Algal Metabolism

Secondary article

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Algal metabolism concerns the biochemical and transport processes by which algae take up nutrients and convert them into the materials needed for growth, reproduction and defence of the organisms.

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Commonality of Algal Metabolism With That of Other Organisms

Algae in the broad sense include the cyanobacteria (blue-green algae) and a range of eukaryotic organisms. The algae are characterized by having oxygen-evolving photosynthesis but they lack the reproductive and developmental features associated with the higher plants or embryophytes. The eukaryotic algae obtained their photosynthetic apparatus (chloroplasts) by the ingestion, retention and genetic integration of cyanobacteria or pre-existing eukaryotic oxygen-evolvers by phagotrophic, non-photosynthetic eukaryotes. Accordingly, as photosynthetic organisms, the eukaryotic algae are polyphyletic, although their photosynthetic apparatus is monophyletic (Bhattacharya and Medlin, 1998). This means that there is likely to be a diversity of metabolic processes in algae as a result of their diverse evolutionary history. So far (June 1999) there is only one example of a completely sequenced genome of a (cyanobacterial) alga, *Synechocystis* sp. strain 6803; knowledge of further genome sequences will help to define this metabolic diversity and its origins (Raven, 1997a).

A key feature that distinguishes the algae from other lower eukaryotes (but see later) is that of oxygen-evolving photosynthesis. Key features of the photosynthetic process are the reactions catalysed by the two reaction centre complexes, the cytochrome b_6–f complex, various lower M_r redox agents, the adenosine triphosphate (ATP) synthetase, and the enzymes of the photosynthetic carbon reduction cycle; these are common to all oxygen-evolvers and are encoded by genes with very significant sequence similarity in all oxygen-evolvers (Falkowski and Raven, 1997). Other photosynthetic catalysts show variation among algae, although embryophytes are much more conservative, having a suite of catalysts resembling their ancestors the green algae.

The photosynthetic reactions produce sugars (as phosphates) which are used by the chemo-organotrophic reactions of cyanobacteria and of the eukaryotes that have obtained chloroplasts (**Figure 1**). The basic chemo-organotrophic metabolism of algae is, of course, very similar to those of all other (eu)bacteria and eukarya.

The photolithotrophic metabolism of the algae is taken to its extreme in the obligate photolithotrophs (e.g. many cyanobacteria and eukaryotes), which cannot be grown in the dark on any of the organic carbon substrates yet tested. In some cases (cyanobacteria) obligate photolithotrophy is correlated with the absence of 2-oxoglutarate dehydrogenase, so that the tricarboxylic acid cycle cannot function in its normal cyclic fashion able to oxidize acetyl coenzyme A (CoA) to two carbon dioxide with ATP synthesis. However, the two remaining linear pathways can still function in the synthesis of essential C skeletons, especially the 2-oxoglutarate needed for the glutamate family of amino acids and the tetrapyrrols (Falkowski and Raven, 1997).

This ability to grow with photons, CO_2, N_2, NH_4^+ or NO_3^-, $H_2PO_4^-$, SO_4^{2-}, and all other essential elements supplied in inorganic form extends to algae that are not obligately photolithotrophic, i.e. can be grown in the light, and rather less frequently, the dark with organic carbon as the major carbon (and, in the dark, energy) source. The loss of functionality of one or more genes essential for photosynthesis among facultatively photolithotrophic algae leads to obligate chemo-organotrophy, which among eukaryotes includes phagotrophy (as was the case for the nonphotosynthetic ancestors of eukaryotic algae) and saprotrophy (including parasitism, usually on other algae). The range of organic carbon compounds that can be used by chemo-organotrophic (or photo-organotrophic) algae varies with the taxon concerned. With respect to nitrogen supply the use of N_2 as nitrogen source is only possible in certain cyanobacteria; eukaryotic algae can only fix N_2 via associations with prokaryotic (generally cyanobacterial) N_2 fixers. Although all algae can use NH_4^+ as nitrogen source, not all can use NO_3^- or NO_2^-. This condition seems to be derived in *Chlamydomonas reinhardtii*, but may be ancestral in *Euglena*.

Other departures from strict photolithotrophy relate to lesions in downstream metabolic processes that make the alga dependent on exogenous supplies of certain 'growth substances' or vitamins, predominantly biotin, thiamin and vitamin B_{12}; in nature these compounds are derived from associated biota that are not autotrophic for these compounds. Ascorbic acid can apparently be synthesized by all algae, albeit involving different pathways from glucose in different eukaryotic taxa.

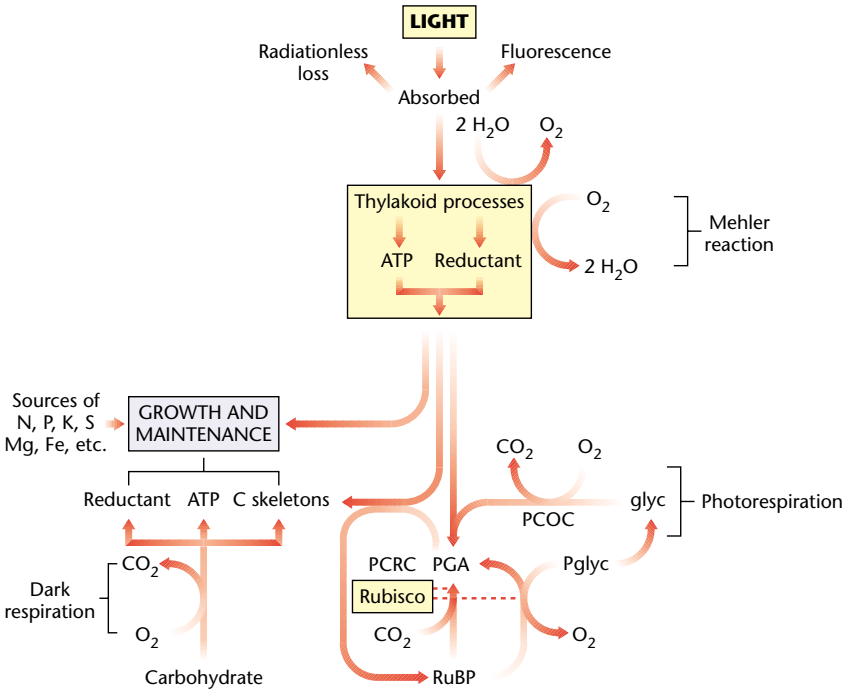

Figure 1 Outline of the pathways of energy, carbon and oxygen in photosynthesis, photorespiration, dark respiration and growth of an alga. No attempt is made to represent stoichiometries. (Abbreviations: Glyc, glycolate; PCOC, photorespiratory carbon fixation cycle (or its equivalent); PCRC, photosynthetic carbon reduction cycle; PGA, 3-phosphoglycerate; Pglyc, phosphoglycolate; RuBP, ribulose bisphosphate; Rubisco, ribulose bisphosphate carboxylase-oxygenase). (Adapted from Raven, 1984.)

Compounds That Only Occur in Algae and Their Metabolism

Overview

Important algal-specific macro- and micromolecules range from light-harvesting pigment protein complexes through redox catalysts of photosynthesis, enzymes and transporters related to inorganic carbon acquisition and enzymes of glycolate metabolism, through to the polyglucan organic carbon stores that act as a metabolic buffer between organic carbon production (or acquisition) and downstream metabolism, and thence to alga-specific end-products such as extracellular structural materials (e.g. agarose, agaropectin, alginic acid and carrageenans) and anti-biophage compounds and compatible solutes of widespread occurrence but with alga-specific synthetic pathways (e.g. dimethylsulfoniopropionate).

Photon harvesting

The ancestral light-harvesting pigment protein complexes of the algae supplying excitation energy to photosystem II and, to a lesser extent, photosystem I are the phycobiliproteins of the cyanobacteria which gave rise to the phycobiliproteins of the eukaryotic red algae, and cryptophytes. The chromophores of these light-harvesting complexes are open-chain tetrapyrrols derived from cyclic tetrapyrrols, and resemble the chromophores of the photomorphogenetic pigment protein complex phytochrome which also occurs in many algae, including cyanobacteria.

In some cyanobacteria *sensu lato* (the prochlorophytes or chloroxybacteria) phycobiliproteins have been replaced by light-harvesting pigment proteins containing chlorophylls *a* and *b* (or divinyl chlorophylls *a* and *b*). The chromophores (other than chlorophyll *a*) involved here are chemically very similar to chlorophyll *a*, with the (divinyl) chlorophyll *b* having a methyl group in (divinyl) chlorophyll *a* oxidized to an aldehyde group. Most, if not all, of the chloroxybacteria also have chlorophyll *c*-like chromophores derived biosynthetically from intermediates of chlorophyll *a* synthesis. The protein of the chloroxybacterial (divinyl) chlorophyll *a*–*b* (–*c*) complex is derived evolutionarily from a chlorophyll *a*-binding protein whose expression in cyanobacteria *sensu stricto* is increased by iron deficiency.

The replacement of phycobiliproteins by chlorophyll *a* and/or *b* and/or *c* proteins as the major light-harvesting complexes has also occurred independently in the eukaryotes, with a common ancestral polypeptide accounting

for the protein component in many eukaryotic algal taxa. The embryophytes can be seen as a very restricted subset of the green algae, let alone algae in general, with respect to chlorophyll-protein light-harvesting complexes; this is especially the case when the diversity of light-harvesting carotenoids associated with other polypeptides is considered. Major light-harvesting carotenoids include siphonenein, siphonoxanthin and prasinoxanthin in green algae, fucoxanthin and its derivatives in heterokont (e.g. brown algae and diatoms) and haptophyte (e.g. coccolithophorid) algae, and peridinin in many dinoflagellates.

Thylakoid redox reactions

Among the redox agents involved in reactions temporally and energetically downstream of primary photochemistry in algae there is, as with light-harvesting, more diversity in algae than in embryophytes. Whereas embryophytes only have the cuproprotein plastocyanin transferring electrons from the cytochrome b_6–f complex to photosystem I, and the iron-sulfur protein ferredoxin transferring electrons from photosystem I to the $NADP^+$ reductase, many algae have facultative or obligate replacement of these redox proteins by the iron-protein cytochrome c_6 and by the metal-free flavoprotein flavodoxin, respectively. Cytochrome c_6 is a member of the (soluble) cytochrome c family widespread among organisms with membrane-associated redox chains. In contrast, both ferredoxin and flavodoxin are widespread among all kingdoms; plastocyanin is confined to (but not ubiquitous in) oxygen-evolvers.

Carbon acquisition and assimilation

Carbon dioxide concentrating mechanisms, which increase the carbon dioxide concentration around the carboxylase ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), and suppress its oxygenase activity, are widespread, and probably polyphyletic, in eukaryotic algae and seem to be ubiquitous in cyanobacteria. Little is known of their mechanism(s) or molecular biology. Carbonic anhydrases occur externally and at a number of internal locations in algae with or without carbon dioxide concentrating mechanisms and derive from both α and β subfamilies of this enzyme. The core carbon dioxide fixing enzyme, Rubisco, of oxygen-evolvers all belong to one family of enzymes, but lateral gene transfers have yielded algal oxygen-evolvers with type I Rubiscos (eight large, eight small subunits) from β-proteobacteria (some cyanobacteria *sensu stricto* and chloroxybacteria and, independently, red algae and the heterokont, haptophyte and cryoptophyte algae which derived their plastids from red algae) and with type II Rubiscos (two large subunits) from β-proteobacteria (dinoflagellates) as well as the type I Rubisco of the cyanobacterial type without lateral gene transfer in most cyanobacteria (*sensu lato*), green algae (including euglenoids) and embryophytes. Rubisco is generally held to require Rubisco activase (an ATP-consuming enzyme) to maximize its catalytic capacity although the complete genome sequence of the cyanobacterium *Synechocystis* sp. strain 6803 does not appear to contain a gene for this enzyme (Raven, 1997a). Raven (1997a) also points out that there is no reported gene for sedoheptulose-1,7-bisphosphate-1-phosphatase in the *Synechocystis* genome, although the transaldolase-dependent variant of the photosynthetic carbon reduction cycle is possible in this cyanobacterium. Alternatively, since the fructose-1,6-bisphosphate-1-phosphatase of higher plants has some sedoheptulose-1,7-bisphosphate-1-phosphatase activity (Ashton, 1998), the presence of the former enzyme could permit the functioning of the transaldolase-independent variant of the photosynthetic carbon reduction cycle in *Synechocystis*.

The carbon dioxide concentrating mechanism(s) (where they occur) do not completely suppress (phospho)glycolate synthesis, and air-equilibrium carbon dioxide and oxygen concentrations certainly permit significant rates of (phospho)glycolate synthesis in algae lacking a carbon dioxide concentrating mechanism. All algae have phosphoglycolate phosphatase and, although some of the resulting glycolate may be excreted to medium, all algae have enzymes capable of oxidizing glycolate to glyoxylate and for further metabolizing glycolate. The ubiquitous glycolate oxidase of the embryophytes is present in many algae (e.g. the Charophyceae, which are the green algae most closely related to the embryophytes, and the brown and red algae), although in others (cyanobacteria, many green algae, *Euglena*, diatoms) the enzyme is a glycolate dehydrogenase. Raven (1997a) suggests that the two enzymes may have at least one subunit in common. Further metabolism of glycolate follows from the complete photosynthetic carbon oxidation cycle pathway, which was first characterized in embryophytes, in at least some green algae, but other reactions may occur in certain other algae.

A final aspect of metabolism related to carbon acquisition in algae concerns anaplerotic CO_2/HCO_3^- fixation. Although acetyl–CoA carboxylase, carbamyl phosphate carboxylase and 5-amino-imidazole ribotide (AIR) carboxylase seem to be ubiquitous among algae, the standard embryophyte ($C_3 + C_1$) carboxylase, i.e. phosphoenolpyruvate carboxylase, appears not to be universal among algae, occurring in the red, green and euglenoid algae, as well as some diatoms and haptophytes, whereas other diatoms and haptophytes and brown algae have phosphoenolpyruvate carboxykinase, and dinoflagellates have either of these carboxylases or pyruvate carboxylase (Raven, 1997a).

Storage compounds and compatible solutes

Turning to the organic carbon compounds acting as reserves or buffers between carbon acquisition and carbon consumption in growth, and in the case of some compounds acting as compatible solutes, the algae use, in the case of green algae, the 'typical' embryophyte polyglucan starch and (often) the 'typical' embryophyte compatible solute sucrose, although the embryophytes as well as the green and other algae have other nonreducing sugars and, especially, sugar alcohols. A few green algae (e.g. *Acetabularia*) have, as well as starch, polyfructans as also found in some embryophytes, whereas the cyanobacteria and red, chlorarachniophyte and cryptophyte algae, and dinoflagellates, have a starch-like polyglucan. Other algae have a β1,3 glucan variously named leucosin (euglenoids), laminarin (brown algae) and chrysolaminarin (other heterokonts; haptophytes); neutral lipid is also an important insoluble energy reserve in some heterokonts and other algae. As for the low M_r solutes acting as cytoplasmic compatible solutes and (if stored in vacuoles as well) as organic carbon reserves, there are some algal classes that use a single or two closely related C, H, O-containing solutes; the brown algae have mannitol supplemented, in five species, by altritol. However, mannitol also occurs in green algae (and in embryophytes). Floridoside or isofloridoside (galactosyl glycerides) occurs in red algae and chrysophytes, and the glycosyl analogue occurs in cyanobacteria. Sugar alcohols are widespread in almost all classes of algae.

Nitrogen storage as soluble low M_r compounds can occur as NO_3^- or as amino acids, betaines or specific low M_r organic nitrogen compounds; many of these can also function (in the cytoplasm) as compatible solutes. Organic nitrogen compounds can also function as intracellular ultraviolet B (UV-B) screens in the form of mycosporine-like amino acids. High concentrations of dimethylsulfoniopropionate (DMSP), a zwitterionic compatible solute, are found in some marine macroscopic green and red algae, and in haptophytes, dinophytes and pelagophytes; although this compound also occurs in embryophytes the biosynthetic pathway is different (Poole and Raven, 1997; Summers *et al*., 1998).

Nitrogen and sulfur assimilation

Nitrogen assimilation in algae resembles that in embryophytes as far as NO_3^- and NO_2^- reductases, and glutamine synthetase and glutamate synthetase are concerned, although there is the possibility that NH_4^+ can be assimilated by an $NADP^+$-specific, high NH_4^+-affinity glutamate dehydrogenase. Most algae can use urea; almost all of them use (like embryophytes) urease, while the Chlorophyceae (division Chlorophyta), like some fungi, use the ATP-consuming urea amidolyase. SO_4^{2-} assimilation in algae generally resembles that in embryophytes.

Growth substrates

There is still controversy over the occurrence of embryophyte-type plant growth substances or 'hormones' in algae, but abscisic acid (ABA) seems to be increasingly accepted as a 'natural' component of several algae. Furthermore, algae were in the forefront in providing evidence for the regulatory role of cyclic AMP in phototrophs (Bradley *et al*., 1991).

Secondary metabolites

Low M_r solutes in algal cells which have a variety of biosynthetic origins and which do not fit obviously into the categories mentioned above are variously described as 'secondary products' or 'antibiophage compounds'; they include the phlorotanins of brown algae, and halocarbons in a diversity of algae, and (probably) the excreted toxins of some cyanobacteria and dinoflagellates.

Cell wall materials

A final category of organic compounds, many of them alga-specific, are cell wall materials *sensu stricto* (i.e. those components that restrain cell turgor) and other extracellular structural (at the organismal level) materials; these are often quantitatively significant components of algae. Algal cell walls are polyphyletic (Raven, 1997b) and have a variety of components that have a role in turgor resistance (e.g. β1,4 glucan; β1,4 glucomannan; β1,3 xylan). The components that probably relate more specifically to whole-organism mechanics, especially in sea water (e.g. agarose, agaropectin, alginates, carrageenans), often have commercial significance and will be considered later.

Algal Metabolism and Extreme Environments

Definition of extreme environments

An extreme environment can be defined for an individual genotype as one that restricts growth and even survival; most ecologically relevant are temporally variable environments where the extremes are only present for a limited fraction of the life cycle (e.g. the marine intertidal).

Ecologically an extreme environment can be defined as one that only permits very limited genetic diversity of organisms of a given life-form and trophic role. The discussion of metabolism in extreme environments will touch on both of these kinds of effects.

Electromagnetic radiation

Algal growth at very low photosynthetic photon flux densities (possibly as low as 10 nmol photons $m^{-2} s^{-1}$,

400–700 nm) generally involves adaptation or acclimation phenomena yielding higher ratios of light-harvesting pigment protein complexes to downstream photosynthetic and chemo-organotrophic biological catalysts, and possibly involves minimizing energy-requiring maintenance reactions, and energy-wasting H^+ leakage and charge recombination in photosystem II. Algal growth at very high photosynthetic photon flux densities (up to 2 mmol photons $m^{-2} s^{-1}$, 400–700 nm) involves lower ratios of light-harvesting pigment protein to downstream, and more expression (when it is present) of a carotenoid cycle which acts in non-photochemical quenching of excessive excitation energy in photosystem II, as well as (when present) 'state transitions' of light-harvesting complex association with photosystem II, thus decreasing the extent of photodamage to photosystem II. State transitions and a carotenoid cycle are ubiquitous in embryophytes. β (and α) carotenes associated with reaction centres are involved in quenching triplet chlorophyll and singlet oxygen in the thylakoid membrane. Extraplastidic β-carotene droplets act as screens of very high levels of (blue) photosynthetically active radiation in algae in very high radiation environments such as tropical terrestrial and marine habitats, and hypersaline lake algae.

Damage to nucleic acids, proteins, quinones and other essential UV-B absorbing materials by incident UV-B radiation can be limited by interposing sacrificial UV-B absorbing materials between the incident radiation and the essential target molecules. This is less readily achieved for small cells than for larger cells if intracellular soluble screening compounds are used; algae generally use the mycosporine-like amino acids rather than the nitrogen-free phenolic compounds used in embryophytes as soluble sacrificial screening compounds (Raven, 1999). Natural waters attenuate UV-B to a greater extent than photosynthetically active radiation, so that UV-B is the greatest problem for terrestrial algae, wherein extracellular UV-B screening involves materials in cyanobacterial sheaths (e.g. scytonemin) and fungal products in lichen symbioses.

Nutrients

Carbon

Growth of photolithotrophic algae at air-equilibrium carbon dioxide and oxygen levels gives high expression of carbon dioxide concentrating mechanisms and of enzymes of (phospho-)glycolate metabolism; algae with no carbon dioxide concentrating mechanisms have even higher expression of glycolate metabolism enzymes. Growth at even lower carbon dioxide levels can lead to even more expression of carbon dioxide concentrating mechanisms, while growth at higher carbon dioxide levels (such as the 10 times air-equilibrium encountered in some freshwaters) suppresses expression of carbon dioxide concentrating mechanisms in many eukaryotes if not in cyanobacteria, and means minimal phosphoglycolate synthesis (and metabolism) even when carbon dioxide always enters by diffusion.

Nitrogen

Nitrogen fixation is restricted to certain cyanobacteria, and although suppression of the energy- and iron- (and usually molybdenum- or vanadium-) demanding nitrogenase by combined nitrogen can occur, the general response to increase nitrogen availability is that fewer nitrogen fixers occur; this is especially the case in the oceans. Among combined nitrogen sources NH_4^+ assimilation is constitutive, although high-affinity NH_4^+ influx may need low nitrogen availability. NO_3^- influx and reduction is generally suppressed when NH_4^+ availability is sufficient to maintain a substantial proportion of the maximum specific growth rate. Many algae can take up and metabolize urea; amino acids can either be taken up and metabolized, or externally deaminated with uptake of NH_4^+.

Phosphorus

Phosphorus deficiency leads to increased capacity of high-affinity inorganic phosphate uptake and sometimes the expression of extracellular phosphatases, giving the algae access to polyphosphates and organic phosphate esters.

Iron

Oxygenated environments have restricted rates, if not final extents, of iron availability, as Fe(III). Iron deficiency increases siderophore (Fe(III) chelater) production, followed by Fe(III) siderophore uptake, by cyanobacteria, and increases surface Fe(III) reduction, followed by Fe(II) uptake, by eukaryotic algae. Acclimation to low iron availability in algae that can produce iron-containing ferredoxin and cytochrome c_6 as well as flavodoxin and plastocyanin involves replacement of the iron-containing by the iron-free redox catalysts, while iron deficiency may make nitrogen fixation, or even NO_3^- assimilation, as high-iron-cost processes, less useful than NH_4^+ scavenging in low iron, low combined nitrogen environments. Adaptation (in instantaneous terms, species replacement) suggests that cyanobacteria and red algae (with high ratios of the iron-demanding photosystem II to photosystem I) nitrogen fixers (large iron requirements) and larger organisms (diffusive iron supply less effective) should be replaced by green or heterokont, NH_4^+-using, smaller algae when iron is limiting.

Temperature

Other things being equal, algae have a smaller amount of the light-harvesting pigment complexes (catalysing the temperature-independent processes of photon absorption, excitation energy transfer and primary photochemistry)

relative to downstream metabolic machinery (catalysing temperature-dependent reactions) when adapted or acclimated to lower temperatures. As with other ectotherms, acclimation to temperature difference maintains membrane fluidity by charged fatty acid in saturation. Compatible solutes such as DMSP also serve as cryoprotectants of proteins.

Osmolarity

Cyanobacteria and eukaryotic algae originated in the oceans, probably at lower osmolarity than that of today's ocean; thus even wall-less marine algae today, isosmotic with the sea water, have compatible solutes in their cytoplasm as well as inorganic ions, related to maintenance of protein function. This requirement applies *a fortiori* to organisms growing in higher-salinity environments, where energy costs of net synthesis of compatible solutes and, if they have a low M_r and cost less per molecule to synthesize, of leakage and replacement, are important. Although not usually regarded as extreme, freshwater osmotic- and volume-regulation constraints can mean that natural selection favours low intracellular osmolarity as a means of limiting energy costs of wall synthesis and, for flagellates, of active water expulsion.

pH

Within the green algal genus *Dunaliella* there are species tolerant of external pH values from 0.5 (*D. acidophilla*) to 10 (e.g. *D. tertiolecta*).

Desiccation and freezing tolerance

The metabolic bases of cytoplasmic tolerance of desiccation are not clear, although dehydrin-type genes are involved at least in cyanobacteria. Desiccation-tolerant (aerophylic, high intertidal) algae use sugar alcohols as compatible solutes rather more commonly than do non-desiccation-tolerant algae, but this is not invariable.

Prevention of free radical synthesis and damage

Damage by UV-B, and photosynthetically active radiation, and (perhaps) by hyperoxia, acts in part by generating O free radicals, whereas NO• free radicals result from NO_3^- assimilation. Quenchers of $^1O_2$ (carotenes), scavengers of •OH (ascorbate, α-tocopherol and other lipid-soluble phenols), and enzymic mechanisms of removing O_2^-•, H_2O_2 and NO•/NO_2•, occur in algae, although the enzymes are (except in the Charophyceae) not necessarily identical to those in higher plants.

Mechanical stresses

The very robust hydrodynamic environment of many marine, and some freshwater, macroalgae may relate to the variety and nature of extracellular polysaccharides involved in organism-level structures (e.g. alginates, agar, carrageenans).

Algal Metabolism and Commercial Use of Algal Compounds

Historically macroalgae have been used as sources of soda for soap and glass manufacture and of iodine; in these cases the organic compounds responsible for the excess of inorganic cations over inorganic anions, and for binding iodine, are lost in burning.

A major present use of marine brown macroalgae is in extraction of alginate, an extracellular copolymer of mannuronate and guluronate, used in soil amelioration and in many commercial products. Sulfated extracellular polysaccharides from marine red macroalgae are used as bases for microbial culture media (agarose, agaropectin) and in the food industry (carrageenans).

The green microalga *Dunaliella* spp. from hypersaline high temperature habitats is cultured as a source of β-carotene (pro vitamin A) for health food use; this alga can be grown outdoors in extreme environments featuring high salinity, thus excluding other phototrophs, and high temperature and irradiance leading to maximum β-carotene content. The glycerol that *Dunaliella* spp. produce as a compatible solute cannot be economically produced in competition with glycerol from petrochemicals.

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