Journal of Environmental Chemical Engineering 13 (2025) 119171

Contents lists available at ScienceDirect

Journal of Environmental Chemical Engineering

journal homepage: www.elsevier.com/locate/jece

Stimulation of microalgae growth and high-value compounds production by magnetic field exposure

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ARTICLE INFO

Keywords:
CO2 uptake
Magnetic field
Microalgal growth
Oxidative stress
Pigment production

ABSTRACT

This study evaluated the effect of magnetic field (MF) intensities of 30, 60, and 120 militeslas (mT) applied for daily exposure times of 1, 2, or 4 h on the growth, CO2 uptake, and pigment production of Chlorella vulgaris, Coelastrella sp., and Arthrospira platensis. The results support the emerging consensus that MF intensities between 30–60 mT generally enhance biological activity, while 120 mT may induce stress and inhibit growth. Specifically, 60 mT significantly enhanced CO2 uptake and O2 production in C. vulgaris and Coelastrella sp., suggesting an intensification of photosynthetic activity. In contrast, 120 mT inhibited growth and CO2 uptake, particularly in A. platensis and Coelastrella sp. However, for C. vulgaris, exposure to 120 mT for 1 h per day produced contrasting effects, with a reduction in biomass productivity and growth, but a 26 % increase in chlorophyll content. At lower intensities, pigment production was also selectively enhanced, with carotenoids in Coelastrella sp. increasing by 51 % at 30 mT for 2 h per day, and phycocyanin in A. platensis rising by 53 % at 30 mT for 4 h per day. These findings indicated the presence of a magnetic "window" where specific field conditions optimized physiological responses in microalgae, supporting the potential use of MF in CO2 capture technologies coupled with the production of high-value biomolecules.

1. Introduction

The uncontrolled release of anthropogenic CO_2 emissions into the atmosphere accounted for 36,300 million tons in 2021, which exceeded the Earth's capacity to capture and fix CO_2. This fact has triggered the need to find sustainable technologies to capture CO_2 and counteract its pernicious environmental and economic effects [1,2]. Recently, the cultivation of photosynthetic microorganisms has demonstrated to be an effective approach to simultaneously recover CO_2 and nutrients from wastewaters or off-gases. More specifically, microalgae stand as a promising biorefinery platform since they can fix CO_2 at a 50-times-higher rate than terrestrial plants and can use inorganic sources of nitrogen and phosphorus for biomass growth [3]. Additionally, the produced algal biomass can serve as a precursor for the synthesis of biofuels or high-value added chemicals including pigments [1,4].

Among the wide range of microalgae species, *Chlorella vulgaris*, *Coelastrella* sp. and *Arthrospira platensis* have demonstrated robustness when cultivated under extreme environments, achieving high biomass growth rates, and specific biomolecules accumulation under certain stress culture conditions. For instance, the rapid growth rate of *C. vulgaris* along with its high CO_2 tolerance has positioned this species as a workhorse for wastewater treatment and biofuel production [5,6]. Moreover, *Coelastrella* sp. has been used in the energy sector due to its rapid growth rate (with an increase of 90–343 mg of volatile suspended solids (VSS) L^{-1} d^{-1}), high lipid accumulation (13–36 % DW) and ability to accumulate carotenoids under stress conditions [7]. On the other hand, *A. platensis,* commonly known as *Spirulina,* is a filamentous cyanobacterium widely studied for CO_2 mitigation, with a growth rate of $\approx$ 800 mg VSS L^{-1} d^{-1} additionally, a high nutritive value and the capacity to produce bioactive substances such as phycocyanin [8,9]. Despite the environmental and techno-economic advantages of microalgae, their large-scale cultivation still presents some drawbacks that must be overcome to make the process profitable. The main challenge of mass cultivation of microalgae is their low photosynthetic efficiency, which typically ranges between 1 % and 2 %.

In this context, different strategies have been implemented to

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https://doi.org/10.1016/j.jece.2025.119171
Received 23 July 2025; Received in revised form 27 August 2025; Accepted 6 September 2025
Available online 9 September 2025

improve microalgae biological performance including new photobioreactor designs [10], genetic engineering [11], and stimulation of microalgae metabolism by the addition of nanomaterials or by physical mechanisms such as exposure to ultrasound or magnetic fields (MF) [12]. Recently, the exposure to MF has emerged as a cost-effective technique to stimulate microalgae metabolism based on its negligible energy consumption and the absence of hazardous by-products. MFs can catalyze biological and physicochemical mechanisms as function of the bioprocess, MF intensity and the exposure time [13–16]. For instance, *Scenedesmus obliquus* was exposed to a MF of 100 milliteslas (mT) for 30 min d^{-1} for 6 days with an increase in biomass and oxygen production of 11.4 and 24.6 %, respectively [15]. Similarly, [14] evaluated the effect of different MF intensities (0, 20, 40, 80 and 150 mT) on the performance of a *C. vulgaris* and *Bacillus* consortium. The exposure to 80 mT increased cellular density by 29 % after 16 days of exposure. Moreover, exposures to 150 mT promoted an oxidative stress response of *C. vulgaris,* which negatively affected EPS secretion and decreased the number of aggregates by 29 % [14]. On the other hand, [17] evaluated the effect of intermittent (1 h d^{-1}) MF exposure on *Chlorella fusca* to 30 and 60 mT, and observed that *C. fusca* growth was increased by 34 %, regardless of the MF intensity. Additionally, CO_2 fixation was increased by 50 % when *C. fusca* was exposed to 60 mT, whilst the protein content in EPS increased by 56 % when exposed to 30 mT. Similarly, [18] observed that the lipid content of *Spirulina* sp. LEB 18 increased by 14 and 45 % when exposed to 30 mT for 12 and 24 h d^{-1}, respectively. In brief, MF has the potential to boost microalgae growth and metabolism by modulating the synthesis of carbohydrates, proteins, and lipids. However, more research is needed to explore the potential of MF to mitigate CO_2 emissions while enhancing the production of high-value-added products.

In this context, the aim of this study was to investigate the effect of different MF intensities (30, 60, and 120 mT) and exposure times (1, 2, and 4 h per day) on the growth and pigment production of *Chlorella vulgaris*, *Coelastrella* sp., and *Arthrospira platensis*. CO_2 fixation, biomass growth and the synthesis of biomolecules (i.e. proteins, carbohydrates, lipids, and pigments) were systematically determined to assess the effect of the MF on microalgal metabolism.

2. Material and methods

2.1. Microalgae strains and culture conditions

C. vulgaris (SAG 211–11b) and *Arthrospira platensis* (SAG 21.99) were originally purchased from the Culture Collection of Algae of the University of Göttingen (SAG, Germany), while *Coelastrella* sp. was obtained from the culture collection MAC-CWU (WDCM 886) of V.N. Karazin Kharkiv National University (Ukraine). Prior to the batch assays, an inoculum of each strain was grown as follows: *C. vulgaris* in BG11 medium, *Coelastrella* in BBM medium, and *A. platensis* in a modified Zarrouk medium with a concentration of 7 g L^{-1} of $NaHCO_3$. The inocula were cultivated in 250 mL serum bottles with an effective mineral salt medium volume of 60 mL and containing 30 % (v v^{-1}) CO_2 in the air headspace. The cultures were incubated at 25 ºC under continuous illumination (≈350 μmol m^{-2} s^{-1}) and agitation at 150 rpm.

2.2. Magnetic field exposure

MF intensities of 30, 60, and 120 mT, and exposure times of 1, 2, and 4 h per day (hereafter referred to as 1, 2, and 4 h d^{-1}) were tested in the three model microalgae. MF were generated by neodymium magnet blocks (60 × 20 × 5 mm) (Superimanes, Spain), and the different intensities were achieved by modifying the number of magnets placed on each side of the glass bottles. The MF intensity was determined by measuring the MF with a Teslameter (KKnoon, Spain) at different points, varying the heights of the measurement sites inside the bottles, obtaining an average MF of 30, 60, and 120 mT for each arrangement of magnets. The results of the average MF intensity at the different measured heights are shown in the supplementary material (Table S1).

2.3. Experimental set-up

Batch experiments were carried out in triplicate in 250 mL serum bottles with an effective liquid volume of 60 mL. The bottles were filled with the respective mineral medium for each microalgae (BG11 for *C. vulgaris*, BBM for *Coelastrella* sp. and modified Zarrouk for *A. platensis*) and sealed with butyl septa and aluminum caps. Then, the headspace of the bottles was replaced by flushing N_2 (Carburos Metalicos, Spain) for 5 min, and subsequently pure CO_2 was injected until a concentration of 30 % (v v^{-1}) was reached in the headspace. Then, the bottles were inoculated with the corresponding microalgae at an initial optical density (OD_{750}) of 0.3, and incubated at 25 ºC and 150 rpm under continuous illumination of ≈ 375 μmol m^{-2} s^{-1} provided by visible LED lights (PHILLIPS, Spain). Gas samples of the headspace (100 μl) were collected twice daily to measure CO_2 and O_2 concentrations, while liquid samples (1 mL) were taken simultaneously to assess OD_{750}, pH, and photosynthetic activity.

The effect of the MF on microalgae growth and metabolism was evaluated by cultivating the strains under subsequently growing cycles of the cultures until a significant change in the patterns of growth, CO_2 uptake, and O_2 release was detected. Specifically, when the CO_2 present in the headspace was completely depleted and the OD_{750} reached a steady state, an aliquot of the culture was collected and used as inoculum for a new batch (fresh medium, 30 % of CO_2 in the headspace, initial OD_{750} of 0.3). This procedure, referred to as "dragging process", was repeated for a total cultivation period of 8–9 days (Fig. 1). The control systems were handled identically to the MF-exposed treatments, except that no MF was applied. Once the last culture cycle was completed, the microalgal biomass was harvested for macromolecular (lipids, protein, and carbohydrates) and pigment analysis.

2.4. Analytical procedures

2.4.1. Microalgae growth and CO_2 fixation

Microalgae growth was determined by daily measuring the OD_{750}. Biomass concentration was then estimated based on an external calibration curve relating OD_{750} to VSS (expressed as g VSS L^{-1}), which represents the organic fraction of the culture and therefore provides a quantitative measure of microalgal biomass. CO_2 and O_2 concentrations were measured twice a day by gas chromatography with thermal conductivity detection (CP-3800 GC-TCD Varian, Palo Alto, USA) according to [19]. The pH and photosynthetic activity (Quantum yield, QY) were determined twice a day with a pH meter SensION™ + PH3 pHmeter (HACH, Spain) and a fluorometer AquaPen AP 110 C (Photon Systems Instruments, Drasov, Czech Republic), respectively.

Microalgae biomass productivity was calculated during the exponential phase according to Eq. (1):

$$\boldsymbol{Px} = \frac{DW1 - DW0}{t1 - t0} \quad (1)$$

where Px is the biomass productivity (g L^{-1} d^{-1}), *DW1* and *DW0* are the biomass dry weight (g VSS L^{-1}) at time t_1 and t_0 (d) during the exponential growth phase.

The specific growth rate was calculated during the exponential phase according to Eq. (2):

$$\boldsymbol{\mu} = \frac{\ln(DW1) - \ln(DW0)}{t1 - t0} \quad (2)$$

where μ represents the specific growth rate (d^{-1}).

2.4.2. Biomass composition and pigment quantification

To determine the protein, carbohydrate and lipid content, the

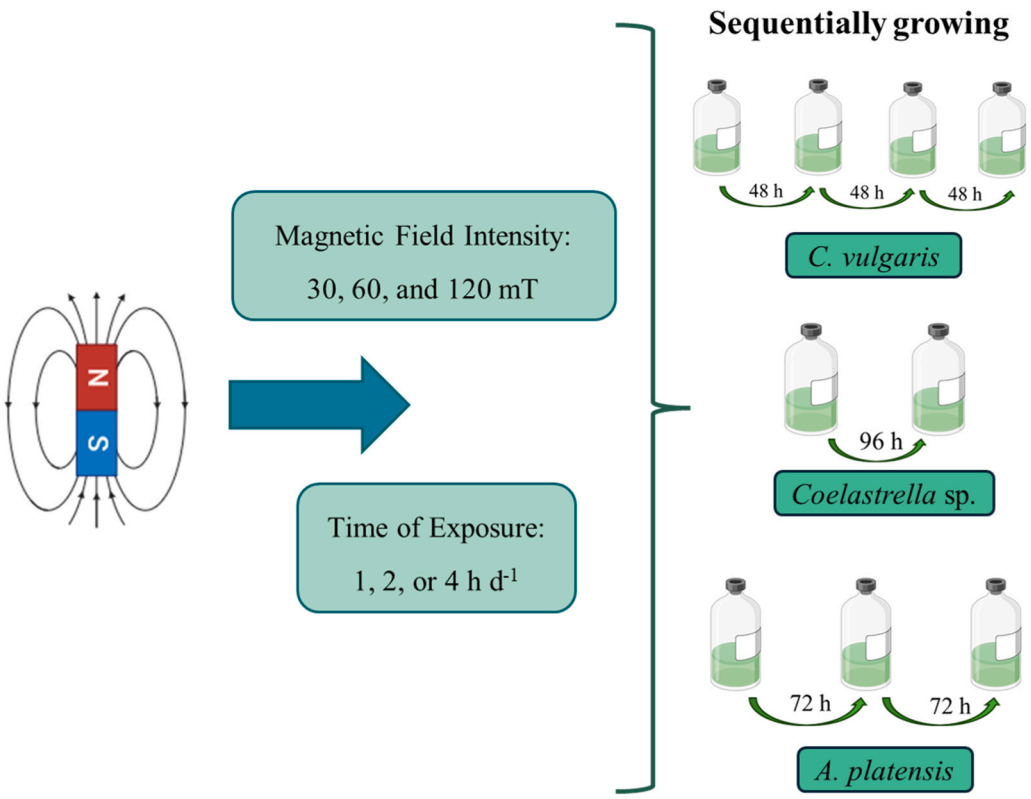

Fig. 1. Magnetic field intensity and time of exposure tested in *Chlorella vulgaris*, *Coelastrella* sp., and *Arthrospira platensis* cultures.

microalgae biomass was centrifuged at 3500 rpm for 15 min, frozen at − 30 °C and finally freeze-dried (− 55 °C, 0.101 mbar). Protein content was determined following the procedure of BCA protein assay kit; carbohydrate content was determined by a modified phenol-sulfuric acid method [20]; and the total lipid content was determined by the phosphovanillin method [21].

Total chlorophyll and carotenoids were extracted with acetone (100 %, v v^{-1}). Briefly, 1 mL of the final biomass of *C. vulgaris* and *Coelastrella* sp. was centrifuged at 10,000 rpm for 10 min, the supernatant was removed and the biomass was resuspended in 1 mL of pure acetone. Then, the samples were incubated at 4 ºC for 24 h and then centrifuged at 10,000 rpm for 10 min. The pigments were quantified by spectrophotometry (spectrophotometer UV - Vis 2550, Shimadzu, Japan) at absorbances of 644 nm (A_{644}) and 661 nm (A_{661}) for Chl, and 470 nm (A_{470}) for carotenoids. The total chlorophyll and total carotenoids concentrations were calculated using Eqs. 3–6 [22]:

$$\text{Total chlorophyll (mg L}^{-1}) = 7.05A_{661} + 18.06A_{644} \quad (3)$$

$$\mathbf{Total carotenoids}\left(\mathbf{mgL^{-1}}\right) = \frac{100 * A_{470} - 1.90Chl_a - 63.14Chl_b}{214} \quad (4)$$

$$\mathbf{Chl_a\ (mg\ L^{-1})} = 11.24A_{661} - 2.04A_{644} \quad (5)$$

$$\mathbf{Chl_b\ (mg\ L^{-1})} = 20.13A_{644} - 4.19A_{661} \quad (6)$$

Final concentration of total chlorophyll and total carotenoids are expressed in the results section in mg $g_{biomass}^{-1}$ by dividing the calculated pigment concentrations by the final biomass content (g VSS L^{-1}).

Phycocyanin (C-PC) was extracted from *A. platensis* as follows: 1 mL sample was centrifuged at 10,000 rpm for 10 min, the supernatant was removed and the biomass was resuspended in 1 mL of phosphate buffer 20 mM, pH 8. Then, the samples were subjected to freeze-thawing periods of 24 h three times. The quantification of C-PC was conducted by spectrometry (spectrophotometer UV - Vis 2550, Shimadzu, Japan) by reading the absorbance at a wavelength of 620 nm (A_{620}). Total C-PC was calculated as follows (Eq. 7) [23]:

$$\mathbf{C-PC}\left(\mathbf{mgg^{-1}}\right) = \frac{A620 * Ve}{3.39 * DWs} \quad (7)$$

where Ve is the total volume of the sample (1 mL) and DWs is the biomass dry weight (g VSS).

2.5. Statistical analysis

The results are presented as mean values ± standard deviation. To assess the impact of the MF on microalgae, a t-student test was conducted to the final kinetic for each strain (after 8 or 9 days of cultivation) by comparing the systems exposed to the MFs with their respective controls, considering *p-value* $\leq$ 0.05.

3. Results and discussion

3.1. Influence of MF intensity and exposure time on microalgae growth

The results presented below correspond to the final cultivation of each strain. The results showed the responses to MF exposure in terms of CO_2 consumption, O_2 production, and biomass. Data from previous cultivation cycles are included in the Supplementary Material (Figs. S1, S2, and S3), which show trends in CO_2 uptake and O_2 production across successive generations of each strain.

The response of *C. vulgaris* cultures to MF stimuli was mainly driven by the exposure time followed by the MF intensity. The exposure of *C. vulgaris* to 30 mT for 2 h d^{-1} induced a 7 % increase in μ compared to the control (Table 1). Concomitantly, oxygen production showed an upward trend at 2 and 4 h d^{-1} of exposure time (Fig. 2d), which was correlated to an increased in biomass concentration by 7 and 5 % after 30 h of cultivation (Fig. 2g). Similarly, Px significantly increased with the exposure time up to 2 h d^{-1} (Table 1). Similarly, pH and QY also increased with longer exposure time (Table S2). The observed trend of

Table 1
Effects of magnetic field (MF) intensity (30, 60, 120 mT) and exposure time (1, 2, 4 h d^{-1}) on biomass productivity (Px) and specific growth rate (μ) after 8 days of cultivation for *C. vulgaris* and *Coelastrella* sp., and after 9 days of cultivation for *A. platensis*.

C. vulgaris

	Px (g L^{-1} d^{-1})			μ (d^{-1})		
	30 mT	**60 mT**	**120 mT**	**30 mT**	**60 mT**	**120 mT**
Control	1.37 ± 0.001	0.93 ± 0.057	1.29 ± 0.048	2.32 ± 0.031	1.41 ± 0.001	2.07 ± 0.015
1 h d^{-1}	1.42 ± 0.012 *	0.75 ± 0.077 *	1.04 ± 0.091 *	2.22 ± 0.073	0.97 ± 0.001 *	1.79 ± 0.081 *
2 h d^{-1}	1.58 ± 0.057 *	1.12 ± 0.039 *	1.28 ± 0.081	2.48 ± 0.058 *	1.63 ± 0.028 *	2.09 ± 0.069
4 h d^{-1}	1.52 ± 0.003 *	1.15 ± 0.021 *	1.45 ± 0.023 *	2.32 ± 0.082	1.69 ± 0.029 *	2.07 ± 0.007

***Coelastrella* sp.**

	Px (g L^{-1} d^{-1})			μ (d^{-1})		
	30 mT	**60 mT**	**120 mT**	**30 mT**	**60 mT**	**120 mT**
Control	0.55 ± 0.043	1.19 ± 0.055	0.63 ± 0.014	0.84 ± 0.021	1.26 ± 0.046	0.93 ± 0.020
1 h d^{-1}	0.57 ± 0.009	0.78 ± 0.009 *	0.72 ± 0.040 *	0.88 ± 0.003	0.75 ± 0.012 *	0.90 ± 0.031
2 h d^{-1}	0.92 ± 0.010 *	0.73 ± 0.001 *	0.74 ± 0.061 *	1.20 ± 0.006 *	0.71 ± 0.049 *	0.98 ± 0.049
4 h d^{-1}	0.58 ± 0.054	0.71 ± 0.018 *	0.63 ± 0.008	0.72 ± 0.022 *	0.79 ± 0.016 *	0.84 ± 0.029 *

A. platensis

	Px (g L^{-1} d^{-1})			μ (d^{-1})		
	30 mT	**60 mT**	**120 mT**	**30 mT**	**60 mT**	**120 mT**
Control	0.78 ± 0.050	0.63 ± 0.039	0.68 ± 0.065	0.97 ± 0.035	0.94 ± 0.002	0.92 ± 0.067
1 h d^{-1}	0.64 ± 0.025 *	0.81 ± 0.065 *	0.61 ± 0.051	0.93 ± 0.009	1.07 ± 0.049 *	0.95 ± 0.044
2 h d^{-1}	0.56 ± 0.003 *	0.86 ± 0.039 *	0.45 ± 0.045 *	0.82 ± 0.010 *	1.05 ± 0.035 *	0.77 ± 0.042 *
4 h d^{-1}	0.52 ± 0.030 *	0.83 ± 0.068 *	0.39 ± 0.064 *	0.88 ± 0.005	1.02 ± 0.053	0.58 ± 0.035 *

* Significant differences compared to the control ($p \leq 0.05$)

increasing QY may reflect subtle improvements in photosystem II (PSII) efficiency and photochemical performance [24]. Together with the observed rise in oxygen concentration and Px, these results point to a coordinated stimulation of carbon assimilation and photobiological processes under MF. Previous studies have suggested that such responses may be linked to improved electron transport such as an enhanced cyclic electron flow or stabilization of PSII/PSI reaction centers [18,24,25].

Similarly, when the MF was increased to 60 mT, CO_2 consumption in *C. vulgaris* cultures was enhanced at 2 and 4 h d^{-1} of exposure (Fig. 2b), resulting in a final biomass concentration of 1.68 and 1.70 g VSS L^{-1}, respectively (Fig. 2h). The parameters μ and Px significantly increased by 20 and 24 % at 4 h d^{-1}, which represented the largest increment recorded at a MF intensity of 60 mT. Consistently, QY values rose by approximately 10–12 % under exposures of 2 and 4 h d^{-1}, suggesting an upregulation in PSII efficiency (Table S2). Interestingly, a shorter daily exposure of 1 h d^{-1} resulted in a marked decrease in μ and Px by 31 and 21 %, respectively, indicating that *C. vulgaris* requires a minimum threshold of exposure to activate beneficial responses. This contradictory effect under 60 mT could be related to acute stress that disturbs redox balance and ion homeostasis, leading to elevated reactive oxygen species (ROS) generation and impaired photosystem performance [26, 27]. However, when exposure is extended 2–4 h d^{-1}, cells may initiate compensatory mechanisms such as enhanced antioxidant activity, remodeling of thylakoid membranes, and acceleration of the repair of the D1 protein in PSII, which collectively stabilize photosynthetic function and promote carbon fixation. Thus, the contrasting outcomes observed at 1 h d^{-1} versus 2 and 4 h d^{-1} of exposure may reflect a time-dependent balance between stress induction and adaptive acclimation. These findings are consistent with previous reports showing enhanced growth of *Chlorella* species under intermediate intensities of MF exposure (20–200 mT), provided that exposure-specific times are needed to trigger adaptive acclimation [14,28,29].

Finally, when the MF was increased to 120 mT, Px in *C. vulgaris* cultures exposed for 4 h d^{-1} increased by 13 %, whilst shorter exposure times (1 and 2 h d^{-1}) resulted in a delayed CO_2 uptake and lower growth (Fig. 2c). Interestingly, exposures of 1 h d^{-1} significantly reduced Px and μ by 20 and 15 %, respectively. This may reflect a threshold adaptation response, where 120 mT MF intensity requires longer exposure time to trigger *C. vulgaris* metabolic adjustments or cellular compensation mechanisms. While *C. vulgaris* benefited from exposures at 30 and 60 mT for both 2 and 4 h d^{-1}, only the longest time of exposure (4 h d^{-1}) at 120 mT mediated positive effects, suggesting that both intensity and duration of MF exposure influence *C. vulgaris* metabolism, but not in a linear or dose-dependent manner. This behavior is consistent with the known resilience of *C. vulgaris* to abiotic stressors, including oxidative, thermal, and salinity fluctuations, suggesting that high-intensity MF may initially act as a stressor, requiring sufficient exposure time to activate protective or acclimatory responses [30].

On the other hand, even if *Coelastrella* sp. is recognized as a robust high-value producer under extreme environmental conditions, its growth was significantly affected by the MF intensity. Similar to *C. vulgaris* cultures, a low exposure time (1 h d^{-1}) induced growth inhibition on *Coelastrella* sp. Nonetheless, exposure to 30 mT for 2 h d^{-1} resulted in the highest Px and μ, which increased significantly by 67 % and 42 %, respectively. QY presented the same tendency, suggesting that the exposure to 30 mT for 2 h d^{-1} enhanced the energy conversion efficiency and improved the PSII performance (Table S3). This improvement may be attributed to an accelerated electron transport or an increased CO_2 permeability across the cell membrane [24,31]. Additionally, MFs influence the solubility and diffusion of CO_2, which is a diamagnetic molecule, by altering its spatial orientation and mobility in the medium. These effects potentially increase the bioavailability of inorganic carbon, thereby supporting photosynthetic activity under magnetic stimulation [32]. However, increasing the exposure time to 4 h d^{-1} caused a 15 % decline in Px likely due to an induced oxidative stress mediated by an excessive ROS production, which impaired metabolic enzymes, membrane integrity, or DNA stability [28,33–37].

The exposure of *Coelastrella* sp. cultures to 60 mT resulted in a significant decrease in the Px by 34, 38, and 40 % at 1, 2, and 4 h d^{-1}, respectively (Table 1). Additionally, QY values dropped alongside pH, with a marked lower final pH with increasing exposure time, indicating both a reduced photosynthetic activity and a potential disruption of bicarbonate uptake mechanisms (Table S3). This was supported by the retarded CO_2 uptake in the cultures exposed to the MF, particularly for 2 and 4 h d^{-1} (Fig. 3b). These results suggest that 60 mT exceeds the physiological tolerance of *Coelastrella* sp., leading to metabolic stress likely mediated by oxidative damage, impaired electron transport, or ionic imbalances [35]. Interestingly, the biomass concentration in the cultures exposed for 2 h d^{-1}, after 84 h of experimentation, was 10 % higher compared to the control (2.23 vs 2.01 g VSS L^{-1}). This uncoupling of carbon assimilation from biomass production suggests that *Coelastrella* sp. may be redistributing internal carbon pools to the production of biomolecules as a protective response to the MF exposure [38]. Finally, increasing the MF to 120 mT resulted in a retarded CO_2 uptake regardless of the exposure time (Fig. 3c). Particularly, at 1 and 4 h d^{-1} of exposure, the oxygen concentration in the headspace significantly decreased, nonetheless the Px increased by 12 % at 2 h d^{-1},

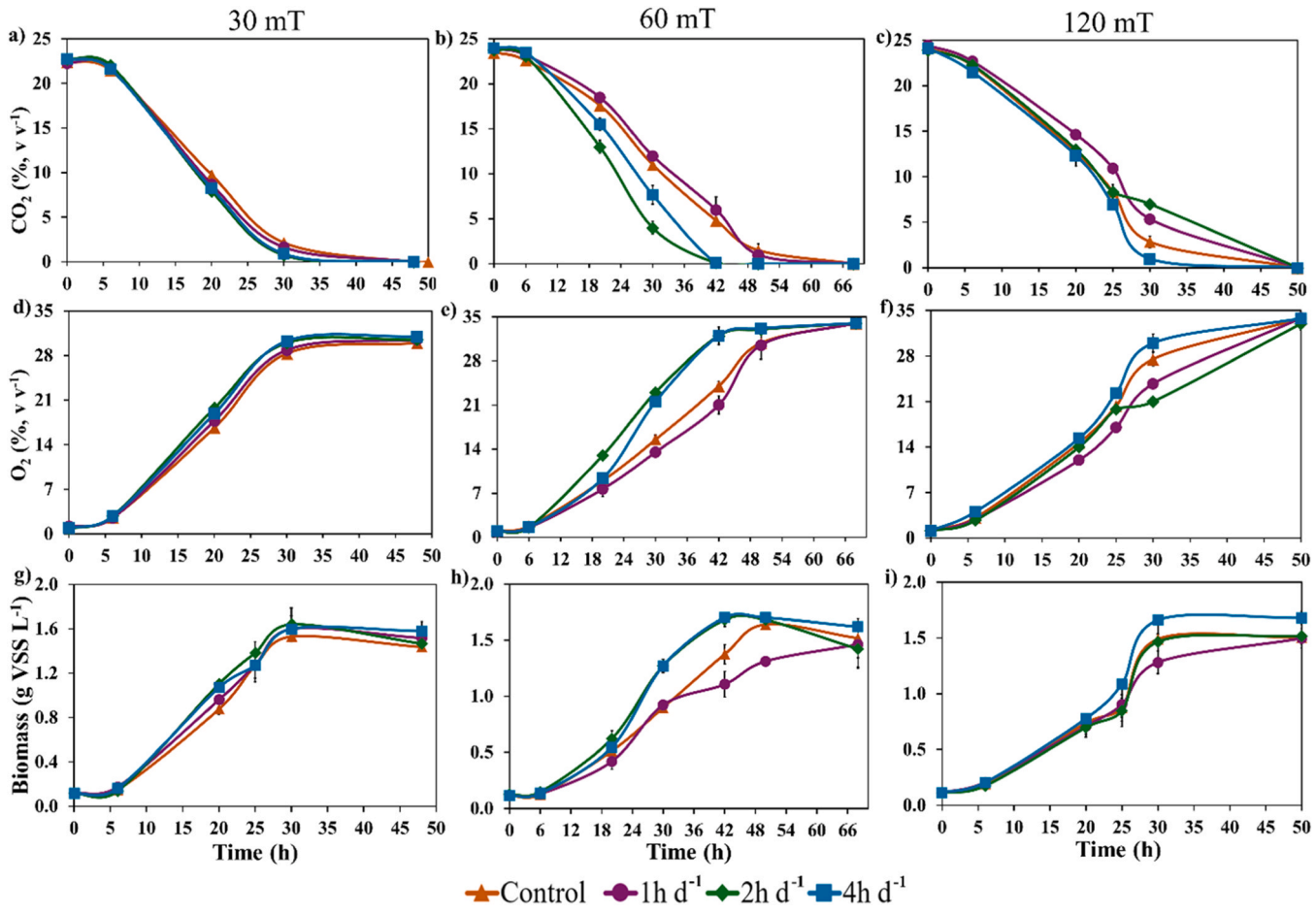

Fig. 2. Time course of the influence of the exposure time of *C. vulgaris* to 30, 60 and 120 mT on CO_2 consumption (a, b, c), O_2 production (d, e, f), and biomass concentration (g, h, i).

which suggested changes in the intramolecular composition of *Coelastrella* sp.

A. platensis cultures exhibited a different response to MF exposure compared to *C. vulgaris* and *Coelastrella* sp., since this cyanobacterium was significantly sensitive to the exposure time at MF intensities of 30 and 60 mT. In this sense, the exposure to 30 mT for 1 and 2 h d^{-1} promoted biomass accumulation, reaching 1.55 and 1.42 g VSS L^{-1}, respectively, which was supported by an increased oxygen production (Fig. 4d). These findings suggest a transient enhancement of photosynthetic activity under short-term MF exposure. QY remained statistically similar to the control at 1 h d^{-1} of exposure, but a decrease in QY was observed at 2 h d^{-1} (Table S4), suggesting the onset of inhibition mediated by ROS accumulation, which could impair PSII reaction center efficiency [24]. In this way, the increased biomass concentration, particularly at 2 h d^{-1} of exposure, suggests an accumulation of specific macromolecules as a protective oxidative response rather than to cell production. Moreover, increasing the exposure time to 4 h d^{-1} resulted in a decline in biomass concentration and oxygen production, along with a sustained 13 % reduction in QY. Hence, the inhibitory effects of the MF on *A. platensis* were extended to carbon assimilation and to the overall metabolic function.

Interestingly, the exposure to 60 mT enhanced *A. platensis* growth, regardless of the time of exposure. The highest biomass concentration was reached after 54 h in the cultures exposed for 2 h d^{-1} (1.53 g VSS L^{-1}), followed by 1 h d^{-1} (1.47 g VSS L^{-1}) and 4 h d^{-1} (1.42 g VSS L^{-1}), and the control (1.17 g VSS L^{-1}). Similarly, Px increased by 29, 38 and 32 % at 1, 2, and 4 h d^{-1} of exposure, respectively. This finding revealed *A. platensis* tolerance to MF, potentially due to its simpler thylakoid organization or robust stress adaptation mechanisms [39,40]. Additionally, the QY values increased in the cultures exposed to MF (Table S3), with a significant increment at 1 h d^{-1} compared to the control, which indicated an enhanced PSII efficiency [24,41].

Contrary, *A. platensis* cultures exposed to 120 mT experienced an inhibitory effect regardless of the daily exposure time (Fig. 4c). The MF reduced *A. platensis* μ and Px with increasing the time of exposure by 5, 30, and 42 % for 1, 2 and 4 h d^{-1}, respectively. This was supported by the decrease in QY values (Table S4), suggesting a progressive impairment of PSII efficiency [24]. The different effects of MF intensity on cyanobacteria metabolism have been extensively reported. For instance, a high-intensity MF may exacerbate the formation of ROS, disrupt membrane integrity, or impair photosynthetic protein complexes, ultimately leading to growth inhibition [42,43]. Previous studies have shown that *Spirulina platensis* experiences reduced μ (up to 11 %) under MF intensities above 100 mT [44], while moderate intensities (5–30 mT) enhance both growth and pigment accumulation [45].

In this context, *A. platensis* exhibited a limited tolerance for low MF intensities and time of exposure, whilst an extended exposure time triggered inhibitory effects. These findings are in agreement with previous studies in cyanobacteria showing that prolonged MF exposure can boost ROS production, leading to oxidative damage in photosynthetic membranes [46]. This heightened sensitivity may stem from the unique physiology of cyanobacteria, particularly due to their vulnerability to redox imbalances. Their cultivation in high-pH media increases CO_2 solubility, which may also induce fluctuations in redox potential, which could compromise CO_2 uptake efficiency. These factors likely contribute to ionic or oxidative imbalances, limiting the potential benefits of MF

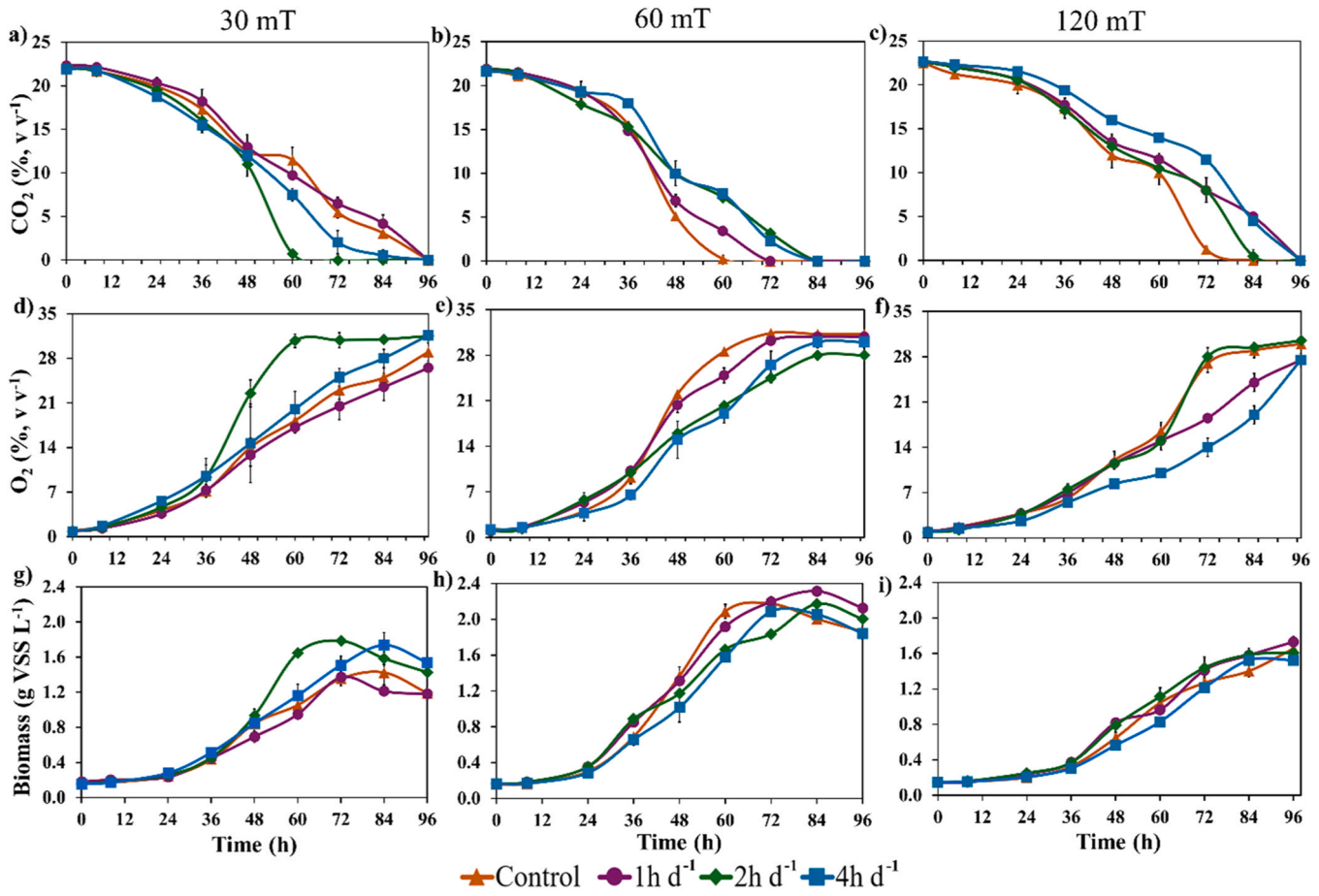

Fig. 3. Time course of the influence of the exposure time of *Coelastrella* sp. to 30, 60 and 120 mT on CO_2 consumption (a, b, c), O_2 production (d, e, f), and biomass concentration (g, h, i).

exposure in *A. platensis* cultures [31,47].

The differential responses observed among *C. vulgaris*, *Coelastrella* sp., and *A. platensis* under MF exposure can be attributed to their inherent physiological and structural differences, which determine how each strain perceives and adapts to electromagnetic stimuli. In *C. vulgaris*, the relatively flexible thylakoid organization and robust redox homeostasis allow cells to tolerate moderate intensities and to engage compensatory mechanisms such as enhanced antioxidant activity and PSII repair when stress thresholds are exceeded. By contrast, *Coelastrella* sp., despite being a robust extremophile, appears highly sensitive to MF intensities above 60 mT, suggesting that its thickened cell wall and distinct carbon assimilation pathways may impose diffusional or ionic constraints that exacerbate ROS accumulation under stronger fields. In cyanobacteria such as *A. platensis*, the simpler thylakoid structure and alkaline growth medium confer short-term tolerance at moderate intensities but also increase vulnerability to oxidative imbalances during prolonged or high-intensity exposures. Together, these species-specific traits—ranging from differences in thylakoid architecture and membrane composition to antioxidant capacity and carbon assimilation strategies—likely underlie the divergent physiological outcomes reported here. This highlights the importance of strain-dependent variability in the response to MF, consistent with previous reports demonstrating that microalgal taxa do not exhibit uniform magnetic sensitivity but instead reflect their unique evolutionary adaptations to environmental stressors [16,17,33].

3.2. Influence of MF intensity and exposure time on biomolecules accumulation

In *C. vulgaris,* MF exposure elicited distinct metabolic reallocations that depended on both intensity and exposure time. At 30 mT exposure, the protein content showed a significant increase with increasing time of exposure (Fig. 5g), with enhancements of 86, 93, and 106 % at 1, 2, and 4 h d^{-1} exposure, respectively. This suggests that the response of *C. vulgaris* to the MF is based on the modulation of the metabolic profile, particularly enhancing protein synthesis for biomass production, which was supported by the increased Px achieved under these conditions. On the other hand, *C. vulgaris* cultures exposed to 60 mT showed a metabolic response shifted toward lipid accumulation, which increased by 75, 125, and 130 % at 1, 2, and 4 h d^{-1} of exposure, respectively, whilst carbohydrate concentration was significantly reduced. These results indicate a diversion of carbon flux from carbohydrates to lipid pathways under oxidative stress conditions that promotes lipid biosynthesis as an adaptive response. Interestingly, these metabolic shifts did not compromise biomass productivity, contrasting with traditional lipid induction strategies based on nitrogen deprivation, which often suppress microalgal growth [48]. Similar enhancements in lipid content under MF exposure have been reported in *Chlorella kessleri* with lipid increments ranging between 22 % and 77 % at MF intensities of 30 and 60 mT for 1 h d^{-1} of exposure, respectively [49]. Moreover, the exposure of *Chlorella homosphaera* to 60 and 30 mT for 1 h d^{-1} increased the lipid content by 108 and 135 %, respectively, reinforcing the potential of MF as a non-invasive lipid induction strategy [50]. Similarly, the exposure of *C. vulgaris* cultures to 120 mT increased the lipid content by 100 and 50 % at 1 and 4 h d^{-1} of exposure, respectively. Notably, protein content

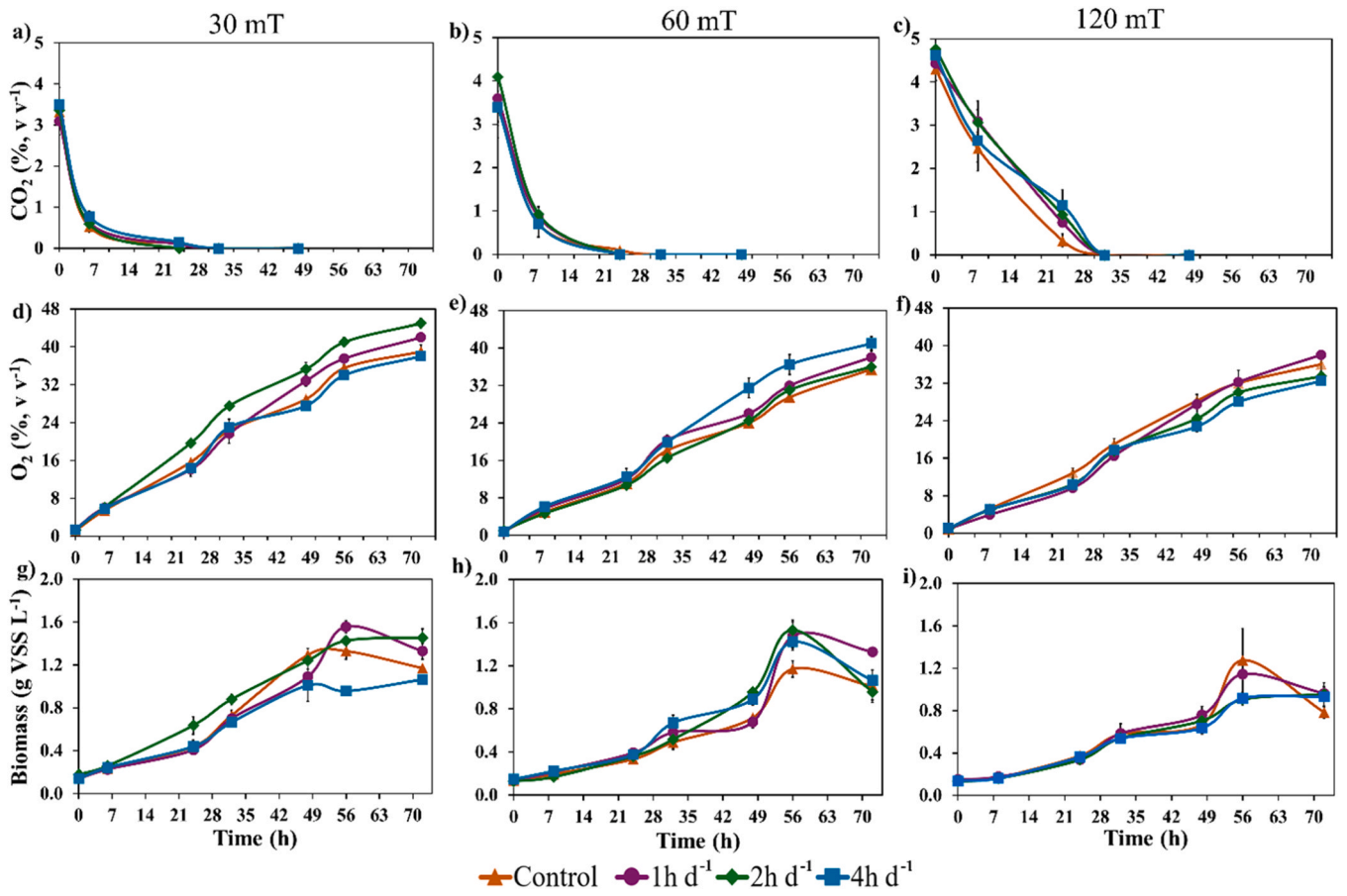

Fig. 4. Time course of the influence of the exposure time of *A. platensis* to 30, 60 and 120 mT on CO_2 consumption (a, b, c), O_2 production (d, e, f), and biomass concentration (g, h, i).

substantially increased under all exposure times, which suggests a greater regulation of biosynthetic activity, possibly due to an enhanced enzyme expression or membrane repair and protein turnover under elevated oxidative pressure. Such responses align with reports of increased expression of stress-protective proteins under strong MF exposure [51]. Together, these findings suggest that *C. vulgaris* can reconfigures its metabolism according to MF intensity and time of exposure: the lower intensity (30 mT) stimulates protein accumulation, the intermediate intensity tested (60 mT) promotes lipid synthesis, and the higher intensity probed (120 mT) activates broader stress responses.

The exposure of *Coelastrella* sp. exhibited more variable and stress-prone responses, reflecting a narrower tolerance window to MF stimulation. At 30 mT for 1 h d^{-1}, the lipid content significantly increased by 18 %. However, this lipid increase compromised biomass growth, suggesting that the exposure to MF resulted in oxidative stress for *Coelastrella* sp. Interestingly, the protein content decreased by 50 % after 2 h d^{-1} of exposure, while 4 h d^{-1} of exposure increased protein concentrations by 28 %. Such contrasting responses suggest a temporal adaptation mechanism, potentially linked to the induction of antioxidative enzymes such as superoxide dismutase (SOD) and peroxidase, as described by [52] in *C. vulgaris* under similar MF conditions. The decrease in protein content may reflect an initial oxidative damage and metabolic reallocation, while the recovery may indicate stress adaptation and reactivation of protein biosynthesis. The variable effects related to the time of exposure to MF could be related to the synthesis of antioxidative enzymes, which could be improved at longer periods of exposure. In this context, Wang and co-workers [52] observed that the exposure to 10–35 mT for 12 h d^{-1} promoted the growth of *C. vulgaris* and regulated the antioxidant defense system to protect the cells, increasing the activity of the SOD and peroxidase. In contrast, a two-fold increase in carbohydrate content, compared to the control, was recorded when *Coelastrella* sp. cultures were exposed to 60 mT for 4 h d^{-1}. Additionally, the protein content increased at 1 and 2 h d^{-1} of exposure by 18 and 25 %, respectively, indicating that moderate MF exposure triggered metabolic reallocation rather than a complete suppression. These findings suggest that MF exposure acted as a strong abiotic stressor for *Coelastrella* sp., as reflected by the reduced Px and QY values (Tables 1 and S2). The preferential accumulation of carbohydrates under stress may serve as a protective mechanism, possibly involving the synthesis of extracellular polysaccharides or cell wall remodeling [25, 53]. Finally, *Coelastrella* sp. cultures exposed to 120 mT consistently experienced a decrease in the carbohydrates, lipids, and proteins content, regardless of exposure time. These results suggest that the high-intensity MF exposure (120 mT) exceeded the physiological tolerance of this particular strain, leading to a widespread metabolic suppression and cellular damage. Thus, while *Coelastrella sp.* shows some adaptive capacity at moderate exposures, it is more sensitive than *C. vulgaris* to MF stress.

The exposure of *A. platensis* cultures also presented a response dependent on the MF intensity but differed from green microalgae. At 30 mT the carbohydrate concentration significantly decreased by 22 and 19 % under 1 and 2 h d^{-1} respectively (Fig. 5c), whereas protein content increased by 39, 22 and 13 % at 1, 2 and 4 h d^{-1} of exposure, respectively (Fig. 5i). This suggests a metabolic shift favoring protein synthesis for biomass production, which is supported by the increase in biomass content, by 14 %, observed at this particular MF intensity (Fig. 4g). When *A. platensis* cultures were exposed to 60 mT for 2 h d^{-1}, the carbohydrate content increased by 11 %, whilst the lipid content significantly increased under 1 and 2 h d^{-1} of exposure. Thereby, the increased biomass concentration under this MF was likely due to *A. platensis*

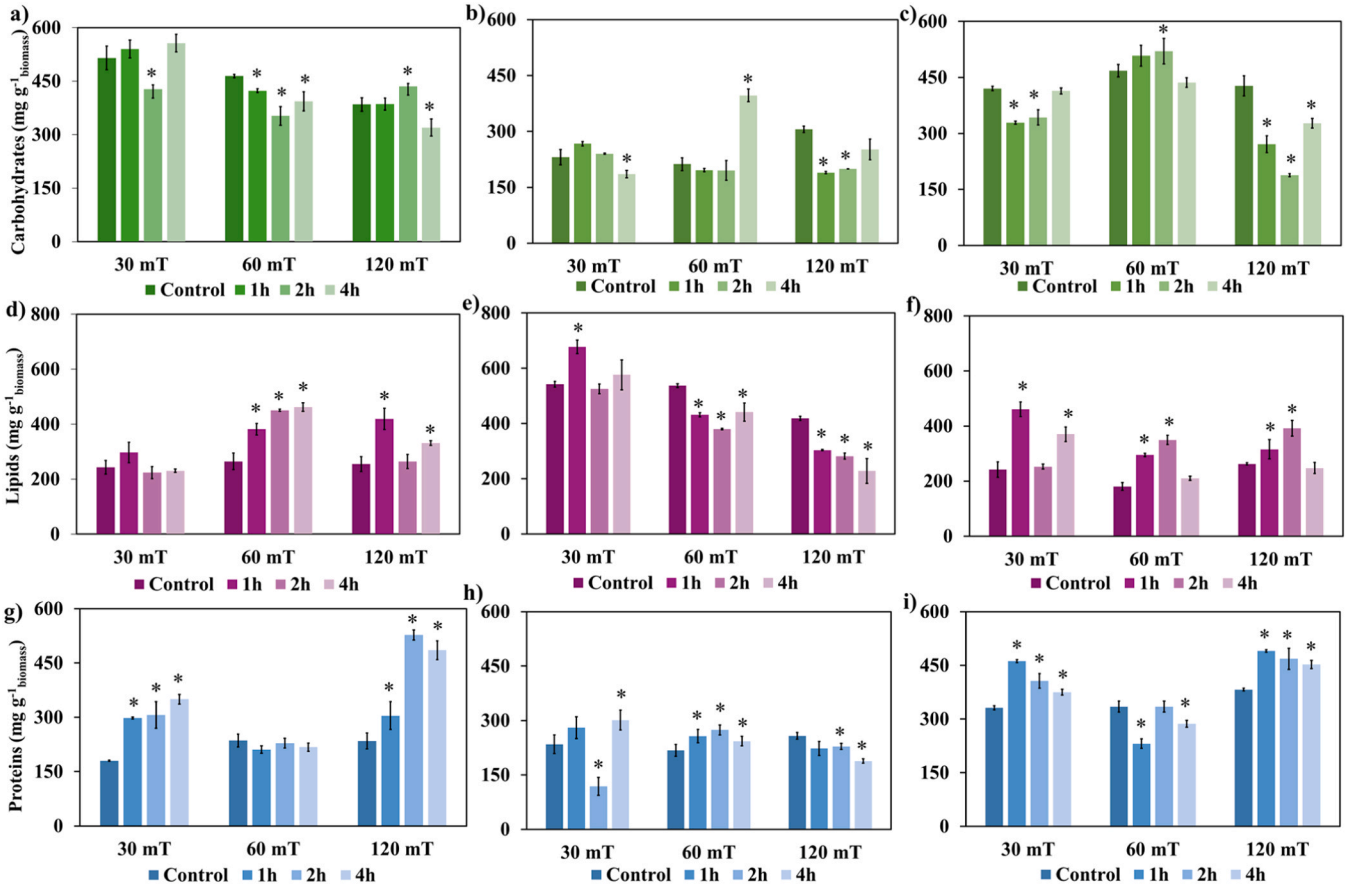

Fig. 5. Influence of MF intensity and exposure time on the final concentrations of carbohydrates (a, b, c), lipids (d, e, f) and proteins (g, h and i) of *C. vulgaris, Coelastrella* sp., *A. platensis*. *Significant difference compared to the control with $p \leq 0.05$.

increase cell size rather than enhance protein content (Fig. 5i). Interestingly, when the MF was increased to 120 mT, the protein content was significantly increased by 28, 22 and 18 % at 1, 2 and 4 h d^{-1} respectively, similarly to the lipid content. On the contrary, the carbohydrate content was significantly decreased regardless of the exposure time. This suggests that exposure to 120 mT in *A. platensis* relocates resources toward stress-related protein and lipid synthesis, potentially through transcriptional upregulation of biosynthetic or repair pathways [45].

The reallocations observed across the three strains can be mechanistically related to the interplay between MF exposure and cellular redox homeostasis. Several studies have suggested that MF can modulate the spin state of radical pairs, thereby altering ROS formation rate and leading to transient oxidative signals within the cell [54]. These ROS bursts serve as secondary messengers, activating the antioxidant defense system and influencing downstream transcriptional regulators and metabolic enzymes [55]. In *C. vulgaris*, the balance between moderate ROS signaling and antioxidant activation appears to favor anabolic processes such as protein or lipid synthesis, depending on the intensity, while *Coelastrella* sp. exhibits a narrower tolerance window in which ROS accumulation exceeds its antioxidant buffering capacity, leading to metabolic suppression. The response of *A. platensis* suggests a cyanobacteria-specific regulation, possibly involving redox-sensitive transcriptional regulators (e.g., RecA and transcriptional repressor LexA, where the former activates auto-cleavage of the latter to induce SOS response) that redistribute carbon fluxes toward protein and lipid biosynthesis under oxidative pressure [56,57]. Additionally, MF-induced changes in membrane potential and ion modulation biosynthetic pathways [35].

Overall, these findings demonstrate that MF exposure may act as a powerful modulator of microalgal growth and metabolic activity, with its effects determined by the interplay between intensity, exposure time, and species-specific tolerance. Rather than functioning solely as a growth enhancer, MF application promotes targeted metabolic reallocations-stimulating protein synthesis, enhancing lipid accumulation, or triggering carbohydrate storage depending on the conditions. Thus, this approach could be applied to a larger-scale cultivation system. For example, photobioreactors with permanent magnets or electromagnetic coils could be integrated into the reactor walls to ensure a homogeneous and adjustable field, while in open raceway ponds, magnetic devices could be positioned along channels or combined with recirculation through magnetically active zones. These strategies highpoint the potential of magnetic field application as a viable technology to enhance biomass productivity in biofuel generation, WWT, and other scale-up biotechnological applications.

3.3. Influence of MF intensity and exposure time on pigment production

The exposure of *C. vulgaris* cultures to MF tends to increase the chlorophyll content regardless of the MF intensity. However, this increment was modulated by both intensity and exposure time (Fig. 6a). Thus, the highest enhancement was recorded at 60 mT for 4 h d^{-1} of exposure, where chlorophyll content was 40 % higher than the control. Interestingly, this increment in chlorophyll content was correlated to an increased biomass concentration. Similar behavior was also observed at 30 mT for 4 h d^{-1}, with 15 % higher chlorophyll content compared to the control, reinforcing the relation between pigment content and photosynthetic efficiency.

The enhancement in chlorophyll content under moderate MF stimulation has been mechanistically associated with an increase in Fe uptake across the plasma membrane, supporting chlorophyll biosynthesis

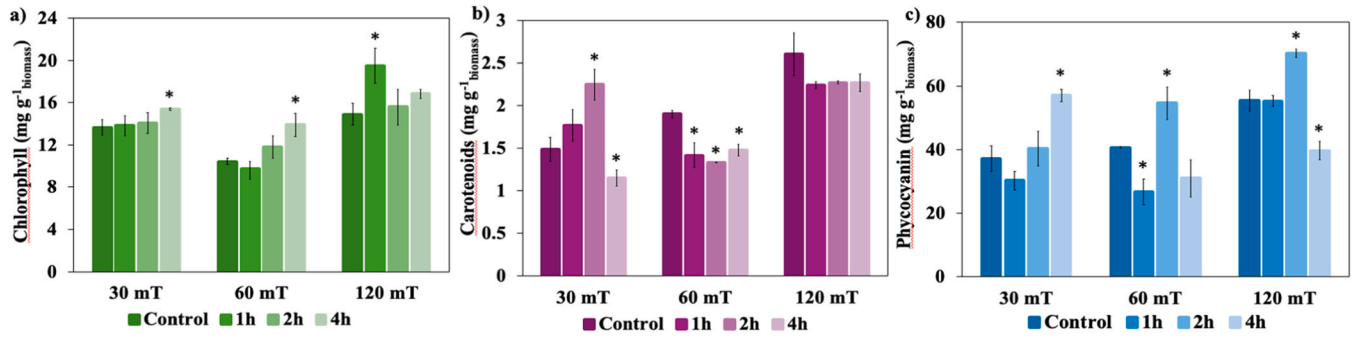

Fig. 6. Influence of MF intensity and exposure time on the chlorophyll content of *C. vulgaris* (a), carotenoid content of *Coelastrella sp*. (b) and phycocyanin content of *A. platensis* (c). * Significant difference compared with control $p \leq 0.05$.

and photosystem assembly [58]. Fe and Mg are essential cofactors for chlorophyll synthesis and photosynthetic protein complexes, indicating that MF induced modulation of ion transport through the cellular membrane transporters, enhancing the photosynthetic capacity [28,59,60].

However, the exposure of *C. vulgaris* cultures to the highest MF intensity (120 mT for 1 h d^{-1}) resulted in a 26 % increase in chlorophyll concentration, despite this condition resulting in significant reductions in Px and μ (Table 1). This decoupling between pigment accumulation and physiological performance suggests that, beyond a certain threshold, increased chlorophyll content does not necessarily translate into enhanced photosynthetic efficiency. In this case, elevated chlorophyll content may impair energy transfer within the photosystems or contribute to photoinhibition. Similar outcomes have been reported by [61], who observed that excessive pigment levels disrupt light harvesting efficiency or increase ROS production.

Overall, these findings suggest that MF stimulation acts at multiple molecular levels: (i) enhancing ion fluxes (Fe^{2+}, Mg^{2+}) that support chlorophyll biosynthesis, (ii) modulating redox-sensitive signaling pathways that regulate photosynthetic protein expression, and (iii) influencing thylakoid membrane organization and electron transport. While moderate stimulation promotes coordinated chlorophyll accumulation and biomass growth, excessive MF disrupts this balance, leading to pigment overaccumulation, impaired energy transfer, and potential ROS-mediated photoinhibition. This dual role highlights MF as a fine-tunable regulator of photosynthetic efficiency rather than a simple stimulant of pigment biosynthesis [58,61].

Carotenoid accumulation in *Coelastrella* sp. was selectively stimulated at 30 mT for 1 and 2 h d^{-1}. However, longer exposure times and higher MF intensities led to significant reductions in carotenoid content (Fig. 6b). Carotenoids are known to function as non-enzymatic antioxidants involved in the scavenging of ROS, generated under stress conditions. Hence, the observed decrease under strong or prolonged MF exposure may reflect a stress response that exceeds the microalgae antioxidant capacity. Alternatively, energy and carbon fluxes may have been redirected from carotenoid biosynthesis to stress mitigation pathways. Nonetheless, the reduced biomass productivity recorded for *Coelastrella* sp. supports the inhibitory effect of the MF.

Carotenoid metabolism may be modulated by MF stimulation through a redox-sensitive pathway. MF promotes controlled ROS generation that activates transcription factors regulating antioxidant and carotenoid biosynthetic enzymes, thereby enhancing pigment accumulation [61,62]. In contrast, strong or prolonged exposure may disrupt redox homeostasis, leading to excessive ROS, oxidation of carotenoids, and diversion of precursors (e.g., isoprenoids) toward stress-related metabolites rather than pigment biosynthesis [25,63,64]. This dual response highlights that MF acts not only as a physical stimulus but also as a regulator of redox signaling and metabolic flux partitioning, determining whether carotenoid accumulation supports photoprotection or is compromised under stress overload.

Finally, C-PC concentration in *A. platensis* cultures was more sensitive to the exposure time rather than to MF intensity (Fig. 6c). For instance, the C-PC content under 30 mT for 4 h d^{-1} was 54 % higher compared to the control. When the MF intensity increased to 60 and 120 mT, the C-PC content was increased by 35 and 27 %, respectively at exposure times of 2 h d^{-1}. The C-PC increase recorded at 60 mT was positively correlated with an enhancement in Px, μ and CO_2 fixation rates, suggesting that under optimized conditions, MF may enhance pigment production while maintaining metabolic balance. In contrast, the increase in C-PC at 120 mT for 2 h d^{-1} was not related to an improved biomass growth or CO_2 fixation, indicating a decoupling of pigment accumulation from photosynthetic efficiency at high pigment concentrations.

C-PC accumulation under optimized MF conditions may be driven by upregulated transcription of phycobiliprotein genes and coordinated assembly of phycobilisomes, enhancing light-harvesting efficiency [65]. Excessive MF, however, can decouple C-PC synthesis from photosynthetic performance, possibly due to ROS-induced damage to photosynthetic membranes or regulatory feedback limiting functional pigment incorporation [66].

Taken together, these highlight that MF exposure can selectively modulate pigment biosynthesis in microalgae, with responses strongly dependent on species, intensity, and exposure time. Moderate MF stimulation favored chlorophyll, carotenoid, and C-PC accumulation in a manner that was often coupled with enhanced photosynthetic efficiency and biomass production, whereas excessive stimulation promoted pigment accumulation without functional benefits. This underscores the potential of MF as a controllable, non-invasive, and energy-efficient strategy tool for optimizing microalgal cultivation for future applications in biofuels, nutraceuticals, and high-value bioproducts. Outside the laboratory scale, the potential of the magnetic field to enhance biomass productivity and influence metabolic activity opens perspectives for industrial applications. Hereafter, microalgal biorefineries could couple electromagnetic coils with cultivation systems to control pigment, lipid, or any other byproduct production according to demand. Also, the combination of magnetic field with magnetic (nano)particles or magnetic support offers a dual benefit: stimulates the microalgae metabolism and at the same time facilitates the downstream harvesting processes for biomolecules recovery. Thus, magnetic field technology is not limited to lab-scale experiments but could be integrated into pilot operations for the sustainable production of high-value biomolecules.

4. Conclusions

The effects found in this study are dependent on the microalgal strain, magnetic field intensity, and exposure time. *C. vulgaris* cultures exhibited a superior tolerance to MF, particularly at exposures of 2 and 4 h d^{-1}. Indeed, the exposure of *C. vulgaris* cultures to 30 and 60 mT resulted in a significant enhancement of CO_2 biofixation and Px. Additionally, protein accumulation was stimulated by ~ 50 % under MF of

30 and 120 mT, while an increase in lipid accumulation by ~ 50 % was recorded at a MF of 60 mT. Interestingly, the exposure to the different MF for 4 h d^{-1} positively affected *C. vulgaris* growth regardless of the intensity of the MF. On the other hand, *A. platensis* exhibited a better tolerance to low MF intensities. The exposure to 30 mT for 4 h d^{-1} significantly increased the C-PC content, although biomass growth was only significantly enhanced when exposed to 60 mT for 1 h d^{-1}. Prolonged exposures of 4 h d^{-1} decreased *A. platensis* growth regardless of the MF intensity, while an exposure to 120 mT decreased *A. platensis* growth regardless of the exposure time. Finally, *Coelastrella* sp. was the most sensitive strain to MF, and the cultures were only stimulated when exposed to 30 mT for 2 h d^{-1}. Interestingly, the response of photosynthetic pigments to MF exposure was highly species-specific and governed by a complex interplay between MF intensity, exposure time, and cellular metabolic capacity. The study reinforces the emerging consensus that 30 and 60 mT can favor biological activity, whereas 120 mT may induce stress and inhibit the growth of some microalgae species. Hence, low intensity MFs represent a scalable and sustainable strategy to enhance biomass and pigment production during CO_2 mitigation process under a photobiorefinery approach. Overall, the study highlights the potential of MF as a scalable and sustainable strategy to enhance biomass and pigment production in microalgae cultivation, contributing to CO_2 mitigation under a photobiorefinery approach. However, successful scale-up will require overcoming significant engineering challenges, particularly ensuring field uniformity in large bioreactors, optimizing electric energy demand, and integrating magnetic field systems without compromising reactor design. In addition, long-term stability of MF effects, potential interactions with light and mixing regimes, and strain-specific variability remain critical issues. Further research is therefore needed to elucidate the molecular mechanisms underlying the observed responses and to establish practical implementation guidelines for industrial application.

CRediT authorship contribution statement

Raúl Muñoz: Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Sonia Arriaga:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Aitor Aizpuru:** Writing – review & editing, Supervision, Investigation, Conceptualization. **Laura Vargas-Estrada:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization. **Estheisy López-Bello:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by the Regional Government of Castilla y León and the EU-FEDER programme (UIC 379). Estheisy López-Bello would like to acknowledge SECITHI for her PhD grant. The authors acknowledge Viktoriia Komarysta for providing the microalgae strain *Coelastrella* sp.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jece.2025.119171.

Data availability

Data will be made available on request.

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