Electromagnetic Radiation Disturbed the Photosynthesis of *Microcystis aeruginosa* at the Proteomics Level

Chao Tang¹,²,³, Chuanjun Yang¹,³, Hui Yu¹,³, Shen Tian¹,³, Xiaomei Huang¹,²,³, Weiyi Wang²,³ & Peng Cai¹,³

Photosynthesis of *Microcystis aeruginosa* under Electromagnetic Radiation (1.8 GHz, 40 V/m) was studied by using the proteomics. A total of 30 differentially expressed proteins, including 15 up-regulated and 15 down-regulated proteins, were obtained in this study. The differentially expressed proteins were significantly enriched in the photosynthesis pathway, in which the protein expression levels of photosystems II cytochrome b559 α subunit, cytochrome C550, PsbY, and F-type ATP synthase (a, b) decreased. Our results indicated that electromagnetic radiation altered the photosynthesis-related protein expression levels, and aimed at the function of photosynthetic pigments, photosystems II potential activity, photosynthetic electron transport process, and photosynthetic phosphorylation process of *M. aeruginosa*. Based on the above evidence, that photoreaction system may be deduced as a target of electromagnetic radiation on the photosynthesis in cyanobacteria; the photoreaction system of cyanobacteria is a hypothetical “shared target effector” that responds to light and electromagnetic radiation; moreover, electromagnetic radiation does not act on the functional proteins themselves but their expression processes.

Electromagnetic radiation is an important environmental factor. On October 2, 2015, the United Nations Economic Commission for Europe (UNECE) issued a paper titled, “The UNECE–ITU Smart Sustainable City Indicators”¹. In the environmental field, electromagnetic radiation was listed as a core indicator, together with solid waste disposal and perception of environmental quality. Electromagnetic radiation not only has a potential long-term effect and threat to public health but may also impact the ecological environment. In recent decades, researchers have carried numerous experiments to evaluate the biological and health effects of *in vitro* and *in vivo* exposure to non-ionizing radiofrequency fields in animals, humans and their isolated cells². Plants were also used in studying the effects of EMF on living organisms, and electromagnetic irradiation induced different alterations in the enzyme activities³, and affected gene expression in plants⁴,⁵.

Photosynthesis is the most basic material and energy metabolism in the biosphere. Light is an electromagnetic wave with an electromagnetic radiation speed of $2.998 \times 10^8$ m/s, which is the speed of light. The wavelength of each radiation is different, and the spectra required for photosynthesis reside in the visible range (380–750 nm). Quantity (duration and intensity) and quality (color or wavelength) of electromagnetic waves are key factors that are involved in regulating growth and physiological processes in photosynthetic organisms⁶. Han investigated the effects of different light colors on photosynthetic pigments of cyanobacteria, and found that red light (660 nm) alters both the amounts and proportions of phycocyanin and allophycocyanin; moreover, cyanobacteria responded to red light by regulating the composition and location of phycobilisomes⁷. Ultraviolet-A (320–400 nm) exposure significantly decreased the photosynthetic parameters of unicellular green alga⁸. Effects of the 300 MHz electromagnetic field were observed on the photosynthetic cells of tobacco, and results showed that the effects generated damage in the membrane of photosynthetic cells in the tobacco leaves, the barricade

---

¹Physical Environment Group, Key Laboratory of Urban Environment and Health, Institute of Urban Environment, Chinese Academy of Sciences, 1799 Jimei Road, Xiamen, 361021, P.R. China. ²University of the Chinese Academy of Sciences, 19 Yuquan Road, Beijing, 100049, P.R. China. ³Xiamen Key Laboratory of Physical Environment, 1799 Jimei Road, Xiamen, 361021, P.R. China. Correspondence and requests for materials should be addressed to P.C. (email: pcai@iue.ac.cn)
thase activity, and electron carrier activity. A detailed list of differential proteins is shown in Table 1.

proteins were mainly related to chlorophyll binding, structural molecular activity, proton-transporting ATP synthase, and electron carrier activity. A detailed list of differential proteins is shown in Table 1.

Differential protein analysis.

Results

Differential protein analysis. Between the treatment and control groups, 30 differentially expressed proteins were determined, 15 of which were up-regulated and 15 were down-regulated. The top 10 different protein expressions contained 4 uncharacterized proteins that were obtained and the molecular functions of the other 6 proteins were mainly related to chlorophyll binding, structural molecular activity, proton-transporting ATP synthase activity, and electron carrier activity. A detailed list of differential proteins is shown in Table 1.

Name | Gene | Protein | CK | E | log2_FC (E/CK) | Pvalue |
--- | --- | --- | --- | --- | --- | --- |
C789_1144 | isiA | Iron stress-induced chlorophyll-binding protein | 1.07 ± 0.07 | 1.57 ± 0.12 | 0.55661 | 0.00245 |
C789_1150 | isiA | Iron stress-induced chlorophyll-binding protein | 1.07 ± 0.07 | 1.57 ± 0.12 | 0.55661 | 0.00245 |
C789_1730 | psbV | Cytochrome c-550 | 0.98 ± 0.03 | 0.78 ± 0.01 | −0.32723 | 0.00047 |
C789_2057 | C789_2057 | Uncharacterized protein | 0.96 ± 0.07 | 1.21 ± 0.14 | 0.331926 | 0.04327 |
C789_2058 | coaD | Phosphopantetheinyltransferase | 1.01 ± 0.08 | 0.80 ± 0.07 | −0.3328 | 0.02801 |
C789_2073 | atpB | ATP synthase subunit a | 1.04 ± 0.03 | 0.83 ± 0.08 | −0.31787 | 0.01645 |
C789_2075 | atpG | ATP synthase subunit b′ | 1.01 ± 0.01 | 0.71 ± 0.09 | −0.50733 | 0.00680 |
C789_2296 | C789_2296 | NUDIX domain protein | 1.01 ± 0.01 | 1.22 ± 0.06 | 0.281262 | 0.00259 |
C789_2366 | specB | Agmatinase | 0.94 ± 0.06 | 1.13 ± 0.03 | 0.264825 | 0.00981 |
C789_2954 | ruvB | Holliday junction ATP-dependent DNA helicase RuvB | 1.04 ± 0.04 | 0.86 ± 0.05 | −0.26628 | 0.01180 |
C789_3280 | C789_3280 | Uncharacterized protein | 1.02 ± 0.04 | 0.71 ± 0.15 | −0.51681 | 0.04331 |
C789_4303 | psbY | Photosystem II protein Y | 1.00 ± 0.01 | 0.76 ± 0.06 | −0.41025 | 0.00312 |
C789_428 | C789_428 | Uncharacterized protein | 0.93 ± 0.06 | 1.17 ± 0.11 | 0.320073 | 0.03007 |
C789_4415 | tpiA | Triosephosphate isomerase | 0.99 ± 0.02 | 1.20 ± 0.03 | 0.282907 | 0.00040 |
C789_4588 | gvpAII | Gas vesicle structural protein | 1.02 ± 0.05 | 0.76 ± 0.08 | −0.42609 | 0.01408 |
C789_4589 | gvpAII | Gas vesicle structural protein | 1.02 ± 0.05 | 0.76 ± 0.08 | −0.42609 | 0.01408 |
C789_4839 | C789_4839 | Uncharacterized protein | 1.01 ± 0.01 | 1.24 ± 0.03 | 0.301737 | 0.00018 |
C789_5042 | hemC | Porphobilinogen deaminase | 0.92 ± 0.10 | 1.12 ± 0.01 | 0.281214 | 0.03221 |
C789_53 | C789_53 | Uncharacterized protein | 1.06 ± 0.05 | 0.74 ± 0.01 | −0.51587 | 0.00034 |
C789_5304 | psbE | Cytochrome b559 subunit alpha | 1.01 ± 0.02 | 0.64 ± 0.12 | −0.6609 | 0.01468 |
C789_549 | C789_549 | Uncharacterized protein | 1.04 ± 0.04 | 0.84 ± 0.04 | −0.31525 | 0.00225 |
C789_639 | porB | S-layer domain protein | 1.03 ± 0.03 | 1.35 ± 0.11 | 0.83678 | 0.00619 |
C789_820 | C789_820 | Uncharacterized protein | 0.99 ± 0.05 | 1.86 ± 0.11 | 0.79031 | 8.70E-05 |
C789_844 | gdhB | Glutathione synthetase | 0.96 ± 0.03 | 1.19 ± 0.06 | 0.30699 | 0.00347 |
C789_87 | C789_87 | Uncharacterized protein | 0.95 ± 0.06 | 1.61 ± 0.18 | 0.759683 | 0.00218 |
C789_895 | C789_895 | Uncharacterized protein | 0.99 ± 0.05 | 0.81 ± 0.02 | −0.2858 | 0.00383 |
C789_898 | mdnF | Methyltransferase small domain protein | 0.92 ± 0.13 | 1.23 ± 0.10 | 0.413078 | 0.04149 |
C789_RS03845 | 0.93 ± 0.10 | 0.80 ± 0.10 | −0.39727 | 0.02415 |

Table 1. Differential protein list.

In the transmission process of electrons in photosynthesis, and decreased potential activity and photochemical efficiency of photosystems II. Microwaves with low power density significantly influenced quantitative increase in the photosynthesis pigment levels of the vegetal cells. Our previous study found that oxidative stress of Microcystis aeruginosa (M. aeruginosa) could be induced under electromagnetic radiation exposure, and regulations on key enzymes of photosynthesis (Rubisco and FBA) by electromagnetic radiation indicated that electromagnetic radiation could affect the photosynthesis of M. aeruginosa cells.

The influence of Electromagnetic wave on living organisms has been observed in different animals and plants species. However, studies on the effects of electromagnetic radiation on photosynthesis have been few and mainly focused on the phenotypic level. Moreover, information is lacking regarding the mechanism of electromagnetic waves on photosynthesis. How electromagnetic radiation or photoelectromagnetic coupling affects photosynthesis and whether electromagnetic radiation and light have a homologous receptor or receptors should be investigated. We tried to observe the mechanism of electromagnetic radiation in photosynthesis at the proteomics level in this novelty study.

M. aeruginosa belongs to the order cyanophyta, which is the dominant population in many bloom-forming lakes, which occupy important niches in the environment and is a common habitat of algae with high environmental sensitivity. The most common and widely used mobile communication frequency in mainland China is 1.8 GHz. In this paper, the effects of 1.8 GHz and 40 V/m electromagnetic radiation on the photosynthetic system protein expression of algal cells were examined through proteomics to explore the mechanism of electromagnetic radiation on photosynthesis.

Results

Differential protein analysis. Between the treatment and control groups, 30 differentially expressed proteins were determined, 15 of which were up-regulated and 15 were down-regulated. The top 10 different protein expressions contained 4 uncharacterized proteins that were obtained and the molecular functions of the other 6 proteins were mainly related to chlorophyll binding, structural molecular activity, proton-transporting ATP synthase activity, and electron carrier activity. A detailed list of differential proteins is shown in Table 1.
in Fig. 1 and the corresponding differentially expressed proteins are listed in Table 3. Results showed that five down-regulated after electromagnetic stress. As shown in Fig. 1, the expressions of cytochrome b559 (Cytb559) and the differential proteins were related to photosynthesis, and the expressions of differential proteins were regulated in pathways such as electron transport chain, oxidation–reduction process, and generation of precursor metabolites and energy.

Differential protein GO enrichment analysis. The treatment group was compared with the control group in terms of cell composition analysis (Table 2). Differential proteins were mainly enriched in the cytoplasmic vesicle, protein complex, organelle membrane, membrane protein complex, proton-transporting two-sector ATPase complex, membrane-bounded organelle, and cytoplasmic vesicle. The cytoplasmic vesicle partial protein was the most enriched, and the number of differential protein was 2, which comprising 14.29% of the total differential protein. Followed by protein complex-related protein, the number of differential protein was 7, comprising 50% of the total differential protein.

From the molecular functional analysis, 1.8 GHz radiofrequency radiation mainly had a significant effect on tetrapterole binding. Moreover, certain effects on the related proteins took place. A significant number of proteins were associated with ATP biosynthesis and metabolic processes, nucleoside triphosphate metabolism and biosynthesis processes, nucleosides, nucleoside monophosphate, nucleotide biosynthesis and metabolism, glutathione metabolic process, protein-heme linkage, protein cofactor connections, and hydrogen transport, glycosylated compounds synthetic processes, cell metabolism processes, biosynthesis, and metabolism.

Analysis of Pathway Enrichment of Differential Proteins. KEGG is a knowledge base for systematic analysis of gene functions, linking genomic information with higher order functional information, which is stored in the PATHWAY database (http://www.kegg.jp/kegg/kegg1.html). Algal cells were exposed to radio frequency electromagnetic radiation and differential proteins mainly focused on the photosynthetic pathways. Based on the enrichment of KEGG pathways, it is significant to note that 1.8 GHz radiofrequency effects can result in changes in the electron transport chain, generation of precursor metabolites and energy, protein complex-related protein, and certain effects were observed on the related proteins.

Table 2. CKP-VS-EP GO Enrichment. The second column is the GO term ID; the third column is the function description of the GO term; the fourth column is the number of differential genes that are noted to a GO term and the percentage of differential genes to the total number of differential genes (number of headings); the fifth is the number of genes annotated to a GO term and the percentage of genes to the total number of genes (number of headings); the sixth column is the P value; the seventh column is the Q value after multiple checks.
for environmental change. Studies have shown that certain natural stresses (such as salt and sulfur deficiency) may reduce light-harvesting and photosynthetic activities, photosynthetic systems I and II, cytochrome b6/f, and ATP synthase gene expression levels. Low-temperature treatment, cytochrome a-b binding protein in the process of photosynthetic light absorption, cytochrome b559α, oxygen-enhanced protein, cytochrome b6-f complex Fe-S protein, and the photosystems I reaction center subunit protein showed significant down-regulation 15–17. Electromagnetic waves also had certain effects on photosynthesis10,11,18. Under the action of a low level radio frequency electromagnetic field of 300 MHz, chlorophyll fluorescence dynamics process and ultra-weak photoemission in tobacco leaf underwent changes. Responses of the fluorescence dynamics parameters, such as $F_{0}$, $F_{V}/F_{0}$, $F_{V}/F_{m}$, $\Delta F_{V}/T$, and $T_{1,2}$, and the amount of ultra-weak photoemission to the radiating power of electromagnetic field appeared to be the characters of non-linear and power windows. Non-thermal effects of electromagnetic field were observed on the photosynthetic cells of tobacco. The effects generated damage in the membrane of photosynthetic cells in the tobacco leaf, the barricade of transmission process of electrons in photosynthesis, and the decrease in potential active and photochemical efficiency of photosystems II10,18. We investigated the proteomics of M. aeruginosa under electromagnetic radiation exposure and found that the differentially expressed proteins were significantly enriched in the photosynthetic pathway (Table 4).

**Figure 1.** M. aeruginosa cells were exposed to radio frequency electromagnetic radiation and differential proteins mainly focused on the photosynthetic pathways, the significant differential proteins are marked by green box. As shown in Fig. 1, the expressions of cytochrome b559 subunit alpha, cytochrome c-550, protein Y, protein ATP synthase subunit α, and protein ATP synthase subunit β were down-regulated. This image is copyright permitted by KEGG12–14, http://www.kegg.jp/kegg/kegg1.html.

**Table 3.** Differential proteins of Photosynthetic pathway.
and other components. PSII is one of the most susceptible parts of the photosynthetic apparatus and is involved in the transmembrane proteins, several hydrophilic peripheral proteins, some small molecular weight protein subunits, and other components. Cytb559 consists of two protein subunits (Mr4400 and 9300) and is important in controlling the redox of Cytb559; moreover, the PsbY protein Cytb559 is only present in its oxidized, and low potential form in vivo.

Table 4. Significant enrichment KEGG Pathway.

In the exclusion of visible light in the environment, the expressions levels of Cytb559 α subunit, cytochrome c-550, and PsbY proteins were down-regulated in photosystems II of *M. aeruginosa* under electromagnetic radiation exposure (Fig. 1). The process of converting light energy into chemical energy by photosynthetic organisms was mainly catalyzed by four multi-subunit membrane-protein complexes: photosystem I (PSI), photosystem II (PSII), cytochrome b6f complex, and F-ATPase. PSII mainly consists of D1, D2, CP43, CP47, Cytb559, other transmembrane proteins, several hydrophilic peripheral proteins, some small molecular weight protein subunits, and other components. PSII is one of the most susceptible parts of the photosynthetic apparatus and is important in the photosynthetic response in higher plants to environmental perturbations and stresses. Moreover, Cytb559 has redox activity that can produce photooxidation and photoreduction. It is a cytochrome molecule that binds to PSI and consists of two polypeptides (Mr4400 and 9300). Cytb559 consists of two protein subunits (PsbE and PsbF) that ligate a heme-group between them. The exact function of this component in PSII has not yet been clarified, but its crucial role for the assembly and photo-protection in prokaryotic complexes has been suggested. Furthermore, a functional role of Cytb559 in the protection of PSI under photoinhibition conditions in *vivo* has been determined. Cytb559 plays an important role in the cyclic electron flow processes that protect PSI from light-induced damage during photo-inhibitory conditions. PsbY protein is important in controlling the redox of Cytb559; moreover, the PsbY protein Cytb559 is only present in its oxidized, and low potential form and plants with PsbY depletion are highly susceptible to photoinhibition. Cytochrome c-550 plays a substantial role in maintaining the stability and function of the manganese cluster in algal PSI. The absence of cytochrome c-550 hinders the balance of photosynthetic system under nitrogen-deficient conditions, which affects the nitrogen tolerance of bacteria.

Expression levels of Cytb559 α subunit, cytochrome c-550, and PsbY protein in photosystem II of *M. aeruginosa* were down-regulated under electromagnetic radiation exposure, which indicated that electromagnetic radiation affects the abovementioned protein synthesis or translation, and this could affect the function of PSI Cytb559, the PSI cycle of electron flow and oxidation and reduction potential, and the function of cytochrome c-550. Therefore, the electromagnetic radiation will affect the light reaction processes of *M. aeruginosa*. In addition, the expression levels of two proteins in ATP synthase were down-regulated under electromagnetic radiation. ATP synthase on the thylakoid membrane, also known as H⁺-ATPase, catalyzed the synthesis process of ATP by ADP and Pi. The pH gradient of the thylakoid membrane, being the driving force of ATP synthesis and phosphorylation, can be blocked by killing venturicidin and similar reagents. Plasma membrane H⁺-ATPase can function in the mitigation of physiological disturbances imposed by salt stress. Electromagnetic radiation may affect the photosynthetic phosphorylation by affecting the ATP synthase on the thylakoid cells of *M. aeruginosa* and thus may affect photosynthetic phosphorylation. Electromagnetic radiation may be one of the reasons that indirectly affect photosynthetic carbon sequestration.

In conclusion, the response of the *M. aeruginosa* cells to electromagnetic radiation is a complex process, wherein differential expression is significantly enriched in photosynthetic pathways. In addition, the differential proteins are mainly related to inositol phosphate metabolism, oxidative phosphorylation, pantothenate and CoA biosynthesis, homologous recombination, glutathione metabolism, fructose and mannose metabolism, arginine and proline metabolism, carbon fixation in photosynthetic organisms, cysteine and methionine metabolism, porphyrin and chlorophyll metabolism, glycolysis/gluconeogenesis, purine metabolism, carbon metabolism, and biosynthesis of amino acid function. The PSI Cytb559 α subunit, cytochrome c-550, PsbY, and F-type ATP synthase (a, b) protein expression levels decreased. Electromagnetic radiation affects the photosynthesis-related
protein synthesis or translation, and could affect the function of photosynthetic pigments, PS II potential activity, photosynthetic electron transport process, and photosynthetic phosphorylation process of *M. aeruginosa*.

Broadly speaking, visible light is within a certain wavelength range of electromagnetic wave (380–750 nm). Certain differences may exist in the electromagnetic radiation effect sites at different frequencies in the growth processes of *M. aeruginosa*. Visible light directly acts on the relevant proteins of photosynthetic system, but microwave electromagnetic radiation (1.8 GHz applied in this study) acts on protein synthesis or translation processes.

Based on the above evidence, the photoreaction system may be a target of electromagnetic radiation on the photosynthesis for cyanobacteria; the photoreaction system of cyanobacteria is a hypothetical "shared target effector" that responds to light and electromagnetic radiation; and electromagnetic radiation does not act on the functional proteins themselves but their expression processes. Furthermore, photosynthesis is associated with energy metabolism. Thus, the correlation between electromagnetic radiation and bioenergy metabolism must be further investigated.

**Methods**

**Experimental Materials.** The experiment involved species from *M. aeruginosa*, and the algal species came from the Institute of Aquatic Biology, Chinese Academy of Sciences, No. FACHB-905. Culture temperature was 25 ± 1 °C with 12 L:12 D light–to-dark ratio, the light intensity was 1000 ± 100 Lux, and the culture medium for high pressure sterilization was BG 11 medium.

**Experimental exposure device.** Radio frequency electromagnetic field (RF-EMF) was generated using a vector signal generator (AgilentE8267DPSG, USA) and a signal amplifier (AV38701E, the 41st Institute of CETC, China). RF-EMF was emitted from an antenna (ETS3180B) that was placed at 24 cm above the sample area. A signal amplifier was used to amplify the RF/MW signal induced by the signal generator. The signal at the sample position was measured using an electromagnetic radiation analyzer (PMM8053B, Narta-STS, Italy) and a signal analyzer (AgilentN9030A). A series of operations was applied to ensure temperature accuracy and stability. First, the temperature probe of the incubator was placed adjacent to the sample so that the incubator would maintain its temperature according to that position. Second, the temperatures of the two incubators for the control and exposure samples were routinely calibrated using the same thermometer. Third, during the exposure periods, the temperature of the sample area was continuously monitored using temperature probes surrounding the control and exposure samples. Fourth, the surface temperature of each sample during the exposure period was checked using a thermal imager (Testo 890). All of the monitoring data showed that the temperature of the control and exposure samples remained stable. Experimental exposure device was shown in Fig. 2. In this study, *M. aeruginosa* cells were exposed to 1.8 GHz RF-EMF through a continuous sine wave. At the position of the *M. aeruginosa* cells, the R F electromagnetic field strength was 40 V/m and the temperature was 25 °C.
Experimental treatment. M. aeruginosa were cultured in the normal light for 30 days (Culture temperature was 25 ± 1°C with 12L:12 D light–to-dark ratio, light intensity was 1000 ± 100 Lux, and the culture medium for high pressure sterilization was BG 11 medium), and were then divided into two parts for exposure and control experiments.

To exclude the impact of light on the experiment, a dark condition was chosen for the experiment. The exposure group was treated with 1.8 GHz and 40 V/m electromagnetic radiation in the dark for 24 hours (based on our previous study result11), whereas the control group was not exposed to electromagnetic radiation and other conditions remained constant.

Experimental roadmap was shown in Fig. 3.

The above treatment was repeated thrice. The control mark was CK and the processing marker was E. Three samples each from the treatment and control groups were sent to GENE DE NOVO Company to extract and identify proteins. The protein identification used Orbitrap Fusion Tribrid mass spectrometer by Gene Denovo Biotechnology Co. (Guangzhou, China).

Data analysis. Database search. The mass spectrometry data were transformed into MGF files with Proteome Discovery 1.2 (Thermo, Pittsburgh, PA, USA) and analyzed using Mascot search engine (Matrix Science, London, UK; version 2.3.2). Mascot database was set up for protein identification using M. aeruginosa DIANCHI905 reference transcriptome. Mascot was searched with a fragment ion mass tolerance of 0.050 Da and a parent ion tolerance of 10.0 PPM.

Protein identification and quantification. The Mascot search results were averaged using medians and quantified. Proteins with fold change in a comparison >1.2 or <0.83 and unadjusted significance level $p < 0.05$ were considered differentially expressed.

Protein functional annotation and enrichment analysis. Proteins were annotated against GO, KEGG and COG/KOG database to obtain their functions. Significant GO functions and pathways were examined within differentially expressed proteins with $p$ value ≤ 0.05.

Data Availability. All data generated or analysed during this study are included in this published article.

References
1. United Nations Economic and Social Council. The UNECE–ITU Smart Sustainable Cities Indicators: http://www.unece.org/fileadmin/DAM/hil/fil/projects/MICRO_CITIES/ECER_HBP_2015_4.pdf (2015).
2. Vijayalaxmi. Biological and health effects of radiofrequency fields: Good study design and quality publications. Mutation Research/Genetic Toxicology & Environmental Mutagenesis 810, 6–12 (2016).
3. Kouzmanova, M., Dimitrova, M., Dragolova, D., Atanasova, G. & Atanasov, N. Alterations in Enzyme Activities in Leaves after Exposure of Plectranthus Sp. Plants to 900 MHZ Electromagnetic Field. Biotechnology & Biotechnological Equipment 23, 611–615 (2009).
4. Vian, A. et al. Microwave irradiation affects gene expression in plants. Plant Signal Behav 1(2), 67–70 (2006).
5. Jangid, R. K. et al. Microwave treatment induced mutations and altered gene expression in Vigna aconitifolia. Biologia Plantarum 54(4), 703–706 (2010).
6. Sammartin, P., Vázquez-Nion, D., Arines, J. & Cabo-Dominguez, L. Controlling growth and colour of phototrophs by using simple and inexpensive coloured lighting: A preliminary study in the Light4Heritage project towards future strategies for outdoor illumination. International Biodeterioration & Biodegradation 122, 107–115 (2017).
7. Han, P. et al. The regulation of photosynthetic pigments in terrestrial Nostoc flagelliforme in response to different light colors. Algal Research 25, 128–135 (2017).
8. White, A. & Jahnke, L. Contrasting effects of UV-A and UV-B on photosynthesis and photoprotection of beta-carotene in two Dunaliella spp. Plant & Cell Physiology 43(8), 877–884 (2002).
9. Xi, G., Yang, C. & Song, Q. The Responses of Chlorophyll Fluorescence Dynamics and Ultraweak Photoemission in Photosynthesis Cell of Tobacco to Low Level Radio Frequency Electromagnetic Field. Acta Photonica Sinica 33, 622–625 (2004).
10. Tufescu, F. & Creanga, D. E. Microwave Effects Upon Vegetal Cell Cultures. Recent Advances in Multidisciplinary Applied Physics 931–941 (2005).
11. Tang, C., Yu, H., Yang, C. & Cai, P. The effects of the electromagnetic environment on oxidative stress and photosynthetic carbon fixation of Microcystis aeruginosa. Acta Scientiae Circumstantiae 37, 3194–3200 (2017).
12. Kanehisa, M., Sato, Y., Kawashima, M., Furumichi, M. & Tanabe, M. KEGG as a reference resource for gene and protein annotation. Nucleic Acids Res 44, 457–462 (2016).
13. Kanehisa, Furumichi, M., Tanabe, M., Sato, Y. & Morishima, K. KEGG: new perspectives on genomes, pathways, diseases and drugs. Nucleic Acids Res 45, 353–361 (2017).
14. Kanehisa, M. & Goto, S. KEGG: Kyoto Encyclopedia of Genes and Genomes. Nucleic Acids Res 28, 27–30 (2000).
15. Zhang, X. Y. Study on Carbon and Nitrogen Metabolism and Proteomics during Growth and Development of Flowering Chinese Cabbage. (South China Agricultural University, 2016).
16. Allakhverdiev, S. I. & Murata, N. Salt stress inhibits photosystems II and I in cyanobacteria. *Photosynthesis research* 98, 529–539 (2008).
17. Zhang, Z., Pendse, N. D., Phillips, K. N., Cotner, J. B. & Khodursky, A. Gene expression patterns of sulfur starvation in *Synechocystis* sp. PCC 6803. *BMC genomics* 9, 344 (2008).
18. Xi, G., Li, Y., Cao, Y. & Song, Q. The Difference of Chlorophyll Fluorescence Dynamics Process and the System of Photosynthetic Pigment in Leaf of Spinach and Tobacco Under the Action of Low Level Microwave Electromagnetic Field. *ACTA PHOTONICA SINICA* 34, 1023–1027 (2005).
19. Nelson, N. & Yocum, C. F. Structure and function of photosystems I and II. *Annu Rev Plant Biol* 57, 521–563 (2006).
20. Ferreira, K. N., Iverson, T. M., Maghlaiou, K., Barber, J. & Iwata, S. Architecture of the photosynthetic oxygen-evolving center. *Science* 303, 1831–1838 (2004).
21. Iwata, S. & Barber, J. Structure of photosystem II and molecular architecture of the oxygen-evolving centre. *Current opinion in structural biology* 14, 447–453 (2004).
22. Baker, N. R. A possible role of photosystem II in environmental perturbations of photosynthesis. *Physiol Plant* 81, 563–570 (1991).
23. Wang, J. Y., Zhu, S. G., & Xu, C. F. Biochemistry. (Higher Education Press, Beijing, 2010).
24. Hung, C. H., Huang, J. Y., Chiu, Y. F. & Chu, H. A. Site-directed mutagenesis on the heme axial-ligands of cytochrome b559 in *Synechocystis* sp. PCC 6803 mutants on the cytoplasmic-side of cytochrome *b*<sub>559</sub> in photosystem II. *Biochim Biophys Acta* 1827, 507–519 (2013).
25. Chiu, Y. F. et al. Spectroscopic and functional characterization of cyanobacterium *Synechocystis* PCC 6803 mutants in the oxygen-evolving centre. *Biochimica et Biophysica Acta* 1857, 1524–1533 (2016).
26. Huang, S. Q. Integration of proteomic and transcriptomic reveals varying pattern of gene expression in *Synechocystis* sp. PCC6803 under salt stress and nitrogen starvation, (Tianjin University, 2013).
27. Shen, J. R., Qian, M., Inoue, Y. & Burnap, R. L. Functional characterization of *Synechocystis* sp. PCC6803 △psbU and △psbV mutants reveals important roles of cytochrome *c*-550 in cyanobacterial oxygen evolution. *Biochemistry* 37, 1551–1558 (1998).
28. Sahu, B. B. & Shaw, B. P. Salt-inducible isoform of plasma membrane H^+ -ATPase gene in rice remains constitutively expressed in natural halophyte, *Suaeda maritima*. *Journal of Plant Physiology* 166, 1077–1089 (2009).
29. Lin, K. W., Yang, C. J., Lian, H. Y. & Cai, P. Exposure of ELF-EMF and RF-EMF Increase the Rate of Glucose Transport and TCA Cycle in Budding Yeast. *Frontiers in microbiology* 7, 1378 (2016).

Acknowledgements
This work was supported by the Science and Technology Innovation Fund Project, Chinese Academy of Sciences (grant numbers CXJJ-16M115) and the Xiamen Science and Technology Project (grant numbers 3502Z20162021). Thanks for getting copyright permission from Kanehisa Laboratories.

Author Contributions
Conceived and designed the experiments: P.C. and C.T. Performed the experiments: C.T., H.Y., S.T., C.Y., X.H. Analyzed data and drew pictures: C.T., C.Y. and S.T. All authors reviewed the manuscript.

Additional Information
Competing Interests: The authors declare that they have no competing interests.

Publisher’s note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2017