

Review

# A Review on Industrial CO<sub>2</sub> Capture through Microalgae Regulated by Phytohormones and Cultivation Processes

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**Abstract:** Microalgae is a promising metabolism microorganism for the fixation of CO<sub>2</sub> from industrial gas while accumulating microalgae biomass. The process of CO<sub>2</sub> fixation by microalgae is able to be significantly improved by the regulation of phytohormones. However, the complex metabolic mechanism of microalgae regulated by phytohormones and abiotic stress on CO<sub>2</sub> fixation deserves to be explored. To systematically understand the existing status and establish a foundation for promoting the technology, this paper reviews investigations on the metabolic mechanism of microalgae regulated by phytohormones. The influences of nitrogen stress, light intensity stress, heavy metal stress, and salinity stress on CO<sub>2</sub> fixation and lipid production are summarized. In addition, a comprehensive overview of the multistage regulation of phytohormones and abiotic stress on CO<sub>2</sub> fixation and lipid production through microalgae is presented. The recent advances in CO<sub>2</sub> transfer reinforcement and light transmission reinforcement in photobioreactors are discussed. This review provides an insight into the enhancement of CO<sub>2</sub> fixation by microalgae regulated by phytohormones, abiotic stress, and mass transfer in multistage photobioreactors.

**Keywords:** microalgae; CO<sub>2</sub> fixation; phytohormones; abiotic stress; multistage regulation; photobioreactor



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## 1. Introduction

Increasing carbon dioxide (CO<sub>2</sub>) emission induced by the consumption of fossil fuels links to global warming, urging the development of CO<sub>2</sub> capture, utilization, and storage (CCUS) technology [1,2]. Microalgae cultivation is an efficient process to convert light energy and CO<sub>2</sub> into glucose in microalgae cells. According to the mass ratio of carbon stored in microalgae biomass, producing 1 ton of microalgae biomass can capture about 0.5 tons of carbon [3,4]. Therefore, microalgae photosynthesis is a potential CO<sub>2</sub> fixation technology [5]. The accumulation rate of organic matter and the CO<sub>2</sub> fixation rate by microalgae are 10–50 times higher than those of terrestrial plants [6]. In addition, microalgae utilizes glucose and nutrients to produce high-value products (proteins, amino acids, carbohydrates, lipids, sugars, nucleic acids, vitamins, chlorophylls and carotenoids, terpenes, lutein, and astaxanthin) [7,8]. The production of high-value products guarantees the economic feasibility of CO<sub>2</sub> capture by the photosynthesis of microalgae [5,9–11]. Nowadays, commercial microalgae cultivation aims to obtain the high-value added products which are applied in the pharmaceutical and cosmetic industries [12,13]. However, the CO<sub>2</sub> fixation from industrial gas of microalgae has not been commercialized [14] due to the low photosynthetic rate of microalgae.

Microalgae, a kind of unicellular photoautotrophic microorganism living in water, is regarded as a microgranular carbon sink [15]. Microalgae suspension, consisting of a large amount of microalgae suspended in water, acts as a continuous carbon sink [16]. The growth rate of microalgal cells and the environmental conditions (abiotic stress factors) are key factors affecting the CO<sub>2</sub> fixation of microalgae suspensions [17]. Particularly, improper temperature and the CO<sub>2</sub> concentration of industrial gas are not suitable to the growth of

microalgae [18]. It has been reported that the maximum CO<sub>2</sub> fixation rate of microalgae suspensions in photobioreactors is 0.8 g·L<sup>-1</sup>·d<sup>-1</sup> [19]. Restrained by the limited volume of the photobioreactor, the efficiency of CO<sub>2</sub> fixation is requested to be enhanced for capturing CO<sub>2</sub> from industrial gas [20].

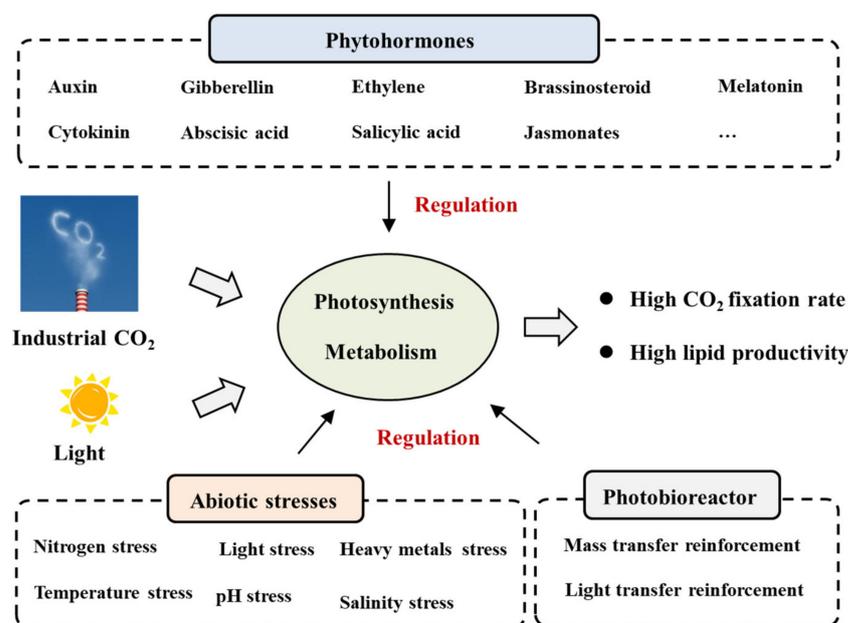
Phytohormones are natural or synthetic chemical modulators that regulate the growth and metabolites of microalgae [21,22]. Several investigations verified that the accumulation of microalgae biomass and the CO<sub>2</sub> fixation rate are significantly promoted 2–3-fold through adding phytohormones with a trace concentration (10<sup>-8</sup>–10<sup>-5</sup> mol/L) [23]. In addition, the limitation of abiotic stresses (light intensity, temperature, pH, and CO<sub>2</sub> concentration) on the growth rate of microalgae can be lowered by phytohormones [17]. Therefore, microalgae cultivation using industrial gas as source is able to be regulated by phytohormones [24]. Particularly, the effect of phytohormones on the growth and carbon sequestration of microalgae is specific to different algae strains [25]. Moreover, the photosynthetic rate of microalgae is also affected by the concentration of phytohormones in the microalgae suspension. For instance, the carbon fixation rate will be reduced when the concentration of phytohormones is higher or lower than the ideal region [26]. In addition to the application of single phytohormones, the coupling of abiotic stresses and phytohormones can also be used to promote the CO<sub>2</sub> fixation of microalgae and the accumulation of organics in microalgae cells [27]. Therefore, it is crucial to propose an optimal method for the industrial CO<sub>2</sub> capture during microalgae cultivation, combining the regulation of environmental factors and the addition of phytohormones.

Based on the growth period, the culture of microalgae can be mainly divided into multiple stages [20]. The regulation of phytohormones and abiotic stresses based on the growth stage of microalgae can promote CO<sub>2</sub> capture and lipid accumulation [28]. During the lag phase of microalgae growth, a low concentration of nutrients and low light intensity can significantly shorten the duration of cell growth [29]. In the exponential growth phase, appropriately enhanced light intensity can increase the rate of growth and the CO<sub>2</sub> fixation of microalgae [30]. Meanwhile, the phytohormones, which can enhance microalgae cell division, should be added in the microalgae suspension [31]. In the stable growth period, using different phytohormones can maintain algal cell growth and promote metabolite synthesis [27,32–34]. However, the synergistic effects of phytohormones and abiotic stresses on the CO<sub>2</sub> fixation and the organic accumulation of microalgae cells are unclear.

Photobioreactors are a place for the photosynthesis of microalgae suspensions, accompanied by the CO<sub>2</sub> fixation, microalgae cell multiplication, and oil accumulation in microalgae cells [28,35]. In photobioreactors, CO<sub>2</sub>, light, a suitable temperature, nutrient substances, and phytohormones are provided in the cultivation of microalgae [36]. The CO<sub>2</sub> fixation rate of microalgae suspensions is affected by the culture conditions, such as the light intensity, concentration of nutrients and phytohormones, and temperature [24]. However, the nonuniform distribution of light intensity and nutrients affects the photosynthetic carbon fixation capacity of microalgae suspensions [37]. In particular, the distribution of phytohormones plays an important role in the photosynthetic carbon fixation of microalgae [29]. It is necessary to optimize the distribution of CO<sub>2</sub> bubbles and reduce the bubble size in photobioreactors so as to promote the gas–liquid mass transfer coefficient of CO<sub>2</sub> [20]. In addition, the CO<sub>2</sub> fixation rate of microalgae suspensions is also affected by the mode of the photobioreactor. Compared to batch photobioreactors, semicontinuous or continuous photobioreactors are more convenient for adjusting the supply mode of phytohormones and environmental conditions based on the cultivation stage of the microalgae [38,39]. Therefore, the operation and the structure of the photobioreactor facilitate the CO<sub>2</sub> fixation and the production of organics of the microalgae suspension with the help of phytohormones.

In this review, recent advances in the synergistic effects of phytohormones and abiotic stresses on the CO<sub>2</sub> fixation and the organic accumulation of microalgae cells in photobioreactors are provided (Figure 1). The effects of abiotic stresses (CO<sub>2</sub> concentration, light intensity, temperature, and nutrient concentration) on the photosynthesis and metabolite

accumulation in microalgae are discussed. On the basis of the growth stage of microalgae, the multistage method of microalgae cultivation is summarized, aimed at promoting the CO<sub>2</sub> fixation rate with the regulation of various phytohormones. Moreover, the operation and the structure of photobioreactors for microalgae cultivation for CO<sub>2</sub> fixation in industrial applications are evaluated. This review provides an opinion on industrial CO<sub>2</sub> fixation through microalgae regulated by phytohormones and culture processes in photobioreactors.



**Figure 1.** Regulation of CO<sub>2</sub> fixation of microalgae in a photobioreactor by phytohormones and abiotic stresses.

## 2. The Metabolic Mechanism of Microalgae Regulated by Phytohormones

Phytohormones are a kind of small molecule, acting as chemical messengers to regulate cell division, growth, and tissue differentiation of the higher plant [21]. As the physiological properties of microalgae are similar to those of the higher plant, phytohormones are also useful to the cell division and metabolism of microalgae [21,40]. In addition, phytohormones are able to avoid the inhibiting effect of abiotic stresses on the growth of microalgae cells, maintaining the CO<sub>2</sub> fixation rate [7,31]. In microalgae suspensions, phytohormones with micro-concentrations can effectively promote the growth, division, and oil accumulation of microalgae cells [41]. Auxin, cytokinin (CK), abscisic acid (ABA), gibberellin (GA), ethylene (ET), and salicylic acid (SA) are common phytohormones for the regulation of the growth of microalgae [42,43]. These phytohormones play different roles in the growth and accumulation of organics.

### 2.1. The Species of Phytohormones

Auxin is a kind of phytohormone that was discovered first [44]. Auxin can regulate the growth and division of microalgae cells [45]. Its main phytohormones include indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), indole-3-acetamide (IAM), indole-3-propionic acid (IPA), and indole-3-naphthylacetic acid (NAA) [46]. Among them, indole-3-acetic acid (IAA) has the most abundant concentration and the broadest distribution in plants [47]. During the photosynthesis of microalgae, the carbon fixation of microalgae is dependent on ribulose-1, 5-diphosphoate carboxylase [48]. The activity of ribulose-1, 5-diphosphoate carboxylase can be efficiently promoted by IAA [49]. In addition, the activity of acetyl-co A carboxylase can be enhanced by IAA, increasing the synthesis of lipids in microalgae cells. Therefore, providing a suitable concentration of IAA is beneficial for the carbon fixation of microalgae photosynthesis.

Cytokinin (CK) is a derivative of adenine, consisting of zeatin, kinetin, and 6-BA [50]. The division and growth of microalgae cells can be regulated by CK to accelerate the growth of plants [51]. CK also enhances the accumulation of photosynthetic pigments, promoting photosynthetic efficiency and biomass production [52]. Particularly, CK is able to regulate the disease resistance of plants [53]. Moreover, CK protects the photosynthesis and metabolism of plants under environmental stresses [54].

Gibberellin (GA) plays an important role in seed germination, cell growth, cell division, photomorphosis, blossoms, and environmental responses [46]. Not only accelerating cell growth and cell division, GA also promotes the synthesis of proteins and lipids [33,55]. According to the position and number of double bonds and hydroxide radicals of molecular structures, GA is divided as GA<sub>1</sub>, GA<sub>2</sub>, GA<sub>3</sub>, GA<sub>4</sub>, GA<sub>5</sub>, GA<sub>6</sub>, and GA<sub>7</sub> [56].

Abscisic acid (ABA) is a sesquiterpenoid existing in higher plants [57]. ABA is mainly used to release the environmental stresses on the growth and metabolism of higher plants [58]. The drought resistance, cold resistance, disease resistance, and salt tolerance of higher plants can be improved by the addition of ABA [44,59,60].

Ethylene (ET) is a phytohormone in the gaseous state [61]. Ethylene can regulate the growth and metabolism of plants while keeping plants alive under biotic stresses or abiotic stresses [62]. The effects of ethylene on cell growth and organic synthesis are dependent on the concentration of ET [63].

In addition to the five typical phytohormones discussed above, several other phytohormones can also improve the capacity of photosynthetic carbon fixation and the organic synthesis of microalgae, such as salicylic acid (SA), brassinosteroid (BRs), jasmonates (JAs), and melatonin (MT) [64,65]. SA is involved in the regulation of seed germination, cell growth, photosynthesis, and nitrogen fixation [66]. Meanwhile, SA induces the adaptability of plants to several abiotic stresses, such as low temperatures, salinity, heavy metals, and dryness, protecting carbon fixation and biofuel synthesis. Brassica sterols (BRs) can improve the antioxidant ability of cells, accelerating the synthesis of proteins, nucleic acids, sugars, and photosynthetic pigments [64,65]. In addition, BRs can also resist abiotic stresses and enhance cell division. Jasmonates (JAs) consist of jasmonic acid (JA) and methyl jasmonate (MJ). JAs are able to promote the synthesis of cyanin and  $\beta$ -carotene [31]. Melatonin (MT) is a natural antioxidant that can promote the photosynthesis and organic synthesis of microalgae under several abiotic stresses [33], such as high light and nitrogen deficiency.

## 2.2. Regulation of Phytohormones on Microalgae Growth

Most phytohormones participate in the physiological processes of microalgal cells, such as resisting oxidative stress and promoting cell growth, cell division, and organic synthesis [67]. Particularly, the effect of one phytohormone on the growth and carbon sequestration of microalgae is dependent on the algal strain. Moreover, the optimal concentration of phytohormones is different for various algal strains during the cultivation process. Table 1 summarizes the biomass production and biocrude production of microalgae cultivation regulated by various phytohormones with different concentrations. The cell density, dry weight, and lipid accumulation are the maximum values observed for microalgae cultures. The CO<sub>2</sub> fixation mass of microalgae ( $\Delta m_{CO_2}$ ) can be calculated by the accumulation of microalgae biomass [68]:

$$\Delta m_{CO_2} = C\% \Delta m_{algae} M_{CO_2} / M_C \quad (1)$$

where C% is the carbon content of the microalgae which is set as 50% [3,4],  $\Delta m_{algae}$  is the accumulate mass of the microalgae biomass (g), and  $M_{CO_2}$  and  $M_C$  are the relative molecular weights of carbon dioxide and carbon.

The effects of phytohormones on microalgae cultivation are dependent on the algal strain [7]. Microalgae suspensions with different algal strains have different biomass productions and lipid productions [22]. Therefore, it is necessary to summarize the specific effects of phytohormones on the biomass production and lipid production of algal strains. Jiang et al. [69] revealed that diethyl aminoethyl hexanoate (DAH) with a concentration

of  $10^{-7}$  mol·L<sup>-1</sup> could obviously promote the biomass productivity and lipid productivity of *Chlorella*, with a maximum lipid yield of 32.5% and 30.3%, respectively. Piotrowska-Niczyporuk and Bajguz [70] indicated that IAA with a concentration of 1 ppm led to the best growth of *Chlorella vulgaris* ( $649.9 \times 10^6$  cells·L<sup>-1</sup>). Meanwhile, GA3 with a concentration of 1 ppm led to the best growth of *Chlorella vulgaris* ( $592.2 \times 10^6$  cells·L<sup>-1</sup>). Trinh et al. [71] reported the effects of IAA and zeatin on the growth of *Nannochloropsis oculata* with a culture period of 35 d. It can be observed that the maximum biomass yield was  $21.0 \times 10^6$  cells/mL regulated by IAA at a concentration of 0.5 ppm. However, the maximum biomass yield was  $22.9 \times 10^6$  cells/mL regulated by zeatin at a concentration of 0.75 ppm. Salama et al. [25] observed that the maximum cell concentration of *scenedesmus obliquus* ( $38.12 \times 10^6$  cells·mL<sup>-1</sup>) was obtained at an IAA concentration and DAH concentration of  $10^{-8}$  mol·L<sup>-1</sup>, while the maximum cell concentration of *Chlorella vulgaris* ( $4.09 \times 10^6$  cells·mL<sup>-1</sup>) was obtained at an IAA concentration and DAH concentration of  $10^{-5}$  mol·L<sup>-1</sup>.

In microalgae cultivation, phytohormones with micro-concentrations efficiently promote the carbon fixation, cell growth, and lipid production of microalgae. Generally, the concentration of phytohormones in microalgae suspensions is in the range of  $10^{-8}$ – $10^{-5}$  mol·L<sup>-1</sup>. Salama et al. [26] found that IAA and diethyl aminoethyl hexanoate (DAH) with a concentration of  $10^{-5}$  mol·L<sup>-1</sup> could obviously promote the growth of *Scenedesmus obliquus*. The biomass yield of *Scenedesmus obliquus* increased by 1.9 and 2.5 times that of the culture solution without IAA and DAH. Trinh et al. [71] regulated the growth of *Nannochloropsis oculata* through providing GA3. The best microalgae cell concentration was  $19.3 \times 10^6$  cells·mL<sup>-1</sup> at a GA3 concentration of 0.25 ppm. Similarly, González-Garcinuño et al. [67] indicated that the maximum CO<sub>2</sub> fixation rate appeared at a GA3 concentration of 60 ppm, with a corresponding microalgae cell concentration and lipid yield of  $82.9.2 \times 10^6$  cells·mL<sup>-1</sup> and 33.1 mg·L<sup>-1</sup>, respectively.

However, when the concentration of phytohormones is higher than a certain value, the carbon fixation and lipid production of microalgae are limited by the phytohormones in suspension. In the cultivation of *Nannochloropsis oceanica*, Udayan and Arumugam et al. [72] found that the microalgae cell concentration increased from  $215.5 \times 10^6$  to  $579.5 \times 10^6$  cells·mL<sup>-1</sup> with an increasing concentration of IAA from 0 to 10 ppm and then decreased from  $579.5 \times 10^6$  to  $520.1 \times 10^6$  cells·mL<sup>-1</sup> with an increasing concentration of IAA from 10 to 50 ppm. Pan et al. [73] found that lipid production ( $880.1$  mg·L<sup>-1</sup>) regulated by ABA with a concentration of 10 ppm was 1.97 times higher than the control group without ABA. However, the accumulation of lipids of the microalgae was limited by ABA when the concentration was 20 ppm, with a lipid production of  $330.5$  mg·L<sup>-1</sup>.

**Table 1.** Effect of phytohormones on the growth and lipid accumulation of microalgae.

Phytohormone	Specific Phytohormone	Species	Concentration of Phytohormone (ppm)	Cell Density (10 <sup>6</sup> Cells/mL)	Dry Weight (mg/L)	Lipid Accumulation (mg/L)	References			
Auxins	IAA	<i>Nannochloropsis oceanica</i>	0	215.5	392.6	120.6	[72]			
			10	579.5	544.1	241.2				
			20	576.5	536.8	291.2				
			30	574.8	526.5	310.3				
			40	536.6	522.0	320.6				
			50	520.1	457.3	273.5				
	IAA	<i>Chlorella vulgaris</i>	0	430.4			[70]			
			1	649.9	/	/				
			0.1	466.9						
			0.01	481.3						
			IAA	<i>Nannochloropsis oculata</i>	0	9.8				[71]
					0.1	13.9				
0.25	15.3	/			/					
0.5	21									
0.75	11.8									
1	11.9									

Table 1. Cont.

Phytohormone	Specific Phytohormone	Species	Concentration of Phytohormone (ppm)	Cell Density (10 <sup>6</sup> Cells/mL)	Dry Weight (mg/L)	Lipid Accumulation (mg/L)	References
ABA	ABA	<i>Chlorella</i> sp.	0			447.1	[74]
			0.5			690.2	
			1	/	/	601.3	
			10			880.1	
			20			330.5	
	ABA	<i>Chlorella saccharophila</i>	0	11.8	157.2	80	[75]
			1	14.1	154.8	82	
			4	14.3	162	87.2	
			10	14.8	150.4	85.6	
			20	14.9	160	91.6	
CKs	Kinetin	<i>Chlorella vulgaris</i>	0	430.4			[70]
			1	667.0			
			0.1	608.9	/	/	
			0.01	601.9			
	Kinetin	<i>Chlorella protothecoides</i>	0			506	[76]
			0.5			543	
			1	/	/	592.7	
			1.5			520	
			2			582.3	
	Zeatin	<i>Nannochloropsis oculata</i>	0	9.8			[71]
			0.1	21			
			0.25	21.1	/	/	
			0.5	21.8			
			0.75	22.9			
GAs	GA <sub>3</sub>	<i>Chlorella vulgaris</i>	0	430.4			[70]
			1	592.2			
			0.1	454.2	/	/	
			0.01	464.7			
	GA <sub>3</sub>	<i>Chlorella protothecoides</i>	0			50.7	[76]
			2.5			50.9	
			5	/	/	48.0	
			10			38.9	
			15			31.9	
	GA <sub>3</sub>	<i>Nannochloropsis oculata</i>	0	9.8			[71]
			0.1	16.7			
			0.25	19.3	/	/	
			0.5	10.7			
			0.75	10.3			
GA <sub>3</sub>	<i>Chlorella ellipsoidea</i>	0	8.5	40.1	9.4	[67]	
		20	18.8	185.0	32		
		40	39.6	193.1	31.1		
		60	82.9	216.2	33.1		
		80	30.3	124.2	24.1		
		120	8.4	48.0	7.2		
GA <sub>3</sub>	<i>Microcystis aeruginosa</i>	0	56.5	0.66		[73]	
		0.001	71.7	0.72			
		0.1	91.5	0.77	/		
		10	101.6	0.98			
		25	111.7	0.98			
Ethylene	Ethephon	<i>Chlorella vulgaris</i>	0		2748.1		[63]
			50	/	2800	/	
			200		2886.42		

### 3. Regulation of Phytohormones on Microalgae under Abiotic Stresses

The growth and carbon fixation of microalgae require suitable environmental conditions, such as light intensity, CO<sub>2</sub> supply, temperature, pH, and nutrients [20]. However,

as large-scale microalgae cultivation is located outdoors, some environmental conditions (light intensity, temperature) rely on the climate [30,77]. When the light intensity and temperature are too high or too low in microalgae cultivation, the carbon fixation rate of the microalgae suspension will be affected [78]. In addition, the concentration of CO<sub>2</sub> (5–15%) in industrial gas is more than 100 times higher than that of the atmosphere. A small amount of SO<sub>x</sub> (0.01–1%) and NO<sub>x</sub> (~1%) also exists in industrial gas [79,80]. Therefore, the pH of the nutrient solution for microalgae cultivation will be reduced during the accommodation of industrial gas, affecting the carbon fixation rate of the microalgae [81]. Moreover, some abiotic stresses are introduced in the cultivation of microalgae to promote the accumulation of lipids, such as high light intensity, nitrogen stress, high temperature, high salt concentration, heavy metal stress, and antioxidant stress [7,31]. In this regard, providing phytohormones is a promising regulation for maintaining the carbon fixation rate during the growth period and the lipid accumulation period, as shown in Table 2.

**Table 2.** Effect of phytohormones on the metabolites of microalgae under abiotic stresses.

Abiotic Stress	Phytohormones	Species	Products	Effects	Refs.	
ND (nitrogen deprived)	ABA	<i>S. quadricauda</i>		“+”, “=”	[82]	
	NAA and IBA	<i>Scenedesmus</i> SDEC-8		“+”, “+”	[83]	
		<i>C. sorokiniana</i> SDEC-18		“+”, “+”		
	IAA DAH	<i>C. sorokiniana</i>		Biomass, lipid	“+”, “+”	[49]
					“+”, “+”	
“+”, “+”						
Z and IAA and GA	<i>Acutodesmus obliquus</i>			“+”, “+”	[84]	
				“+”, “+”		
HL intensity	MT	<i>Monoraphidium</i> sp.	Biomass, lipid	“=”, “+”	[32]	
	DAH	<i>H. pluvialis</i>		“−”, “=”	[86]	
Heavy metals	Z	<i>Chlorella vulgaris</i>	Number of cells, carotenoid	“+”, “+”	[87]	
	K			“+”, “+”		
	IAA			“+”, “+”		
	GA			“+”, “+”		
Salt stress	2-4-D	<i>D. tertiolecta</i>	Lipid	“+”, “+”	[34]	
				“+”, “+”	[45]	

+, increased; =, sustained; −, decreased.

### 3.1. Effect of Phytohormones on Microalgae under Nitrogen Stress

Although nitrogen stress accelerates the lipid accumulation of microalgae biomass, it limits the biomass productivity and the carbon fixation rate [88]. Therefore, it is necessary to regulate the rate of the microalgae biomass production by phytohormones under nitrogen stress conditions. Babu et al. [49] adjusted the concentration of NH<sub>3</sub>NO<sub>3</sub> in the culture medium (BG11) to investigate the effects of nitrogen stress on the productivity of biomass and lipids for *C. Sorokiniana*. In the range of nitrogen stress from 12.5% to 100%, IAA (10<sup>−5</sup> M) and DAH (10<sup>−9</sup> M) were used to accelerate biomass production [49]. When the concentration of NH<sub>3</sub>Cl in the culture medium was 50% of the BG11, the biomass productivity (201 mg·L<sup>−1</sup>·d<sup>−1</sup>) and lipid productivity (69 mg·L<sup>−1</sup>·d<sup>−1</sup>) regulated by IAA were 22% and 49% higher than that of the cultivation without IAA, respectively. In addition, the biomass productivity (236 mg·L<sup>−1</sup>·d<sup>−1</sup>) and lipid productivity (86 mg·L<sup>−1</sup>·d<sup>−1</sup>) regulated by DAH were 43% and 84% higher than that of the cultivation without DAH, respectively. Sulochana and Arumugam [82] explored that ABA with a concentration of 2 μM prevented the rapid reduction in microalgae biomass under nitrogen stress. The concentration of microalgae biomass regulated by ABA under nitrogen stress was 38 × 10<sup>6</sup> cell·mL<sup>−1</sup>, 1.4 times higher than that without ABA. Yu et al. [83] revealed that the combination of IBA and NAA was able to reduce nitrogen stress on the cultivation of *Scenedesmus* SDEC-8 and *Chlorella*

*sorokiniana* SDEC-18. The production rates of lipids for the SDEC-8 and SDEC-18 were 26.7 and 25.9 mg·L<sup>-1</sup>·d<sup>-1</sup>, respectively. The results revealed that the damage of microalgae cells caused by nitrogen depletion could be reduced by phytohormones. Renuka et al. [84] demonstrated that the biomass productivity of *Acutodesmus obliquus* regulated by kinetin (1 mg/L) and zeatin (0.1 mg/L) was promoted by 50% and 60.7% under nitrogen stress, respectively. In addition, the lipid production of *Acutodesmus obliquus* regulated by kinetin (1 mg/L) and zeatin (0.1 mg/L) was promoted by 64.95% and 63.06%, respectively. Renuka et al. [85] proposed the optimal cultivation of *Acutodesmus obliquus* under nitrogen stress regulated by the phytohormone mix of zeatin (0.5 mg L<sup>-1</sup>), IAA (1.0 mg L<sup>-1</sup>), and GA (5.0 mg L<sup>-1</sup>). The results revealed that the biomass yield and lipid yield were promoted by 49.07% and 77.20%, respectively. In this situation, zeatin was found as the most influential phytohormone on the acceleration of the biomass yield of *Acutodesmus obliquus* under nitrogen stress.

### 3.2. Effect of Phytohormones on Microalgae under Other Stresses

The growth rate and CO<sub>2</sub> fixation rate of microalgae are limited in environments with a high light intensity. However, some specific phytohormones can reduce the limitation of the CO<sub>2</sub> fixation and biomass production of microalgae under light stress. Li et al. [32] investigated the effect of melatonin on the accumulation of lipids, carbohydrates, and proteins in *Monoraphidium* sp. QLY-1. The maximum lipid yield (49.6%) increased by 1.32 times when regulated by melatonin under high light stress (30 μmol·m<sup>-2</sup>·s<sup>-1</sup>). Meanwhile, the protein content decreased from 57.21% to 47.96%, while the carbohydrate content decreased from 53.4% to 37.71%. The physiological analysis revealed that the enzyme activity for accelerating lipid accumulation was induced by the combination of high light intensity and melatonin. Ding et al. [86] proposed the strategy of combining DAH with high light (150 μmol photons·m<sup>-2</sup>·s<sup>-1</sup>) to realize the high and efficient accumulation of astaxanthin. When the concentration of DAH was 0.1 mM, the astaxanthin content (30.95 mg·g<sup>-1</sup>) was 2.01-fold higher than that of the control one (15.43 mg·g<sup>-1</sup>).

Heavy metals inhibit the growth, organic accumulation, and enzymatic and nonenzymatic antioxidant function of microalgae. However, the negative effects of heavy metals on the growth and lipid accumulation of microalgae could be reduced by phytohormones. Piotrowska-Niczyporuk et al. [87] indicated that auxin, cytokinin, gibberellin, jasmonic acid, and polyamine—arginine could maintain the growth and metabolites of microalgae. The results show that phytohormones were able to inhibit the absorption of heavy metals by the microalgae, releasing the heavy metal stress. In addition, phytohormones have antioxidant activity to protect the cells against reactive oxygen species under heavy metal stress. Tiwari et al. [34] indicated that kinetin obviously reduces the effects of toxicity induced by chromium on the growth of *N. muscorum*. In this situation, the accumulation of chromium in the microalgae cells was reduced, significantly improving the photochemistry of the photosynthetic pigments.

Salinity stress can promote the accumulation of lipids and reduce the biomass productivity of microalgae. Arroussi et al. [45] found that the lipid productivity of *D. tertiolecta* under salinity stress (2 M NaCl) increased by 50% more than that without salinity stress. On this basis, the combination of 2,4-D and NaCl with a concentration of 2 M promoted the lipid yield of *D. tertiolecta* to 69.6%.

## 4. Multistage Regulation of Phytohormones on CO<sub>2</sub> Fixation through Microalgae

During the cultivation process, the metabolism of microalgae is dependent on the stages of cultivation which are mainly divided into the stage of carbon fixation in photosynthesis and the stage of lipid accumulation [20,89,90]. It is necessary to provide a suitable light intensity and CO<sub>2</sub> and nutrient substances for each cultivation stage of the microalgae.

Multistage cultivation is beneficial to promote the carbon fixation and growth rate of microalgae suspensions. Zhou et al. [89] cultivated *Chlorella* sp. NJ-18 in a 70 L photobioreactor for 20 days using a semi-continuous cultivation method. As the concentration

of the microalgae suspension was higher than  $1 \text{ g}\cdot\text{L}^{-1}$ , 30 L, the microalgae suspension was replaced by fresh nutrient medium. In this situation, the light shading induced by the microalgae suspension with a high concentration was reduced, leading to the growth rate of the microalgae being kept at  $0.09 \text{ g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ . Russo et al. [90] carried out a semi-continuous culture of *C. vulgaris*. Microalgae suspensions were extracted in a volume ratio of 30% every day, and the same volume of culture medium was replaced to maintain a growth rate of  $0.34 \text{ g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$  for 7 days.

In addition, multistage cultivation is beneficial to promoting the lipid productivity of microalgae suspensions. Pedro et al. [91] carried out microalgae cultivation with two stages: the first stage was with abundant nitrogen and then with scarce nitrogen, promoting the carbon fixation rate and the accumulation rate of lipids. Mujtaba et al. [92] confirmed that the lipid yield of microalgae could be promoted by multistage cultivation. During an experiment, abundant nutrients were provided to cultivate the microalgae, and nitrogen stress conditions were controlled. The lipid accumulation of *Chlorella* was  $71.1 \text{ mg}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$  under the two-stage cultivation, significantly higher than that under the single-stage ( $31.5 \text{ mg}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ ). Ratha et al. [93] cultivated microalgae using nitrogen-rich medium in the first 24 days and then using nitrogen-poor medium in the last 8 days. The results revealed that the lipid yield of the two-stage mode was 40–50% higher than that of the one-stage mode. Yang et al. [94] investigated the biomass yield and lipid yield at different concentrations of NaCl (0, 20, 40, and 60 g/L) in the logarithmic phase of microalgae. The lipid yield of microalgae under salt stress (20 g/L) was 10% higher than that without salt stress. Arroussi et al. [45] regulated the cell division and growth of *D. tertiolecta* at the first stage. Then, NaCl was added into the microalgae suspension to create a salt stress condition at the late logarithmic growth stage. The results revealed that the accumulation of microalgae biomass increased by 40% in the first stage, and the salt stress at the second stage increased the accumulation of lipids from 24% to 70%.

In general, the establishment of a multistage cultivation system of microalgae is beneficial for meeting the requirements of microalgae for  $\text{CO}_2$  fixation and lipid accumulation. However, literature on the regulation of microalgae cultivation with multiple stages by phytohormones is lacking. Therefore, it is urgent to propose regulating strategies of phytohormones for microalgae cultivation with multiple stages.

## 5. Photobioreactors for $\text{CO}_2$ Fixation through Microalgae

### 5.1. $\text{CO}_2$ Transfer Reinforcement in Photobioreactors

The  $\text{CO}_2$  transfer from bubbles to microalgae suspensions in photobioreactors plays an important role in the photosynthetic carbon fixation of microalgae [20,36]. The  $\text{CO}_2$  transfer performance in photobioreactors is largely dependent on the  $\text{CO}_2$  bubble size, retention time of  $\text{CO}_2$  bubbles, and flow field. Recently, several researchers optimized the structure of photobioreactors to optimize the flow field, promoting the mass transfer of  $\text{CO}_2$ . Rahman et al. [95] proposed a rectangular bubble column photobioreactor with horizontal baffles. The baffles placed in staggered layers reduced the bubble size and velocity of the  $\text{CO}_2$  bubbles while homogenizing the distribution of the  $\text{CO}_2$  bubbles. The results show that the *Synechococcus* HS-9 growth was 2.17 times higher in the photobioreactor with the baffles than in the photobioreactor without the baffles. Xia et al. [96] designed a flat-plate photobioreactor with perforated inverted arc trough (PIAT) internals for enhancing the  $\text{CO}_2$  fixation from industrial gas in the microalgae suspension. The PIAT internals promoted the  $\text{CO}_2$  gas–liquid contact time and generated periodic aeration in the microalgae suspension. When 15%  $\text{CO}_2$  ( $v/v$ ) was aerated at a rate of  $15 \text{ mL}\cdot\text{min}^{-1}$ , the dissolved  $\text{CO}_2$  concentration and the  $\text{CO}_2$  fixation rate in the microalgae suspension were improved by 26.0% and 26.2% ( $36.6 \text{ mg}\cdot\text{L}^{-1}\cdot\text{h}^{-1}$ ) in the photobioreactor with PIAT internals, respectively. Yaqoubnejad et al. [97] developed a novel hexagonal airlift flat-plate (HAFF) photobioreactor for the improvement of microalgae growth that simultaneously enhanced  $\text{CO}_2$  biofixation. Compared to traditional flat-plate (TFP) photobioreactor, microalgae cultivated in the HAFF photobioreactor showed a drastic improvement in growth

and CO<sub>2</sub> biofixation. For instance, the maximum CO<sub>2</sub> biofixation was 0.85 g·L<sup>-1</sup>·d<sup>-1</sup> in the HAFP photobioreactor which was 70% higher than that in the TFP photobioreactor. To enhance CO<sub>2</sub> transfer and microalgal biomass yield, Cui et al. [19] proposed a tangent double-tube photobioreactor (TDTP) and a concentric double-tube photobioreactor (CDTP) on the basis of the traditional tube photobioreactor (TTP). A 10-day cultivation experiment showed that the maximum CO<sub>2</sub> fixation rate of microalgae in TDTP was 0.8 g·L<sup>-1</sup>·d<sup>-1</sup>, which was 33.3% and 293% more than that in CDTP and TTP. Meanwhile, the microalgal biomass yield in TDTP (2.81 g/L) was 51.2% and 124.8% more than that in CDTP and TTP.

CO<sub>2</sub> bubble generators influence the initial bubble size and the dispersity of CO<sub>2</sub> bubble clusters which are regarded as key components affecting the mass transfer of CO<sub>2</sub> in photobioreactors. Cheng et al. [98] developed a three-stage shear-serrated aerator (TSA) which is able to break CO<sub>2</sub> bubbles. TSAs were installed in the raceway reactor, resulting in an increased mass transfer coefficient (by 25.5%) and microalgal biomass yield (46.8%). Wu et al. [99] proposed a microbubble-driven photobioreactor to optimize the growth of *Haematococcus pluvialis* and CO<sub>2</sub> biofixation through minimizing the CO<sub>2</sub> bubble size. The results show that the algal biomass yield increased by five times.

### 5.2. Light Transfer Reinforcement in Photo-Bioreactor

Light intensity is recognized as an important parameter during microalgae cultivation for CO<sub>2</sub> fixation, biomass yield, and lipid productivity in photobioreactors [30]. It is necessary to provide a sufficient light intensity for microalgae cultivation. However, the microalgae cells suspended in the microalgal suspension carry out light absorption and light scattering. In this situation, the light intensity appears as an exponential attenuation along with the light path within the microalgae cultivation, causing a nonuniform distribution of light intensity in the microalgae suspension which obeys the Lambert–Beer law [100]:

$$I = I_0 \cdot \exp[-(k_b C_b + k_w)l] \quad (2)$$

where  $I$  is the located light intensity,  $I_0$  is the incident light intensity of the photobioreactor,  $k_b$  is the optical attenuation coefficient induced by the microalgae cells,  $k_w$  is the optical attenuation coefficient induced by the culture medium [101],  $C_b$  is the concentration of microalgae cells, and  $l$  is the length away from the incident light point.

The nonuniform distribution of light intensity is not beneficial to microalgae cultivation. In this regard, several light transfer reinforcements are carried out in photobioreactors. Sun et al. [102] inserted a light guide plate (LGP) with light scattering nanoparticles into a flat-plate photobioreactor. The light distribution coefficient (1.95 kg·m<sup>-3</sup>) was increased by 7.22 times more than that in the flat-plate photobioreactor without LGP, while the concentration of microalgae cells (3.05 g·L<sup>-1</sup>) was 220% higher than that in the flat-plate photobioreactor without LGP. On this basis, Sun et al. [30] proposed light feeding strategies based on the growth phase of microalgae in the flat-plate photobioreactor with LGP. A low light intensity (0–1 d), medium light intensity (1–4 d), and high light intensity (4–6 d) were supplied based on the growth rate and lipid content of *Chlorella vulgaris* FACHB-31. The maximum biomass concentration and lipid productivity were 5.32 g·L<sup>-1</sup> and 312.92 mg·L<sup>-1</sup>·d<sup>-1</sup>. In addition, LGP was introduced into a lab-scale open-raceway pond for the cultivation of *Nannochloropsis oculata* [103]. The biomass yield (2.31 g·L<sup>-1</sup>) and lipid yield (1258.65 mg·L<sup>-1</sup>) increased by 193.33% and 443.71% compared with that in the open raceway pond without LGP.

The light/dark cycle is another key factor affecting the growth of microalgae. Liao et al. [104] proposed a tubular photobioreactor with periodic light and dark regions along the flow direction of the microalgae suspensions. The CO<sub>2</sub> fixation rate and growth rate could increase by 22%. Ye et al. [105] optimized light/dark cycle 900 L tangential spiral-flow column photobioreactors (TSCP) to promote the CO<sub>2</sub> fixation of *Arthrospira* sp. cells. The light distribution and light/dark cycle of the microalgae cells were calculated by a solar irradiation model. The biomass yield (1.705 g/L) and CO<sub>2</sub> fixation rate (0.655 g/L/d) were 45% and 59% more than in ordinary column photobioreactors. Chen and Su [106]

revealed that the maximum CO<sub>2</sub> fixation rate of *Haematococcus lacustris* was obtained at an L/D of 1:5 with a light intensity of 50, 110, and 220  $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Under high light intensities, Liu et al. [107] indicated that 2/2 h light/dark cycle treatment led to the highest specific growth rate of *Haematococcus lacustris* at a light intensity of 18  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ .

### 5.3. Prediction and Optimization through the CFD Model

Based on the mass transfer of CO<sub>2</sub> bubbles, light transmission, and the light/dark cycle in photobioreactors, several computational fluid dynamic (CFD) models were constructed to predict and optimize the CO<sub>2</sub> fixation rate, growth rate, and lipid productivity of photobioreactors [108–115].

Raceway ponds are a typical photobioreactor for microalgal biomass production and CO<sub>2</sub> fixation on a large scale [116]. Recently, several CFD models have been established to simulate the flow field, light/dark cycle, and light distribution of microalgae suspensions in raceway ponds, providing guidance for the optimization of CO<sub>2</sub> fixation efficiency. Zhang et al. [108] designed an airfoil baffle and guide plate for raceway ponds. According to the results of CFD simulations, the volume of microalgae suspensions with a low velocity decreased by 60%, while the growth rate of microalgae biomass increased by 30%. Cheng et al. proposed a raceway pond with upward guide plates and downward guide plates. The plates induce the vortex flow [109] of the microalgae suspension in raceway ponds, promoting liquid mixing and gas–liquid mass transfer velocity. Chen et al. [110] installed spiral spoilers in the bottom of the raceway pond. The mixing time was reduced by 41%, and the gas–liquid mass transfer coefficient increased by 38%. Guo et al. [111] established a CFD model combined with a DO radiation model to simulate the flow field and microalgae biomass yield of a raceway pond with disturbed flow cones. The CO<sub>2</sub> fixation rate of the microalgae suspension increased by 40% in the novel raceway pond compared with that of traditional raceway ponds.

Enclosed photobioreactors are used for microalgae cultivation with efficient CO<sub>2</sub> fixation and high-value added biomass production. They mainly consist of flat-plate photobioreactors, air-lift reactors, column reactors, and horizontal tube reactors [112]. For instance, Ye et al. [113] proposed a CFD model and a miniature Doppler velocimeter (MDV) to simulate the spiral flow pattern, mixing time, mass transfer coefficient, and bubble diameter. The maximum CO<sub>2</sub> fixation rate in TSCP ( $1.12\text{ g}\cdot\text{L}^{-1}\cdot\text{d}^{-1}$ ) increased by 53%. Shen et al. [114] carried out a CFD model to optimize the flow field structure and enhance the cells' light/dark cycle. In the parallel spiral-flow column photobioreactor, the light/dark cycle frequency increased by 33.3%, while the biomass yield and CO<sub>2</sub> fixation rate of *Spirulina* sp. increased by 81.5% and 100.5%, respectively. Moreover, a bionic fractal structure was designed to optimize the photobioreactor efficiency. Then, a CFD model was established to investigate the hydrodynamic characteristics of the microbubbles and large bubbles in the tree-like photobioreactor [115]. The results reveal that the tree-like photobioreactor has an outstanding capacity to optimize the CO<sub>2</sub> fixation and biomass productivity for microalgae cultivation.

In general, studies mainly focus on the mass transfer enhancement of CO<sub>2</sub> and the optimization of light conditions to promote the CO<sub>2</sub> fixation efficiency of microalgae suspensions in photobioreactors. However, the CO<sub>2</sub> fixation performance of microalgae suspensions in photobioreactors under the regulation of phytohormones deserves to be further explored to contribute to the establishment of industrial photobioreactors for CO<sub>2</sub> fixation.

## 6. Prospective

The regulation of phytohormones is beneficial to maintain the stability of large-scale microalgae cultivation for CO<sub>2</sub> fixation from industrial gas. However, the species of phytohormones are specific to the growth of algal strains and carbon sequestration of microalgae suspensions [25,26]. In addition to the utilization of single phytohormones, the coupling of abiotic stresses with two or more phytohormones can also be used to promote

the productivity of microalgae biomass and lipids [27]. To guarantee the carbon sink at a high intensity, the kinetics of microalgae growth, CO<sub>2</sub> fixation rate, and lipid production are requested to be established. Moreover, it is urgent to propose a synergistic regulation of multiple phytohormones and environmental factors on the photosynthetic carbon fixation of specific algae species.

The optimal requirements of microalgae for the culture conditions (light, CO<sub>2</sub>, and nutrients) are dependent on the various growth stages. In the adaptation period of microalgae growth, a low concentration of nutrients and a low light intensity can significantly reduce the cell growth and improve the productivity of the microalgae biomass [29]. In the exponential growth stage, the growth rate and photosynthetic CO<sub>2</sub> fixation rate increase with an increase in light intensity [30]. In this situation, the addition of phytohormones can promote the CO<sub>2</sub> fixation rate. In the stable period, abiotic stresses such as nitrogen stress can reduce the growth rate and promote the lipid productivity of the microalgae. In this situation, the addition of phytohormones can promote the CO<sub>2</sub> fixation rate while maintaining the lipid production rate. Therefore, it is crucial to establish a control strategy for various factors in cultivation processes based on the growth stage of microalgae, such as light, CO<sub>2</sub>, nutrients, and phytohormones. Particularly, continuous photobioreactors enable the cultivation processes to be regulated conveniently [91]. Nowadays, continuous photobioreactors for the photosynthetic carbon sequestration and lipid production of microalgae regulated by phytohormones in multiple stages deserves to be developed.

The transportation of CO<sub>2</sub>, light, and nutrients in photobioreactors is crucial to the photosynthetic CO<sub>2</sub> fixation and growth of microalgae. During microalgae cultivation regulated by phytohormones, it is crucial to keep the micro-concentration of phytohormones in a suitable range. However, the micro-concentration of phytohormones is difficult to regulate in large-scale photobioreactors. Therefore, it is necessary to redesign the structure of photobioreactors and to optimize the effects of phytohormones coordinated with the growth kinetics and the CO<sub>2</sub> fixation rate of microalgae suspensions. On the basis of the reinforcement of light transfer and CO<sub>2</sub> transfer, guide plates and static mixers can be added in the photobioreactors for the enhancement of phytohormone transfer. In addition, the feed type of the nutrients and phytohormones, such as continuous feeding and batch feeding, should be obedient to the synergistic effect of phytohormones and abiotic stresses on the multistage microalgae cultivation.

## 7. Conclusions

Phytohormones with a low concentration ( $10^{-8}$ – $10^{-5}$  mol·L<sup>-1</sup>) can obviously promote the growth rate and the lipid productivity of microalgae, contributing to the CO<sub>2</sub> fixation of industrial gas. IAA and ABA are the most effective phytohormones to improve the biomass production and lipid production of microalgae, respectively. The effects of phytohormones on microalgae cultivation are specific to the algal strain. *Chlorella* appears to be the most convenient for cultivation regulated by phytohormones. The combination of phytohormones and nitrogen stress can significantly increase the accumulation of lipids while maintaining the CO<sub>2</sub> fixation rate. Multistage systems for microalgae cultivation have the potential to optimize the regulating strategy of phytohormones and abiotic stresses on the CO<sub>2</sub> fixation and lipid accumulation of microalgae. The reinforcement of light and mass transfer in photobioreactors is crucial to guarantee the effects of regulation by phytohormones on the CO<sub>2</sub> fixation and lipid accumulation of microalgae.

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