8 g) > NO_3^- (17.4 g); Chlorophyll: NH_4^+ (20 μg/cm²) > NO_3^- (16 μg/cm²)	NH_4^+ improves leaf growth and chlorophyll content
Peterson et al. (2022)	NH_4^+ vs. NO_3^-	*V. corymbosum* L.	Higher NH_4^+ uptake in hydroponic systems	NH_4^+ is preferred in hydroponics
Arias et al. (2024)	$^{15}NH_4^+$ vs. $^{15}NO_3^-$	'Blue Ribbon'	N accumulation: NH_4^+ (243.5 mg/plant) > NO_3^- (213.6 mg/plant); ^{15}N recovery rate ↑ 10.7% with NH_4^+	Greater N use efficiency with NH_4^+
González et al. (2018)	NH_4^+ vs. NO_3^-	*V. meridionale.* Swartz	Shoots/plant: NH_4^+ (22) > 50:50 (20); Higher N% with NH_4^+ (1.72%), ↑ Net assimilation rate (NAR), LAI, dry matter	NH_4^+ improves shoot development, N accumulation and better photosynthetic performance
Alt et al. (2017)	NO_3^-	'Alapaha' and 'Sweetcrisp'	Growth ↓ by 30% – 60% with NO_3^-; low nitrate reductase activity	NO_3^- assimilation is limited because of enzyme inefficiency
Rosen et al. (2019)	NO_3^-	'Northblue'	Higher dry weight of plant parts at pH 6.5	NO_3^- can be effective at neutral pH
Messiga et al. (2021)	High NO_3^-	'Duke'	↓ Fruit set and quality	High NO_3^- can negatively affect reproductive traits
Imler et al. (2019)	NH_4^+ vs. NO_3^-	'Emerald'	NH_4^+ acidifies rhizosphere; NO_3^- increases pH	pH shifts affect nutrient availability and uptake
Anwar et al. (2024); Xu et al. (2021)	2:1 NH_4^+:NO_3^-	'Emerald' and 'Nangao Z9'	↑ Chlorophyll (1.2 mg/g FW), crown width ↑ 11%	A 2:1 ratio is optimal for vegetative growth
Yañez-Mansilla et al. (2015)	$NH_4^+NO_3^-$	'Legacy' and 'Bluegold'	Root N: Legacy (15 g/kg) > Bluegold (8 g/kg)	Cultivar-specific N responses
Yuan-Yuan et al. (2021)	Various NH_4^+:NO_3^- ratios	'Northsky'	Improved bud, root development and photosynthesis	Balanced ratios support overall plant health
Vargas & Bryla (2015)	NH_4^+ vs. urea	'Bluecropb'	Berry weight: NH_4^+ (2.22 g) > urea (2.17 g)	NH_4^+ is linked to better cellular growth when fertigation system with a split application method is used

Source: Adapted from Vargas & Bryla (2015), Yañez-Mansilla et al. (2015), Alt et al. (2017), González et al. (2018), Imler et al. (2019), Rosen et al. (2019), Osorio et al. (2020), Messiga et al. (2021), Xu et al. (2021), Yaun-Yaun et al (2021), Peterson et al. (2022), Arias et al. (2024), Anwar et al. (2024) available in this article's full reference list, https://doi.org/10.4102/jomped.v9i1.293

Blueberry growth and yield responses to different N sources

Nitrogen form plays a critical role in determining blueberry growth and yield responses. As shown in Table 2, numerous studies have investigated the effects of different N sources, including NH_4^+, NO_3^- and combinations thereof, on various blueberry cultivars and developmental parameters. Overall, NH_4^+-N tends to be more favourable than nitrate-N in most studies (Alt et al. 2017; Anwar et al. 2024; Arias et al. 2024; González et al. 2018; Imler et al. 2019; Messiga et al. 2021; Osorio et al. 2020; Peterson et al. 2022; Rosen, Allan & Luby 2019; Vargas & Bryla 2015; Xu et al. 2021; Yañez-Mansilla et al. 2015; Yuan-Yuan et al. 2021), with consistent improvements in shoot growth, chlorophyll content, leaf dry mass and yield. This trend may be attributed to the limited nitrate reductase activity in *Vaccinium* species, as well as their preference for acidic soils, which complements the acidifying effect of NH_4^+ nutrition.

Moreover, a combination of N sources, particularly NH_4^+:NO_3^- ratios of 2:1 or 1:1, has demonstrated synergistic effects on physiological and yield-related traits (Anwar et al. 2024). These ratios often outperform singular forms by enhancing N recovery, leaf area index and net assimilation rate without the adverse effects seen with high NO_3^- concentrations (Xu et al. 2021). Table 2 summarises these findings, offering insight into the understanding of blueberry N nutrition. However, recent studies seem to be placing increased emphasis on physiological responses, such as N uptake efficiency and photosynthetic activity, in addition to yield attributes. While cultivar-specific responses and environmental factors (such as soil pH and substrate) can modulate outcomes, the preference for NH_4^+-dominated nutrition or a combination of forms remains a consistent recommendation for optimising blueberry production.

Nitrogen sources on berry phenolic compounds

The antioxidant compounds anthocyanins, phenolic acids and polyphenols, which are present in blueberry plants, provide multiple health advantages (Krishna et al. 2023). Anthocyanin accumulation serves as a protective response for N-deficient plants by making leaves more light-sensitive through chlorophyll reduction. The presence of anthocyanins in plants enhances their ability to withstand N deficiency stress (Liang & He 2018). The accumulation of anthocyanin is triggered by N deficiency but also results from different nutritional imbalances, making it a useful crop nutrient status indicator (Jezek et al. 2023). Low N availability has been shown to enhance secondary metabolite production in plants by redirecting excess carbon (C) energy towards biosynthesis pathways, including flavonoid synthesis (Li et al. 2021).

Contrarily, high N availability can lead to decreased anthocyanin levels and reduced reproductive development. In blueberries, findings vary; while high N may reduce anthocyanin accumulation, Gonzalez et al. (2018) observed increased anthocyanin levels in specific N treatments, such as a balanced 50:50 NH_4^+:NO_3^- ratio, as shown in Table 3. NO_3^--based sources generally favour C allocation towards flavonoid production, whereas NH_4^+ sources tend to enhance N assimilation, potentially at the expense of flavonoid synthesis. Studies on blackberries show that distinct N forms impact the expression of genes involved in flavonoid biosynthesis, specifically dihydroflavonol 4-reductase (DFR) and chalcone synthase (CHS). Ammonium (NH_4^+) increases gene activity related to phenolic compound production (Duan et al. 2023).

As research specifically investigating the effect of different N sources on phenolic compound accumulation in blueberries

TABLE 3: Effects of nitrogen forms on phenolic compound biosynthesis.

Source	Plant	Nitrogen source or condition	Key findings	Implications
Gonzalez et al. (2018)	Blueberry	100% NO_3^-, 100% NH_4^+, 50:50 NH_4^+:NO_3^-	100% NO_3^-: 11.68 mg/100 g FW anthocyanin 100% NH_4^+: 1.90 mg/100 g FW 50:50 mix: 12.79 mg/100 g FW (highest)	NO_3^- favours anthocyanin synthesis over NH_4^+; balanced N form most effective.
Liang & He (2018)	General	N deficiency	Anthocyanin accumulation increases under N deficiency as a stress response; reduces chlorophyll; increases light sensitivity	Anthocyanins serve as protective metabolites under N stress.
Jezek et al. (2023)	General	Nutritional imbalances, including N deficiency	Anthocyanin accumulation reflects multiple nutrient imbalances, not just N deficiency	Anthocyanins are effective biomarkers for nutrient status.
Leitzke et al. (2015)	Blueberry ('O'Neal')	High N availability	Increased anthocyanin production observed alongside pH drop and toxic Al accumulation	Excess N can stimulate anthocyanin synthesis but also cause soil acidification.
Arias et al. (2024)	Blueberry	NO_3^- treatment	Lower biomass (leaves, stems, roots) and reduced secondary metabolite production, including anthocyanins	NO_3^- may suppress overall plant growth, negatively impacting secondary metabolites.
Duan et al. (2023)	Blackberry	Urea, ammonium sulphate, calcium nitrate	NH_4^+ and urea: ↑ anthocyanins, ellagic acid Ca $(NO_3)_2$: ↑ flavonoid biosynthesis and antioxidant capacity	N-form affects specific bioactive compound production differently. NO_3^- promotes carbon reallocation to secondary metabolism.
Huang et al. (2022)	General	N deficiency	N deficiency triggers C metabolism activation and energy accumulation	Explains why secondary metabolite biosynthesis increases under N deficiency.
Li et al. (2021)	General	N deficiency	Energy surplus from C metabolism promotes flavonoid synthesis to rebalance C/N metabolism	Flavonoids help regulate energy balance under nutrient stress.
Kishorekumar et al. (2020)	General	NH_4^+ vs. NO_3^- assimilation pathways	NH_4^+: directly assimilated; NO_3^-: energy-costly reduction to NH_4^+; influences phenolic synthesis differently	NH_4^+ may supply more precursors but less energy, whereas NO_3^- impacts resource allocation more strongly.

Source: Leitzke et al. (2015), González et al. (2018), Liang & He (2018), Kishorekumar et al. (2020), Li et al. (2021), Huang et al. (2022), Duan et al. (2023), Jezek et al. (2023), Arias et al. (2024) available in this article's full reference list, https://doi.org/10.4102/jomped.v9i1.293

is limited, data from studies on related species have been included to provide a broad context. These trends are summarised in Table 3, presenting several studies on how different N sources and conditions influence phenolic compound accumulation across various plants.

Plant physiological responses to different N sources

The response of blueberry plants to different N forms shows N availability as a critical factor that affects both growth and photosynthesis (González et al. 2018; Osorio et al. 2020; Yuan-Yuan et al. 2021). Adequate N supply remains essential because chlorophyll synthesis depends on N to enable light absorption and photosynthetic efficiency. The use of NH_4^+ as a nutrient source has been shown to increase stomatal conductance in blueberries, which leads to better gas exchange and supports photosynthesis (Osorio et al. 2020). The application of NH_4^+ resulted in better gaseous exchange parameters than NO_3^-, and Yuan-Yuan et al. (2021) demonstrated that a 5:1 NH_4^+:NO_3^- ratio produced the best photosynthetic and stomatal performance.

However, the advantage depends on concentration because excessive NH_4^+ leads to metabolic imbalance and oxidative stress and impaired photosynthetic functions (Yañez-Mansilla et al. 2015). Excessive NH_4^+ stress disrupts electron transport and reduces carboxylation efficiency, thus decreasing CO_2 assimilation (Wang et al. 2019). The assimilation of NO_3^- requires more energy than NH_4^+ but enables sustained photosynthesis through its ability to generate Adenosine Triphosphate (ATP) and Nicotinamide Adenine Dinucleotide Phosphate (NADPH) needed for the Calvin cycle (Kishorekumar et al. 2020). The study by Cárdenas-Navarro et al. (2024) demonstrated that blueberry plants supplied with NO_3^- nutrition showed better carbon fixation rates and electron transport activity.

Urea-based fertilisers, which are hydrolysed into NH_4^+ in the soil, have shown photosynthetic outcomes like NH_4^+ sources (Nasraoui-Hajaji & Gouia 2014). The controlled N release from urea leads to higher chlorophyll content and better C assimilation (Kozos & Ochmian 2016). The photosynthetic response extends longer because N from urea becomes available more gradually than from NH_4^+ or NO_3^- (Smolander, Martikainen & Henttonen 2022). The most successful approach to maximise photosynthetic efficiency while preventing N-related stress in blueberries involves maintaining balanced NH_4^+:NO_3^- inputs.

Effects of nitrogen source on water-use efficiency and drought tolerance in plants

Different N sources influence water-use efficiency (WUE), transpiration and osmotic adjustment in blueberry plants; these are key processes for maintaining water status under drought (Ruiz-Romero et al. 2024). NH_4^+ nutrition enhances blueberry plant drought resistance through multiple physiological processes. The increased root abscisic acid content in drought-stressed NH_4^+-fed plants leads to better WUE (Ding et al. 2016). Accumulation of osmolytes such as proline and soluble sugars helps sustain root development to reach deeper soil water (Zaher-Ara, Boroomand & Sadat-Hosseini 2016).

Highbush blueberry cultivars showed different levels of drought resistance after drought stress reduced their photochemical efficiency and increased proline content (Balboa, Ballesteros & Molina-Montenegro 2020).

Under water-limited conditions, NH_4^+ nutrition controls stomatal conductance to minimise excessive water loss through transpiration while allowing sufficient CO_2 uptake for photosynthesis to support plant development (Torralbo et al. 2019). The drought resistance of *Malus prunifolia* increased with higher NH_4^+ uptake but lower NO_3^- uptake, indicating the importance of NH_4^+ in drought tolerance (Huang et al. 2018). Similarly, in other crops, high NH_4^+ concentrations cause ion imbalances, which lead to toxicity and damage the plant's water stress tolerance (Shilpha et al. 2023). Research conducted by Faralli et al. (2023) demonstrated that NO_3^--based fertilisation enhances plant development under sufficient irrigation by improving transpiration efficiency. The positive effects of NO_3^--nutrition on transpiration reached their peak when water availability was sufficient, yet NO_3^- does not provide drought tolerance at the same level as NH_4^+. Plants that received NH_4^+ nutrition demonstrated superior drought tolerance compared to those receiving NO_3^- under water-stressed conditions (Ding et al. 2016). However, plants treated with NO_3^- still maintained positive hydration status because NO_3^- enabled proper stomatal conductance for efficient CO_2 uptake and reduced water loss during photosynthesis (Ding et al. 2016).

Recommendations

Future research should also explore the interactions between N sources and secondary metabolite production, especially phenolic compounds, which are important for blueberry quality and human health benefits. Knowledge of the mechanisms through which N influences phenolic synthesis could provide new ways of improving fruit quality through fertilisation practices. Selection of an N source is the main factor in improving plant growth and physiological performance; hence, it is important to explore this area of research, particularly in blueberry secondary metabolite accumulation, which is relatively scarce in the current available literature.

Conclusion

The selection of N sources, along with application methods, determines the most effective method to promote blueberry production while maintaining environmental sustainability. The combination of NH_4^+ with NO_3^- or NH_4^+ alone results in superior plant growth and fruit quality compared to NO_3^- alone, particularly when the soil conditions are acidic, which is favourable for blueberry cultivation. Further research should investigate how different blueberry cultivars respond to the combination of N forms under varying acidic conditions. The practice of split fertiliser applications and fertigation systems enhances nutrient utilisation efficiency while reducing nutrient loss. However, the long-term effects of continuous NH_4^+ fertilisation on soil acidification and associated changes in nutrient dynamics under blueberry production remain under-investigated, highlighting the need for further research.

Acknowledgements

The authors would like to show appreciation to the Cape Peninsula University of Technology (CPUT) for affording support and research facilities. This article is partially based on Asemahle Mshweshwe thesis entitled 'The effect of different nitrogen sources and growth media on water use of blueberry cultivated under shade net', towards the degree of Master of Agriculture, Cape Peninsula University of Technology with supervisors: Prof F.B. Lewu and Ms N Mfeka. It will be available at: https://etd.cput.ac.za/.

Competing interests

The authors reported that they received funding from the Water Research Commission (WRC), which may be affected by the research reported in the enclosed publication. The authors have disclosed those interests fully and have implemented an approved plan for managing any potential conflicts arising from their involvement. The terms of these funding arrangements have been reviewed and approved by the affiliated university in accordance with its policy on objectivity in research.

Authors' contributions

Asemahle Mshweshwe contributed to conceptualisation, methodology, writing – original draft, writing – review and editing. Nonkululeko Mfeka, Francis B. Lewu and Mbappe Tanga contributed to conceptualisation, methodology, writing, review and editing, and supervision. Francis B. Lewucontributed to funding acquisition.

Funding information

This research study was supported by the Water Research Commission (WRC), project number: 2022/2023-00838, and the National Research Foundation (NRF).

Data availability

Derived data supporting the findings of this study are available from the corresponding author, Nonkululeko Mfeka, on reasonable request.

Disclaimer

The views and opinions expressed in this article are those of the authors and are the product of professional research. They do not necessarily reflect the official policy or position of any affiliated institution, funder, agency or that of the publisher. The authors are responsible for this article's results, findings and content.

References

Ahmadi, A.Y., 2023, 'Relations of legumes with soil health and succeeding crops', *Open Access Journal of Agricultural Research* 8(4), 1–9. https://doi.org/10.23880/oajar-16000333

Alt, D.S., Doyle, J.W. & Malladi, A., 2017, 'Nitrogen-source preference in blueberry (*Vaccinium* sp.): Enhanced shoot nitrogen assimilation in response to direct supply of nitrate', *Journal of Plant Physiology* 216, 79–87. https://doi.org/10.1016/j.jplph.2017.05.014

Anwar, A., Zheng, J., Chen, C., Chen, M., Xue, Y., Wang, J. et al., 2024, 'Effects of NH_4^+-N:NO_3^--N ratio on growth, nutrient uptake and production of blueberry (*Vaccinium* spp.) under soilless culture', *Frontiers in Plant Science* 15, 1438811. https://doi.org/10.3389/fpls.2024.1438811

Arias, M.I., Nario, A., Rojas, K., Blanc, P. & Bonomelli, C., 2024, 'Newly established blueberry plants: The role of inorganic nitrogen forms in nitrogen and calcium absorption', *Horticulturae* 10(11), 1168. https://doi.org/10.3390/horticulturae10111168

Balboa, K., Ballesteros, G.I. & Molina-Montenegro, M.A., 2020, 'Integration of physiological and molecular traits would help to improve the insights of drought resistance in highbush blueberry cultivars', *Plants* 9(11), 1457. https://doi.org/10.3390/plants9111457

Bashir, M.R., Alomran, M., Gill, A.N., Tufail Khan, Q.A., Jameel, S., Rafiq, M.U. et al., 2024, 'Rising nitrogen dioxide (NO_2): A growing threat to environment and plant health', *Journal of Agriculture and Biology* 2(1), 76–83. https://doi.org/10.55627/agribiol.002.01.01023

Cárdenas-Navarro, R., Luna-Béjar, J.A., Castellanos-Morales, V.d.C., Bravo-Hernández, N.L. & López-Pérez, L., 2024, 'Effect of the concentration and ionic form of nitrogen (N) on photosynthesis, growth and fruit production of blueberry (*Vaccinium corymbosum* L.)', *Biotecnia* 26(3), e2325. https://doi.org/10.18633/biotecnia.v26.2325

Ding, L., Li, Y., Wang, Y., Gao, L., Wang, M., Chaumont, F. et al., 2016, 'Root ABA accumulation enhances rice seedling drought tolerance under ammonium supply: Interaction with aquaporins', *Frontiers in Plant Science* 7, 1206. https://doi.org/10.3389/fpls.2016.01206

Duan, Y., Yang, H., Yang, H., Wu, Y., Fan, S., Wu, W. et al., 2023, 'Integrative physiological, metabolomic and transcriptomic analysis reveals nitrogen preference and carbon and nitrogen metabolism in blackberry plants', *Journal of Plant Physiology* 280, 153888. https://doi.org/10.1016/j.jplph.2022.153888

Faralli, M., Bianchedi, P.L., Moser, C., Bontempo, L. & Bertamini, M., 2023, 'Nitrogen control of transpiration in grapevine', *Physiologia Plantarum* 175(2), e13906. https://doi.org/10.1111/ppl.13906

Glass, J.B. & Rousk, K., 2024, 'Microbial nitrogen transformation processes across environments: More than just a cycle', *Trends in Microbiology* 32(6), 519–521. https://doi.org/10.1016/j.tim.2024.04.006

González, L.K., Rugeles, L.N. & Magnitskiy, S., 2018, 'Effect of different sources of nitrogen on the vegetative growth of Andean blueberry (*Vaccinium meridionale* Swartz)', *Agronomía Colombiana* 36(1), 58–67. https://doi.org/10.15446/agron.colomb.v36n1.69304

Huang, L., Li, M., Zhou, K., Sun, T., Hu, L., Li, C. et al., 2018, 'Uptake and metabolism of ammonium and nitrate in response to drought stress in *Malus prunifolia*', *Plant Physiology and Biochemistry* 127(1), 185–193. https://doi.org/10.1016/j.plaphy.2018.03.031

Helm, M., Alaba, T., Klimis-Zacas, D., Izuora, K. & Basu, A., 2023, 'Effect of dietary berry supplementation on antioxidant biomarkers in adults with cardiometabolic risks: A systematic review of clinical trials', *Antioxidants* 12(6), 1182. https://doi.org/10.3390/antiox12061182

Huang, W.T., Zheng, Z.C., Hua, D., Chen, X.-F., Zhang, J., Chen, H.H. et al., 2022, 'Adaptive responses of carbon and nitrogen metabolisms to nitrogen deficiency in *Citrus sinensis* seedlings', *BMC Plant Biology* 22(1), 370. https://doi.org/10.1186/s12870-022-03759-7

Imler, C.S., Arzola, C.I. & Nunez, G.H., 2019, 'Ammonium uptake is the main driver of rhizosphere pH in southern highbush blueberry', *HortScience* 54(5), 955–959. https://doi.org/10.21273/HORTSCI13764-18

Jezek, M., Allan, A.C., Jones, J.J. & Geilfus, C., 2023, 'Why do plants blush when they are hungry?', *New Phytologist* 239(2), 494–505. https://doi.org/10.1111/nph.18833

Jiang, Y., Zeng, Q., Wei, J., Jiang, J., Li, Y., Chen, J. et al., 2019, 'Growth, fruit yield, photosynthetic characteristics, and leaf microelement concentration of two blueberry cultivars under different long-term soil pH treatments', *Agronomy* 9(7), 357. https://doi.org/10.3390/agronomy9070357

Jose, E., Soni, K.B., Alex, S., Pillai, P.S., Beena, R. & Stephen, R., 2023, 'Molecular frameworks of nitrogen response in plants: A review', *International Journal of Environment and Climate Change* 13(12), 380–390. https://doi.org/10.9734/ijecc/2023/v13i123694

Kishorekumar, R., Bulle, M., Wany, A. & Gupta, K.J., 2020, 'An overview of important enzymes involved in nitrogen assimilation of plants', *Methods in Molecular Biology* 2057, 1–13. https://doi.org/10.1007/978-1-4939-9790-9_1

Kozos, K. & Ochmian, I., 2016, 'The influence of fertilization urea phosphate on growth and yielding bush of two highbush blueberry cultivars (V. corymbosum)', *Folia Pomeranae Universitatis Technologiae Stetinensis Agricultura, Alimentaria, Piscaria et Zootechnica* 325(37), 29–38. https://doi.org/10.21005/AAPZ2016.37.1.04

Krishna, P., Pandey, G., Thomas, R. & Parks, S., 2023, 'Improving blueberry fruit nutritional quality through physiological and genetic interventions: A review of current research and future directions', *Antioxidants* 12(4), 810. https://doi.org/10.3390/antiox12040810

Leitzke, L.N., Picolotto, L., Pereira, I.D.S., Vignolo, G.K., Schmitz, J.D., Vizzotto, M. et al., 2015, 'Nitrogen fertilizer affects the chemical composition of the substrate, the foliar nutrient content, the vegetative growth, the production and fruit quality of blueberry', *Científica* 43(4), 316–324. https://doi.org/10.15361/1984-5529.2015v43n4p316-324

Li, S., Huang, Y.Z., Liu, X.Y. & Fu, X.D., 2021, 'Genetic improvement of nitrogen use efficiency in crops', *Yi Chuan = Hereditas* 43(7), 21–064. https://doi.org/10.16288/j.yczz.21-064

Liang, J. & He, J., 2018, 'Protective role of anthocyanins in plants under low nitrogen stress', *Biochemical and Biophysical Research Communications* 498(4), 946–953. https://doi.org/10.1016/j.bbrc.2018.03.087

Machado, R.M.A., Bryla, D.R. & Vargas, O., 2014, 'Effects of salinity induced by ammonium sulphate fertilizer on root and shoot growth of highbush blueberry', *Acta Horticulturae* 1017, 407–414. https://doi.org/10.17660/ActaHortic.2014.1017.49

Messiga, A.J., Nyamaizi, S., Yu, S. & Dorais, M., 2021, 'Blueberry yield and soil mineral nitrogen response to nitrogen fertilizer and nitrification inhibitors under drip-fertigation systems', *Agronomy* 11(11), 2144. https://doi.org/10.3390/agronomy11112144

Muratore, C., Espen, L. & Prinsi, B., 2021, 'Nitrogen uptake in plants: The plasma membrane root transport systems from a physiological and proteomic perspective', *Plants* 10(4), 681. https://doi.org/10.3390/plants10040681

Nasraoui-Hajaji, A. & Gouia, H., 2014, 'Photosynthesis sensitivity to NH_4^+-N change with nitrogen fertilizer type', *Plant, Soil and Environment* 60(6), 274–279. https://doi.org/10.17221/7418-PSE

Osorio, R., Cáceres, C. & Covarrubias, J.I., 2020, 'Vegetative and physiological responses of "Emerald" blueberry to ammoniacal sources with a nitrification inhibitor', *Journal of Soil Science and Plant Nutrition* 20(2), 507–515. https://doi.org/10.1007/s42729-019-00135-7

Peterson, L.A., Stang, E.J. & Dana, M.N., 2022, 'Blueberry response to NH_4-N and NO_3-N', *Journal of the American Society for Horticultural Science* 113(1), 9–12. https://doi.org/10.21273/jashs.113.1.9

Pienaar, L., Smit, P., Hattingh, J. & Cloete, K., 2022, *Developing economic models for South African blueberry industry: Outlook 2022–2031*, *Report commissioned by BerriesZA*, Bureau for Food and Agricultural Policy (BFAP), Paarl.

Pinheiro, R.B., Cantarutti, R.B., Villani, E.M.d.A., Cavalcante, V.S. & Fontes, M.P.F., 2020, 'Nitrate mobility in variable-charge tropical soils', *Communications in Soil Science and Plant Analysis* 51(16), 2163–2173. https://doi.org/10.1080/00103624.2020.1820025

Rosen, C.J., Allan, D.L. & Luby, J.J., 2019, 'Nitrogen form and solution pH influence growth and nutrition of two *Vaccinium* clones', *Journal of the American Society for Horticultural Science* 115(1), 83–89. https://doi.org/10.21273/jashs.115.1.83

Ruiz-Romero, R., De la Peña, M., Ayala-Díaz, I., Montoya, C. & Romero, H.M., 2024, 'Genotype and nitrogen source influence drought stress response in oil palm seedlings', *Agronomy* 14(9), 2082. https://doi.org/10.3390/agronomy14092082

Shilpha, J., Song, J. & Jeong, B.R., 2023, 'Ammonium phytotoxicity and tolerance: An insight into ammonium nutrition to improve crop productivity', *Agronomy* 13(6), 1487. https://doi.org/10.3390/agronomy13061487

Smolander, A., Martikainen, P.J. & Henttonen, H.M., 2022, 'Half-a-century effects of a slow-release nitrogen fertilizer, ureaformaldehyde, on stand growth and soil processes in a Scots pine stand', *Forest Ecology and Management* 519, 120320. https://doi.org/10.1016/j.foreco.2022.120320

Spiers, J.M., 2022, 'Effects of pH level and nitrogen source on elemental leaf content of "Tifblue" rabbiteye blueberry', *Journal of the American Society for Horticultural Science* 103(6), 523–525. https://doi.org/10.21273/jashs.103.6.705

Tarkanyi, P.C., Bordean, D.M., Catargiu, A. & Poiana, M.A., 2019, 'Blueberries – Pleading for health', *Journal of Agroalimentary Processes and Technologies* 25(4), 187–194.

Torralbo, F., González-Moro, M.B., Baroja-Fernández, E., Aranjuelo, I. & González-Murua, C., 2019, 'Differential regulation of stomatal conductance as a strategy to cope with ammonium fertilizer under ambient versus elevated CO_2', *Frontiers in Plant Science* 10, 597. https://doi.org/10.3389/fpls.2019.00597

Vargas, O.L. & Bryla, D.R., 2015, 'Growth and fruit production of highbush blueberry fertilized with ammonium sulfate and urea applied by fertigation or as granular fertilizer', *HortScience* 50(3), 479–485. https://doi.org/10.21273/HORTSCI.50.3.479

Wang, F., Gao, J., Shi, S., He, X. & Dai, T., 2019, 'Impaired electron transfer accounts for the photosynthesis inhibition in wheat seedlings (*Triticum aestivum* L.) subjected to ammonium stress', *Physiologia Plantarum* 167(2), 159–172. https://doi.org/10.1111/ppl.12878

Xu, J., Fang, Y., Tavakkoli, E., Pan, X., Liao, F., Chen, W. et al., 2021, 'Preferential ammonium:nitrate ratio of blueberry is regulated by nitrogen transport and reduction systems', *Scientia Horticulturae* 288, 110345. https://doi.org/10.1016/j.scienta.2021.110345

Yañez-Mansilla, E., Cartes, P., Reyes-Díaz, M., Ribera-Fonseca, A., Rengel, Z., Lobos, W. et al., 2015, 'Leaf nitrogen thresholds ensuring high antioxidant features of *Vaccinium corymbosum* cultivars', *Journal of Soil Science and Plant Nutrition* 15(3), 574–586. https://doi.org/10.4067/S0718-95162015005000025

Yang, H., Wu, Y., Zhang, C., Wu, W., Lyu, L. & Li, W., 2022, 'Growth and physiological characteristics of four blueberry cultivars under different high soil pH treatments', *Environmental and Experimental Botany* 197, 104842. https://doi.org/10.1016/j.envexpbot.2022.104842

Ye, J.Y., Tian, W.H. & Jin, C.W., 2022, 'Nitrogen in plants: From nutrition to the modulation of abiotic stress adaptation', *Stress Biology* 2(1), 4. https://doi.org/10.1007/s44154-021-00030-1

Yuan-Yuan, Z., Jun-Ping, T., Jun, C., Yu-Hui, H. & Yu-Shi, L., 2021, 'Effects of different NH_4^+/NO_3^- ratios on the photosynthetic and physiological responses of blueberry (*Vaccinium* spp.) seedlings', *Journal of Plant Nutrition* 44(6), 854–864. https://doi.org/10.1080/01904167.2021.1871754

Zaher-Ara, T., Boroomand, N. & Sadat-Hosseini, M., 2016, 'Physiological and morphological response to drought stress in seedlings of ten citrus species', *Trees* 30(3), 985–993. https://doi.org/10.1007/s00468-016-1372-y

Zhang, J., Cai, Z. & Müller, C., 2018, 'Terrestrial N cycling associated with climate and plant-specific N preferences: A review', *European Journal of Soil Science* 69(3), 488–501. https://doi.org/10.1111/ejss.12533