Abiotic stress in algae: response, signaling and transgenic approaches

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Abstract

High salinity, nutrient deficiency, heavy metals, desiccation, temperature fluctuations, and ultraviolet radiations are major abiotic stress factors considered inhospitable to algal growth and development in natural and artificial environments. All these stressful conditions cause effects on algal physiology and thus biochemical functioning. For instance, long-term exposure to hyper/hypo salinity conditions inhibits cell differentiation and reduces growth. Photosynthesis is completely blocked in algae's dehydrated state, resulting in photoinhibition or photodamage. The limitation of nutrients in aquatic environments inhibits primary production via regulating phytoplankton community development and structure. Hence, in response to these stressful conditions, algae develop plenty of cellular, physiological, and morphological defences to survive and thrive. The conserved and generalized defence responses in algae include the production of secondary metabolites, desaturation of membrane lipids, activation of reactive species scavengers, and accumulation of compatible solutes. Moreover, a well-coordinated and timely response to such stresses involves signal perception and transduction mainly via phytohormones that could sustain algae growth under abiotic stress conditions. In addition, the combination of abiotic stresses and plant hormones could further elevate the biosynthesis of metabolites and enhance the ability of algae to tolerate abiotic stresses. This review aims to present different kinds of stressful conditions confronted by algae and their physiological and biochemical responses, the role of phytohormones in combatting these conditions, and, last, the future transgenic approaches for improving abiotic stress tolerance in algae.

Keywords Abiotic stress · Salinity · ROS · Phytohormones · Lipid production · Transgenic

Introduction

Stress is described as a "disparity from nominal conditions for as long as homeostasis allows" (Borowitzka 2018). Nutrient deficiency, especially nitrogen deprivation, low/high light intensity, low/high temperature, low/high salinity levels, and pH variations, are all considered physiologically stressful conditions for algae as they reduce the growth rate. The impact of these environmental factors, whether negative or positive, may significantly affect microalgal physiology and biochemical processes (Rosenberg et al. 2008). Acute variations in temperature, irradiance, salinity, or pH will disturb cellular homoeostasis by affecting cellular integrity and bio-molecular composition (Jauzein and Erdner 2013).

Under salinity stress, the turgor pressure, ion distribution, and organic solutes in the cell are disrupted, resulting in reactive oxygen species (ROS), which induce cell oxidative damage (Liu and Pang 2010). Long-term exposure to hyper/hypo salinity conditions inhibits cell differentiation and decreases growth (Kumar et al. 2010).

Similarly, light intensity affects algal growth through its impact on photosynthesis (Stockenreiter et al. 2013). The growth rate of algae is maximum at saturation intensity and decreases with both rising and fall in light intensity. Microalgae undergo photoadaptation/photoacclimation, which results in a change in cell properties and increased photosynthetic activity. This will help the microalgae to survive in changed conditions of light intensity. Photoadaptation (a change in genotype that occurs over many generations in response to a change in light intensity) can occur through various processes, including changes in pigment types and quantities, growth rate, dark respiration rate, and essential fatty acid supply (Fábregas et al. 2004). Reversible

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phenotypic adjustments such as changes in cell volume and the number of thylakoid membranes per stack accompany morphological photoacclimation (Berner et al.1989).

Moreover, ultraviolet (UV) light (wavelengths 215–400 nm) has harmful effects on algae (Pessoa 2012). At comparable intensities, UV-B (215–380 nm) does more significant damage to the cells than UV-A (380–400 nm) (Pessoa 2012). UV-B radiation causes direct damage to DNA molecules, whereas UV-A radiation induces indirect damage by generating reactive oxygen and hydroxyl radicals. Self-shading through mat formation, migration to greater water depth (lower UV-levels), activation of anti-oxidative processes involving enzymatic and non-enzymatic strategies, or the synthesis of specific secondary metabolites such as mycosporine-like amino acids (MAAs), scytonemin, and carotenoids comprising myxoxanthophyll, β-carotene, and its derivatives (such as echinenone and zeaxanthin) are all established acclimation mechanisms in algae and cyanobacteria (Rastogi et al. 2014).

Environmental stress can cause significant damage and trigger responses that result in either acclimation or programmed cell death. Algae use various stress control and repair techniques, including modifying fatty acid saturation to change membrane fluidity, synthesising chaperonins for correct folding of denatured proteins, accumulating compatible solutes to sustain cell osmolality and controlling photosynthesis to regulate energy output and consumption. This review highlights the different kinds of abiotic stress conditions faced by algae and their physiological and biochemical responses. The role of phytohormones to combat abiotic stress and lipid production during these conditions is also discussed. In addition, transgenic approaches to cope with these stressful conditions are also considered in this review.

High salt stress

When algae are subjected to high salt stress, their photosynthetic activity is significantly reduced. This kind of inhibition appears in the photosystem II (PSII) complex. Reduced PSII activity was linked to state-2 transition in the green alga *Dunaliella tertiolecta* (Gilmour et al. 1984, 1985). Endo et al. (1995) confirmed this and proposed that the reduction of quantum yield of PSII electron transport in *Chlamydomonas reinhardtii* caused by salinity stress is connected to the state-2 transition. Lu and Vonshak (2002) demonstrated that the damage to phycobilisome and shifted the distribution of excitation energy favouring PSI in *Arthrospira* (*Spirulina*) *platensis* due to inhibition of the electron transport at donor and acceptor sides of PSII under salt stress.

Moreover, stress due to high salt concentration also leads to ROS generation and deficiency of different cations (such as potassium (K^+), calcium (Ca^{2+}), and manganese

(Mn^{2+})), thus decreasing photosynthetic activity by interfering with several physiological and biochemical processes (Sudhir and Murthy 2004; Fal et al. 2022). Light-harvesting complexes (LHCs) of PSI and proteins of PSII involved in oxygen (O_2) evolution are damaged by ROS at high salt concentrations in *C. reinhardtii* (Subramanyam et al. 2010; Neelam and Subramanyam 2013). However, to eliminate the ROS and misfolded protein production, the salt-stressed cells of *C. reinhardtii*, undergo upregulation of several genes such as glutathione transferase, glutaredoxin, plastid Fe superoxide dismutase 1 (SOD), thioredoxins, a GrpE family protein, heat shock protein HSP20 and heat shock factor binding proteins (Perrineau et al. 2014). In response to a spike in salt concentration, *Dunaliella salina* a salt-tolerant microalga, increases the Chlorophyll-*a* (Chl-*a*) content to raise the photosynthetic activity (Talebi et al. 2013).

Different responses are reported in algal species to combat salinity stress, as shown in Fig. 1.

Khona et al. (2016) reported that when *C. reinhardtii c*ells are exposed to high salt stress, they undergo a temporary stage known as "palmelloid" (Fig. 2). Palmelloid form has undergone several structural changes, including the loss of flagella, cell clustering having a minimum of two cells per cluster, increased secretion of exopolysaccharide (EPS), surrounding cells by EPS matrix, and individual cell wall thickening. The synthesis of EPS requires a lot of energy; however, the EPS matrix's protection permits to survive the stressed cells under adverse conditions. EPSs accelerate water accumulation and decrease ion influx, protecting the membrane system on palmella formation in *D. salina* (Wei et al. 2017).

Algal genera like *Dunaliella* and *Chlorella* have alternative strategies for dealing with salt stress. As *Dunaliella* does not have a cell wall, allowing the cells to rapidly alter volume during severe salinity stress by altering internal ion and glycerol content, restoring the cells' osmotic pressure (Ben-Amotz and Avron 1980; Katz and Avron 1985; Kaçka and Dönmez 2008). On the other hand, *Chlorella* cells employ osmoregulation to maintain osmotic homeostasis by producing organic solutes and accumulating inorganic ions due to rigid cell walls. These solutes, also known as compatible solutes, are typically small organic compounds with a neutral charge and minimal toxicity at significant concentrations. Glycerol is an excellent example of an effective compatible solute generated by algal species during high salt stress. Glycerol accumulation in *Chlamydomonas* HS-5 was proportional to salt concentration, with higher salt concentration resulting in higher glycerol content (Miyasaka et al. 1998). Starch breakdown correlated closely with glycerol formation in *Chlamydomonas pulsatilla*, suggesting that glycerol was synthesised by the breakdown of starch (Hellebust and LIN 1989).
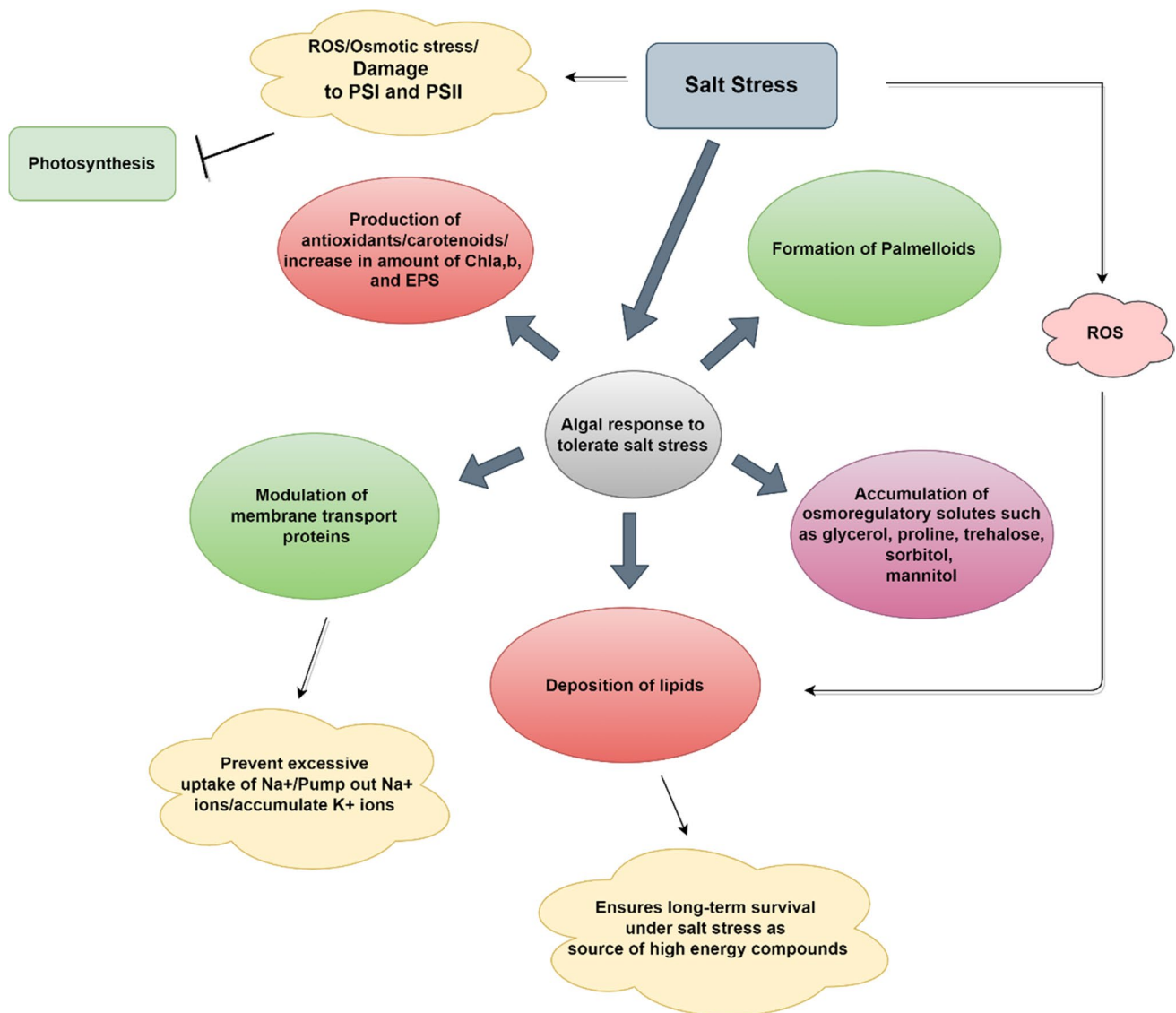
Fig. 1 Algal response to tolerate high salt stress

Proline is another osmoregulatory solute whose content increases linearly with increasing salt in algae (Brown and Hellebust 1978). Exogenous proline application reduces the adverse effects of high salinity by decreasing sodium (Na^+) and chloride (Cl^-) accumulation in *C. reinhardtii* (Reynoso and De Gamboa 1982). During salt stress, *Picochlorum oklahomensis* (Henley et al. 2004) and *Picochlorum* SE3 (Foflonker et al. 2016) both showed up-regulation of genes involved in proline synthesis. In contrast to *Chlamydomonas* sp. and *D. salina*, where glycerol is the primary osmolyte and starch degradation increases, proline is the primary osmolyte in *Picochlorum* species, and starch synthesis is increased (Xia et al. 2014; Foflonker et al. 2016). Besides proline and glycerol, trehalose also has a recognised involvement in the stability of proteins by raising the

transition temperature of proteins and as an osmoregulatory molecule (Kaushik and Bhat 2003). High salt stress in *Chlamydomonas* (Wang et al. 2018a), *Chlorella*, and *Scytonema* increased trehalose production (del Pilar Bremauntz et al. 2011). Other polyols such as mannitol and sorbitol are also crucial in osmoregulation (Foflonker et al. 2016).

Another critical technique for dealing with salt stress is ion uptake and export via the cell membrane, which helps to maintain intracellular ion balance (Reed et al. 1981; Talebi et al. 2013). In hypersaline conditions, *Dunaliella* is reported to use a redox-driven sodium pump to remove Na^+ ions (Katz and Pick 2001). High Na^+ concentrations can interfere with the absorption of other cations, particularly K^+ (Chakraborty et al. 2016). As K^+ is involved in a variety of physiological activities in plants, maintaining

Fig. 2 Conceptual diagram that shows the clustering of *C. reinhardtii c*ells (Palmelloid stage) upon salt stress
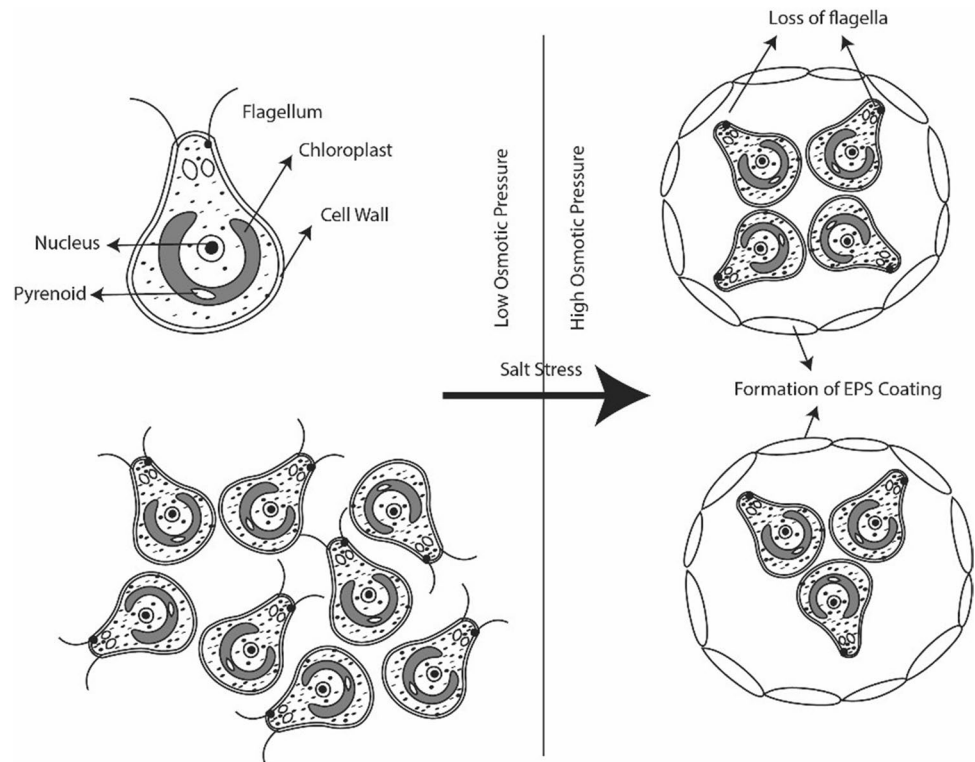
the cytosolic K^+/Na^+ ratio is very critical in salty circumstances (Degl'Innocenti et al. 2009). By transporting K^+ ions through membrane transport proteins, upregulation of membrane transport proteins can give resistance to high salinity in halotolerant algal species. Salt-adapted mutants of *C. reinhardtii* showed increased expression of numerous membrane transport proteins, as reported by Sithtisarn et al. (2017). When salt-sensitive *C. reinhardtii* cells were subjected to salt stress, genes for K^+ ion transport were dramatically increased (Wang et al. 2018a), perhaps compensating for the disruption in K^+ absorption induced by elevated Na^+ ion concentrations. In addition to membrane transport proteins, the amount of two plasma membrane proteins, P150 and P60, increased significantly with increasing salt content in *D. salina* (Fisher et al. 1996). Furthermore, the induction of these proteins correlated with enhanced growth immediately after a severe hyperosmotic shock, indicating their role in salt acclimation.

Most green algae exhibit storage lipid buildup when subjected to salt stress. Several researches have been conducted on using high salinity conditions to improve algal lipids production. *Chlamydomonas* sp. JSC4 is a salt-tolerant strain obtained from a marine environment that exhibits substantial lipid accumulation when subjected to extreme salt stress. This strain was used to investigate the mechanism of lipid production in extreme salt stress (Ho et al. 2014). Under salt stress, *Chlamydomonas* sp. JSC4

exhibits a highly selective transition from starch synthesis to lipid synthesis (Ho et al. 2017).

Carotenoids act as antioxidants situated inside the chloroplast envelope and protect the PSII (primarily the de novo synthesis of D1 protein required to repair PSII) and LHC from the damage induced by ROS. In response to high salt stress *D. salina* synthesizes a high amount of carotenoids, which is exploited in industries for carotenoid production (Massyuk 1965; Borowitzka et al. 1985, 1990; Avron and Ben-Amotz 1992; Borowitzka 1995; Ye et al. 2008). At moderate levels of salt stress (0.05 M–0.15 M), *C. reinhardtii* and *Chlorella vulgaris* also show high carotenoid production (Annamalai et al. 2016).

Several studies showed that low salinity conditions also affect various physiological processes of marine algae. For instance, Wilson et al. (2004) reported the decrease in the photosynthetic efficiency (F_v/F_m) of the red alga *Lithothamnion glaciale* after 5-week exposure to a salinity of 3. Despite an initial reduction in photosynthetic parameters and an increase in respiration, the physiology of the *Gelidium coulteri* was reported to be partially recovered after a 5-week exposure to a low-salinity environment (Macler 1988). In the brown algae, *Alaria esculenta*, a reduction in photosynthetic efficiency was detected in the microscopic zoospores but not during adult life stages when exposed to a salinity of 20 (Fredersdorf et al. 2009). Moreover, Burdett et al. (2015) investigated the effect of low salinity on the intracellular

concentration of dimethylsulphoniopropionate (DMSP), pigment composition and photosynthetic characteristics in *L. glaciale*. No significant difference in intracellular DMSP concentrations was observed. However, photosynthetic parameters (comprising pigment composition) exhibited a mixed response, indicating some degree of photosynthetic resilience to decreased salinity. This study shows evidence of intracellular mechanisms adopted by *L. glaciale* in response to reduced salinity.

Nutrient stress in algae

The limitation of nitrogen (N) and phosphorus (P) in aquatic environments inhibits primary production via regulating phytoplankton community development and structure (Harke et al. 2016). In algae, depending on which nutrient is reduced and to what degree, significant differences in biochemical composition can be found under conditions of nutrient limitation. Nitrogen and phosphorus deficiency, for example, causes lipid metabolism to switch from membrane lipid synthesis to neutral lipid storage. As a result, the overall lipid content of green algae rises, although the lipid contents in the plasma membrane decrease. Studies have shown that P-stressed cells upregulate gluconeogenesis over glycolysis transcriptionally. Trehalose concentrations rise dramatically in P-stressed cells. P-stressed cells displayed higher taurocholate levels, indicating that P-stress promotes triacylglycerol (TAG) mobilization (McLean et al. 2021). Moreover, phosphorus-containing lipids (P-lipids) of membranes are reported to get replaced with other non-P substitutes under situations of P deficiency in the diatom *Thalassiosira pseudonana* (Martin et al. 2011; Hunter et al. 2018). This response permits the phytoplankton to decrease its P demands in P-limited environments (Van Mooy et al. 2009).

Microalgae degrade nitrogen-containing macromolecules such as proteins, mainly when nitrogen is low. As a result of the lack of nitrogen, microalgae accumulate vast quantities of carbohydrates and fats. Current research has used nutrient limitation approaches (such as sulfur, nitrogen, and phosphate) to induce microalgae to convert protein or peptides into carbohydrates to enhance carbohydrate accumulation (Dragone et al. 2011; Harun and Danquah 2011). The carbohydrate content of the microalga *C. vulgaris* rose to 22.4% from the normal content of 16.0% on a dry weight basis under nutritional (nitrogen) stress, which is more acceptable in terms of the biomass required to create bioethanol (Kim et al. 2014).

Depending on the nutritional composition of the growth medium, the same algal strain might be a source of various fatty acids. Saturated fatty acids, particularly palmitic acid and total lipid content in the green alga *Scenedesmus obliquus*, are affected by Na, iron (Fe), cobalt (Co), and molybdenum (Mo). High potassium and magnesium trigger the production of the most polyunsaturated acids (PUFA) and oleic acid, whereas nitrogen and phosphorus trigger the least. The maximum levels of monounsaturated acids (MUFAs), particularly α-linolenic acid (ALA), are acquired when nitrogen and phosphorus deficiency retards development and results in a buildup of fatty acids that form MUFAs, particularly elaidic acid (Darki et al. 2017).

Microalgae growth and phosphate absorption are also directly related to biomass production (Solovchenko et al. 2016). Chu et al. (2013) showed that in phosphate-sufficient circumstances, the lipid yield of *C. vulgaris* for biodiesel generation was 58.39 mg L^{-1} day^{-1}, which was more significant than in phosphate-deficient situations. Consequently, it is possible to deduce that phosphate is a crucial macronutrient for the production of microalgal lipids. However, due to a lack of light and a decline in carbon dioxide (CO_2) and O_2 levels in the growth medium, the phosphorus absorption rate by microalgae can achieve saturation (Chu et al. 2013).

Few experimental studies in the literature highlight the effect of high concentrations of nutrients on the physiological processes of algae. Reef et al. (2012) reported the effect of nutrient enrichment (N and P) on the growth rate, photosynthesis, nucleic acid composition, and elemental stoichiometry of three coral reef macroalgae (*Caulerpa serrulata*, *Laurencia intricata*, *Sargassum polyphyllum*). They observed that nutrient enrichment had positive effects on photosynthetic rates and investment in RNA. However, no correlation of growth was found with either photosynthetic rates or RNA content. Macroalgae, especially *L. intricata*, accumulated P to very high levels (> 0.6% of dry weight). Negative effects of P accumulation on growth were observed above 0.21%. N was not stored, but evidence of futile cycling (significant reduction in N signatures following the enrichment) was observed. The ability to store large amounts of P is probably an adaptation to the tropical oceans' patchy and low nutrient environment. Moreover, nutrient enrichment of lakes leads to eutrophication, which results in the growth of harmful and undesirable algal species. It causes changes in the physical and chemical quality of water and sediments, affecting the entire ecohydrology of lakes along with variations in diversity, composition and richness of algal species (Dubey and Dutta 2020).

Desiccation stress

Water-stressed environments lead to desiccation in certain poikilohydric plants such as algae and lichens quickly, as they cannot manage their water content actively. In the dehydrated state of algae, photosynthesis is completely blocked, and due to which, it cannot use any absorbed energy for

electron excitation, which results in photoinhibition or photodamage. Allakhverdiev et al. (2008) reported different desiccation sensitive sites in the photosynthetic machinery of cyanobacteria, green algae, lichens, and mosses. These sites include the photosystems, particularly PSII with its oxygen-evolving complex, ATP-generation, and carbon assimilation processes. Due to desiccation in algae, the supply of CO_2 used in carbon fixation may also decrease, resulting in the decrease of the D1 protein repair by inactivating the translation machinery (Takahashi and Murata 2008). Hence, it is not the photodamage but the loss of repair mechanism responsible for reducing photosynthesis in green algae during desiccation.

Terada et al. (2021) reported that the photosynthetic response to dehydration stress differs between two heteromorphic life-history stages of the red alga *Neopyropia yezoensis* f. *narawaensis* collected from Saga, Kyushu Island, Japan. In the microscopic sporophyte, the effective quantum yield of photosystem II dropped to zero after a 5-min of acute emersion (~ 1440-min) under 50% humidity and did not recover to initial values regardless of a following 24 h immersion in seawater. However, the macroscopic gametophyte almost recovered to initial values after the subsequent 24 h immersion in seawater. Thus, their results suggest that the photochemical efficiency in microscopic sporophytes appears to be sensitive to dehydration stress, unlike the macroscopic gametophyte.

Gasulla et al. (2013) found ultrastructural alterations in *Asterochloris erici* cells after 3 h of rehydration following quick (60 min) or gradual (5–6 h) desiccation. Delayed dehydration led to an increase in the number of lipid bodies (with a decrease in their size), the amount of starch deposits and electron-dense deposits in the chloroplasts (Gasulla et al. 2013). The plasma membrane remained somewhat retracted from the cell wall in the progressively dried and rehydrated cells. Rapidly dried *Asterochloris* cells, on the other hand, showed a clear degenerate ultrastructure after being rehydrated. The cytoplasm was highly vacuolated and filled with lipid bodies. The cytoplasm and the chloroplasts still appeared shrunken, thylakoids were swollen or fused, and numerous starch deposits were visible (Gasulla et al. 2013). It also exhibited extensive plasmolysis and cytolysis. However, even with this damage, the cells survived the dehydration treatment.

Recently, Terlova et al. (2021) found that the degree of recovery from dehydration followed by short- and long-term rehydration in the case of the green algae *Tetradesmus* spp. was dependent on the habitat of origin and the dehydration scenario in terrestrial, but not in aquatic species. During dehydration and rehydration, both aquatic and desert species maintained their cell ultrastructure uniformly, but staining with an amphiphilic styryl dye showed damage to the plasma membrane due to osmotically induced water loss in aquatic species. Thus, their analyses indicate that terrestrial *Tetradesmus* possess a vegetative desiccation tolerance phenotype, making them suitable for comparative omics studies to investigate the origins of the desiccation machinery in that group.

One method against desiccation of aeroterrestrial and aquatic green algae is to prevent dehydration through self-protection. *Klebsormidium*, an aeroterrestrial filamentous green algae, can form multi-layered mat-like structures on top of or interwoven with the upper millimetres of soil in natural conditions, resulting in a high degree of self-shading and reduced water loss from individual filaments within such a population. Arctic *Zygnema* sp. is also reported to form mats (Pichrtová et al. 2013) and provides desiccation tolerance in the field-collected *Zygnema ericetorum* in the Alps (Aigner et al. 2013).

Temperature stress response of algae

Like higher plants, numerous metabolic activities of algae are affected due to fluctuations in temperature. Many studies highlight the effect of temperature change on photosynthetic activity (Zheng et al. 2020), the composition and production of lipids (Calhoun et al. 2021), and many other macromolecules of algae (Zhao et al. 2020a). Zhang and Liu (2016) have reported that the activity of PS II was reduced with increasing temperature (from 25 to 37 °C) due to its structural damage, while the activity of PSI was increased and synchronized with high O_2 production in the marine cyanobacterium *Arthrospira (Spirulina)*. However, on increasing the temperature to 40 °C, the rate of photosynthetic O_2 evolution was decreased, and severe reduction in PSII activity, but the rise in PSI activity was reported. Thus, photosynthetic activity of *Arthrospira* increased at heat stress (30–37 °C) by upregulating the PSI electron transport activity, and it was decreased at strong heat stress (40 °C) due to inhibition of PSII electron transport activity. *Chlorella pyrenoidosa* is cultivated largely due to its commercial importance. In *C. pyrenoidosa*, high temperature (38 and 41 °C) stimulates the production of active oxygen species that damage photosynthetic machinery due to the suppression of activities of antioxidant enzymes at 41 °C (Ma et al. 2020).

Algae also show broad acclimations and tolerance to changing temperatures (Zheng et al. 2020), such as changes in lipids and fatty acid proportions with fluctuating temperatures. With increasing temperature, the amount of PUFA reported being reduced in *Navicula,* a diatom collected from Antarctica (Teoh et al. 2013) and in *Nannochloropsis* sp. (Hu and Gao 2006). In addition, a decrease in temperature increased the proportion of unsaturated and short-chain fatty acids in algae has also been documented in several studies (Mühling et al. 2005; Mangelsdorf et al. 2009).

A study on a high-temperature tolerant strain of *Pyropia haitanensis* showed that high-temperature response depends upon the length of exposure to stress. Short-term exposure caused changes in transcriptome profile simultaneous reduction in photosynthesis and utilization of energy, while long-term exposure induced an anti-oxidative response with an increase in energy utilization (Wang et al. 2018b). Tolerance to high temperature in some algal species may depend upon the biogeographical distribution that has also been reported. For instance, a difference in tolerance capacity to high temperature has been observed in two strains of the dinoflagellate *Alexandrium tamarense* collected from Japan and Malaysia (Kobiyama et al. 2010). Malaysian strains could survive at a higher temperature range (15- 30 ℃) than Japanese strains (0 -25℃), delineating their biogeographical boundaries.

The low-temperature stress is less explored than the high temperature in the case of microalgae (Ermilova 2020). However, some recent studies have focused on finding the effects of cold stress in *C. reinhardtii* (Zalutskaya et al. 2019; Li et al. 2020), a unicellular green alga, the best available model for studying the response to temperature fluctuations (Ermilova 2020). A change in the production of heat shock proteins (HSPs) as a low-temperature acclimation has also been reported in *C. reinhardtii* (Maikova et al. 2016). It shows variations in the expression of 3471 genes responsible for various biological processes, including cell cycle, protein synthesis, and protein kinase-based phosphorylation under cold stress (Li et al. 2020). The *C. reinhardtii* showed a decrease in growth due to photo-oxidative damage of several macromolecules under low temperatures (Zheng et al. 2020). A recent study by Calhoun et al. (2021) on a halotolerant microalga *Scenedesmus* reported an increase in the expression of genes that encode fatty acids, metabolic enzymes, and variations in the levels of amino acids under cold stress. Menegol et al. (2017) demonstrated increased ω3-fatty acids production due to low temperature in *Heterochlorella luteoviridis*.

CO$_2$/pH/ocean acidification stress

The process in which a rise in atmospheric CO_2 leads to a drop in the pH of the ocean surface is known as ocean acidification. CO_2 uptake by the ocean changes the carbonate chemistry of seawater following a reduction in pH (Raven et al. 2005). Experiments have shown that increasing pCO_2 causes decreased calcification of crustose coralline algae (Anthony et al. 2008). Burdett et al. (2012) examined the effect of low pH on the red coralline alga *L. glaciale* on epithelial cell morphology and DMSP/DMS(P) production. No change in DMS(P) production was observed at low pHbut cracks were observed between the cell walls of the algal

skeleton. They proposed that this structural change may cause membrane damage that allows DMS(P) to leak from the cells into the water column, with subsequent implications for the cycling of DMS(P) in coralline algae habitats. Kamenos et al. (2013) observed the coralline algae survived by enhancing their rate of calcification during the day to compensate for the dissolution that happens during the night at low pH. Moreover, when the low pH change occurred at a fast rate, they observed the weakening of the calcite skeleton. The weakening of the structure decreases the potential of the alga to withstand wave energy (Ragazzola et al. 2012). *Lithothamnion glaciale* also show changes in the structure after incubating under increasing pCO_2 (589 µatm). In the case of *Chlorella ellipsoidea* the carbohydrate content attained its maximum value at alkaline pH while the pigment content decreased. Moreover, vitamin E content was higher at pH 10 than at pH 6, but there was a significant reduction in vitamin C content of *C. ellipsoidea* both at pH 6 and pH 10 (Khalil et al. 2010).

Different macroalgae respond differently to increasing pCO_2. The red alga *Lomentaria articulata*, *Gracilaria* spp and *Porphyra yezoensis* show an increase in the growth rate under increasing CO_2 concentration (Gao et al. 1991, 1993; Kübler et al. 1999). Several macroalgae are reported to show neutral effects on the growth at elevated CO_2 levels (Roleda et al. 2012). Moreover, coralline alga *Arthrocardia corymbosa* showed the highest growth rate at pH 8.05; however, at pH 7.65, the growth rate was lowest (Roleda et al. 2007). In the coralline alga *Lithophyllum cabiochae* respiration was unaltered by pCO_2, but photosynthesis was decreased under elevated pCO_2 whereas calcification responds differently depending on the season; net calcification decreased with increasing temperature under elevated pCO_2 but increased under ambient pCO_2 with rising temperature (Martin et al. 2013).

Some experimental results of ocean acidification effects on calcareous marine macroalgae are listed in Table 1. Most studies indicate a negative effect of low pH and high CO_2 on calcification.

Heavy metal (HM) stress

Metals at low concentrations are essential for algal cells to carry out cellular functions as they act as cofactors for nitrogen assimilation (Fe, V and Mo in nitrogenase (Bothe et al. 2010)), DNA transcription, RNA polymerase (such as Zn (Zinc) (Sunda 2012)), and CO_2 fixation (Zn in carbonic anhydrase). However, high concentrations of HMs such as Chromium (Cr), Lead (Pb), Cadmium (Cd), Arsenic (As), Mercury (Hg) in algal cells show adverse effects like blockage of cell division, reduction in photosynthesis and

Table 1 Effects of ocean acidification on calcareous marine macroalgae

Algal Species	pH	CO_2	Effects	Source
Corallina officinalis	8.30	384	At a high CO_2 level, low relative growth	(Hofmann et al. 2012)
Corallina sessilis	8.4	380	At high CO_2, calcification is low and lowers the phycoerythrin and Chl-*a*	(Gao and Zheng 2010)
Hydrolithon sp.	7.91	765	At high CO_2, coralline recruitment loss	(Kuffner et al. 2008)
Lithothmnion cabiochae	8.06	417	No effect of CO_2 on calcification	(Martin and Gattuso 2009)
Porolithon onkodes	7.90	613	At high CO_2, caused bleaching	(Diaz-Pulido et al. 2012)

inhibition of various thiol group-containing enzyme activities (Monteiro et al. 2012).

Multiple studies highlight the effect of HMs on algae exist in the literature (Table 2). For instance, the effect of HMs such as copper (Cu) and Cd was carried out on the diatom *Amphora coffeaeformis*. These HMs drastically decreased the protein and carbohydrate content. The lipid and amino acid content were also reduced. Thus, high concentrations of these HMs affect the diatom by reducing its growth and biochemical composition (Anantharaj et al. 2011). On the other hand, Cd plays a beneficial role in diatoms; they use Cd as a catalytic metal atom in carbonic anhydrase (CA), where Zn is nearly depleted in oceans (Park et al. 2007; Xu et al. 2008). In *Ulva lactuca* exposure to high Cr (VI) concentration decreased cell viability and altered thallus cell morphology. When the cells were treated with 1 and 5 mM of Cr (VI), the amount of necrotic cells increased around 76.93% and 84.23%, respectively (Ünal et al. 2010).

Table 2 Effects of different heavy metals on the algal species

Algal species	HM	Concentrations that cause effect	Effects	Source
Amphora coffeaeformis	Cu and Cd	10 ppm	Reduction in the amount of proteins, carbohydrates, lipids and amino acids	(Anantharaj et al. 2011)
Acutodesmus obliquus	Pb	500 µM	Growth inhibited	(Piotrowska-Niczyporuk et al. 2017)
A. obliquus	Pb	100 µM	Disturbance in phytohormone homeostasis (severe depletion of auxins, cytokinins and gibberellin and increase in abscisic acid content)	(Piotrowska-Niczyporuk et al. 2020)
Alexandrium pacificum	Zn, Pb, Cu and Cd	6 µM	Changes in membrane proteomes, cell growth and morphometry	(Chetouhi et al. 2020)
Chlorella sorokiniana	Pb, Cd	250 µM	Deformed chloroplast and lipid droplets in the cytoplasm	(Carfagna et al. 2013)
Chlorella vulgaris	Zn and Cu	Zn: 100 mg dm^{-3} Cu: 0.15 mg dm^{-3}	Reduction of photosynthetic pigments	(Kondzior and Butarewicz 2018)
C. vulgaris	Cr, Cd, Cu, Pb and Zn	5 µmol L^{-1}	Growth inhibited	(Ouyang et al. 2012)
Desmidium	Zn	10 µM	Mitochondria enlargement	(Andosch et al. 2015)
Gomphonema pseudoaugur	Selenium (Se) and Pb	Not mentioned	Induces deformities in diatom frustules and increased lipid body size	(Gautam et al. 2017)
Microcystis aeruginosa	Pb	0.5 mg L^{-1}	Effect on photosynthesis, decrease in bound extracellular polysaccharides (bEPS)	(Wang et al. 2021)
Phaeocystis antarctica	Cu	5.9 µg L^{-1}	Increased in cell size and granularity	(Gissi et al. 2015)
Raphidocelis subcapitata	Cu, Ni and Zn	Cu: 0.15 mg L^{-1} Ni: 0.50 mg L^{-1} Zn: 0.20 mg L^{-1}	Growth inhibition	(Filová et al. 2021)
Zygnema sp.	Cd and Zn	66 mM	Decrease in quantum yield (F_V/F_M); inhibition of photosynthesis	(Hernandez 2016)

Recently, the influence of Zn and Cu HMs on the reduction of photosynthesis pigments in cells of *C. vulgaris* has been shown (Kondzior and Butarewicz 2018). After 7 days of incubation, at the highest Cu concentration, *C. vulgaris* cells contain less carotenoid, Chl-*a* and Chl-*b* content by 60%, 63% and 58% respectively. The influence of Zn concentration shows that *C. vulgaris* reduced carotenoid content by 79%, while Chl-*a* and Chl-*b* were reduced by 88% in 79%, respectively, compared to the control. Hernandez (2016) reported that the primary photosynthetic processes of *Zygnema* were sensitive to Zn and Cd. However, in cultures treated with Zn and Cd (66 mM), the potential quantum yield (F_V/F_M) of PS II and relative fluorescence decline ratio (RFd) was decreased, the PS II centres still shown photosynthetic activity even after 5 h 40 min exposure to the heavy metals. Thus they concluded that *Zygnema* is relatively resistant to these heavy metals. Moreover, Chen et al. (2016) reported that the Hill reaction activity (HRA) of chloroplast was decreased at a high concentration of Cu (II) under both dark and illuminating conditions in *C. vulgaris*. Content of malondialdehyde (MDA) and activities of catalase (CAT) and SOD were also reduced at high Cu^{2+}, accompanied with the formation of ROS, thus inhibiting the algal growth. However, Cu is an essential element at low concentrations and acts as a cofactor in several enzymes such as cytochrome *c* oxidase, plastocyanin, Cu/Zn superoxide dismutase, polyphenol oxidase, amino oxidase and laccase (Yruela 2005).

In *Gracilaria tenuistipitata*, the addition of sub-lethal concentrations of Cd^{2+} and Cu^{2+} for the short-term causes increased oxidative stress, decreasing growth and increasing lipids and proteins oxidation. However, algae respond to this oxidative stress by increasing the activity of the reactive oxygen metabolism. As Cu^{2+} addition has increased SOD, CAT, and ascorbate peroxide (APX) activities, while the addition of Cd^{2+} only induced the catalase activity. Additionally, the amount of β-carotene and lutein has increased by adding both HMs (Collén et al. 2003).

UV-A and B stress on algae

Increasing the amount of ultraviolet radiation (UVR) on the earth's surface has a significant direct negative effect on photoautotrophs like plants and algae, as they cannot escape light because it is needed for photosynthetic processes. This UVR caused morphological alterations in certain macroalgal species. In *Laminaria ochroleuca*, high UVR induced tissue deformation, blistering, lesions, and thickening of the meristematic tissues of the lamina (Roleda et al. 2006). However, many organisms, such as cyanobacteria and algae, have evolved a variety of strategies to minimise UVR damage, including behavioural avoidance, photoprotection, and DNA repair mechanisms. Many photosynthetic organisms have evolved coping mechanisms against such changes, including the synthesis of UV defensive compounds such as MAAs, phlorotannins, antioxidants, phenolics, HSPs, DNA repair mechanisms, and microRNA regulation. Many Arctic and Antarctic strains of *Zygnema* have been shown to produce sporopollenin as extracellular cell walls of zygospores in response to UV exposure. An extracellular mucilage coating in some polar *Zygnema* strains acts as a protective sheath. *Zygnema* also has macroscopic mat production to self-shade and shield cells from excessive radiation (Holzinger et al. 2009).

Effects of UV-B radiation on algae

Effects on photosynthesis Under increased UV-B (280-315 nm), the marine microalgae *Tetraselmis* (*Platymonas*) *subcordiformis* and *Nitzschia closterium* show a decrease in growth rates, Chl-*a* content, and carotenoid content (Zhang et al. 2005). When measured using the Chl-*a* fluorescence technique, photosynthetic output in some of the Arctic and Antarctic strains of *Zygnema* was reduced at increased UV to photosynthetically active radiation (PAR), likely due to a reduction in PS-II efficiency under UV stress (Pichrtová et al. 2013). Overall photosynthesis decreases when vertical mixing brings deeper organisms to the surface and vice versa, as photoinhibition of deep-water algal species occurs, and upper dwellers travel deeper, where light becomes a limiting factor for them. UVR causes mild photosynthetic inhibition in eulittoral species, but substantial inhibition in sublittoral species and eulittoral species recover faster from stress than sublittoral species. Reproductive cells also are more vulnerable to increased UVR than gametophytic stages, and the impact is species-specific, as *Condrus* carpospores were more sensitive to increased UVR than *Mastocarpus* carpospores (Roleda et al. 2013).

Damage to DNA UV-B causes DNA to modify its molecular structure. Formation of dimers and pyrimidine primidone photoproducts, which modify DNA and interfere with proper transcription and replication, as well as being misread into genetic codes, resulting in mutations and death. In *D. salina*, UV-B directly damaged cellular DNA, causing physiological damage and elevated death rates (Tian and Yu 2009). High UV to PAR ratio causes DNA damage in Arctic and Antarctic *Zygnema* strains (Pichrtová et al. 2013).

ROS production The majority of microalgae suffer from oxidative damage by increased UV-B levels. Higher amounts of thiobarbituric acid reactive substance (TBARS) and hydrogen peroxide (H_2O_2) have been reported in *D. salina* in response to increased UV-B levels, but no such change in controls, indicating acclimation to reduce UV or solar

radiation levels (Tian and Yu 2009). ROS generation and oxidative stress are also seen in Z*ygnema* strains from the Arctic and Antarctic (Pichrtová et al. 2013).

Suppression of antioxidant system Non-enzymatic antioxidants such as carotenoids and glutathione (GSH) were reported to decrease under increased UV-B in *T. subcordiformis* and *N. closterium*. In both *species* enzymatic antioxidants like SOD and CAT were also reduced as UV-B radiation levels increased. UV irradiation has different adverse effects depending on the species. For *N. closterium*, increased UV-B is more harmful than for *P. subcordiformis* (Zhang et al. 2005).

Adaptations against harmful UV radiations in algae

DNA repair Algae primarily use photoenzymatic repair in which DNA photolyase monomerizes cyclobutane dimers in the presence of UV-A or visible light to repair damaged DNA. Nucleotide excision repair is enrolled to recognise damaged DNA strands, then excision and resynthesis of the damaged portions by DNA polymerase enzyme. Damaged DNA is repaired by the recombinational repair mechanism, bypassed by the replication mechanism (Karentz et al. 1991). In certain arctic and Antarctic *Zygnema* strains, photodamage to DNA activates multiple DNA repair pathways (Pichrtová et al. 2013).

Adaptations for photosynthesis Short-term acclimation, such as fluorescence or heat dissipation via the xanthophyll cycle, or energy redistribution between the two photosystems, are made to protect the photosynthetic system against excessive UVR. To protect macroalgal species from ROS,

defensive mechanisms such as antioxidant enzymes, carotenoid production inside cellular membranes, and the creation of water-soluble reductants occur in the cytosol during long-term UVR exposure (Dunlap and Chalker 1986). UVR damages PS-II directly, resulting in ROS generation, which slows protein synthesis, particularly of PS-II D1 proteins, which are necessary to replace damaged D1 proteins (Nishiyama et al. 2004). Photodamage caused by high UVR is controlled by the steady-state oxidation–reduction of the main quinone acceptor (QA). Seaweeds in the sublittoral zones are particularly vulnerable to UVR because they cannot downregulate photosynthesis via photoprotection (Hanelt and Nultsch 2003).

Production of mycosporine- like amino acids MAAs are chemical compounds with a low molecular weight that absorb the most light in the UV range of 310-365 nm. They are called MAAs because they're similar to mycosporines found in terrestrial fungi. Some of the MAAs that have been identified in algal species are included in the table below (Table 3). They are essentially sunscreen chemicals that protect organisms from damaging UV radiation and act as antioxidants that scavenge toxic ROS.

The percentage of MAAs reported being greatest in red algae and with the most MAAs kinds and numbers (Sun et al. 2021). MAAs in macroalgae have been found in the arctic to tropical species. MAAs levels have been observed to be decreasing in species that grow at greater depths and in species that live at higher latitudes. The distribution of MAAs in macroalgae is mainly based on three patterns: Initially high MAAs content with no further growth in their amount after light treatment, increased MAAs content with

Table 3 Common MAAs occur in algal species

MAAs	Algal species	Reference
Palythinol	*Porphyra endiviifolium, Hydropuntia corhea*	(Hoyer et al. 2002; Álvarez-Gómez et al. 2019)
Mycosporine-glycine, Palythenic acid, Porphyra-334	*Gyrodinium aureolum, Gyrodinium galatheanum, Gyrodinium venificum*	(Llewellyn and Airs 2010)
Two hexose-bound palythine-threonine derivatives	*Nostoc commune*	(Nazifi et al. 2013, 2015)
Shinorine	*Scytonema* cf. *crispum*	(D'Agostino et al. 2016)
Mycosporine-Glycine	*Aphanothece halophytica*	(Ngoennet et al. 2018)
7-O-(β-arabinopyranosyl)-porphyra-334, Hexose-bound porphyra-334	*Nostoc commune*	(Li and Guo 2018)
Asteria-330	*Gracilariopsis longissina*	(Álvarez-Gómez et al. 2019)
Asterina-330, Shinorine	*Lyngbya* sp.	(Fuentes-Tristan et al. 2019)
Porphyra-334, Shinorine, Mycosporine-Glycine, Palythine, Asterina-330	*Nostoc commune, Alexandrium excavatum, Mmicrocystis aeruginosa, Aphanothece halophytica*	(Kageyama and Waditee-Sirisattha 2019; Geraldes et al. 2020)
Gadusol, Shinorine, Palythine, Porphyra-334, Palythenic acid	*Bangia fusco-purpurea, Gelidium amansii, Gracilaria confervoides, Gracilaria* sp.	(Sun et al. 2021)

increasing light treatment but no initial MAAs or generation after light treatment (Sinha et al. 2001).

Antioxidant production Increased UV radiation favoured a rise in Chl-*a* in case of *D. salina* at first, although carotenoid content did not appear to alter. Many green microalgae, such as *Chlamydomonas nivalis* (Bidigare et al. 1993), *Chlorella* sp. (Sayed and Hegazy 1992), *Chlamydomonas nivalis* (Remias et al. 2010), can accumulate secondary carotenoids under stress. Some Arctic and Antarctic strains of *Zygnema* also exhibit higher quantities of secondary carotenoids, but no secondary carotenoids or MAAs have been found in Zygnematophyceae (Remias et al. 2012).

Haematococcus pluvialis accumulates astaxanthin in cytoplasmic globules. β-carotene synthesised in the chloroplast is first transported to the cytoplasm for oxygenation, where the keto group is added to C4 and C4', as well as hydroxyl groups to C3 and C3'. This is done using the products of *crto/bkt*, and *crt R-b*, which are nuclear genes that encode phytoene desaturase. Nuclear factor X regulates the expression of these genes. Three distinct bkt genes have been identified, each of which is up-regulated at different amounts in response to stress. The presence of numerous bkt genes has been shown to be critical for *H. pluvialis*' production of significant quantities of astaxanthin under stressful conditions (Huang et al. 2006). When green algae, such as *H. pluvialis*, are stressed, they produce secondary ketocarotenoids such as canthaxanthin and astaxanthin. Astaxanthin storage is a cost-effective way to store energy and carbon in less demanding environments. Furthermore, the high quantity of astaxanthin prevents oxidative stress generated by various stressors, including UV-B radiation, making it a multifunctional stress response (Lemoine and Schoefs 2010).

Production of phenolics The production of phenolics in several arctic and Antarctic *Zygnema* species represents a stress adaptation. Because phenolics are stored in electron-dense particles and vacuoles at the cell's perimeter, they operate like UVR screens, safeguarding its internal organelles. After UV exposure, Antarctic strains exhibit the largest quantities of phenolics and have high variable fluorescence by maximum fluorescence (F_V/F_M) ratio, indicating that phenolics preserve photosynthetic machinery. *Zygnemopis decussata* with high phenolic content has a high F_V/F_M ratio and the best photosynthetic rates (Figueroa et al. 2009). Phenolics, as phlorotannins, are widely found in brown algae (Abdala-Díaz et al. 2006), can serve as cell wall components (Schoenwaelder 2002), deter herbivores (Targett and Arnold 1998), and protect from UVR (Pavia et al. 1997). Several studies have found that the release of phlorotannin in response to UV exposure varies depending on the species, season, and stage of thalli formation. After two weeks of UV-B treatment, the concentration of phlorotannin in *Ascophyllum*

nodosum (Pavia et al. 1997) increased by 30%. However, no similar effect of UV-B on the concentration of phlorotannin was found in another investigation of *Fucus gardneri* juveniles and embryos (Henry and Van Alstyne 2004). Lack of phlorotannin accumulation in *Fucus vesiculosus* under UV-B exposure is linked to lack of overexpression of genes Pks-III and other genes involved in phlorotannin modifications such as *ast6* and *vbpo*, implying that this metabolism is not activated and only constitutive accumulation of phlorotannins occurs during the development of *F. vesiculosus* rather than inducible processes (Creis et al. 2015). Several Chlorophyceae and Rhodophyceae have been shown to have phlorotannins, which operate as UVR absorbers.

MicroRNA regulation Because most of the UV adaptation in algae has focused on physiological control and linked protein-coding genes, there have been few publications on connected protein non-coding genes. Heat stress caused Cre-miRNA to be downregulated, responsible for heat shock adaptation. Using qPCR and bioinformatics computing, the function of Cre-miR914 and its target gene was determined under UV stress. Cre-miR914 was downregulated, resulting in increased expression of its target gene, ribosomal protein L18 (RPL18), promoting UV-B adaptation in *Chlamydomonas* (Fig. 3). So, overexpression of Cre-miR914 lowered UV-B tolerance in algae, but overexpression of RLP18 increased UV-B tolerance and lowered ROS and MDA levels (Wang et al. 2019a).

Mechanical stress

Macroalgae experience considerable mechanical stress in the form of hydrodynamic movements (acceleration, drag, and lift). Studies as early as 1932 (Delf 1932; Koehl 1982, 1986) have shown that although the seaweeds are dependent upon ambient seawater flow for the transport of nutrients and are generally adapted to hydrodynamic stress, occasional wave actions could be powerful enough to shear the thallus ("pruning"), especially in wave-swept rocky shores. In general, benthic macroalgae are more susceptible to hydrodynamic stresses than planktonic species. Among diatoms, studies have shown that nonfilamentous species have higher resistance than filamentous ones against mechanical stress (Biggs and Thomsen 1995).

Various adaptations against mechanical stress have been documented in marine algae, including the cell wall composition of long-chain polysaccharides (Janot and Martone 2016) and the ability to secrete viscous mucilage. Recently discovered porous helical microstructure of mineralized coralline alga *Jania* sp. might also play roles in mechanical stress resistance as an adaptation (Bianco-Stein et al. 2020). A morphological convergence in the form of
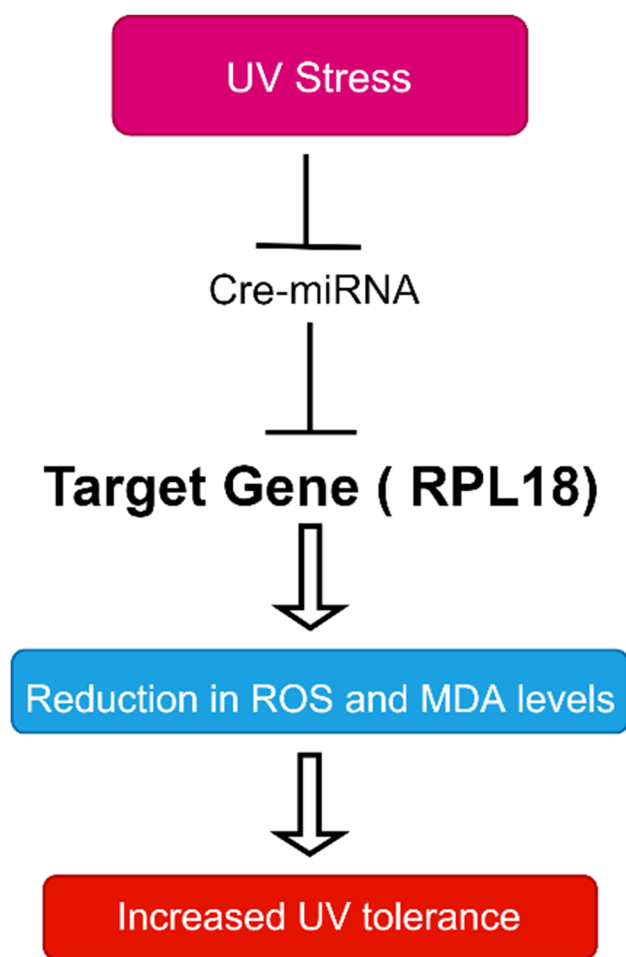
Fig. 3 Schematic diagram showing miRNA regulation under UV stress in *Chlamydomonas*

cellulosic secondary cell-wall in coralline algae at wave-swept habitats has also been described recently (Martone et al. 2019). Phylogenetic analysis of character evolution of uncalcified joints (genicula) in coralline red algae indicated three independent origins as a bending strategy to cope with the hydrostatic force (Janot and Martone 2018). Benthic seaweeds at turbulent coasts like *Chondracanthus exasperates* tend to have softer, extensible and flexible tissues that act as a shock absorber and stipes that can be twisted and bent (Koehl 2000). The red seaweed *Mastocarpus papillatus* has been shown that its stipe had similar thickness throughout (to avoid a single point prone for shear), and its thallus had a streamlined shape to flow along with waves (Carrington 1990). Mechanical forces were also reported to constrain the size of intertidal seaweeds in wave-swept habitats (Gaylord et al. 1994). Such physiological adaptations are expected to have ramifications in the form of trade-offs with other physiological processes, including photosynthesis, in the so-called 'form-function hypothesis' (Dudgeon et al. 1995). Morphological switch from one thallus morphology

to another in response to stress is a well-known adaptation in marine algae. For example, the brown seaweed *Ecklonia radiata* have shown that the species had wide, thin thallus at sheltered habitats while narrow, thick thallus with thick stipes at exposed habitats (Fowler-Walker et al. 2006). Reciprocal transplantation of algae from one habitat to another also confirmed this morphological plasticity in response to environmental constraints. Similar morphological plasticity in response to exposure gradients has also been reported for *Laminaria longicruri*s (Gerard and Mann 1979) *Durvillaea potatorum* (Cheshire and Hallam 1989), *F. vesiculosus* (Bäck 1993) and *Egregia menziesii* (Blanchette et al. 2002). A recent study approached physiological adaptation to the wind-swept habitat in a more integrative fashion, combining biomechanics with seasonality and herbivory in kelp *E. menziesii* (Burnett and Koehl 2019). They suggest correlated physiological strategies with season and herbivory, such as higher growth rate (leading to more softer tissues) during summer months when the wave action is comparatively weaker, while lower growth rate (leading to hardened tissue) during winter when wave action is stronger.

Self-pruning of algal thalli has been suggested as a possible adaptation for helping the alga to reduce the size and reducing the risk of dislodgement from substratum (Black 1976; Demes et al. 2013). However, a recent study suggested this conjecture is flawed because on a long run, unpruned individuals of kelp *E. menziesii* survived better than the pruned individuals (Burnett and Koehl 2020). Yet another recent study revealed that the attachment strength of isomorphic red alga *Chondrus verrucosus* differs with its life-history stages. The tetrasporophyte stage of this alga tends to have weaker stipe-holdfast junctions rendering them more susceptible to thallus dislodgement compared with the gametophyte stage (Bellgrove and Aoki 2020).

There have been a few experimental studies to assess the hydrodynamic effects on microalgae. The green microalga *Dunaliella* sp. has been shown to be sensitive to increasing specific bubble rates in tubular airlift photobioreactor, that can be minimized by the addition of carboxymethylcellulose and agar (Silva et al. 1987). Photosynthetic rate, growth rate and cellular morphology of green cyanobacterium *A. platensis* also has been shown to be affected with the hydrodynamic flow rate (Mitsuhashi et al. 1994). Higher rates of mechanical agitation also have been shown to induce cell damage in the chrysophyte *Ochromonas malhamensis* (Yang and Wang 1992) and the red microalga *Porphyridium cruentum* (Camacho et al. 2000).

On the other hand, studies conducted on several fresh-water red algae have shown that no preferential advantage was apparent for one morphological form over the other for the hydrodynamic stress resistance, perhaps indicative of the adaptations that these various species have been going through for a very long period (Sheath

and Handbook 1988). Such algae of various morphological forms, including tufts, mucilaginous filament, nonmucilaginous erect filament and so on, might have evolved through independent mechanisms for hydrodynamic resistance. Studies of the red seaweeds *Chondrus crispus* and *Mastocarpus stellatus* also concluded that no clear relationships exist between algal morphology and its responses to environmental variation (Dudgeon et al. 1995). However, algal thallus morphology should not be assessed for its adaptations from hydrodynamic stress in isolation, as most of the algal communities exist in nature as large canopies consisting of multi-species communities. Studies of the red alga *C. crispus* have shown that although bushy morphology in isolated thalli increases the drag- seemingly a counter-intuitive to resist the wave-action, this morphology significantly reduce the drag when in canopy (Johnson 2001). A recent study contextualized the adaptation strategies of windswept kelps within the broader evolutionary framework of avoidance-tolerance spectra. The study concluded that kelps are either strong and tenacious (tolerance-dominant) or streamlined (avoidance-dominant), but not both concurrently, thus indicating a trade-off between these two strategies (Starko and Martone 2016).

Algal hormones involved in response to stress

A well-coordinated and timely response to various abiotic stresses in plants involves signal perception and transduction mainly via plant hormones, that is, phytohormones. Phytohormones comprise a wide array of signaling compounds present in minute quantities in cells, playing crucial roles in minimizing environmental stresses by facilitating growth, developmental processes and coordinating various signal transduction pathways during stress responses. The main classes of phytohormones include (1) classical phytohormones such as auxin (AUX), abscisic acid (ABA), brassinosteroids (BRs), ethylene (ET), gibberellins (GAs), and cytokinin (CK); (2) molecular phytohormones, for example, jasmonic acid (JA), salicylic acid (SA), and nitric oxide (NO); and (3) newly discovered karrikins (KARs), and strigolactones (SLs) (Smith and Li 2014; Pandey et al. 2016). In different phylogenetic groups of algae, all known plant hormones are found. Generally, phytohormones of various algal groups are poorly understood because of the extreme diversity of this group and difficulties in working methodologies due to their small size. So here in this review, we tried to summarize the published data elucidating the role of phytohormones in algae in combating various abiotic stress conditions.

Nitrogen stress Certain hormones such as GA_3, triacontanol (TRIA), kinetin (K), and zeatin (Z) promote cell elongation, cell division, growth and photosynthesis under nitrogen deficiency (Park et al. 2013; Babu et al. 2017; Renuka et al. 2017). Indole-3-acetic acid (IAA), GA, K, 1- TRIA improved biomass in nitrogen-deficient *C. reinhardtii* (Park et al. 2013). This treatment with several coupled hormones increased the F_V/F_M and relative electron transport rate (rETR) of certain algae under nitrogen limitation conditions. Thus, the combination of several phytohormones may enhance algal growth and lipid production under abiotic stress more efficiently than one phytohormone alone by regulating oxidative stress and photosynthetic rate. By keeping in view, zeatin and kinetin enhanced algal growth and lipid production in *A. obliquus* (Renuka et al. 2017) under nitrogen stress. Babu et al. (2017) reported that under nitrogen limitation, the low doses of IAA and diethyl aminoethyl hexanoate (DAH) treatments in *C. sorokiniana* showed the highest enhancement in biomass productivity over the control. Yu et al. (2018) reported that the combination of the phytohormones such as naphthylacetic acid (NAA) and indolebutyric acid (IBA) has positive effects on growth and lipid production in *Scenedesmus* sp. SDEC-8 and *C. sorokiniana* SDEC-18 under nitrogen starvation. Salama et al. (2014) demonstrated that the biomass was increased by 1.9- and 2.5-fold, and the PUFA content was enhanced by up to 56% and 59% at $10-5$ M by the application of IAA and DAH, respectively. The treatment with these coupled hormones induced antioxidant enzyme activities, which protect cells from damage caused by abiotic stresses, and significantly upregulated the levels of RuBisCO and ACCase under N limitation.

ROS Fulvic Acid (FA) appeared to promote microalgal lipid biosynthesis significantly by regulating cellular ROS levels. The application of FA, melatonin (MT), butylated hydroxyanisole (BHA), and butylated hydroxytoluene (BHT) reduced high light intensity and nutrient deficiency stress resulting in increased biomass and enhancement of various pigments such as astaxanthin, β- carotene and lipids in *H. pluvialis* (Ding et al. 2018a; b; 2019; Zhao et al. 2018b; 2019a; b). These studies indicated that the application of phytohormones could sustain or induce cell growth and metabolite accumulation in microalgae under abiotic stress conditions, mainly by regulating oxidative stress.

HM stress In response to HM stress in microalgae, the application of several hormones such as Z, K, IBA, GA, JA, IAA, NAA and phenylacetic acid (PAA) are involved in the induction of cellular growth and division and augmentation of photosynthetic activity (Bajguz 2011; Piotrowska-Niczyporuk et al. 2012) and can alleviate stress symptoms by preventing HM biosorption. Cr stress is alleviated by

K in *Nostoc muscorum*. Here K application significantly improved the dry weight and carotenoid production of the cyanobacterium *N. muscorum* (Tiwari et al. 2018). The possible reason for this change is that K triggers photosynthesis and antioxidant enzyme activities while depressing respiration and oxidative stress in algae. The endogenous levels of auxins (IAA) and CKs (transzeatin, tZ) were reduced in the green alga, *C. vulgaris* (Bajguz 2011) and *A. obliquus* (Piotrowska-Niczyporuk et al. 2017) when subjected to the higher concentration (100 µM) of Pb. In this case, the endogenous application of auxin and CKs mitigated toxicity, promoted growth and development, and regulated HM sorption in *C. vulgaris* (Piotrowska-Niczyporuk et al. 2012) and *A. obliquus* (Piotrowska-Niczyporuk et al. 2018a). Exogenous CKs were found to protect proteins and scavenge various components of photosynthetic apparatus (Chls, carotenoids, xanthophylls) and significantly reduce damaging effects of HMs on green algae, *C. vulgaris* (Piotrowska-Niczyporuk et al. 2012), and *A. obliquus* (Piotrowska-Niczyporuk et al. 2018b). CKs alleviated HM toxicity by inhibiting ROS formation in *C. vulgaris* when challenged by Cd, Cu, or Pb (Piotrowska-Niczyporuk et al. 2012).

Not many reports are available regarding the biological functions of GAs in algae; however, their presence has been confirmed in multiple microalgae strains (Stirk et al. 2013). GA_3 showed the positive effect on growth, protein contents, Chl-*a* and *b,* carotenoids, and monosaccharides in *C. vulgaris* exposed to HMs (Falkowska et al. 2011; Piotrowska-Niczyporuk et al. 2012). Here in this study, GA_3 activated defence responses and decreased oxidative damages by promoting the production of thiol compounds which could bind to HM ions (Bajguz 2002) in cells of *C. vulgaris* (Falkowska et al. 2011; Piotrowska-Niczyporuk et al. 2012). These results indicate that GA_3 can help algae to withstand the toxic concentrations of Cd and Pb based upon the efficiency of cellular division in *C. vulgaris* (Falkowska et al. 2011). Exogenous presence of JA exacerbated Cd, Cu, or Pb toxicity accompanied by an increase in metal biosorption, lipid peroxidation and H_2O_2 level in *C. vulgaris*. In response to JA treatment under HM exposure, several indicators of cell health and their ability to deal with HM, like cell number, Chl levels, carotenoids, monosaccharides, soluble proteins, ascorbate and GSH content, and antioxidant enzyme activity, were considerably reduced (Piotrowska-Niczyporuk et al. 2012). These findings concluded that high amounts of JA accelerated the senescence program and algal cell death (Czerpak et al. 2006).

Heat stress BRs enhanced the level of ABA in *C. vulgaris* in response to short term (3 h) heat stress (30–40 °C) (Bajguz 2009). Exogenous BL partially overcomes the inhibitory effect of HMs on *C. vulgaris*, reducing the accumulation of HMs in the cells and increasing ABA, IAA and zeatin

content (Bajguz 2011). Endogenous level of BRs increases in response to salt and low temperature (15 °C) stress in several species of algae such as *Chlorococcum ellipsoideum*, *Gyoerffyana humicola*, *Nautococcus mamillatus*, *Acutodesmus acuminatus*, *Protococcus viridis* and *C. vulgaris*. The response of algal cultures was observed within 30 min of the salt shock.

In macroalgae, studies regarding the role of phytohormones are limited. Application of ACC (the ethylene precursor 1-aminocylopropane1-carboxylic acid) repressed gametophytes and enhanced tolerance to oxidative stress in *Pyropia yezoensis* (Uji et al. 2016). Gene expression profiles of small heat shock proteins in *P. yezoensis* showed that exogenous application of ACC could significantly increase the expression levels of small heat shock proteins (Uji et al. 2019) against heat stress. Wang et al. (2019b) showed that SA and jasmonic acid (JA) could promote the growth of algae and enhance the resistance of *P. haitanensis* against temperature stress. Transcriptome data showed that the phytohormones GA and ABA played essential roles in responding to temperature stress in *P. yezoensis* (Sun et al. 2014; Wang et al. 2017).

Plant hormones are also associated with signal transduction pathways, including pathways that use NO, Ca^{2+}, mitogen-activated protein kinase (MAPK) and specifically stress hormones (ABA, SA and GA), which form a complex signalling network connected to growth, metabolic, and stress tolerance in higher plants (Peleg and Blumwald 2011; Lu et al. 2014; de Zelicourt et al. 2016; Wani et al. 2016; Raja et al. 2017). These stress hormones may promote cell growth by improving photosynthetic activity by increasing Chl content (Lu and Xu 2015). NO, and Ca^{2+} are cellular second messengers that mediate oxidative stress and metabolite synthesis in algae under abiotic stress conditions (Zhang et al. 2017; Kováčik and Dresler 2018). Figure 4 shows the signal transduction pathway of phytohormones that includes the NO and Ca^{2+} as second messengers during abiotic stress conditions.

Abiotic stress to stimulate lipid production

Algae are widely studied due to their ability to accumulate high content of lipids and bioactive compounds under various abiotic stress conditions such as temperature, nutrient deprivation, UV-radiation, salinity, pH, phytohormones and HMs (Paliwal et al. 2017; Dong et al. 2019). Microalgae have attracted particular interest due to their high-value applications in nutraceuticals, pharmaceuticals, biofuel production, and capacity to accumulate a large amount of lipids, high growth rate, economical and environmentally friendly (mitigating fossil CO_2 pollution) (Yu
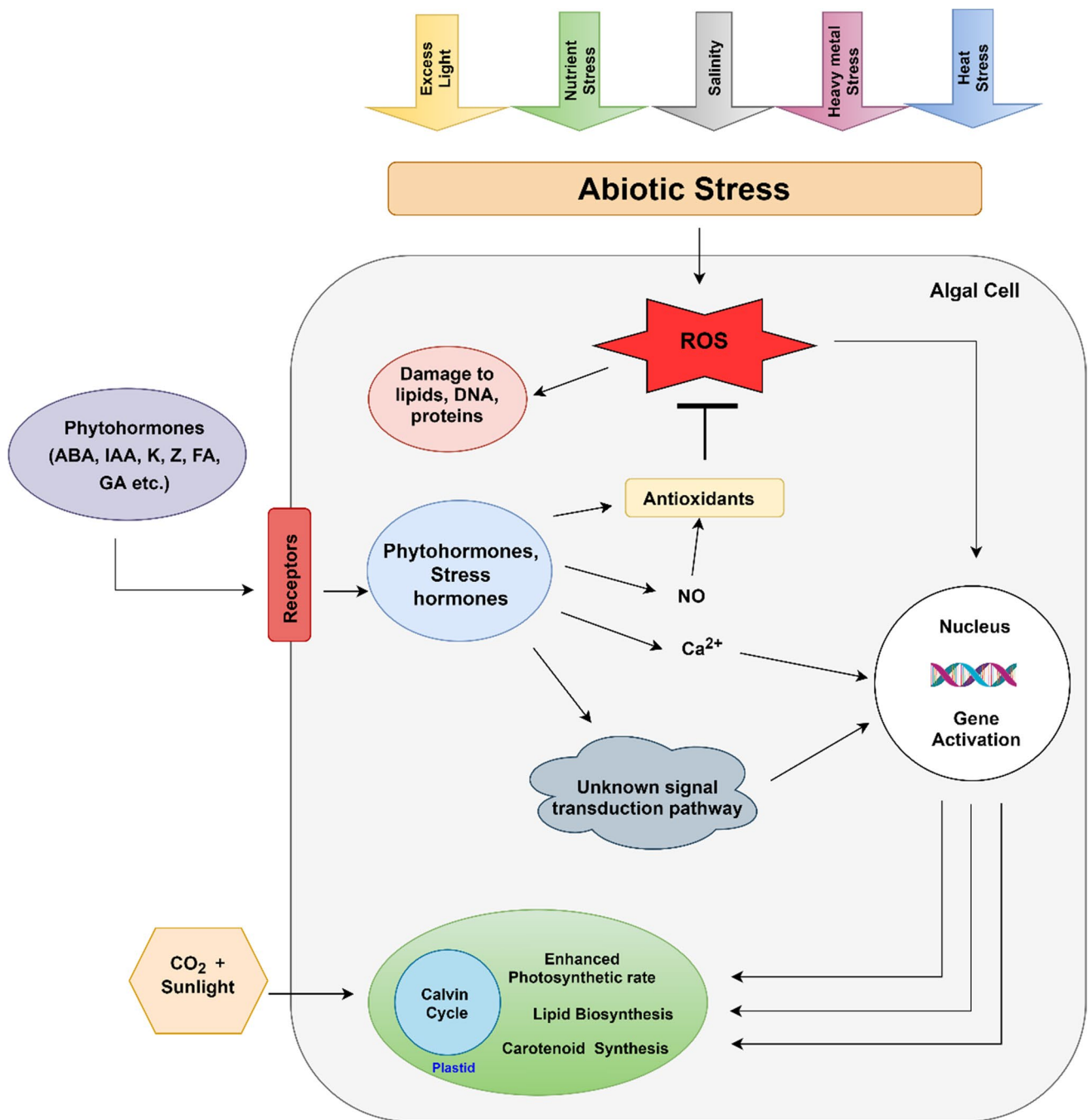
Fig. 4 Role of phytohormones in abiotic stress conditions

et al. 2012; Barati et al. 2019). During abiotic stresses, algae modulate their metabolites in their physiology and biochemistry to survive through adaptation (Roleda et al. 2013; Bermejo et al. 2018). Upon exposure to numerous abiotic stresses, algae influenced their intracellular concentration of lipids, antioxidant enzymes, carotenes, and other metabolites (Rothschild and Mancinelli 2001; Forján et al. 2015). However, under prolonged stress conditions, the algal growth ceases and leads to programmed cell

death (PCD) or apoptosis (Zuppini et al. 2010; Markou and Nerantzis 2013; Bermejo et al. 2018; Barati et al. 2019).

Microalgae are a potential biofuel producing source as they are not dependent on fertile land, can begrown in wastewater, and offer higher productivities. However, large-scale production of lipids is facing a cost-related bottleneck because of low biomass production, high water footprint, high nutrient input, low cell density, and harvesting issues. Currently, several strategies have been explored to overcome

the challenges and achieve maximum growth and large-scale production of lipids (Kim et al. 2016; Wang et al. 2016; Babu et al. 2017). Recently, advanced strategies have been employed to overcome this kind of problem, which are a combination of two different stresses; two-stage cultivation; co-culturing with other organisms; and the addition of phytohormones (ABA, IAA, CKs, GAs, and ET), salts, and flue gases (CO_2, NO_x, SO_x) (Lu and Xu 2015; Li et al. 2017; Salama et al. 2018). The two-stage cultivation strategy has been extensively used, in which cells are firstly grown in nutrient-sufficient conditions (for higher biomass), and then stress conditions are induced, which stimulates the accumulations of higher amounts of proteins, carbohydrates, lipids, fatty acids and other bioactive compounds (Fig. 5) (Chen et al. 2011; Aziz et al. 2020).

Microalgal lipids are categorized into structural lipids such as PUFAs, and storage lipids like non-polar saturated fatty acids (SFAs) and MUFAs. Storage lipids (PUFAs), primarily stored in the form of TAGs, are transesterified to produce biofuel (Thompson Jr 1996). Moreover, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are the most valuable fatty acids in the microalgae, which make them suitable for high biofuel production (Gimpel et al.

2015). Nutrient starvation (primarily nitrogen and phosphate) and salinity have been well documented to stimulate TAG accumulation in microalgae (Li et al. 2008; Yeesang and Cheirsilp 2011; Paliwal et al. 2017; Shi et al. 2017; Wase et al. 2017). The algal lipid production under varying abiotic stress factors is summarised below (Table 4).

Transgenic approaches for stress resistance in algae

Significant breakthroughs in genetic modification of green microalgae have been made over the years (Mayfield and Golden 2015), as evidenced by the synthesis of omega-3 fatty acids, carotenoids, biofuels, and better photosynthetic growth (Gimpel et al. 2015). Following the development of advanced automated sequencing technology over the last two decades, genomics has become a potent tool. Bioinformatics is used to assemble DNA sequences and evaluate gene structure and expression. In the case of microalgae, whole-genome sequencing of strains with commercial potential will allow scientists to apply other omics technologies to gain a better knowledge of high-value cell components,

Fig. 5 Two-stage cultivation of algae to enhance pigment and lipid production
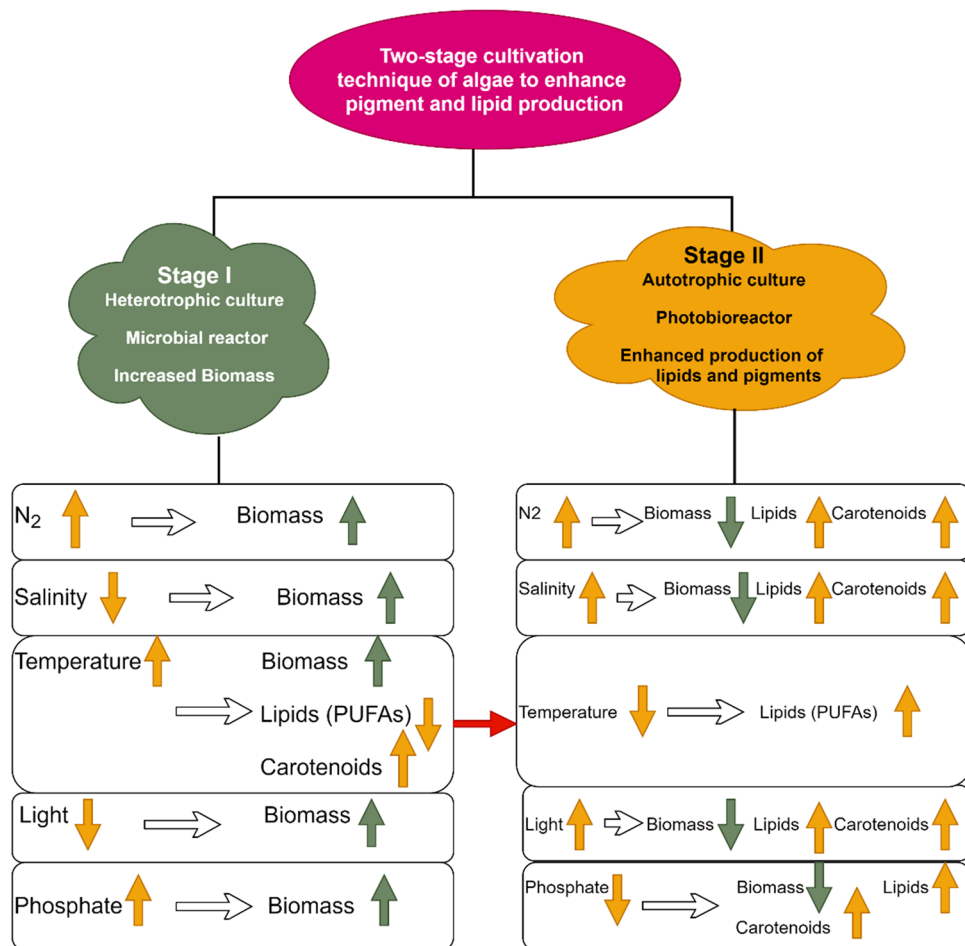
Table 4 The effect of varying abiotic stress factors on algal lipid production

Algal species	Abiotic stress factors	Operation strategy	Lipid production	References
Acutodesmus dimorphus	N deficiency	N starvation (2 days)	29.92%	(Chokshi et al. 2017)
A. dimorphus	Temperature-induced oxidative stress	Temperature 38 °C than at 25 °C	22.7%	(Chokshi et al. 2015)
Acutodesmus obliquus	N limitation + phytohormone	Z (0.5 mg L^{-1}), IAA (1.0 mg L^{-1}), and GA (5.0 mg L^{-1}) + -(N)	77.20%	(Renuka et al. 2018)
Chlamydomonas reinhardtii	N deficiency + melatonin	5 µM melatonin + no N	66.7%	(Meng et al. 2020)
C. reinhardtii	Salinity stress	100 mM NaCl/100 mM CaCl$_2$	73.4%	(Mori et al. 2020)
Chlorella minutissima	N limitation	0.3 g L^{-1} of N	579.86 mg L^{-1}	(Chandra and Ghosh 2019)
Chlorella sorokiniana	N deficiency + IAA + Diethyl aminoethyl hexanoate (DA-6)	IAA (10^{-5} M) or DA-6 (10^{-9} M) + N limitation	69 mg L^{-1} day^{-1} (49% increase)	(Babu et al. 2017)
C. sorokiniana	Salinity	30 g L^{-1} NaCl	0.36 g L^{-1}	(Kim et al. 2016)
C. sorokiniana	Low temperature + glycine betaine (GB)	18 °C + GB at 500 mg L^{-1}	376.2 mg L^{-1}	(Wang et al. 2016)
C. sorokiniana SDEC-18	N deficiency + phytohormone	20 mg L^{-1} NAA and IBA	55.76%	(Yu et al. 2017)
Chlorella sp. HS2	Heat Shock	12 h heat-shock at (50 °C)	2.64 g l^{-1} day^{-1}	(Kim et al. 2020)
Chlorella vulgaris	High Temperature + (BRs)	2, 4- epibrassinolide (EBL) + 25 °C	50%	(Liu et al. 2018)
C. vulgaris	N modulation	250 mg L^{-1} of total nitrogen (TN)	70 mg/L^{-1}	(Cho et al. 2019)
Coccomyxa melkonianii	pH	pH 4.0 and 8.0	24 and 22%	(Soru et al. 2019)
Coccomyxa onubensis	Salinity	100 mM NaCl	416.16 mg g^{-1} dw	(Bermejo et al. 2018)
C. onubensis	PAR + UVA	Continue PAR + UVA 8.7 W m^{-2})	487.26 mg g^{-1} dw	(Bermejo et al. 2018)
Haematococcus pluvialis	High-light and N deficiency + BHT	120 µmol photons m^{-2} s^{-1}, 2 mg L^{-1} BHT	46%	(Zhao et al. 2018b)
H. pluvialis	High-light and nitrogen-deficiency + BHA	50 µmol photons m^{-2} s^{-1}, 2 mg L^{-1} BHA	42.84%,	(Ding et al. 2019)
H. pluvialis	Low light + glycerol	Low light + 1 mL L^{-1} glycerol	36.8%	(Zhang et al. 2020)
Monoraphidium sp. QLY-1	N deficiency + melatonin	N deficiency + 1 µM melatonin	51.38%	(Zhao et al. 2018a)
Monoraphidium sp. QLY-1	Melatonin + Photoinduction	1 µM melatonin	49.6%	(Li et al. 2017)
Monoraphidium sp. QLY-1	Salinity + FA	20 g L^{-1} NaCl + 1.20 g L^{-1} FA	59.53%	(Li et al. 2019)
Monoraphidium sp. QLY-1	N deficiency + JA + strigolactone (SL)	1 µM SL + 25 µM JA	312.35 mg L^{-1} day^{-1}	(Song et al. 2020)
Monoraphidium sp. QLY-1	HM Cd	80 µM and 40 µM Cd	96.75 mg L^{-1} day^{-1}	(Zhao et al. 2019a, b)
Monoraphidium sp. QLY-1	HM Cd + GABA	2.5 mM GABA + Cd	55.37%	(Zhao et al. 2020b)
Nannochloropsis oceanica	low-temperature + Bicarbonate	Bicarbonate (1.0 g L^{-1}) + low-temperature (16 °C)	57%	(Yuan et al. 2019)
Nannochloropsis oculata	High light + N deficiency	250 µmol photons m^{-2} s^{-1} (high light + (-) N	402 mg g^{-1} DW	(Ma et al. 2016)
N. oculata	UV radiation + quizalofop	120 min for 1×10^5 cells m L^{-1}	58.38 mg g^{-1} DW	(Moha-León et al. 2019)
N. oculata	Magnetic fields (MF) and nitrate	MF (20 mT) and N (150 mg L^{-1})	38 mg L^{-1} day^{-1}	(Chu et al. 2020)
Scenedesmus sp.	HM Pb	1 mg/L Pb	31%	(Pham et al. 2020)
Scenedesmus sp. CCNM 1077	Salinity	400 mM NaCl	33.13%	(Pancha et al. 2015)

Table 4 (continued)

Algal species	Abiotic stress factors	Operation strategy	Lipid production	References
Scenedesmus sp. SDEC-8	N deficiency + Phytohormone	20 mg L^{-1} NAA and IBA	56.17%	(Yu et al. 2017)

lipid metabolism, and overall cell activity under stress and non-stress conditions. The genomes of *Botryococcus braunii Showa, Botryococcus braunii UTEX 572, C. reinhardtii, Chlorella sp. NC64A, Coccomyxa sp. C-169, D. salina, Micromonas pusilla, N. oceanica* and *Ostreococcus tauri* were recently sequenced.

The understanding of mechanisms for the adaptation of microalgae to extreme environments has been contributed by comparative genome analysis. Microalgae genomes can be altered in the nuclear, chloroplast, or mitochondrial genomes (Specht et al. 2010). The majority of enzymes involved in secondary metabolism are encoded in the nuclear genome, although others are directed to the chloroplast to accomplish their function (Heydarizadeh et al. 2013). In these circumstances, the nuclear or plastid genomes might be modified to confer a particular metabolic function (Johanningmeier and Fischer 2010). The major ways for delivering DNA to microalgae include electroporation, shaking with glass beads, and particle gun bombardment (biolistic), with the letter proving to be the only effective way for chloroplast transformation thus far (Purton et al. 2013).

The pursuit of stress-tolerant lines has led to an unprecedented rise in algae genetic modification for peptides, enhanced photosynthesis, and key metabolic routes, including the production of lucrative dietary supplements, pharmaceuticals, and hydrocarbons (Gangl et al. 2015). Moreover, genetic sequence omics have assisted in efficient algal modification. Despite enormous accomplishments, only a few algae species continue to display strong and stable expressions of foreign proteins. There are several microalgal gene silencing methods, including oppressive histone H3 lysine alteration, DNA cytosine modification, RNA interference, and miRNA gene regulatory systems to eliminate highly unstable external transcription proteins. *Chlamydomonas* has been shown to have effective but simple nuclear gene targeting mechanisms (Zorin et al. 2009). Various promoters, and 5`UTR modifications, such as the 16S rRNA promoters and the atpA 5`UTR, were shown to allow sufficient heterogeneous genome editing and efficient transgenic protein production within the *C. reinhardtii* plastid (Tissot-Lecuelle et al. 2014). Codon enhanced gene regulation hemH and lba throughout the plastid of *C. reinhardtii* for optimum biohydrogen production is evidence of genetic manipulation in microalgae (Wu et al. 2010). Furthermore, chemically synthesized promoters were created to induce high levels of nuclear gene expression in *Chlamydomonas* (Scranton et al. 2016). Moreover, increased targeted genomic alteration in

C. reinhardtii has been described using zinc finger nuclease enzymes, activator effectors, and the recently discovered clustered, regularly interspersed short palindromic repeat (CRISPR) pathway (Jiang et al. 2014).

Although most genetic engineering strategies are aimed at enhancing the production of high-value metabolites (such as antioxidant pigments and PUFAs) and biofuel molecules (such as hydrogen and TAG), a few attempts have been made toward developing resilient strains for applications such as HM mitigation and CO_2 sequestration. A moth lentil d1-pyrroline-5-carboxylate synthetase (P5CS) allele, for instance, was already found to be primarily expressed in *Chlamydomonas* transformants used to have 80 times better free-Pro levels, exponential growth at detrimental Cd concentration levels, and remarkable binding at four-fold higher Cd densities than wild-type cell types. The findings suggest that free-Proasan antioxidant plays a function in Cd-stressed cells, with greater GSH levels promoting more excellent phytochelatin production and Cd sequestration. Speedy genomic manipulation of such algae was being utilized to increase HM susceptibility and binding selectivity for contaminated water bodies and sediments. Changing both the large and small subunits of Rubisco (rbcS and rbcL) as possibilities for enhancing net CO_2 uptake (photosynthesis) and sequestration through growth promotion received a lot of interest (Whitney et al. 2011). *Chlamydomonas* is a significant host genetic manipulator in this regard since it can cause alterations in both the rbcS and rbcL genes. Hybrid Rubiscos, for instance, have indeed been created by combining plant's small (rbcS) subunits with algae large (rbcL) subunits by transforming a *C. reinhardtii* mutant deficient in the rbcS gene. Despite an increase in CO_2/O_2 binding of 3–11 per cent, the transgenic enzyme retains high Vmax ratios and enzymatically efficient Rubisco. Genetically modified strains, on either hand, are deficient in plastid pyrenoids and also have restricted photosynthesis. Continued research to build and evaluate better Rubiscos, according to (Whitney et al. 2011), would mainly rely on algae in vitro experiments, especially *Chlamydomonas*.

Conclusion

Algae are considered a source of many bioactive compounds with attractive properties, including pigments, carbohydrates, lipids, proteins, and vitamins. They are studied as encouraging feedstocks to satisfy future sustainable

energy demands as they have a high ability to absorb CO_2, no need for arable land, and year-round cultivation that make them attractive for commercial exploitation. However, the growth and development of algae may be inhibited by adverse stresses such as high salinity, nutrient deficiency, HMs, low or excessive water, temperature fluctuations, and UVRs. These stressful conditions cause a variety of metabolic, physiological, biochemical and molecular alterations, subsequently causing oxidative damage and ultimately declining cell growth and biomass. It has been reported that the algal species respond to these stressful conditions by modifying their metabolites. Nitrogen and phosphorus deficiency, for example, causes lipid metabolism to switch from membrane lipid synthesis to neutral lipid storage. Salinity stress causes the accumulation of various osmoregulatory solutes (like glycerol, proline, trehalose), antioxidants, and lipids. The increase in temperature is considered the most tuning factor for polyunsaturated fatty acid production, whereas a decrease in temperature increases the composition of unsaturated and short-chain fatty acids. In recent years, phytohormones emerged as a topic of intense focus in microalgae research. They could sustain the growth of microalgae under abiotic stress conditions. Moreover, it is widely studied that the abiotic stress conditions (such as a two-stage cultivation strategy) can be used to produce lipids and high-value by-products in microalgae.

Recent advancement in our understanding of the molecular mechanisms underlying the responses of algae to abiotic stresses emphasizes their multilevel nature that involves multiple processes such as sensing, signaling, transcription, transcript processing, translation and post-translational protein alterations. However, there is considerable uncovered ground in understanding how algae signal each other to start the cascade of pathways that will improve survival. Moreover, comparative genome analysis has contributed to understanding mechanisms for the adaptation of microalgae to extreme environments. Further, studies integrated with next-generation sequencing strategies and directed experimental evolution approaches will continue to raise and deepen our knowledge of how algae respond and adapt to stressful conditions.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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