

Review

EFFECT OF CHEMICAL AND PHYSICAL FACTORS ON MICROALGAE METABOLISM

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Background. Modifying the metabolism of microalgae through chemical and physical environmental factors to obtain useful substances.

Objective. To summarize literature data on the effects of elevated concentrations of heavy metal ions on the biosynthesis of carotenoids, chlorophylls, and unsaturated fatty acids in microalgae, and to analyze the influence of lighting regimes as well as ultrasonic, ultraviolet, and gamma irradiation on the performance of various microalgae species.

Methods. A review and synthesis of literature data on the impact of increased heavy metal ion concentrations, lighting conditions, and exposure to ultrasound, UV, and gamma radiation on both the performance of different microalgae species and the biosynthesis of carotenoids, chlorophylls, and unsaturated fatty acids.

Results. The influence of physical and chemical environmental factors on nutrient biosynthesis in microalgae is species-specific. Elevated metal ion concentrations may either stimulate or inhibit the biosynthesis of various metabolites, including lipids, carotenoids, chlorophylls, proteins, and carbohydrates. Variations in light spectrum and intensity, as well as the frequency and duration of exposure to ultrasound, UV, and gamma radiation, can alter the metabolic pathways of microalgae in a species-dependent manner.

Conclusions. The metabolism of microalgae is influenced by cultivation parameters, species type, and the composition of the growth environment. Optimizing microalgae cultivation by adjusting physical and chemical abiotic factors for enhanced nutrient production requires a species-specific approach. The presented analysis forms a foundation for further research and the development of technological solutions aimed at boosting the biosynthesis of valuable compounds in microalgae.

Keywords: microalgae; heavy metal ions; lighting; ultrasound; UV irradiation; gamma radiation; carotenoids; chlorophylls; fatty acids.

Introduction

Microalgae demonstrate a high ability to adapt to changing environmental conditions. This changes the metabolism of cells, which leads to the synthesis of certain types of valuable nutrients, in particular fatty acids, pigments and proteins. These substances are used in many industries including pharmaceutical, food, cosmetic and biofuel [1–3].

The influence of chemical and physical factors on microalgae metabolism is one of the key strategies used to stimulate the synthesis of nutrients by microalgae. Clarification of the dependence of the influence of various environmental factors, such as the presence of an excessive amount of metal ions in the nutrient medium, the illumination mode, irradiation with ultrasonic waves, ultraviolet light and γ irradiation, on the biosynthesis of specific products by microalgae is of great importance for the industrial use of these organisms [4–7].

It is known [8–10] that heavy metal ions in excess amounts can have both negative and posi-

tive effects on the biosynthesis of metabolites such as carotenoids, chlorophylls, fatty acids by activating or inhibiting the action of enzymes of the corresponding biochemical processes. Microalgae can counteract the effects of heavy metals by synthesizing antioxidant enzymes, thereby mitigating the harmful effects of free radicals on their cellular structure [11]. Low concentrations of heavy metals can stimulate the growth of microalgae and the synthesis of useful substances, while high concentrations of metals are often toxic to microalgae, they lead to the suppression of photosynthesis, cell division and a decrease in the concentration of pigments [12].

Light is also an important factor that affects microalgae metabolism. Different spectra and intensity of illumination can both stimulate and inhibit the growth and metabolic activity of microalgae. For example, in [13] it is shown that the light spectrum can affect the metabolism of *Nannochloropsis gaditana* at the level of gene expression. High light intensity can promote the growth of microalgae cells

by enhancing photosynthesis, but can also lead to an increase in superoxide and hydrogen peroxide, which causes oxidative damage to some metabolites, in particular polyunsaturated fatty acids [14].

Also, the development of microalgae and the increase of their biomass is affected by exposure to different frequencies [15–17]. The frequency and duration of exposure to ultrasound, UV and γ radiation have an impact on the physiology of microalgae and can have both a positive and negative effect on the metabolism of various types of microalgae [18–20].

By changing the culture conditions of microalgae, the yield of useful metabolic products can be optimized. This allows you to determine the most rational conditions for cultivation and develop effective technologies for obtaining valuable substances that are used in various industries.

This study aims to analyze the impact of physicochemical factors on the synthesis of carotenoids, chlorophylls, and unsaturated fatty acids in microalgae. To achieve this, the following objectives were set:

- summarize the literature on the effects of elevated concentrations of heavy metal ions on the biosynthesis of carotenoids, chlorophylls, and unsaturated fatty acids in microalgae;
- analyze the impact of light regimes and exposure to ultrasonic frequencies, UV radiation, and γ -irradiation on the productivity of various microalgae species.

The effect of metal concentrations on metabolite synthesis in microalgae

Metal ions in low concentrations are essential for the development of microalgae cells, as they participate in the functioning of many enzymatic systems. Specifically, they serve as components for photosynthetic electron transport proteins (Cu, Fe) and photosynthetic water oxidation centers (Mn), or are part of vitamins (Co) [21]. Moreover, they act as cofactors for enzymes involved in CO₂ fixation (Zn in carbonic anhydrase), DNA transcription (Zn in RNA polymerase), as well as N₂ assimilation (Mo, Fe, V in nitrogenase), and nitrate reduction (Mo in nitrate reductase and Fe in nitrite reductase) [21–23]. It is believed that particularly Fe, Zn, Mn, Cu, Co, and Ni, which are more common in nature, have played a key role in biological evolution in general and in the evolution of photobiological systems and algae in particular [22, 24]. However, high concentrations of heavy metal ions

lead to negative consequences, such as disruption of the photosynthetic mechanism, blockage of cell division, and inhibition of enzyme activity in microalgae cells [22, 25].

The accumulation of metals in microalgae cells involves two main mechanisms: adsorption on the cell wall surface and uptake into the cells through transport systems [22, 23, 26]. These mechanisms protect against the harmful effects of metal ions, which can include forming reactive oxygen species such as hydroxyl radicals, superoxide anions, singlet oxygen, and hydrogen peroxide [22]. Microalgae cells respond to metal-induced oxidative stress by synthesizing chelating agents such as phytochelatins, and antioxidants including pigments, glutathione, and ascorbate, as well as enzymes like superoxide dismutase and catalase [27].

Chelators, such as phytochelatins, form complexes with metal ions, preventing their interaction with biological macromolecules [28]. Additionally, microalgae cells synthesize antioxidants capable of scavenging reactive oxygen species and reducing metal ions to less reactive forms [29].

Pigments such as chlorophylls, carotenoids, and phycobilins not only harvest light for photosynthesis but also function as antioxidants [30]. The presence of metals in the environment can affect the pigment content in microalgae cells. For example, the addition of copper, iron, or other metal ions can increase pigment concentration, reflecting the cells' adaptation to oxidative stress but can also impact the growth and survival of these organisms [8, 10, 31, 32]. The addition of metals, particularly cadmium or copper, to the culture medium, can significantly increase the lipid content in microalgae cells. Studying their effects could lead to the development of technologies to produce cultures with higher lipid content for biodiesel production [33, 34].

Additionally, elevated metal ion concentrations in the culture medium compared to standard cultivation media alter the fatty acid profile in microalgae cells. For instance, exposure to cadmium or cobalt ions can lead to an increase in monounsaturated fatty acids (MUFA) [29] and free fatty acids (FFA) [30] in the cells, which could be utilized to develop technologies for producing products for various industries [34, 35].

A review of studies on the impact of elevated metal ion concentrations in the culture medium on the development and metabolism of microalgae is presented in Table 1.

Table 1: The effect of increased concentration of metal ions on the synthesis of metabolites in microalgae

Microalgae culture	Metal	Concentration	The effect on metabolic products and growth of microalgae with increasing concentration of metal ions	Source
<i>Chlorella pyrenoidosa</i> , <i>Chlorella sorokiniana</i>	Fe ₂ O ₃ nanoparticles	10–30 mg/L	<i>Chlorella pyrenoidosa</i> : increased biomass concentration (maximum 33.75% at 20 mg/L), lipid content (maximum 13.77% at 30 mg/L), and chlorophyll content (maximum 41.66% at 20 mg/L). <i>Chlorella sorokiniana</i> : growth inhibition and decreased metabolite production even at 2 mg/L	[36]
<i>Chlorella sorokiniana</i>	Pb ²⁺	50–600 mg/L	Decreased dry biomass by 35% at maximum concentration. Increased lipid productivity by 67%, carbohydrate content by ~17%, and decreased protein content by ~27 %. Decreased chlorophyll-a and b by ~50%	[37]
<i>Chlorella minutissima</i>	Cd ²⁺ Cu ²⁺ Zn ²⁺ Mn ²⁺	Cd ²⁺ : 0.2–0.6 mM Cu ²⁺ : 0.2–1 mM Zn ²⁺ : 2–6 mM Mn ²⁺ : 2–6 mM	Cd ²⁺ : increased biomass at 0.2 mM and 0.4 mM (maximum 12 % at 0.4 mM). Increased lipid content at all concentrations (maximum 94% at 0.4 mM). Cu ²⁺ : increased biomass at all concentrations (maximum 11% at 0.4 mM). Increased lipid content at all concentrations (maximum 21% at 0.4 mM). Zn ²⁺ : decreased biomass at all concentrations. Decreased lipid content at 2 mM and 4 mM. Increased lipid content by 18% at 6 mM. Mn ²⁺ : increased biomass at all concentrations (maximum 14% at 6 mM). Decreased lipid content at all concentrations	[33]
<i>Chlorella sorokiniana</i>	Fe ₂ O ₃ NP	5–200 mg/L	At low concentrations, growth, and nutrient content are similar to control. At high concentrations, increased total carbohydrate content and significantly decreased unsaturated fatty acids	[38]
<i>Chlorella vulgaris</i>	Fe ₂ O ₃ NP	0.1–100 mg/L	At low concentrations, growth and total lipid content are similar to control. Decreased biomass by 41.2% and 83.7% at 50 and 100 mg/L, respectively. Increased total lipid content by 39.7% and 25.5%. Decreased C16, C16:1, C18:1, C18:2 fatty acids	[39]
<i>Chlorella vulgaris</i>	Cu ²⁺ , Cr ⁶⁺ , Zn ²⁺ , Cd ²⁺ , Pb ²⁺	0.05–5 mM	Toxicity sequence after 24 hours: Cu ²⁺ > Cd ²⁺ > Pb ²⁺ > Cr ⁶⁺ > Zn ²⁺ . After 96 hours: Cu ²⁺ > Cr ⁶⁺ > Cd ²⁺ > Zn ²⁺ > Pb ²⁺ . Cu ²⁺ and Cr ⁶⁺ : decreased chlorophyll content at maximum concentrations, stimulation at lower concentrations. Zn ²⁺ and Cd ²⁺ : increased chlorophyll content at all concentrations. Pb ²⁺ : increased chlorophyll content at all concentrations compared to control	[31]
<i>Chlorella vulgaris</i>	Zn ²⁺ Cu ²⁺	0.025 Cu ²⁺ : 0.025– 0.15 mg/L Zn ²⁺ : 6.25– 100 mg/L	Decreased chlorophyll and carotenoid content at all concentrations. Maximum decrease at the highest concentration. Cu ²⁺ : decreased chlorophyll-a by 37%, chlorophyll-b by 42%, and carotenoids by 40%. Zn ²⁺ : decreased chlorophyll-a by ~1400 times, chlorophyll-b by ~216 times, no carotenoids at maximum concentration	[40]

Continuation of Table 1

Microalgae culture	Metal	Concentration	The effect on metabolic products and growth of microalgae with increasing concentration of metal ions	Source
<i>Chlorella vulgaris</i>	Cu ²⁺ , Pb ²⁺ , Zn ²⁺ , Mg ²⁺ NP	Cu ²⁺ : 10–50 mg/L Pb ²⁺ : 50–200 mg/L Zn ²⁺ : 50–200 mg/L Mg ²⁺ : 50–200 mg/L	<p>Cu²⁺: highest specific biomass at 20 mg/L. Maximum decrease in chlorophylls by 87%, carotenoids by 89%, and lipids by 27% at 50 mg/L.</p> <p>Pb²⁺: highest specific biomass at 100 mg/L. Maximum decrease in chlorophylls by 32% at 25 mg/L, carotenoids by 83% at 25 mg/L, increase in lipids (maximum 20% at 100 mg/L).</p> <p>Zn²⁺: highest specific biomass at 50 mg/L. Decreased chlorophylls by 52%, carotenoids by 94% at 200 mg/L, and increase in lipids (maximum 26% at 100 mg/L).</p> <p>Mg²⁺: highest specific biomass at 50 mg/L. Maximum decrease in chlorophylls by 73% at 150 mg/L and carotenoids by 72% at 50 mg/L and 150 mg/L, increase (maximum 35% at 150 mg/L). Metal concentrations above 100 mg/L inhibit growth</p>	[41]
<i>Dunaliella salina</i> CCAP 19/18, <i>Dunaliella salina</i> Hoze-soltan	Se ⁴⁺	100–1600 µm	With increasing Se ⁴⁺ content, decreased chlorophyll by 4.95 times for <i>Dunaliella salina</i> CCAP 19/18 and 2.26 times for <i>Dunaliella salina</i> Hoze-soltan compared to control, an increase in carotenoid content (three times higher in <i>Dunaliella salina</i> CCAP 19/18 than in <i>Dunaliella salina</i> Hoze-soltan)	[9]
<i>Dunaliella salina</i>	Fe ²⁺ , Mn ²⁺	0.1–2 ppm	<p>Fe²⁺: increased carotenoid content, maximum β-carotene 3 times at 0.6 ppm.</p> <p>Mn²⁺: increased carotenoid content, maximum β-carotene 1.5 times at 0.8 ppm</p>	[10]
<i>Dunaliella tertiolecta</i>	Zn ²⁺	5–25 mg/L	Decreased carotenoids (maximum 86% at 25 mg/L), chlorophyll (maximum 48% at 25 mg/L), and saturated and unsaturated fatty acids (maximum 80% at 25 mg/L) with increasing concentration	[42]
<i>Haematococcus pluvialis</i>	Zn ²⁺	10–200 mg/L	Decreased chlorophyll-a (maximum 63% at 200 mg/L), carotenoids (maximum 43% at 200 mg/L), and astaxanthin (maximum 48% at 200 mg/L)	[43]
<i>Haematococcus pluvialis</i>	Al ³⁺ Li ⁺ Mg ²⁺	0.01–10.00 mg/L	Increased carotenoid content with increasing concentration for all metals. Carotenoid content correlated proportionally with the number of cells. Order of increase in the number of cells and carotenoids: Mg ²⁺ > Li ⁺ > Al ³⁺	[32]
<i>Haematococcus pluvialis</i>	Zn ²⁺	10–200 mg/L	Increased lipid content. Maximum lipid content 329.9% at 200 mg/L	[44]
<i>Isochrysis galbana</i>	Cr ⁶⁺	0.5–10 mg/L	Increased chlorophyll content at low concentrations (0.5–5.0 mg/L), maximum increase of 14% at 0.5 mg/L. Decrease in chlorophyll content by 78% at higher concentrations (10 mg/L)	[45]

End of Table 1

Microalgae culture	Metal	Concentration	The effect on metabolic products and growth of microalgae with increasing concentration of metal ions	Source
<i>Raphidocelis subcapitata</i>	Cd ²⁺ Co ²⁺	Cd ²⁺ : 0.22–1.11 mM Co ²⁺ : 0.98–4.37 mM	Cd ²⁺ : increased wax esters, phospholipids, and aliphatic hydrocarbons (total lipid content maximally increased by 40% at 0.8 mM). Decreased chlorophyll-a content at 0.89 and 1.11 mM (maximum 33% at 0.89 mM). Increased chlorophyll-a content by 23% at 0.22 mM. Co ²⁺ : increased wax esters, structural lipids, and free fatty acids (total lipid content maximally increased by 95% at 1.8 mM). No significant effect on chlorophyll-a content	[35]
<i>Scenedesmus acutus</i> , <i>Chlorella sp.</i>	Pb ²⁺	1.95×10 ⁻⁹ M <i>Chlorella sp</i> 0.4×10 ⁻⁹ M <i>Scenedesmus acutus</i>	<i>Chlorella sp.</i> : decreased photosynthesis productivity by 59%. <i>Scenedesmus acutus</i> : decreased photosynthesis productivity by 6%	[46]
<i>Selenastrum gracile</i>	Cd ²⁺	9.8×10 ⁻¹³ –1.18 mM	Increased saturated fatty acid content (maximum 30.3% at 9.8×10 ⁻¹³ mM). Increased monounsaturated fatty acid content (maximum 45.9% at 1.18 mM). Increased polyunsaturated fatty acid content (maximum 45.7 % at 0.29 mM). Maximum overall increase in total fatty acid content by 24.2 % at 9.8×10 ⁻¹³ mM	[34]
<i>Spirulina platensis</i>	Zn ²⁺	1–8 mg/L	Decreased biomass (maximum 70.33% at 8 mg/mL). Increased the proportion of saturated and polyunsaturated fatty acids (maximum at 8 mg/mL), decreased chlorophyll-a (maximum 81% at 8 mg/L), different carotenoid profile at different concentrations (increase at 1 and 4 mg/L, maximum 9% at 1 g/L; decrease at 2, 6, and 8 mg/L, maximum 71% at 8 mg/L)	[47]
<i>Spirulina platensis</i>	Fe ²⁺ , Cu ²⁺ , Zn ²⁺	10 times more than in the culture medium	Fe ²⁺ : decreased chlorophyll-a content by 7 %, decreased carotenoid content by 18%. Cu ²⁺ : increased chlorophyll-a content by 71%, increased carotenoid content by 54%. Zn ²⁺ : increased chlorophyll content by 21%, decreased carotenoid content by 57%	[48]
<i>Spirulina platensis</i>	Ni ²⁺ , Zn ²⁺ Cu ²⁺	1–3 mg/L	Ni ²⁺ : increased chlorophyll content by 54% at 1 mg/L, similar to control at 2.5 mg/L, decreased chlorophyll content by 19% at 1.5, 2, and 3 mg/L, increased carotenoid content at 1, 2, 2.5, 3 mg/L (maximum 30% at 2.5 mg/L), a slight decrease at 1.5 mg/L. Zn ²⁺ : decreased chlorophyll content at all concentrations (maximum 60% at 3 mg/L), decreased carotenoid content at all concentrations (maximum 90% at 3 mg/L). Cu ²⁺ : decreased chlorophyll content at all concentrations (maximum 100% at 2 mg/L), decreased carotenoid content at all concentrations (maximum 90% at 3 mg/L). Metal toxicity order Cu ²⁺ > Zn ²⁺ > Ni ²⁺	[49]

The general effect of metals on the yield of useful substances in microalgae can be quite diverse and depends on the specific type of microalgae, metal ion and its concentration in the culture medium. Generally, the following trends are observed: Cadmium and Copper increase the lipid content in *Chlorella minutissima* [33]. Cadmium also increases fatty acids in *Selenastrum gracile* and *Raphidocelis subcapitata* but inhibits photosynthesis in these organisms [34, 35]. However, cadmium stimulates photosynthesis in *Chlorella vulgaris* [23]. Iron promotes lipid accumulation in *Chlorella pyrenoidosa* [36] and carotene in *Dunaliella salina* [10], but may inhibit the yield of valuable substances in *Chlorella sorokiniana* [36, 38]. Lead increases lipid and carbohydrate content but decreases proteins and chlorophylls in *Chlorella sorokiniana* and *Chlorella vulgaris* [37, 41]. Lead also inhibits photosynthesis in *Scenedesmus acutus* and *Chlorella sp.* [46]. Zinc shows mixed effects. It stimulates photosynthesis in *Chlorella vulgaris* [31], yet other studies [40, 41, 43] indicate that even low concentrations reduce chlorophyll and carotenoid content but increase the lipid content in *Chlorella vulgaris* and *Haematococcus pluvialis*. In *Dunaliella tertiolecta*, lower zinc concentrations boost metabolite content, while higher concentrations inhibit nutrient accumulation [42]. Nickel: lower concentrations promote growth and pigment accumulation in *Spirulina platensis*, but higher concentrations can inhibit growth and nutrient yield [49].

Given this diversity of effects, detailed studies considering the specifics of each microalgae species and their cultivation conditions are necessary to optimize microalgae cultivation and maximize the yield of valuable substances.

The effect of light spectrum and intensity on metabolite synthesis in microalgae

Light, as the main source of energy for microalgae, plays an important role in regulating their growth and development. Algae absorb only specific parts of the solar spectrum, particularly light in the range of 400 to 700 nm. The wavelengths absorbed by microalgae vary depending on the species [50, 51]. This is because algal pigments absorb light energy, which stimulates photochemical transformations. Each photosystem includes a specific set of pigments that form a unique absorption spectrum [52–55].

Lighting of different intensity can affect the growth and photosynthetic activity of microalgae in different ways. The intensity of light directly de-

termines the rate of photosynthesis described by the logarithmic curve. The increase in light intensity leads to a near-linear increase in the rate of photosynthesis [56]. However, with a certain light intensity, an additional increase in light does not lead to a further increase in the rate of photosynthesis and can lead to photoinhibition [57]. During photoinhibition, the production of reactive oxygen species (ROS), which have high reactivity, can increase [14]. In response to oxidative stress, algae cells may synthesize antioxidant enzymes, phytohormones, and other photoprotective compounds [57]. Changes also occur in the photosystems and the composition of the light-harvesting complex. Oxidative stress can significantly influence the biosynthesis of metabolites by microalgae. Therefore, achieving an optimal balance between their growth rate and the accumulation of biochemically valuable compounds is a crucial task [53, 58, 59].

When analyzing the regulatory impact of light on microalgae growth, it is essential to consider the light source, radiation range, intensity, and photoperiod, as the effect of different light parameters on the physiological properties of microalgae is diverse.

A detailed review of recent research on the impact of light spectrum and intensity on microalgae is presented in Table 2.

The effect of different light spectra on the growth and biochemical composition of microalgae is a complex process determined not only by intensity but also by specific light characteristics, such as wavelength. As shown in Table 2, for various microalgae species, the impact on metabolism depends on the light spectrum and other factors, including the species, cultivation conditions, and other physical and chemical parameters. For example, *Chlorella ellipsoidea* exhibits maximum increases in chlorophyll-a, chlorophyll-b, β -carotene, and lipid content under blue LED light, with pigment increases following the order: blue > green > white > red [60]. In contrast, for *Botryococcus braunii*, red light significantly enhances photosynthesis efficiency, nitrogen uptake rate, and accumulation of lipids and carbohydrates, with increases in chlorophyll and lipids in the order: red > white > blue > green [61]. These studies indicate that the spectral composition of light significantly affects microalgae physiology and can be used to optimize their productivity for various industrial applications. Studies on *Arthrospira platensis*, *Chlorella vulgaris*, and *Scenedesmus obliquus* demonstrate that different microalgae species respond differently to light spectra, highlighting the need for tailored approaches to optimize cultivation conditions for each species [63].

Table 2: The effect of light spectrum and intensity on metabolite synthesis in microalgae

Microalgae culture	Light characteristics	Effect	Source
The effect of different spectrum			
<i>Chlorella ellipsoidea</i>	White, green, blue, red	Maximum yield of chlorophyll-a, chlorophyll-b, β -carotene, and lipids under blue LED light. An increase in all pigments and lipids occurs in the following order: blue > green > white > red	[60]
<i>Botryococcus braunii</i>	White, green, blue, red	Maximum photosynthetic efficiency, nitrogen consumption rates, and lipid and hydrocarbon accumulation under red light. Increase in chlorophyll and lipid yield occurs in the following order: red > white > blue > green	[61]
<i>Pavlova lutheri</i> , <i>Chlorella vulgaris</i> , <i>Porphyridium cruentum</i>	Violet, blue, green, yellow, red	For all cultures, an increase in lipid yield was observed in the following order: yellow > green > red. Minimum lipid yield was observed under blue light for <i>Pavlova lutheri</i> , <i>Chlorella vulgaris</i> , and under green light for <i>Porphyridium cruentum</i>	[62]
<i>Arthospira platensis</i> , <i>Chlorella vulgaris</i> , <i>Scenedesmus obliquus</i>	Blue, green, yellow, red, white	Maximum chlorophyll-a content was recorded in <i>Chlorella vulgaris</i> under red LED light. Green light led to higher chlorophyll-b and carotenoid content in <i>Arthospira platensis</i> , <i>Chlorella vulgaris</i> , and <i>Scenedesmus obliquus</i> . Total carbohydrate content was highest under blue light. Maximum protein content was observed under blue and green light	[63]
<i>Chlorella vulgaris</i> , <i>Chlorella pyrenoidosa</i> , <i>Scenedesmus quadricauda</i> , <i>Scenedesmus obliquus</i>	Red, blue, white	Maximum yield of chlorophyll-a, chlorophyll-b, lutein under blue light. Maximum lipid content in <i>Chlorella vulgaris</i> and <i>Chlorella pyrenoidosa</i> under red light, and in <i>Scenedesmus quadricauda</i> and <i>Scenedesmus obliquus</i> under white light	[64]
<i>Phaeodactylum tricornutum</i>	White, red, yellow	Maximum lipid yield under yellow light. An increase in lipid yield occurs in the following order: yellow > red > white	[65]
<i>Chlamydomonas reinhardtii</i>	Blue, red-orange	Maximum lipid concentration under blue light, no significant changes in carbohydrate and protein content. Combined light increases lipid and carbohydrate content. Alternating blue/red-orange (24/24 h) significantly increases protein content compared to alternating red-orange/blue	[66]
<i>Isochrysis zhanjiangensis</i>	Green, blue, red, white, yellow	Maximum chlorophyll content under green light, maximum protein content under white light, maximum carbohydrate content under blue light	[50]
<i>Picochlorum</i> sp. (<i>Trebouxiophyceae</i> , <i>Chlorophyta</i>)	White, green, blue, red	Maximum pigment concentration under green light	[67]
<i>Muriellopsis</i> sp.	White, red, blue	Stimulation of lutein and other carotenoid synthesis under blue light. Direct correlation between lipid accumulation and high light intensity. The highest antioxidant activity was observed under high-intensity white light	[68]
<i>Chlamydomonas reinhardtii</i> , <i>Galdieria sulphuraria</i> , <i>Porphyridium purpureum</i>	Red, green, blue	<i>Chlamydomonas reinhardtii</i> : The optimal ratio of red, blue, and green light is approximately 80–90% red, 0–20% green, and 0–10% blue. <i>Galdieria sulphuraria</i> : Red light maximally stimulates photosynthesis <i>Porphyridium purpureum</i> : Maximum pigment yield achieved at approximately 30–50% red, 40–70% green, and 0–20% blue light	[69]

Continuation of Table 2

Microalgae culture	Light characteristics	Effect	Source
<i>Oscillatoria</i> sp. (SRA), <i>Oscillatoria</i> sp. (CWA), <i>Ankistrodesmus</i> sp.	White, green, blue, red, yellow	For all algae: maximum biomass and pigment concentration under blue light, maximum lipid accumulation under yellow light	[70]
<i>Spirulina platensis</i>	White, red, blue, yellow	Maximum chlorophyll and phycocyanin under blue light. Increase in chlorophyll yield in the following order: blue > red > white > yellow. Increase in phycocyanin yield in the following order: blue > red > yellow > white. Increase in vitamin B ₁₂ yield in the following order: blue > red > white > yellow	[71]
<i>Spirulina platensis</i>	White, red, blue	Increase in protein content: blue > white > red. Increase in carbohydrate content: blue > red > white	[72]
<i>Monoraphidium braunii</i>	White, blue, green, red	Maximum amount of unsaturated fatty acids and higher concentration of all identified pigments under white, blue, and green light, which included blue-green light, compared to irradiation with red light	[73]
<i>Acutodesmus obliquus</i>	No light, white, yellow, orange, red	Maximum pigment and fatty acid yield under blue-green light. Maximum chlorophyll yield under white light	[74]
<i>Chlorella vulgaris</i>	Blue, green, red, white	Maximum amount of chlorophyll-a and chlorophyll-b in cultures illuminated with green light, astaxanthin in those illuminated with blue light	[75]
<i>Chlorella vulgaris</i>	Green, red, blue, white	Maximum amount of chlorophyll-a and chlorophyll-b in cultures illuminated with green light, astaxanthin in those illuminated with red light	[76]
The effect of different light intensity			
<i>Phaeodactylum tricornutum</i>	60 to 750 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Maximum biomass concentration and eicosapentaenoic acid content are not dependent on light intensity. Lipid yield decreased at higher light intensities ($>100 \mu\text{mol m}^{-2}\text{s}^{-1}$). The highest yield of tetraglycerides was observed at the lowest tested light intensity ($60 \mu\text{mol m}^{-2}\text{s}^{-1}$)	[77]
<i>Rhodomonas</i> sp.	60 to 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$	The light intensity had no effect on fatty acid composition. Maximum production rates of eicosapentaenoic acid and docosahexaenoic acid were obtained under high light intensity ($600 \mu\text{mol m}^{-2}\text{s}^{-1}$)	[78]
<i>Isochrysis galbana</i>	50 to 325 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased protein content with increased light intensity; high light intensity ($325 \mu\text{mol m}^{-2}\text{s}^{-1}$) promotes rapid growth and accumulation of carbohydrates and lipids, as well as total carotenoid content and antioxidant activity	[79]
<i>Desmodesmus</i> sp. <i>Scenedesmus obliquus</i>	50 to 300 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased light intensity led to increased biomass in <i>Desmodesmus</i> sp. and <i>Scenedesmus obliquus</i> and to higher fatty acid content. Fatty acid profile analysis showed increased oleic acid and decreased linolenic acid content with increasing light intensity	[80]
<i>Phaeodactylum tricornutum</i>	150 to 750 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased pigment production (chlorophyll and carotenoids) and production of polyunsaturated fatty acids (PUFAs) at $150 \mu\text{mol m}^{-2}\text{s}^{-1}$. Irradiation at $750 \mu\text{mol m}^{-2}\text{s}^{-1}$ led to increased saturated fatty acids (SFAs) and decreased PUFA concentration	[81]

End of Table 2

Microalgae culture	Light characteristics	Effect	Source
<i>Entomoneis paludosa</i> NCC18.2, <i>Nitzschia alexandrina</i> NCC33, <i>Staurosira</i> sp. NCC182	30 to 400 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Irradiation from 100 to 400 $\mu\text{mol m}^{-2}\text{s}^{-1}$ stimulates lipid accumulation in <i>Entomoneis paludosa</i> and <i>Nitzschia alexandrina</i> , while in <i>Staurosira</i> sp. it stimulates carbohydrate accumulation. Irradiation at 400 $\mu\text{mol m}^{-2}\text{s}^{-1}$ reduces protein and pigment synthesis	[82]
<i>Scenedesmus obliquus</i>	36.7 to 102.3 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Maximum protein content, total phenols, and total carotenoids were observed at 65.9 $\mu\text{mol m}^{-2}\text{s}^{-1}$	[83]
<i>Nostoc calcicola</i>	21 to 63 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased total carotenoid and carbohydrate content with increasing light intensity, while biomass, chlorophyll-a, phycoerythrin, phycocyanin, allophycocyanin, and total protein content decreased. Similar effects were observed with increased photoperiod duration. Interaction of increased light intensity and photoperiod led to increased carbohydrate and total carotenoid content and decreased chlorophyll-a, phycoerythrin, phycocyanin, allophycocyanin, and total protein content	[84]
<i>Phormidium</i> sp.	2000, 8000 lux	Increased phycocyanin, phycoerythrin, and allophycocyanin and biliprotein content under 2000 lux. Chlorophyll-a content was higher under lower light intensity compared to total carotenoids	[85]
<i>Ettlia</i> sp.	200 to 800 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased capric, palmitic, and linolenic acid content with a decrease in stearic, palmitoleic, oleic, linoleic, and alpha-linolenic acids with increasing light intensity	[86]
<i>Chlorella zofingiensis</i>	50 to 400 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased astaxanthin content with increasing light intensity	[87]
<i>Tetraselmis</i> sp. CTP4	33 to 280 $\mu\text{mol m}^{-2}\text{s}^{-1}$	β -carotene content was higher at low light intensity (33 $\mu\text{mol m}^{-2}\text{s}^{-1}$), while lutein content increased at higher light intensity (170 and 280 $\mu\text{mol m}^{-2}\text{s}^{-1}$). The highest total carotenoid and lutein content was observed at 170 $\mu\text{mol m}^{-2}\text{s}^{-1}$	[88]
<i>Dunaliella salina</i> Y6	100 to 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Lipid content increased by 6% under 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$ compared to 100. Maximum lipid productivity was observed at a light intensity of 405 $\mu\text{mol m}^{-2}\text{s}^{-1}$. The fatty acid composition was similar across different light intensities. Saturated and unsaturated fatty acid content increased by 43.7% and 11.7%, respectively. β -carotene content increased by 31.5% and lutein by 95.9% under 200 $\mu\text{mol m}^{-2}\text{s}^{-1}$	[7]
<i>Chlorella vulgaris</i>	130 to 520 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Increased solar radiation led to higher lipid and protein content. Additionally, increased light intensity with red-white LED lamps led to higher lipid content. Protein, fiber, ash, and moisture content remained relatively constant	[89]
<i>Choricystis</i> sp. AL045	135 to 675 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Maximum lipid productivity was observed at a light intensity of 405 $\mu\text{mol m}^{-2}\text{s}^{-1}$. The fatty acid composition was similar across different light intensities	[90]
<i>Dunaliella salina</i> UTEX 2538, <i>Dunaliella salina</i> CCAP 19/30, <i>Dunaliella salina</i> D-Factory DF15 <i>Dunaliella salina</i> DF17, <i>Dunaliella salina</i> DF40	200 to 1500 $\mu\text{mol m}^{-2}\text{s}^{-1}$	Total chlorophyll content in cells decreased, while carotenoid content increased with increasing light intensity for all five <i>Dunaliella</i> strains. β -carotene content increased with increasing light intensity in all strains except UTEX 2538	[91]

Most studies [60, 68, 70, 73] show increased carotenoid content with blue light, while chlorophyll content increases with green light [50, 63, 67, 75, 76]. However, findings in [75, 76] are contradictory, as for *Chlorella*, astaxanthin content increases under red light [76] but under blue light [75]. For increasing carotenoid and chlorophyll content, different species require different light spectrum ratios [69]. Lipid synthesis is stimulated by yellow and blue light, with maximum lipid synthesis under blue light observed in *Chlorella ellipsoidea* [60], *Chlamydomonas reinhardtii* [66], and *Acutodesmus obliquus* [74], and under yellow light in *Pavlova lutheri*, *Chlorella vulgaris*, *Porphyridium cruentum* [62], *Phaeodactylum tricornutum* [65], *Oscillatoria* sp. (SRA), *Oscillatoria* sp. (CWA), and *Ankistrodesmus* sp. [64]. However, [64] also noted lipid synthesis stimulation in *Chlorella vulgaris* under red light, which does not correlate with [62].

Studies on the effect of light intensity on microalgae show that carotenoid content increases at $65.9 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Scenedesmus obliquus* [83], at $63 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Nostoc calcicola* [84], at $170 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Tetraselmis* sp. CTP4 [88], and up to $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Chlorella zofingiensis* [87]. Chlorophyll content increases at $150 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Phaeodactylum tricornutum* [81] but decreases at $63 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Nostoc calcicola* [84], is higher at 2000 lux in *Phormidium* sp. [85], and decreases to $1500 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Dunaliella salina* [91]. Increased light intensity up to $800 \mu\text{mol m}^{-2}\text{s}^{-1}$ in *Ettlia* sp. increases capric and palmitic acid content, while other acids decrease [86]. In *Rhodomonas* sp., the maximum production rates of eicosapentaenoic and docosahexaenoic acids are observed at $600 \mu\text{mol m}^{-2}\text{s}^{-1}$ [78]. Increased light intensity often promotes higher carotenoid and lipid content but can reduce chlorophyll and other compounds. For example, in *Phaeodactylum tricornutum*, the highest triglyceride yield is observed at the lowest tested light intensity, specifically $750 \text{ m}^{-2}\text{s}^{-1}$ [81].

Thus, increasing light intensity can affect microalgae due to biochemical processes within the cells. Some microalgae show a positive response to increased light intensity, enhancing the accumulation of beneficial compounds [7, 79, 80, 87], while others may experience saturation or reduced compound content at high light intensity [77, 82, 85]. These findings help better understand and optimize microalgae cultivation conditions to maximize their potential for various industrial applications.

Overall, studies on the impact of light spectrum and intensity on microalgae are a crucial step in understanding their physiology and determining

parameters for enhanced biosynthesis of valuable compounds.

The effect of ultrasound, ultraviolet spectrum radiation, and γ -radiation on metabolite synthesis in microalgae

Ultrasound is a physical method widely applied in the microalgae industry. Research indicates that ultrasonic treatment enhances biomass and lipid content in microalgae and improves lipid extraction efficiency [92, 93]. Ultrasound is used in extraction processes as it breaks cell walls, releasing valuable products from cells [94]. However, ultrasonic treatment during cultivation improves enzyme activity, cell permeability, and substrate transport [95]. The use of ultrasound for algae processing aims to improve extraction processes by increasing cell permeability and substrate transport or by rupturing cells to release their compounds, such as lipids [96]. Less common is the use of ultrasound to stimulate microalgae growth to increase their biomass and lipid production. Although there are few studies on the effect of ultrasonic frequencies on biomass growth and lipid content, several works confirm this effect [97].

For example, ultrasonic treatment stimulated the growth of *Anabaena variabilis* under phototrophic conditions [98]. Ultrasonic treatment of *Scenedesmus* sp. during the growth phase led to increased biomass and lipid production [96]. Ultrasonic treatment alters cell membrane permeability, affecting cell activity and product synthesis [99]. It also affects photosynthetic pigments, such as chlorophyll-a and carotenoids, increasing the cells' ability to absorb light, enhancing photosynthesis rates and cell division, and providing a protective mechanism against stressful conditions [18].

Analyzing the effects of irradiation on microalgae reveals various impacts on the physiological and biochemical parameters of these organisms. Specifically, applying ultraviolet radiation (UV-R) is identified as a strategy to increase lipid content in microalgae. UV-R consists of UV-A, -B, and -C, which affect growth, photosynthesis, lipid content, and fatty acid composition in microalgae by ROS such as hydrogen peroxide (H_2O_2), hydroxyl radical ($\cdot\text{OH}$), and superoxide ($\text{O}_2^{\cdot-}$) [100–102]. However, research results can contradict each other depending on the species and/or cultivation conditions and may also depend on nitrogen concentration or other stress conditions.

Additionally, γ -irradiation has been found to affect microalgae. Studies have shown that γ -radia-

tion can stimulate the synthesis and distribution of essential phytochemicals for potential radioprotection and cell survival. Transcriptomics and proteomics studies also reveal the molecular mechanisms by which radiation affects microalgae cells, including changes in gene and protein expression responsible for photosynthesis, metabolism, and stress response [103, 104].

Some studies have shown that UV and γ -radiation can lead to an increase in algal cell size, which may be related to the production of various secondary metabolites [105, 106]. However, such changes in cell size may also occur due to impaired photosynthesis and other physiological parameters.

A detailed review of recent studies on the impact of ultrasound and irradiation on the yield of carotenoids, chlorophylls, and unsaturated fatty acids in microalgae is presented in Table 3.

Ultrasonic irradiation has a significant impact on the content of carotenoids, chlorophylls, and saturated and unsaturated fatty acids in microalgae. For *Nannochloris* sp. 424-1, the maximum increase in unsaturated C18 fatty acids was achieved with 3 minutes of daily exposure to 1 W ultrasound [107]. In the case of *Scenedesmus* sp., an ultrasound power of 20 W resulted in a 49% increase in lipids and a 16% increase in chlorophylls [92]. For *Scenedesmus* sp. Z-4, optimal ultrasound parameters (20 W, frequency 20 Hz, interval 2 s) provided maximum biomass concentration, lipid content (37% higher than the control), chlorophyll-a by 23.3%, and chlorophyll b by 18.4% [96]. The results of the study [19] correlate with those of [92] for *Scenedesmus* sp. at a power of 20 W, a frequency of 18 Hz, and a duration of 10 minutes,

showing a 44% increase in lipids and a 126% increase in biomass, which also contributed to better nutrient removal and the development of microbiological symbionts.

Ultraviolet (UV) and gamma (γ) radiation has proven to be effective strategies for increasing lipid content in microalgae such as *Chlorella sorokiniana* and *Fistulifera solaris*. Studies have shown that UV radiation accelerates the synthesis of neutral lipids, while γ -radiation promotes the accumulation of unsaturated fatty acids [108, 109]. It has been found that UV radiation can also enhance biomass productivity and promote lipid accumulation in microalgae, as presented in the study on *Ettlia* sp. [20]. The application of γ -radiation can have a dual effect on microalgae. On the one hand, low doses of γ -radiation can stimulate growth and antioxidant enzyme activity, while high doses can lead to reduced growth and phenolic activity, as well as changes in algal pigmentation, as shown in the study on *Chlorella* sp. [110]. The toxic effects of UV radiation were observed in a study where *Chlorella vulgaris* and *Chlorococcum humicola* demonstrated a decrease in chlorophyll and carotenoid content under UV exposure, indicating a stress response [112]. Short-term γ -irradiation leads to suppressed photosynthetic productivity and the formation of reactive oxygen species in *Chlamydomonas reinhardtii*, indicating initial physiological stress [113].

The obtained results confirm the importance of studying the effects of irradiation on microalgae for their further use in biotechnological processes. They provide valuable information for optimizing microalgae cultivation to enhance the productivity of useful compounds.

Table 3: The effect of irradiation on metabolite synthesis in microalgae

Microalgae culture	Radiation characteristics	Effect	Source
The effect of ultrasound			
<i>Nannochloris</i> sp. 424-1	Power: 1 W Time: 60 to 300 s Power: 10 W Time: 6 to 30 s	Maximum biomass productivity increase (by 45%) was observed with 3 min daily exposure at 1 W. Daily irradiation at 10 W led to a 27% increase in biomass productivity compared to the control after 30 s of ultrasound exposure. There was an increase in fatty acids and changes in the fatty acid profile, especially with 1 W ultrasound (decrease in C16 unsaturated fatty acids and increase in C18 unsaturated fatty acids for both irradiation modes). When 10 W ultrasound was applied, both categories of unsaturated acids decreased	[107]
<i>Scenedesmus</i> sp.	Power: 0–50 W Time: 0–10 min	Lipid content increased by 49% and chlorophylls by 16%, with a slight increase in carotenoids at 20 W (mode: 2 s with ultrasound irradiation/2 s without ultrasound irradiation)	[92]

Continuation of Table 3

Microalgae culture	Radiation characteristics	Effect	Source
The effect of ultrasound			
<i>Scenedesmus</i> sp. Z-4	Power: 10 to 50 W Frequency: 18 to 30 Hz Time: 1–5 s	Maximum biomass concentration (28.5% higher than the control) and lipid content (37% higher than the control) at 20 W ultrasound power, 20 Hz frequency, and 2 s interval. Microscopic analysis showed that ultrasound irradiation caused tiny cracks or holes on the cell wall surface but did not damage the integrity of the algal cell structure. Membrane permeability and nutrient transport improved after ultrasound stimulation. Chlorophyll <i>a</i> increased by 23.3% and chlorophyll <i>b</i> by 18.4%. However, excessive ultrasound irradiation significantly inhibited cell growth and lipid accumulation in microalgae	[96]
<i>Scenedesmus</i> sp.	Power: 20 W, Frequency: 18 Hz, Time: 10 min	Lipid content increased by 44%. Biomass increased by 126%. Ultrasound treatment also significantly improved nutrient removal and facilitated the development of micro-biological symbionts in the medium	[19]
The effect of irradiation			
<i>Chlorella sorokiniana</i>	UV: 0.25 to 2 J/cm ² γ -irradiation: 0.5 to 4 kGy	Maximum lipid increase by 1.56 times under UV irradiation (1 J/cm ²) and by 1.73 times under γ -irradiation (1 kGy). UV radiation stimulated the accumulation of saturated fatty acids, while γ -radiation stimulated the accumulation of unsaturated fatty acids (particularly essential omega-3)	[108]
<i>Fistulifera solaris</i>	UV: 0 to 200 mJ/cm ² Wavelengths: λ = 248 to 277 nm	UV irradiation accelerated the synthesis of unsaturated fatty acids. For 248 nm irradiation, maximum fatty acid increase at 10 mJ/cm ² . For 255 nm, 268 nm, and 277 nm, maximum fatty acid increase at 5 mJ/cm ² . After irradiation, the content of unsaturated fatty acids was 62.2% at 255 nm, 66.8% at 268 nm, and 70.8% at 277 nm	[109]
<i>Ettlia</i> sp.	UV	UV irradiation increased biomass productivity and stimulated lipid accumulation. Lipid productivity increased by 43.7% and lipid content by 33.7% compared to the control. However, the ratio of saturated to unsaturated fatty acids was higher under UV treatment than in the control	[20]
<i>Chlorella</i> sp.	γ -irradiation: 0.01 to 0.075 kGy ⁶⁰ Co	Higher doses of γ -irradiation led to reduced growth, total phenolic, flavonoid, antioxidant activity, free radical scavenging, and changes in pigmentation, while doses up to 0.075 kGy showed inhibition of beneficial substance synthesis. Protein content and antioxidant enzyme activity, chlorophyll, carotenoid, and protein synthesis were stimulated at 0.075 kGy	[110]
<i>Anabaena</i> sp. PCC7120	γ -irradiation: 6 kGy ⁶⁰ Co	γ -irradiation negatively affects photosynthesis, as determined by cytosolic proteome analysis	[111]
<i>Chlorella vulgaris</i> , <i>Chlorococcum humicola</i>	UV-B	UV-B had a toxic effect on the algae <i>Chlorococcum humicola</i> and <i>Chlorella vulgaris</i> . Chlorophyll and carotenoid content in <i>Chlorella vulgaris</i> and <i>Chlorococcum humicola</i> decreased under UV radiation with increasing exposure time. Lipid yield in <i>Chlorococcum humicola</i> was higher than in <i>Chlorella vulgaris</i> under UV exposure	[112]

End of Table 3

Microalgae culture	Radiation characteristics	Effect	Source
<i>Chlamydomonas reinhardtii</i>	γ -irradiation: 0.49 to 1677 mGy/h Time: 6 h	Short-term γ -irradiation leads to inhibition of photosynthetic productivity and the formation of reactive oxygen species (ROS) in microalgae	[113]
<i>Dunaliella salina</i> KU5, <i>Dunaliella salina</i> KU18, <i>Dunaliella salina</i> KU20, <i>Dunaliella salina</i> KU37	UV-C 0.4 mmol m ⁻² s ⁻¹	UV radiation significantly increased β -carotene content in mutant strains of microalgae. By 1.62 times for <i>Dunaliella salina</i> KU5, by 2.03 times for <i>Dunaliella salina</i> KU18, by 1.32 times for <i>Dunaliella salina</i> KU20, and by 1.21 times for <i>Dunaliella salina</i> KU37 compared to the wild-type strain. The <i>Dunaliella salina</i> KU18 mutant showed significant differences in chlorophyll and total carotenoid ratio	[114]

Conclusions

Microalgae metabolism depends on changes in cultivation parameters, the type of microalgae and the content of components of the growth medium. The analysis demonstrates the importance of understanding and optimizing physicochemical factors to increase the productivity of biosynthesis of useful substances by microalgae.

Low concentrations of metals can stimulate the growth of microalgae, while high concentrations can lead to toxic effects or stress. Ferum to a concentration of 50 mg/l has a positive effect on *Chlorella vulgaris* [39], *Chlorella pyrenoidosa* [36] and *Dunaliella salina* [10], stimulating their growth and biosynthesis of useful substances. A similar positive effect is observed for copper to a concentration of 20 mg/l for *Chlorella vulgaris* [41, 31], but at a concentration of 50 mg/l inhibits growth and reduces the content of chlorophylls and carotenoids [41]. Cadmium at concentrations up to 0.4 mM promotes the growth of biomass and lipid content in *Chlorella minutissima* [33], and zinc to a concentration of 6 mM in *Chlorella minutissima* [33] and up to 50 mg/l in *Chlorella vulgaris* [41] increases the lipid content. At concentrations above 100 mg/l, most metals inhibit the growth of microalgae. The mechanism of action of metal ions is associated with their ability to influence the activity of enzymes involved in biosynthesis. At the same time, high concentrations of heavy metals can lead to the formation of reactive oxygen species that cause oxidative stress and damage to cellular structures, but the action of short-term abiotic stress factors can stimulate the metabolism of microalgae. Increasing the content of metal ions can act as an activator and inhibitor of the biosynthesis processes of various metabolites: lipids, carotenoids, chlorophylls, proteins and carbohydrates.

Light from different spectra has different effects on the synthesis of carotenoids, chlorophylls, and lipids in microalgae, with the blue spectrum generally increasing carotenoids [60, 68, 70, 73], the green spectrum increasing chlorophylls [50, 63, 67, 75, 76], and the yellow and blue spectrum increasing lipids [60, 62, 65, 66, 74], although there are conflicting results regarding specific species and conditions. The effect of light intensity also varies: an increase in light intensity often contributes to an increase in the content of carotenoids and lipids, but may reduce the content of chlorophylls and other compounds.

Ultrasonic irradiation and UV/ γ radiation can increase lipid and biomass content in microalgae. So, ultrasound at low power can increase the content of lipids and chlorophylls, but at strong power it inhibits growth and metabolism in microalgae [19, 92, 96]. The mechanism of action of ultrasound is associated with mechanical effects on cell walls, which facilitates the transport of nutrients and the release of metabolites. UV radiation accelerates the synthesis of neutral lipids, while γ radiation promotes the accumulation of unsaturated fatty acids, but can also cause stress reactions depending on the dose, since excessive radiation can cause oxidative stress due to the formation of reactive oxygen species. γ radiation in small doses can stimulate the growth and synthesis of lipids, while higher doses lead to a decrease in biomass due to DNA damage [20, 110, 114]. The mechanism of action of γ radiation involves the induction of mutations and the activation of stress responses, which can both stimulate and inhibit biosynthesis.

In general, the spectrum and intensity of illumination, the frequency and duration of exposure to ultrasound, UV and γ radiation have an effect on the physiology of microalgae and have a positive or negative effect on the metabolism of various types of microalgae.

The potential of utilizing the aforementioned chemical and physical factors in microalgae cultivation biotechnologies lies in the ability to fine-tune the conditions for maximum synthesis of biologically active compounds. This opens new possibilities for their industrial use, particularly in the food industry for the production of dietary supplements, in the pharmaceutical sector for the manufacturing of medicinal products and bioactive substances, as well as in bioenergy for biofuel production.

Optimization of microalgae cultivation by physical and chemical action of abiotic factors for

maximum yield of useful substances should be based on an individual approach to each type of algae.

The presented analysis is the basis for further research and development of technological solutions for increasing the biosynthesis of useful substances by microalgae.

Interests disclosure

The authors have no conflicts of interest to declare.

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ВПЛИВ ХІМІЧНИХ І ФІЗИЧНИХ ФАКТОРІВ НА МЕТАБОЛІЗМ МІКРОВОДОРОСТЕЙ

Проблематика. Зміна метаболізму мікроводоростей під дією хімічних і фізичних факторів середовища для отримання корисних речовин.

Мета. Узагальнення літературних даних щодо впливу підвищеного вмісту іонів важких металів, режимів освітлення, ультразвукового, ультрафіолетового та гамма-опромінення на продуктивність різних видів мікроводоростей та біосинтез каротиноїдів, хлорофілів і ненасичених жирних кислот мікроводоростями.

Методика реалізації. Аналіз літературних джерел щодо впливу підвищених концентрацій іонів важких металів та дії різних режимів освітлення, ультразвукового, ультрафіолетового та γ -опромінення на біосинтез корисних речовин мікроводоростями.

Результати. Вплив хімічних і фізичних факторів середовища на біосинтез корисних речовин у мікроводоростях є індивідуальним для кожного виду. Підвищений вміст іонів металів може виступати як активатором, так й інгібітором процесів біосинтезу різних метаболітів: ліпідів, каротиноїдів, хлорофілів, білків і вуглеводів. Спектр та інтенсивність освітлення, частота і тривалість опромінення ультразвуком, ультрафіолетом і гамма-опроміненням приводять до зміни метаболізму мікроводоростей, характерного для певного виду.

Висновки. Метаболізм мікроводоростей залежить від змін параметрів культивування, виду мікроводоростей і вмісту компонентів середовища вирощування. Оптимізація культивування мікроводоростей за хімічної та фізичної дії абіотичних факторів для максимального виходу корисних речовин має базуватись на індивідуальному підході до кожного виду водоростей. Представлений аналіз є підґрунтям для подальшого дослідження та розробки технологічних рішень підвищення біосинтезу корисних речовин мікроводоростями.

Ключові слова: мікроводорості; іони важких металів; освітлення; ультразвук; УФ-опромінення; гамма-опромінення; каротиноїди; хлорофіли; жирні кислоти.