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A Brief Review of Nitrogen Manipulation in Microalgae: Effects on Growth, Biomass, and Biochemical Composition

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Abstract

Microalgae are microorganisms with the potential to produce high-value compounds while providing environmental benefits. Nitrogen availability plays an important role in regulating growth, photosynthetic efficiency, and intracellular carbon allocation. This review examines the effects of nitrogen manipulation on microalgal growth, metabolism, and the production of biomass and biochemical compounds. Literature published between 2015 and 2026 was retrieved from PubMed, Scopus, Web of Science, and Google Scholar based on its relevance to nitrogen metabolism, growth, and biomass production. Nitrate generally supports growth and biomass production, whereas ammonium requires pH control to reduce toxicity. Urea has the potential to enhance lipid and carotenoid accumulation in certain species. In contrast, nitrogen limitation redirects carbon allocation toward energy-storage compounds, particularly triacylglycerols (TAGs) and carbohydrates. Two-stage cultivation offers a potential strategy for balancing biomass production and biochemical accumulation, although its effectiveness depends on the species and cultivation conditions. Differences in research designs limit comparisons among studies, highlighting the need for species-specific optimization. Overall, nitrogen manipulation is an important strategy for optimizing microalgal growth, biomass production, and the development of high-value bioproducts.

Keywords: *Microalgae; Nitrogen Metabolism; Nitrogen Regulation; Biomass*

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INTRODUCTION

Microalgae are increasingly viewed as a sustainable biomass source and a promising biotechnology platform due to their ability to grow rapidly and utilize CO2, water, waste, and non-arable land, while simultaneously producing a variety of high-value compounds relevant to the food, feed, pharmaceutical, cosmetic, and bioenergy industries (Siddiki et al., 2022; Olguin et al., 2022). Microalgal dry biomass accumulates carbohydrates (8–69.7%), proteins (5–74%), and lipids (7–65%), depending on the strain and culture parameters (Siddiki et al., 2022). These biochemical components can be utilized to produce various bioenergy vectors, such as biodiesel from the lipid fraction, bioethanol from carbohydrates, and biogas via anaerobic degradation.

Nitrogen is an important nutrient and regulator of intracellular carbon allocation and metabolism. In the absence of nitrogen limitation, fixed carbon is preferentially allocated to cell division, protein synthesis, and photosynthetic machinery components. Under nitrogen limitation, however, this process can be subjected to metabolic rewiring, i.e., the assimilated carbon is reallocated from growth to carbon storage forms such as triacylglycerols (TAGs) and carbohydrate accumulation (Remmers et al., 2018). This response is associated with changes in photosynthetic activity, chlorophyll content, protein synthesis, and carbon metabolism (Liu et al., 2022). For example, nitrogen limitation in Phaeodactylum tricornutum promotes TAG and carbohydrate accumulation at the expense of growth and cellular protein content (Remmers et al., 2018). However, the extent of this metabolic shift depends on the severity and duration of nitrogen limitation, as well as the physiological characteristics of the microalgal species (Maltsev et al., 2023). Thus, nitrogen availability determines not only the amount of biomass produced but also how cellular carbon is distributed between growth and the formation of storage compounds.

Although numerous studies have investigated the effects of nitrogen availability on microalgal growth and biochemical composition, the findings remain variable depending on the nitrogen source, microalgal species, nitrogen concentration, and cultivation conditions. Previous studies have examined the effects of different nitrogen sources, such as nitrate, ammonium, and urea, on growth and biochemical composition (Yuniarti et al., 2023; Salbitani & Carfagna, 2021), while other studies have focused primarily on nitrogen limitation and its effects on lipid accumulation and metabolic responses (Remmers et al.,

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2018; Liu et al., 2022). Furthermore, studies on two-stage cultivation have demonstrated the potential of combining nitrogen sufficiency and nitrogen deprivation to balance biomass production and lipid accumulation (Nayak et al., 2019). However, the combined relationships among nitrogen source selection, photosynthetic regulation, intracellular C/N balance, and the allocation of carbon toward TAG, carbohydrates, and carotenoids have not been sufficiently synthesized in the context of nitrogen management strategies. Addressing this gap is important for identifying nitrogen management strategies that can balance biomass production with the formation of high-value biochemical products.

This review thus critically examines the effect of the nitrogen source and availability on the growth and biochemistry of microalgae. Furthermore, the review addresses nitrogen management approaches to provide insight into the strategies to optimize biomass and biochemical production.

RESEARCH METHOD

Research Design

The study used a modified systematic and narrative review method to identify, evaluate, and synthesize the available evidence on microalgal carbon capture and lipid accumulation. This was so because the approach is systematic and transparent in identifying relevant publications producing and approaching their findings as well as their synthesis of evidence from the pertinent literature (Musifa et al., 2025).

Inclusion and Exclusion Criteria

The inclusion criteria cover peer-reviewed articles published between 2015 and 2026 that examine carbon capture by microalgae and the mechanisms involved in lipid accumulation. Conversely, the exclusion criteria encompass publications irrelevant to the research objectives, specifically those that do not address microalgae, biomass, growth curves, or lipid accumulation as well as articles for which the full-text information is unavailable or inaccessible.

Study Selection and Search Strategy

The filtered papers were screened by reviewing titles and abstracts to start selecting studies. Articles that matched the pre-defined inclusion criteria were then full-text reviewed for their relation to the research objectives. Also, literature search was conducted utilizing multiple databases like PubMed, Scopus, Web of Science and Google Scholar. The search was performed using keywords such as “nitrogen manipulation,”

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"lipid accumulation in microalgae," and "microalgae growth." Boolean operators (AND and OR) were used to create combinations of keywords to broaden or refine the search results to locate relevant publications.

Data Extraction and Analysis

Finally, data were taken from the relevant literature on the topic, mainly the mechanisms and consequences of nitrogen modification on microalgae development. The data were then systematically organized. This study uses a qualitative method to highlight patterns, reported achievements and limitations of carbon capture and lipid production by microalgae. Furthermore, a descriptive analysis was performed in an effort to develop a complete narrative based on the available facts. The results are compiled to provide a critical summary and insight into the mechanisms of carbon capture and lipid buildup in microalgae.

RESULT AND DISSCUSSION

Nitrogen Sources

Nitrate is generally used because as a culture it has more stability and control of the process, partly because to a lesser danger of ammonia toxicity and smaller reduction of pH than ammonium (Yuniarti et al., 2023). However, nitrate does not always result in maximum growth, as cells must first reduce nitrate to ammonium before it can start amino acid biosynthesis. Although ammonium is the most metabolically efficient supply, this advantage is typically lost during actual cultivation because of acidification and toxicity problems (Salbitani et al., 2021). However, ammonium can promote biomass, protein content or nitrogen removal at optimum doses or in combination with nitrate, with continuous culture systems showing very species-specific responses. Urea is often used as a cheap and versatile alternative, with studies reporting similar or better growth rates than nitrate, average cost savings up to 72.6% and in the case of *Chlamydomonas reinhardtii* improved photosynthesis under mixotrophic conditions (Yuniarti et al., 2023).

Urea is not a universal solution as it can diminish final yields or PUFA content in some marine microalgae. The metabolic basis of nitrogen consumption is different amongst nitrogen sources. Before it can be incorporated into amino acids, nitrate has to be reduced to ammonium, through the successive action of nitrate reductase and nitrite reductase. Ammonium can also be directly assimilated into glutamine and glutamate

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through the glutamine synthetase-glutamate synthase (GS-GOGAT) pathway; however, this assimilation can affect cellular ion balance and culture pH. Urea must be degraded by urease or other urea utilization pathways to release ammonium for assimilation. Therefore its effects should be assessed strain by strain and target product by target product. Other organic nitrogen sources have been investigated and the optimal source is not only dependent on the type of nitrogen but also on the specific metabolic architecture of each species (Luthfi at al., 2025). In practice, nitrate is suitable for stable cultures, ammonium is suitable when the pH and dosage are controlled, urea is often more cost-efficient, and mixed nitrogen sources can offer optimal performance for biomass production and wastewater treatment (Castro-Varela et al., 2021).

1.1. Nitrogen Manipulation Strategies

Nitrogen manipulation causes a change in carbon flux away from cell division and toward the production of energy-storage molecules such as triacylglycerols and carbohydrates (Remmers et al., 2018). Nitrogen limitation causes the suppression of the photosynthetic system and the creation of functional proteins, forcing the cell to undergo a coordinated metabolic reconfiguration to maintain energy homeostasis (Scarsini et al., 2022). In the absence of nitrogen or nitrogen deficiency, the metabolic pathway of porphyrin and the enzyme porphobilinogen deaminase are repressed, which greatly lowers the production of chlorophyll (Rai et al., 2017). This loss corresponds to a decrease in the amount of key enzymes involved in photosynthetic carbon fixation, such as ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), phosphoribulokinase and sedoheptulose-1,7-bisphosphatase. Cells degrade ribosomal polypeptides, light-harvesting pigments and thylakoid membrane proteins via autophagy processes to cope with external nitrogen limitation (Scarsini et al., 2022). Cells channel carbon skeletons from TCA cycle intermediates to incorporate nitrogen into certain amino acids like glutamate, aspartate, and arginine. Accumulation of arginine is an intermediate intracellular nitrogen pool, and a protective mechanism against oxidative stress in cells.

Different nitrogen sources have different metabolic basis for nitrogen consumption. Nitrate is first reduced to ammonium by nitrate reductase and nitrite reductase and then assimilated into amino acids. Conversely, ammonium can be directly assimilated into glutamine and glutamate via the glutamine synthetase-glutamate synthase (GS-GOGAT) pathway. However, ammonium assimilation can impact the ion

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balance and pH of the culture. The mechanisms are efficient not only depending on the nitrogen source but also on the species-specific metabolic capability and the cultivation circumstances such as nitrogen concentration, pH, salinity, light intensity, and medium composition. Interactions account for the variability of optimal nitrogen source among microalgal species and culture strategies. Therefore its effects should be assessed strain by strain and target product by target product. Other organic nitrogen sources have been investigated and the optimal source is not only dependent on the type of nitrogen but also on the specific metabolic architecture of each species (Luthfi at al., 2025).

1.2. Nitrogen Sufficiency

Under nitrogen-replete conditions, the "optimal" concentration is not universal and is highly species-dependent; meta-analyses emphasize that the same N level can be sufficient for one strain and limiting for another (Maltsev et al 2023). The basic pattern, however, is evident. Enough nitrogen keeps the exponential phase longer, leading to larger biomass and better production of protein and chlorophyll (Truong et al 2024).

- In *Isochrysis galbana*, 72 mg/L yields the highest carbohydrate and lipid productivity, whereas reduced nitrogen levels lower growth, pigment content, and protein levels (Zarrinmehr et al., 2020).
- In *Phaeodactylum tricornutum*, high nitrogen extends the exponential phase and increases biomass productivity by approximately 2.7-fold compared to nitrogen-depleted conditions (Truong et al., 2024).
- In *Chlorella zofingiensis*, nitrogen-rich medium maintains rapid growth and stable chlorophyll levels, whereas nitrogen starvation inhibits both (Zhu et al., 2013).

Nitrogen sufficiency generally promotes microalgal growth by maintaining protein synthesis, chlorophyll production, and cell division. However, the growth response is species-dependent and species' optimal nitrogen requirements; so, increasing nitrogen concentrations do not always lead to higher growth. The nitrogen excess may not increase the biomass output after reaching the appropriate concentration (Maltsev et al., 2023). Growth performance must be assessed using different parameters. Biomass concentration (g L^{-1}) is the quantity of biomass per unit of culture volume, specific growth rate (day^{-1}) is the rate of change of biomass per unit of time, biomass productivity (g L^{-1} day^{-1}) is the biomass produced per unit of volume per unit of time, and biomass composition (% dry cell weight) is the quantity of the cellular components (e.g. protein,

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lipid, carbohydrate) in relation to the total dry weight of the biomass. These metrics need to be reported separately, as they represent various elements of microalgal growth and production.

Nitrogen Limitation

The degree of nitrogen limitation elicits a graded response, ranging from the suppression of N metabolism under mild limitation to damage to the photosynthetic apparatus and a major shift toward lipid accumulation under severe limitation or starvation. Duration also determines the outcome: brief stress often offers the best compromise between biomass and lipid yields, whereas prolonged starvation tends to reduce protein and chlorophyll levels as well as growth rates (Liu et al., 2022).

- Mild limitation allows for the maintenance of biomass: in *Chlorella vulgaris*, dry cell weight (DCW), biomass, pigments, proteins, and lipids remain virtually unchanged until nitrate levels drop below 21.66 mg/L; in *Scenedesmus*, biomass remains relatively stable until nitrate levels fall to approximately 30.87 mg/L or after 3 days of limitation (Liu et al., 2022).
- Severe limitation or starvation reduces photosynthesis, protein, and chlorophyll levels while increasing lipid (TAG) and carbohydrate content.
- The optimal duration is typically short to moderate: 3 days of starvation is most suitable for *C. vulgaris*, 5 days maximizes lipid content in *Scenedesmus obliquus*, and in *Nannochloropsis*, peak lipid accumulation occurs around day 12. These physiological changes are also clearly reflected in the comparison of biomass and lipid levels under varying nitrogen concentrations (Palanisamy et al., 2023).

Nitrogen limitation reduces protein and chlorophyll synthesis, which negatively affects photosynthetic activity and carbon fixation. Consequently, the intracellular C/N ratio increases, promoting the redistribution of available carbon from cell growth toward the synthesis of storage compounds, particularly triacylglycerols (TAGs) and carbohydrates. This metabolic shift represents an adaptive response to nitrogen deficiency (Remmers et al., 2018). The response to nitrogen limitation varies among microalgal species and depends on stress duration. Short-term limitation may stimulate lipid accumulation while maintaining biomass, whereas prolonged starvation can reduce

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cell growth and biomass productivity (Liu et al., 2022). Therefore, nitrogen limitation should be optimized to balance lipid accumulation and biomass production.

Nitrogen Repletion

When nitrogen is resupplied following starvation, microalgae typically recover rapidly: photosynthesis, amino acid, protein, and pigment levels rise again within hours to days, while stored TAGs and carbohydrates are mobilized to support cell division. Therefore, the most effective production strategy often involves two-stage cultivation: a nitrogen-rich first phase to build biomass, followed by a nitrogen-poor second phase to trigger the production of target metabolites (Nayak et al., 2019).

- In *Scenedesmus acuminatus*, following the re-addition of $NaNO_3$ on day 9, Fv/Fm, soluble proteins, amino acids, and pigments recovered within 12 hours, and biomass increased rapidly after a 2-day lag (Zhang et al., 2019).
- In *Vischeria* sp. WL1, cells previously subjected to nitrogen starvation exhibited rapid growth recovery; within 3 days, nitrogen content rose from 0.83% to 2.93%, and the C/N ratio dropped from 76.6 to 20.5 (Rao et al., 2025).
- Two-stage cultivation often improves the productivity trade-off: for *Chlorella* sp. HS2, a regimen of 5 days under nitrogen-replete (N^+) conditions followed by 4 days under nitrogen-deplete (N-) conditions yielded a lipid content of 36.7% and a productivity of 216.9 mg L^{-1} d^{-1} (Nayak et al., 2019)

Resupply of nitrogen stimulates the protein synthesis, chlorophyll creation, photosynthetic activity and cell division, promoting the recovery of nitrogen-starved microalgal cells. In this process, intracellular triacylglycerols (TAGs) and carbohydrates are digested to produce energy and carbon precursors for cellular regeneration and growth. This response was found in *Chromochloris zofingiensis*, where TAG and starch degradation was accompanied by increased chlorophyll, protein and biomass production (Mulders et al., 2015), and in *Nannochloropsis oceanica*, where TAG degradation was associated with cell-cycle reactivation and photosynthetic recovery (Zienkiewicz et al., 2020). Compared with the traditional two-stage cultivation, nitrogen repletion may be more favorable when the purpose is mainly to repair nitrogen-depleted cells and recover biomass productivity, in particular in repeated-batch systems. Conversely, two-stage cultivation is more appropriate when nitrogen limitation is deliberately imposed to induce TAG accumulation following biomass formation. The technique selected should be

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based on the culture target, either biomass recovery or the accumulation of value-added metabolites (Tsai et al., 2018; Zienkiewicz et al., 2020), as nitrogen resupply may decrease the stored lipid reserves through TAG degradation.

Effects of Nitrogen Manipulation on Microalgal Growth

The effects of different nitrogen sources and availability on microalgal growth, biomass production, and biochemical composition are summarized in Table 1. The findings highlight the species-specific responses of microalgae to nitrogen manipulation and demonstrate the importance of selecting appropriate nitrogen sources and concentrations for achieving the desired cultivation outcomes.

Table 1. Effects of Nitrogen Manipulation on Microalgal Growth, Biomass Production and Biochemical Compositions.

Nitrogen Source	Microalgal Species	Culture Condition	Growth Response	Dry Biomass and Biochemical Compositions	Key Findings and Physiological Responses	Reference
Nitrate salts (concentration-dependent; up to 1,440 mg/L)	*Chlorella sorokiniana* AM-02	BBM medium	Specific growth rate reached 1.07 day^{-1}, with increased cell density	Biomass productivity of 0.41–0.50 g/L/day in standard BBM medium	Increasing nitrate availability supported cell growth	Ziganshina et al. (2025)
Nitrate salts (8.82 mM)	*Phaeodactylum tricornutum*	not specified	Cell density reached 1.1 × 10^7 cells/mL,	Dry biomass reached 2.76 g/L, approximately 2.7 times	promoted biomass accumulation and upregulated fucoxanthin-chlorophyll-	Wu et al. (2019)
Nitrate salts (0.075 g/L)	*Porphyridium purpureum*	F/2-based medium	Maximum 0.386 g/L/day at 0.075 g/L $NaNO_3$ and 100 µmol m^{-2}	Biomass yield reached 5.403 g/L, with a productivity of 0.386 g/L/day;	Nitrate limitation stimulated phycoerythrin accumulation,	Wu et al. (2022)
Ammonium	*Chlorella sorokiniana* AM-02	Modified BBM	Specific growth rate reached 1.26 day^{-1}	Cellular protein content remained stable at up to 42% of dry cell weight	Direct ammonium assimilation supported growth and protein	Zhiganshina et al. (2022)
Urea (minimum supply: 18 mg/L/day)	*Chlorella* sp. A2	BG-11 medium	A minimum urea supply of 18 mg/L/day	Neutral lipid productivity increased by 74–416%	Urea supplementation supported lipid accumulation	Ansari et al. (2025)
Urea (12 mg/L)	*Chlorella vulgaris*	not specified	Highest growth was	carotenoid content	Urea supplementatio	Musifa et al. (2026)

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Nitrogen Source	Microalgal Species	Culture Condition	Growth Response	Dry Biomass and Biochemical Compositions	Key Findings and Physiological Responses	Reference
			observed at 12 mg/L urea, with an optical density of 0.537 on day 8	doubled, with β-carotene accounting for 30.91%	n enhanced carotenoid accumulation	
Nitrogen-rich liquid digestate (ammonium-rich; 8.3 g/L as reported)	*Chlorella vulgaris*	laboratory glass-column photobioreactors and outdoor photobioreactor	Up to 0.93 g/L/day; areal productivity 7–10 g/m^2/day in the thin-layer photobioreactor	Dry biomass reached 10–14 g/L, with a productivity of 0.93 g/L/day	Ammonium uptake caused medium acidification, which was controlled through NaOH titration	Pulgarin et al. (2021)

The comparative findings indicate that the effects of nitrogen manipulation are strongly dependent on microalgal species, nitrogen sources, and cultivation conditions. Although nitrate generally supports cell division and biomass production, its effects on biochemical composition may differ among species. For example, nitrate supplementation promoted biomass accumulation in Chlorella sorokiniana and Phaeodactylum tricornutum, whereas nitrate limitation in Porphyridium purpureum was associated with increased phycoerythrin accumulation. Similarly, urea supported neutral lipid productivity in Chlorella sp. A2 and increased carotenoid content in Chlorella vulgaris. These differences suggest that nitrogen availability does not produce a uniform metabolic response across microalgae. Instead, the outcome depends on the species-specific capacity for nitrogen assimilation and carbon allocation. Therefore, nitrogen concentration and source should be optimized according to the target species and desired product rather than applying a single nitrogen manipulation strategy to all microalgae.

CONCLUSION

Control of microalgal growth, biomass output and biochemical composition is significantly impacted by nitrogen modulation. The effects of nitrogen sources and availability are species- and cultivation-condition specific. Generally, nitrogen sufficiency favors cell division, protein synthesis, chlorophyll formation, and biomass accumulationThe two-stage cultivation method, the first phase being nitrogen-sufficient, and the second phase being nitrogen-limited, is a potential technique to compromise

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between the biomass production and the accumulation of high-value metabolites; nonetheless, it should not be taken as a universal solution. Therefore, more research is required to optimize nitrogen contents, transition timing, pH management and total biomass and metabolite productivity, particularly in large scale cultivation conditions.

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