Condition-specific genes of Ulva compressa under light intensity and temperature stress

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Abstract

The experiment aimed to explore the possible life activities of *Ulva compressa* under different environmental conditions, e.g., light intensity and temperature stress. Orthogonal experiment of three temperature levels and three light intensity levels were designed, and there were a totally nine groups. The transcriptome of *U. compressa* was studied in specific genes after RNA extraction, sequencing, transcriptome assembly, annotation, and expression analysis. It was showed that *U. compressa* was selectively expressed condition-specific genes under certain conditions, thereby maintaining related life activities, which was different from the algae in the Yellow Sea green tide. Two categories of condition-specific genes were divided according to the results, wherein one type of genes was more obviously expressed under the influence of light, while the other one was obviously influenced by temperature. It seemed that these changes might benefit for *U. compressa* to temporarily increase the efficiency of photosynthesis and have more gene expression in terms of reproduction and nutrition, laying the foundation for further exploration of its environmental adaptability different from other algae.

1 Introduction

Green tide is a widespread phenomenon of algal blooms in coastal areas, which seriously endangers the marine ecological environment and causes immeasurable losses to offshore tourism, aquaculture, and ecosystems(Xuelei, et al. 2021). A large number of indoor work and marine surveys have shown that the formation of the green tide is caused by the drift, accumulation, and over-proliferation of macroalgae, and the most representative macroalgae is *Ulva Prolifera*(Blomster, et al. 2002, Merceron, et al. 2007, Nelson, et al. 2008).

It belongs to Chlorophyta, Cholophyceate, Ulvales, and Ulvaceae(Rengcheng, et al. 2018). At present, there are more than 80 known species of prolifera in the world, mainly from marine products, and a few species are distributed in brackish water or rivers, while there are 19 known species of prolifera in China, and the main ones are related to *Ulva. line*, *U. prolifera*, *U. compressa*, *Ulva flexuosa*, and so on, some of them appear in the green tide of the Yellow Sea in China all year round(Leliaert, et al. 2009, Liu, et al. 2013, Liu, et al. 2012, Masini, et al. 1995). The identification at the molecular level shows that the outbreak of green algae in the South Yellow Sea first appeared in 2008. With time, the green tide constituent species appeared in population succession during the floating process(Xiaolin, et al. 2011). In general, *U. compressa*, *U. line*, and *U. flexuosa* were in the early population, but finally, *U. prolifera* developed into the dominant species and the last surviving species of its growth rate advantage (Wang, et al. 2018).

Although it is not eye-catching during the green tide eruption and succession in the Yellow Sea, it is the first prolifera species to publish the complete genome sequence. It has a lot of research data in morphogenesis, environmental ecology, and molecular biology, and is one of the representative species of Ulva. In terms of photosynthetic physiology, *U. compressa* is relatively resistant to low temperatures (Yangyang, et al. 2010). And with the changes in seawater temperature and light intensity, high temperature and high light intensity inhibit the growth of *U. compressa*, gradually eliminated in the green

tide formation process(Wang, et al. 2018). In this paper, transcriptome data of *U. compressa* under different growth conditions were analyzed to study the gene expression changes of *U. compressa* under the influence of light intensity and temperature and to explore the molecular mechanism of adaptation of *U. compressa* to changes in light and temperature environment.

2 Materials And Methods

2.1 Experimental materials and pre-culture

The material in this experiment was collected from the Qingdao sea area in July 2008 (East longitude: 120.19 degrees, North latitude: 36.04 degrees), selected healthy algae, clean the algae and remove surface attachments, take the same mass (5g). The fresh-weight algae were divided into 9 groups (3 parallels in each group) for treatment and were cultured in 1.5L conical flask with VSE medium. The culture conditions in the light incubator were shown in Table 1. Because the optimum growth conditions of E. platypus were: temperature 10 ± 1℃, 100μmol·$m^{-2}s^{-1}$, so B5 was the positive control group. During the experiment, each group was exposed to light for 12 h, and the light cycle was L/D = 12:12 h. Afterwards, the algae were sub-packaged, quick-frozen in liquid nitrogen, and stored at -80°C for subsequent RNA extraction.

Table 1
Experimental design of orthogonal transcriptome of *U. compressa* under temperature and light intensity stress

temperature **light intensity**	**30℃**	**10℃**	**4℃**
400μmol·m^{-2}·s^{-1}	B1	B4	B7
100μmol·m^{-2}·s^{-1}	B2	B5	B8
20μmol·m^{-2}·s^{-1}	B3	B6	B9

2.2 Experimental method

2.2.1 RNA extraction and sequencing

Add DNase I to digest the DNA in the sample, then enrich the mRNA with magnetic beads containing Oligo(dT), add the breaking reagent to the Thermomixer, and use the broken mRNA as a template to synthesize the first cDNA, and then use the two-stranded synthesis system to further synthesize the double-stranded cDNA. Then the kit was used for purification and recovery, sticky end repair, adding A base "A" to the cDNA3 'end, and connecting the connector. After selecting the fragment size, PCR amplification was carried out to construct the cDNA library. Agilent 2100 Bioanalyzer and ABI StepOnePlus Real-Time PCR System were used to check the constructed cDNA. After qualified, Illumina

HiSeq™ 2000 was used for double-terminal sequencing of the constructed cDNA library(Wang, et al. 2009).

2.2.2 Transcriptome assembly and annotation

The short reads were assembled using the software Trinity (http://trinityrnaseq.sourceforge.net/), and the obtained sequence was unigene, using Tgicl (http://sourceforge.net/projects/tgicl/files/tgicl%20v2.1/) Remove redundancy and further complete the splicing. Secondly, cluster homologous transcripts to obtain effective Unigenes. At the same time, parallel samples are sequenced, and the assembled unigenes are further sequenced by sequence clustering software to remove redundancy. Additional processing, and clustering of homologous transcripts, resulted in as long as possible non-redundant unigenes, in which only unigene sequences with p-value < 0.05 and |Log2FoldChange|>1 were considered significantly different. The obtained unigene sequences were then functionally annotated (e-value < 0.00001) through protein databases NR, Swiss-Prot, KEGG, and COG (http://blast.ncbi.nlm.nih.gov/Blast.cgi).

2.2.3 Transcriptome expression annotation

The expression quantity of unigene is calculated by FPKM (Fragments Per KB Per Million Fragments). Its calculation formula is:

$$FPKM = \frac{10^6 C}{NL/10^3}$$

2.1

Among them, FPKM(A) is the expression level of unigene A, C is the number of fragments uniquely aligned to unigene A, N is the total number of fragments uniquely aligned to all unigenes, and L is the number of bases of unigene A.

2.2.4 Homology alignment

Multiple sequence analysis was performed on the known unigene gene sequences with the same function by DNAMAN software.

3 Results And Analysis

3.1 Transcriptome sequencing, assembly, and annotation

A total of 43,290,792,180 nt of data were generated by sequencing on the Illumina Hiseq2000 platform. A total of 92,790 Unigenes were obtained by the assembly, with a total length of 158,854,805nt, an average length of 1,712nt, and an N50 of 2,940nt. Annotating Unigene functions to NR, NT, Swiss-Prot, KEGG, COG, and GO libraries are 51,884, 9,200, 35,580, 38,453, 32,981, 21,772, and the Unigenes on all

annotations are 52,679 individual. A total of 5,519 SSRs. The statistical results of data processing are shown in Table 2.

Table 2 The yield statistics of orthogonal transcriptome sequencing of *U. compressa* under temperature and light intensity stress

Samples	Total Raw reads	Total clean Reads	Total clean Nucleotides(nt)	Q20 percentage(%)	GC percentage(%)
B1	57,959,152	53,893,110	4,850,379,900	97.84	58.11
B2	59,233,936	55,278,410	4,975,056,900	97.82	57.97
B3	58,968,570	55,062,386	4,955,614,740	97.91	57.76
B4	56,196,420	52,125,072	4,691,256,480	97.71	56.87
B5	55,631,066	51,649,190	4,648,427,100	97.70	56.71
B6	57,876,244	54,744,178	4,926,976,020	98.31	58.11
B7	56,074,990	52,650,014	4,738,501,260	97.95	57.46
B8	58,358,300	54,159,594	4,874,363,460	98.20	57.60
B9	55,563,802	51,446,848	4,630,216,320	98.17	57.98

Note: 1. Total Reads and Total Nucleotides represent the number of filtered reads and bases;

1. Q20 percentage indicates the proportion of bases with quality of not less than 20 after filtering;
2. GC percentage indicates the ratio of bases G and C to the total number of bases after filtering.
3. Total Clean Nucleotides = Total Clean Reads1×Read1 size + Total Clean Reads2×Read2 size

3.2 Transcriptome expression analysis

Through the analysis of the expression of the transcriptome of *U. compressa*, it was found that some of the unigene genes were not expressed under B5 (normal conditions), but were only expressed under special conditions, which were called condition-specific expression genes. In previous studies, the analysis of differential genes was mostly performed, that is, under normal conditions, the expression of genes of key enzymes of the organism was up-regulated or down-regulated in the treatment group, to find out that there may be emerging biological processes. In previous studies, through transcriptome sequencing analysis, the up-regulation or down-regulation of carotenoid-related genes in *U. prolifera*, it was found that high temperature and low temperature can activate the synthesis of carotenoids, which provides a reference for the analysis of other metabolic pathways(Yuan, et al. 2018); the up-regulation and down-regulation of key enzyme genes in photosynthesis of *U. line*, and found the significance of C_4 pathway in CO_2 assimilation(JianFang, et al. 2013); the up-regulation of genes in photosynthesis and glycolysis in *U. compressa*. It was concluded that it may provide sufficient energy for long-term low-salt tolerance(Xing, et al. 2021). In the analysis of transcriptome data in this paper, an interesting

phenomenon was found. Among the many condition-specifically expressed genes, the expression levels of some genes showed regular changes with temperature or light intensity. Through further functional analysis of these condition-specific genes, it is possible to infer the biological processes that are taking place in each group, which provides direction for understanding the molecular tolerance mechanism of *U. compressa* under extreme conditions.

3.2.1 Genes that change with light intensity under extreme temperature conditions

Such condition-specific expression genes can be expressed under extreme light intensity conditions, and the expression level is always the largest in B1, the smallest in B3, and B7 > B9. The genes with known functions are shown in Table 3. These genes are shown in Table 3. The functions expressed are mostly anti-stress and signal transduction. For example, unigene17011_All is heat shock 70 kDa protein 6 (chloroplastic), unigene27131_All has the function of an uncharacterized protein, and unigene34085_All is annotated as profilin-1, which can bind to actin, and it can be determined by the concentration of high and low. Affects the structure of the cytoskeleton. unigene30740_All has the function of ran-binding protein 1 homolog a, and unigene23679_All and unigene33974_All function as formin-like protein 14 and formin-like protein 3, which can regulate cell activity. Others include short-chain dehydrogenase TIC 32 (chloroplastic), chlorophyll ab binding protein L1818 (chloroplastic), 3-isopropyl malate dehydratase, serine/threonine-protein kinase SAPK10, 26S proteasome regulatory subunit 4 homolog B, etc. The specific expression of these genes, by affecting the cytoskeleton and regulating activity, plays an important role in the growth process of *U. compressa*, enabling it to temporarily adapt to extreme conditions to survive for some time. This is also consistent with the mechanism of the adaptation to salinity stress in the related literature(Xing, et al. 2021), but there is no report on condition-specific genes for its tolerance.

Table 3
Genes that changed with light intensity under extreme temperature conditions

gene	function	annotation number	Swissprot-E-value
unigene5844_All	wd repeat-containing protein LWD2	sp|Q38960|LWD2_ARATH	1.00E-18
unigene34958_All			4.00E-11
unigene20376_All	vegetative cell wall protein gp1	sp|Q9FPQ6|GP1_CHLRE	1.00E-16
unigene20405_All			2.00E-06
unigene9924_All			3.00E-29
unigene13685_All			2.00E-19
unigene33653_All			9.00E-14
unigene27164_All			4.00E-12
unigene17011_All	heat shock 70 kDa protein 6, chloroplastic	sp|Q9STW6|HSP7F_ARATH	3.00E-82
unigene30541_All	chlorophyll a-b binding protein L1818, chloroplastic	sp|Q03965|L181_CHLMO	3.00E-51
unigene225_All			1.00E-49
unigene27131_All	uncharacterized protein	sp|P0C8Z0|Y8359_ORYSI	1.00E-06
unigene6266_All	40S ribosomal protein S12	sp|Q9XHS0|RS12_HORVU	1.00E-33
unigene34085_All	profilin-1	sp|P49231|PROF1_PHAVU	8.00E-35
unigene30740_All	ran-binding protein 1 homolog a	sp|Q9LMK7|RBP1A_ARATH	8.00E-40
unigene23723_All	dynein 8 kDa light chain, flagellar outer arm	sp|Q39580|DYL1_CHLRE	5.00E-42
unigene13240_All	20 kDa chaperonin, chloroplastic	sp|O65282|CH10C_ARATH	1.00E-41
unigene27075_All	peptide methionine sulfoxide reductase B2, chloroplastic	sp|Q9C5C8|MSRB2_ARATH	2.00E-39
unigene13846_All	small ubiquitin-related modifier 1	sp|P55857|SUMO1_ORYSJ	2.00E-17
unigene34046_All	branched-chain-amino-acid aminotransferase 5, chloroplastic	sp|Q9FYA6|BCAT5_ARATH	4.00E-86
unigene27210_All	glutathione S-transferase Z2	sp|Q9ZVQ4|GSTZ2_ARATH	1.00E-12
unigene23679_All	formin-like protein 14	sp|Q9C6S1|FH14_ARATH	4.00E-10
unigene10207_All	short-chain dehydrogenase TIC 32, chloroplastic	sp|A2RVM0|TIC32_ARATH	3.00E-49
unigene20031_All	3-isopropylmalate dehydratase	sp|Q94AR8|LEUC_ARATH	0

gene	function	annotation number	Swissprot-E-value
unigene30563_All	serine/threonine-protein kinase SAPK10	sp|Q75H77|SAPKA_ORYSJ	2.00E-50
unigene20380_All	26S proteasome regulatory subunit 4 homolog B	sp|Q9SL67|PRS4B_ARATH	0
unigene33974_All	formin-like protein 3	sp|Q7G6K7|FH3_ORYSJ	5.00E-08

Among the genes that change with light intensity under extreme temperature conditions, there are more genes related to the function of the Vegetative cell wall protein gp1, and there are 6 genes. Further analysis of their homology found that the consistency was 30.71% in DNAMAN, and the homology was 30.71%. The sex is not high. unigene5844_All and unigene34958_All express the same function: wd repeat-containing protein LWD2. The homology comparison found that the consistency is 50.95%. These genes do not belong to one class, and may have formed different Categories; unigene30541_All and unigene225_All are annotated as chlorophyll ab binding protein L1818 (chloroplastic), and the homology comparison found that the consistency is 84.65%, the homology is high, and it may be a class of genes.

In addition to the above genes, there are still some genes with unknown functions that enable the growth of E. prolifera under extreme conditions, including unigene30667_All, unigene27474_All, unigene26919_All, unigene10018_All, unigene23770_All, unigene34014_All, unigene13559_All, etc.

The expression levels of these genes under high light intensity are higher than those under low light intensity, which may be because the stress of high light intensity is more extreme for *U. compressa*, which leads to the need for more gene expression levels to adapt to high light intensity stress, but it still needs to be further proved by follow-up experiments.

3.2.2 Genes only expressed at high temperature

These genes were only expressed at high temperatures, that is, the samples were only expressed in B1, B2, and B3. Most of these genes are related to stress resistance and signal transduction, and a few are related to cell division and cell components. It can be seen that under high-temperature conditions, to maintain the growth of *U. compressa* level. The genes with known functions are shown in Table 4. Among them, the genes such as unigene35167_All and unigene36939_All are respectively formin-like protein 5 and formin-like protein 20 according to the annotations, and they all have the function of regulating cell activity; unigene26553_All, unigene28750_All, unigene46434_All, unigene9437_All, etc. All genes have the function of vegetative cell wall protein gp1, thus constituting cell components. According to the homology comparison, the consistency of these genes is only 22.96%, and the homology is not high.

There are also some genes directly related to resistance to external adverse environments. Among them, unigene17608_All has the function of lectin OS = Ulva pertusa according to the annotation. The activity of the protein was not affected within 30min at 30–70°C, which could protect *U. compressa* from

temporarily adapting to high-temperature environment; unigene19720_All and unigene19717_All both have the function of proline-rich receptor-like protein kinase PERK2, which acts as a protein kinase to temporarily resist the influence of certain adverse environments. These genes all have different expression levels under high temperatures, and they all help *U. compressa* to temporarily adapt to the high-temperature environment from different angles. This may be a special gene formed in the long evolutionary process, but in terms of growth rate, the growth rate of *U. compressa* was much lower than that of other *U. prolifera* at high temperatures(Jianjun, et al. 2015). It is speculated that the condition-specific gene expression mechanism of *U. compressa* may be different from the differential gene mechanism of other *U. prolifera*, resulting in a slow growth rate. Therefore, *U. compressa* mostly appeared in the early green tide of the Yellow Sea, and then with the increase of temperature, resulting in a slow growth rate. *U. compressa* gradually lost its status of the dominant species(Wang, et al. 2018).

Table 4
Genes that were only expressed at high temperatures

gene	function	annotation number	Swissprot-E-value
unigene26553_All	vegetative cell wall protein gp1	sp|Q9FPQ6|GP1_CHLRE	5.00E-20
unigene28750_All			5.00E-07
unigene46434_All			1.00E-14
unigene9437_All			4.00E-22
unigene35167_All	formin-like protein 5	sp|Q84ZL0|FH5_ORYSJ	4.00E-10
unigene36939_All	formin-like protein 20	sp|Q9FLQ7|FH20_ARATH	2.00E-08
unigene17608_All	lectin OS = Ulva pertusa	sp|Q6T6H8|LEC_ULVPE	6.00E-15
unigene19720_All	proline-rich receptor-like protein kinase PERK2	sp|Q9LK03|PERK2_ARATH	2.00E-07
unigene19717_All			5.00E-07

3.2.3 Genes that change with temperature under constant light intensity

The expression level of such genes is not expressed in samples B4 and B5 but is expressed in B1, B2, B3, B6, B7, B8, and B9. When the light intensity is constant, the expression level gradually decreases with the decrease of temperature, that is, Under the same light intensity, to adapt to the change of temperature, this kind of specific genes of *U. compressa* began to express and B1 > B7, B2 > B8, B3 > B6 > B9. Genes with known functions are shown in Table 5. Such genes are mainly related to cellular components and signal transduction, including unigene27211_All, unigene23849_All, unigene23949_All, unigene6286_All, unigene888_All, unigene26935_All, unigene6099_All, unigene17243_All and unigene229_All. The functions of these genes are related to vegetative cell wall protein gp1, which is involved in the formation

of the cell wall. According to the homology comparison, it is found that the consistency is 34.39%, and the homology is not high.

At the same time, the unigene30603_All and unigene10500_All genes are xyluloses 5-phosphate/phosphate translocator, chloroplastic and secretory carrier-associated membrane protein 1 respectively according to their annotation functions, and both have the role of transport.

U. compressa can grow at low temperatures, and the growth rate is higher than other U. prolifera, but the growth rate is lower than other *U. prolifera* at high temperatures. Therefore, the high expression level of these genes may inhibit the growth of U. compressa, which makes *U. compressa* withdraw from the early stage of the green tide.

Table 5
Genes that changed with temperature under constant light intensity

gene	function	annotation number	Swissprot-E-value
unigene27211_All	vegetative cell wall protein gp1	sp|Q9FPQ6|GP1_CHLRE	1.00E-10
unigene23849_All			4.00E-20
unigene23949_All			2.00E-12
unigene6286_All			7.00E-06
unigene888_All			3.00E-10
unigene26935_All			4.00E-15
unigene6099_All			1.00E-07
unigene17243_All			2.00E-09
unigene229_All			2.00E-24
unigene30603_All	xylulose 5-phosphate/phosphate translocator, chloroplastic	sp|Q9LF61|XPT_ARATH	1.00E-83
unigene10500_All	secretory carrier-associated membrane protein 1	sp|Q8H5X5|SCAM1_ORYSJ	7.00E-39

3.3 Homology alignment of genes with the same function expressed under different conditions

It can be seen from the above results that different specific genes expressed in *U. compressa* have the same function under different conditions. Among them, there were 19 specific genes related to vegetative cell wall protein GP1 function, with a consistency of 23.19%, all of which did not have homology. In the evolution of *U. compressa*, these genes had undergone great changes.

4 Discussion

Through laboratory culture conditions and transcriptome analysis, it was found that under the stimulation of short-term light intensity and temperature, some genes of *U. compressa*, which is also consistent with the results obtained(Yangyang, et al. 2010). Studies have shown that for *U. prolifera*, *U. flexuosa*, and *U. line*, under the stimulation of short-term light intensity and temperature, the genes related to photosynthesis will be significantly up-regulated or down-regulated, and temperature changes have a certain tolerance, and maximize the photosynthetic efficiency in their respective ways(Masini, et al. 1995, Tao, et al. 2017, Wenzhong, et al. 2009). In this study, the genes related to photosynthesis in *U. compressa* are unigene30541_All and unigene225_All. According to the annotation, they both express the function of chlorophyll ab binding protein L1818 (chloroplastic), and both are condition-specific genes expressed at extreme temperatures. In DNAMAN software analysis, the consistency is 84.65%, with homology. The accumulation of chlorophyll has great consistency with the change rate of chlorophyll ab-binding gene expression, but it is not affected by light below the photosynthetic threshold(Hermsmeier, et al. 1991), which is consistent with the fact that the content of chlorophyll ab does not change with light intensity obtained in this experiment. The results were consistent. At the same time, increasing the expression of two condition-specific expression genes with homology only at extreme temperatures was beneficial to increasing the rate of change in gene expression, thereby improving its ability to cope with adverse environments.

In this study, genes related to the function of vegetative cell wall protein gp1 appeared frequently. Studies have shown that when Chlamydomonas reinhardtii is cultured in a medium with alternating light and dark cycles, the synthesis period of cell wall proteins is during cell division, and shortly after cells are separated., and at this time, cells use 15% of their protein synthesis capacity to make cell wall proteins(Lang and Chrispeels 1976). In 2003, Nicolas et al. found an Arabidopsis gene in the genomes of Arabidopsis and rice as encoding a new type of cell wall protein. Phylogenetic analysis of the conserved domain found that the protein encoded by this gene is in Before monocotyledonous and dicotyledonous plants differentiate, there are two branches, one is "reproductive", which is specifically expressed in Arabidopsis pollen; the other is "vegetative", which is expressed in spore organoids(Baumberger, et al. 2003). It can be seen that cell wall proteins may have a certain relationship with reproduction (division, spore release). The expression of conditional specific genes related to cell wall proteins was different under different conditions. unigene20376_All, unigene20405_All, unigene9924_All, unigene13685_All, unigene33653_All and unigene27164_All were expressed under extreme light intensity. unigene26553_All, unigene28750_All, unigene46434_All, and unigene9437_All were expressed at high temperatures. According to DNAMAN sequence analysis, the homology of these specific genes was less than 50%. However, according to the annotation, they all play a role in the formation of the cell wall. According to the analysis of the image, it is found that these fragments with high homology are concentrated in the middle of the gene fragment, and the length of the DNA sequence at both ends is different These specific genes without homology may be more suitable for the growth and reproduction of *U. compressa* under different conditions, which is consistent with the in-situ germination of *U. compressa* under related stimuli(Steen 2004).

The functions of other regular condition-specific genes are mostly related to resistance to stress. The specific expression of these genes helped *U. compressa* to grow under extreme conditions. Compared with the rise of other predominant species of *U. prolifera*, *U. compressa* was still in a weak position in growth and development. From these regular changes, it can be seen that under unsuitable conditions, most of the genes expressed by *U. compressa* are anti-stress and signal transduction specific genes to maintain normal growth and development, which also confirms the tolerance of *U. compressa's* wide range, and strong survivability(Wang, et al. 2018).

5 Conclusion

Through this study, it was found that there are indeed some changes in the expression of some condition-specific genes under different growth conditions. Related genes, to cope with extreme temperature changes, express two condition-specific expression genes with higher homology, that is, genes related to cell wall proteins. Different condition-specific expression genes are expressed under different stresses so that *U. compressa* can adapt to changes in the environment in terms of reproduction and nutrient supply so that it can temporarily maintain normal growth and development. To further explore the condition-specific genes of *U. compressa*. The relationship with environmental tolerance provides a reference.

Declarations

Ethical Approval and Consent to participate

In no case human participants whose consent to participate was needed were involved.

Human and Animal Ethics

Not applicable.

Consent for publication

In this study, human participants whose consent for publication was needed were not involved.

Availability of supporting data

All the specimens herein studied were deposited at Shanghai Ocean University, China.

Competing interests

Not applicable.

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Authors' contributions

All authors contributed to the study’s conception and design. Material preparation, data collection, and analysis were performed by Dong ao and Zhou lingjie. The first draft of the manuscript was written by Dong ao and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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References

1. Baumberger N, Doesseger B, Guyot R, Diet A, Parsons RL, Clark MA, Simmons MP, Bedinger P, Goff SA, Ringli C, Keller B (2003) Whole-Genome Comparison of Leucine-Rich Repeat Extensins in Arabidopsis and Rice. A Conserved Family of Cell Wall Proteins Form a Vegetative and a Reproductive Clade Plant Physiology. 131:1313–1326. 10.1104/pp.102.014928. 3
2. Blomster J, Back S, Fewer DP, Kiirikki M, Lehvo A, Maggs CA, Stanhope MJ (2002) Novel Morphology in Enteromorpha (Ulvophyceae) Forming Green Tides American. J Bot 89(11):1756–1763. 10.3732/ajb.89.11.1756
3. Hermsmeier D, Mala E, Schulz R, Thielmann J, Galland P, Senger H (1991) Antagonistic Blue- and Red-Light Regulation of Cab-Gene Expression During Photosynthetic Adaptation in Scenedesmus

Obliquus Journal of photochemistry and photobiology. B Biology 11(2):189–202. 10.1016/1011–1344(91)80260-o

4. JianFang X, XiaoWen Z, NaiHao Y, Zhou Z, ShanLi M, MeiTao D, Dong X, JinLai (2013) M Activities of Principal Photosynthetic Enzymes in Green Macroalga Ulva Linza: Functional Implication of C-4 Pathway in Co2 Assimilation Science China-Life Sciences. 56(6): 571–580. 10.1007/s11427-013-4489-x
5. Jianjun C, Jianheng Z, Yuanzi H, Lingjie Z, Qing W, Liping C, Kefeng Y, Peimin H (2015) Adaptability of Free-Floating Green Tide Algae in the Yellow Sea to Variable Temperature and Light Intensity Marine Pollution Bulletin. 101:660–666. 10.1016/j.marpolbul.2015.10.033. 2
6. Lang WC, Chrispeels MJ (1976) Biosynthesis and Release of Cell Wall-Like Glycoproteins During the Vegetative Cell Cycle of Chlamydomonas Reinhardii Planta. 129:183–189. 10.1007/bf00390026. 2
7. Leliaert F, Zhang X, Ye N, Malta E-j, Engelen AH, Mineur F, Verbruggen H, De Clerck O (2009) Research Note: Identity of the Qingdao Algal Bloom Phycological Research. 57:147–151. 10.1111/j.1440-1835.2009.00532.x. 2
8. Liu F, Pang S, Chopin T, Gao S, Shan T, Zhao X, Li J (2013) Understanding the Recurrent Large-Scale Green Tide in the Yellow Sea: Temporal and Spatial Correlations between Multiple Geographical, Aquacultural and Biological Factors Marine Environmental Research. 83:38–47. 10.1016/j.marenvres.2012.10.007
9. Liu F, Pang SJ, Zhao XB, Hu CM (2012) Quantitative, Molecular and Growth Analyses of Ulva Microscopic Propagules in the Coastal Sediment of Jiangsu Province Where Green Tides Initially Occurred Marine Environmental Research. 74:56–63. 10.1016/j.marenvres.2011.12.004
10. Masini RJ, Cary JL, Simpson CJ, McComb (1995) Effects of Light and Temperature on the Photosynthesis of Temperate Meadow-Forming Seagrasses in Western-Australia Aquatic Botany. AJ:239–254. 10.1016/0304–3770(94)00432-l. 4
11. Merceron M, Antoine V, Auby I, Morand P (2007) In Situ Growth Potential of the Subtidal Part of Green Tide Forming Ulva Spp. Stocks Sci Total Environ 384(1–3):293–305. 10.1016/j.scitotenv.2007.05.007
12. Nelson TA, Haberlin K, Nelson AV, Ribarich H, Hotchkiss R, Van Alstyne KL, Buckingham L, Simunds DJ (2008) Ecological and Physiological Controls of Species Composition in Green Macroalgal Blooms Ecology. 89:1287–1298. 10.1890/07-0494.1. Fredrickson K5
13. Rengcheng Y, Song S, Tian Y, Mingjiang Z (2018) Progesses and Perspctives on Green-Tide Studies in the Yellow Sea Oceanologia Et Limnologia Sinica. 49:942–94905
14. Steen H (2004) Interspecific Competition between Enteromorpha (Ulvales: Chlorophyceae) and Fucus (Fucales : Phaeophyceae) Germlings: Effects of Nutrient Concentration, Temperature, and Settlement Density Marine Ecology Progress Series. 278(89–101. 10.3354/meps278089
15. Tao Z, Juhong T, Jianyi Z, Zonggen S (2017) A Study on the Effect of Temperature on the Photosynthetic Physiology of Attached Green Algae in the South Yellow Sea. J Changshu Inst Technol 31(04):95–99. 10.16101/j.cnki.cn32-1749/z.2017.04.022

16. Wang S, Huo Y, Zhang J, Cui J, Wang Y, Yang L, Zhou Q, Lu Y, Yu K, He P (2018) Variations of Dominant Free-Floating Ulva Species in the Source Area for the World's Largest Macroalgal Blooms, China: Differences of Ecological Tolerance Harmful Algae. 74:58–66. 10.1016/j.hal.2018.03.007
17. Wang Z, Gerstein M, Snyder M (2009) Rna-Seq: A Revolutionary Tool for Transcriptomics. Nat Rev Genet 10(1):57–63. 10.1038/nrg2484
18. Wenzhong T, Xingshu L, Haiyan H, Chuner C, Yuanzi H, Peimin H (2009) Effects of Different Light Intensity and Temperature Treatment on Photosynthesis and Chlorophyll Fluorescence in Ulva Line. J Fishries China 33(05):762–769
19. Xiaolin T, Yuanzi H, Liping C, Jianhua H, Jianhen Z, Rui J, Hong L, Jinhui W, Reng X, Jianqiang Y, Xiang H, Jianmeng F, Jiahai M (2011) Molecular Detection and Analysis of Green Seaweeds from Rudong Coasts in Jiangsu Province Chinese Science Bulletin. 56:309–317Peimin HZ1
20. Xing Q, Bi G, Cao M, Belcour A, Aite M, Mo Z, Mao Y (2021) Comparative Transcriptome Analysis Provides Insights into Response of Ulva Compressa to Fluctuating Salinity Conditions. J Phycol. 10.1111/jpy.13167-21-001
21. Xuelei J, Xiaojian Z, Jianing l, Zhenjun K (2021) Research Progress in the Ecological Consequences of Ulva Prolifera Green Tides in the Yellow Sea Marine Environmental Science. 40:647–652. 10.13634/j.cnki.mes.2021.04.023. Qing l04
22. Yangyang W, Yuanzi H, Jiachun C, Liping C, Peimin H (2010) Influence of Low Temperature and Low Light Intensity on Growth of Ulva Compessa. J Fish Sci China 17(03):593–599
23. Yuan H, Yafeng M, Yu D, Songdong S (2018) Differential Gene Expression for Carotenoid Biosynthesis in a Green Alga Ulva Prolifera Based on Transcriptome Analysis. BMC Genomics 19(1):916–916. 10.1186/s12864-018-5337-y