BACTERIOLOGICAL REVIEWS, Mar. 1973, p. 32-101
Vol. 37, No. 1

Printed in U.S.A.

Physiology and Cytological Chemistry of Blue-Green Algae

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INTRODUCTION

This review grew out of an interest in developmental phenomena in certain filamentous blue-green algae (823–825). In these algae, vegetative cells can differentiate into heterocysts, and sometimes also into spores. Differentiation involves major changes in certain of the cytochemical and physiological characteristics of the vegetative cells, whereas other such characteristics change little if at all. A first step toward understanding the transition from the metabolic state of a vegetative cell to that of a heterocyst or spore is to learn the characteristics of those end points.

The positions of the heterocysts and spores along the algal filaments form well-defined patterns. These developmental patterns, at least in *Anabaena cylindrica*, are dependent upon interactions between cells, as well as intracellular changes. Study of development may therefore be expected to be assisted by consideration of other phenomena, e.g., movement and nitrogen fixation, which involve coordinated activities of, and within, cells of algal filaments.

Thus, a survey of information pertinent to study of differentiation and pattern formation in blue-green algae expanded to encompass much of their physiology and cytological chemistry. This review is perforce a primer because of the restrictions of contemporary knowledge. It is written with the hope that it will help to "prime" the maturation of developmental studies of these algae.

In recent years, Lang (484) has reviewed the cytology, and Holm-Hansen (390) the physiology and ecology of blue-green algae. Other reviews will be cited where they are pertinent.

CYTOLOGY AND CYTOLOGICAL CHEMISTRY

Outer Layers

Side walls. The structural features of the cells of blue-green algae—or *Cyanophyta*—which can be observed with the light microscope include a central region ("centroplasm, nucleoplasm") which is rich in nucleic acid, and which interdigitates with a peripheral region ("chromatoplasm") containing the photosynthetically active pigments; various inclusions; and circumferential layers including a plasmalemma, a pellicular wall, and often, a layer of mucilaginous material (250). Figure 1 is a survey electron micrograph of a blue-green algal cell, showing with greater resolution the features cited above. The following sections will discuss the fine structure and chemical composition of the component parts of these cells, beginning with the cell wall.

Between the plasmalemma and the extracellular mucilage is a wall layer, termed the "inner investment" (250), which has been resolved by the electron microscope into four layers, L_I through L_{IV} (438; Fig. 1). This terminology appears now to be generally accepted (e.g., 12, 335, 484). L_{IV} is discussed below. Layers L_I and L_{III} are electron transparent, and vary from about 3 nm each in thickness (429) to about 10 nm (438). L_I may possibly be an artifact of preparation (12; but cf. 107). A parallel array of fibrils, 6 to 9 nm in diameter, is present in the region of, and apparently constitutes, layer L_{II} of *Oscillatoria princeps* (335). The thickness of L_{II} ranges from 10 nm or less in *Oscillatoria rubescens* (438) and *Anacystis nidulans* (516) to about 200 nm in *O. princeps* (335). This layer thickens at

least fivefold during akinete differentiation in *Cylindrospermum* sp. (427).

Rows of pores are frequently visible on both sides of the loci of ingrowth of end walls, in filamentous blue-green algae. These pores are 7 to 20 nm in diameter (179, 543), or may be elongated at the outside (616), and may taper toward the inside (616) or toward the outside (335). In *Microcoleus vaginata*, hormogone production involves tearing of the wall along just such a circumferentially positioned set of pores (482). It has been suggested, but with little supporting evidence, that these pores are involved in mucilage secretion (179, 543). However, no such pores were seen in a study of the ultrastructure of members of the *Stigonemataceae* (107). It was suggested that the mucilage of these algae may be extruded as "blebs" of material.

Blue-green algae can be lysed by growing them in penicillin (e.g., 237, 241, 254, 470), which interferes with deposition of peptidoglycan into bacterial walls. Moreover, lysozyme, which breaks down this material in bacterial walls, can cause lysis of blue-green algae (254), a fact which has permitted isolation of protoplasts (61, 161, 779) or spheroplasts (187, 276, 331, 633) of these algae. Since simultaneous treatment with ethylenediaminetetraacetate (EDTA) (187) or prior lyophilization (297) sometimes greatly increases the effect of lysozyme, it appears that the sensitive layer is not directly at the cell surface. Although initial results suggested that L_I was the lysozyme-sensitive layer of the cell wall (241), it has now been clearly demonstrated that the layer destroyed by lysozyme is L_{II} (429; cf. also 516).

After it was found that the constituents of peptidoglycan (670, 730), including diaminopimelic acid (831; and cf. 395), are present in blue-green algae, Frank et al. (240, 241) and later workers analyzed the composition of the peptidoglycan-containing layer of the wall (Table 1). There is little divergence from the ratio of constituents expected if the backbone of the peptidoglycan is, as in most bacteria (606), a repeating sequence of *N*-acetyl muramic acid and *N*-acetyl glucosamine.

Carbohydrates detected in isolated walls of blue-green algae are listed in Table 2.

Some authors have pointed out the existence of a membrane-like layer L_{IV}, approximately 75 to 80 Å thick, external to the peptidoglycan layer ("outer membrane," reference 200; "*Scheidenlamella*," reference 438; see also 654). This layer is, however, not always seen (654). The layer may have either a dark-light-dark pattern, typical of "unit membranes" following permanganate fixation (438), or the image of only a single dark line (200). Undulation of this membrane (107, 200) may be an artifact, since its appearance is smooth following freeze-etching (438; cf. also 657). A layer of similar location and appearance in gram-negative bacteria consists of lipopolysaccharide (606), and it has been found that 2 to 3% of the dry weight of *Anacystis nidulans* is a wall-associated lipopolysaccharide of which about 60% is carbohydrate, principally mannose but with glucosamine, 2-amino-2-deoxyheptose, 2-keto-3-deoxyoctonate, and other sugars also present (800).

Based on the content of mannose and amino sugars in cells and walls, Dunn et al. (191) estimated that 10 to 20% of the dry weight of vegetative cells of *A. cylindrica* is wall material (exclusive of mucilage). Walls of blue-green algae contain a variety of amino acids and thus, presumably, protein (388, 643).

End walls; division. The end walls of unicellular blue-green algae do not differ in ultrastructure from the side walls (e.g., 12, 200, 420). In filamentous species, a peptidoglycan-containing (241) L_{II} layer is present, sandwiched between L_I layers which are continuous from the side walls of the two adjacent cells (438; cf. also 332, 333, 506). The result is a three-layered end wall (254, 332, 333, 438, 572). In *Stigonema*, the L_{II} layer may subsequently be divided part of the way in from the periphery of the end wall by an ingrowth of layers L_{III} and L_{IV} (107).

Pores (10–20 nm) were observed in chromic acid-treated end walls of *Oscillatoria sancta* and in end walls of *Cylindrospermum*, *Microcoleus*, and *Oscillatoria limosa* (179, 180, 543). Hagedorn (333) found 35 to 40 pores per μm^2. Intercellular "plasmodesmata" 17 nm in width were observed in thin sections of *Symploca muscorum* by Pankratz and Bowen (616). It is unknown if these structures play any role in intercellular communication.

The end walls are formed by irislike ingrowth of the side walls (332), beginning with the plasmalemma (616). Ingrowth of the L_{II} layer may be either as a continuation of the L_{II} layer of the side walls (333) or from a ring-formed deposit (438), such as is sometimes found at the junction of completed end walls with side walls (252, 572) in filamentous forms. Division in *Agmenellum quadruplicatum* strain BG-1 takes place by simultaneous invagination of all wall layers (420), and in *Anacystis nidulans*, another unicellular blue-green alga, by forma-

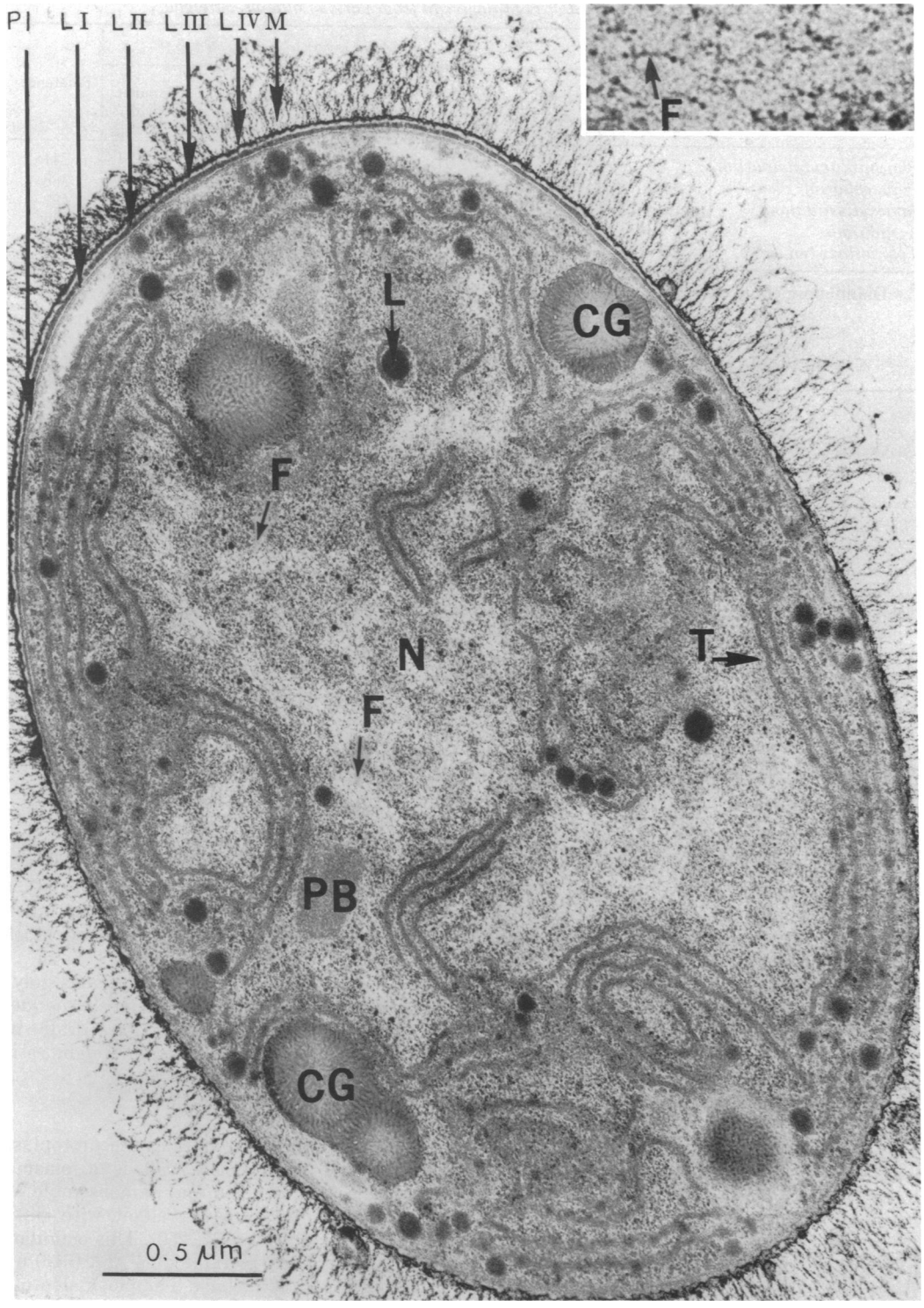

FIG. 1. *A survey electron micrograph of a cell of Anabaena variabilis showing mucilage (M); wall layers (L_I-L_{IV}); plasmalemma (Pl); thylakoids (T); DNA-containing regions (N), with fine fibrils (F) visible in certain areas (see inset); cyanophycin granules (CG); a polyhedral body (PB); and other inclusions, possibly lipid in nature (L). Courtesy of L. V. Leak (500); with permission.* ×48,000. *Inset,* ×272,000.

TABLE 1. *Composition of peptidoglycan from various blue-green algae*

Organism	Peptidoglycan/ Isolated Wall (% wt)	Molar ratio[a]						Reference
		Muramic acid	Glucosamine	Diaminopimelic acid	Glutamic acid	Alanine	Aspartic acid	
Phormidium uncinatum	52	0.63	1.0	1.0	0.94	2.0	0.94	241
P. foveolarum	32	0.8	1.1	1.0	1.1	1.85		388
Anacystis nidulans	28	1.47	1.34	1.0	1.52	2.4		187
A. nidulans	22	0.9	1.9	1.0	1.1	2.0		388
Tolypothrix tenuis	25–30	0.8	1.1	1.0	1.1	1.9		388

[a] Diaminopimelic acid = 1.

TABLE 2. *Sugars in wall polysaccharides from various blue-green algae*

Organism	Sugars										Reference
	Mannose	Glucose	Galactose	Xylose	Ribose	Arabinose	Rhamnose	Fucose	Galactosamine	Unknown	
Phormidium foveolarum	+	+									388
Tolypothrix tenuis	+	+	+	+							388
Anacystis nidulans	+[a]	+	+	+	+	+	+		+		388
A. nidulans	+++	+								+	186
Anabaena cylindrica (vegetative cells)[b]	50%	35%	5%	8%				2 ± 1%			192

[a] A highly purified peptidoglycan fraction was still rich in mannose.
[b] Carbohydrate accounted for ca. 18% of detergent-washed walls.

tion of a three-layered end wall (see above), which is then transected by ingrowth of the L_{III} and L_{IV} layers (12).

When a cell of *Pleurocapsa fuliginosa* forms endospores, many small groupings, each of which contains thylakoid fragments and a nuclear region, become distinguishable within the cell. These groupings are then separated by ingrowth of the cell wall (49).

Mucilage/sheath. A layer of mucilage surrounds the cells or filaments of many blue-green algae. In shadow micrographs (248, 543, 685, 708) and in thin sections (481, 501, 775), mucilage has a fibrillar appearance, but the presence of fibrils 30 Å wide, and wider, may be due to binding together of individual fibrils by the act of drying (438). Chemical studies of presumptive mucilage are described in Table 3. (It is difficult to ascertain the origin of all of the material extracted with hot water or hot alkali.) It is not presently understood, in chemical terms, why certain mucilages of blue-green algae are diffluent (192), whereas other mucilages—referred to as sheath (729)—are much denser.

Substances, presumably mucilaginous polysaccharide, produced by *Anabaena flos-aquae*, and capable of reducing friction (drag) in turbulent flow, have a molecular weight estimated to be about 100,000 (417).

Membranes

Plasmalemma. Surrounding the protoplast and internal to the cell wall is a plasma membrane or plasmalemma, demonstrable at the light microscope level, albeit with difficulty, by plasmolysis (137, 250). This boundary (Fig. 1) is variously estimated as 70 Å (616) up to 100 to 150 Å (200) thick. The plasmalemma is apparently not the sole permeability barrier

TABLE 3. *Composition of putatively extracellular mucilaginous polysaccharides from various blue-green algae*

Alga	Mode of extraction	Monomers												Reference
		Glucose	Mannose	Galactose	Xylose	Fucose	Ribose	Arabinose	Rhamnose	"Uronic acids"	Mannuronic acid	Glucuronic acid	Unknown	
Rivularia	100 C, H_2O	+						+		+?				623
Calothrix	100 C, H_2O		+?	+						+?				623
Phormidium tenue	100 C, H_2O	+	+?	+?					+		+			624
Nostoc	100 C, H_2O	+		20–	25%				10%	30%			+	415
Anabaena flos-aquae	Ethanol precipitation	67%		30%	30%		2.3%					0.8%		553
Anabaena cylindrica (Fogg strain)	100 C, 4% NaOH	31%	0	6%	25%			6%	6%			25%		68
Anabaena cylindrica (Wolk strain)	Centrifugation, ethanol wash	47%[a]	25%	6%	21%	trace		0	0			0		192

[a] These figures refer to the polysaccharides; 5 ± 1% amino compounds and ca. 7% ash were also found.

in algal cells, since protoplasts of *A. nidulans* were found to take up nucleic acid precursors more rapidly than do intact cells (633). Instances of apparent fusion of photosynthetic lamellae to the plasmalemma have been reported (11, 616, 681) but may have arisen as artifacts of fixation and sectioning. However, following degeneration of lamellae in *O. rubescens*, renewed formation of lamellae originates in invaginations from the plasmalemma. These in turn develop secondary invaginations which grow and then disperse as small vesicles. The vesicles enlarge into photosynthetic lamellae (438). Structures of appearance similar to the invaginations mentioned have been likened to mesosomes (204, 629).

Photosynthetic lamellae (thylakoids). Although detectable with the light microscope (292), the photosynthetic lamellae of the blue-green algae were seen first with the electron microscope, initially in shadowed preparations (108) and later in thin sections (572, 573).

The lamellae are closed discs (332, 438, 654) termed thylakoids (541; Fig. 1). The appearance of the lamellae, when adjacent membranes are appressed, varies with the fixative employed. Following permanganate fixation, the appearance of a double membrane, as seen in section, is of three parallel lines of thickness 20, 40, and 20 Å, between which are spaces of 30 to 35 Å (506, 616), whereas following osmic acid fixation such a length appears as two parallel lines, each 35 ± 5 Å (506) to 65 ± 5 Å (616) thick, separated by a space of about 50 Å (cf. also 654).

On occasion, reticulate configurations of lamellae are seen (487, 541; cf. also 485). Although most often seen closely appressed, the thylakoid discs can swell greatly (225, 654, 806), a condition apparently correlating with growth at high light intensity (225, 806). In this case, the "vacuolar space" within the disc is aqueous (438). The plane of the membranes can be parallel or orthogonal to the cell surface (572). Although lamellae usually appear to be both numerous and discrete within a cell, instances are known in which only a single peripheral lamella is found (43), and in which a single thylakoid spirals around the centroplasm (337; cf. also 485).

Jost (438) has presented preliminary evidence that the outer face of the lamellae consists of 50 to 70 Å subunits; that 100 to 200 Å particles, relatively thickly packed, are present on the inner face of the membrane; and that these are separated by an "unstructured" membrane. In contrast, Fuhs (256) has maintained that the membranes are comprised of spherical subunits. It would appear that the detailed substructure of the membranes merits much further investigation.

All, or almost all, of the cellular chlorophyll, and much or all of the carotenoids, are localized in the lamellae (11, 693), which may be isolated by differential centrifugation (693, 703). Schmitz (677) has presented a detailed chemical analysis of thylakoids from *Oscillatoria chalybea*, including an amino acid analysis of their protein. Since chlorophyll accounted for 2.2% of the dry weight of intact

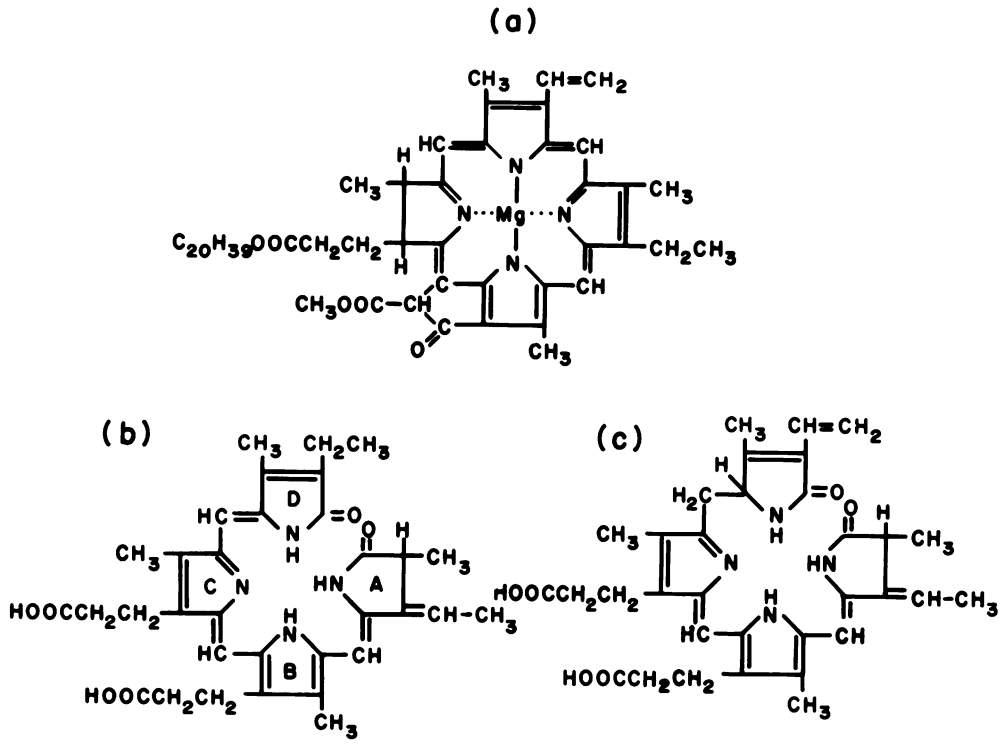

FIG. 2. *Tetrapyrrole pigments of blue-green algae. (a) Chlorophyll a, (b) phycocyanobilin, and (c) phycoerythrobilin.*

cells and for 8.5% of the dry weight of isolated thylakoids, the thylakoids accounted for about 26% of the dry weight of the intact cells (cf. also 754).

Thornber (761) solubilized a chlorophyll *a*-protein complex from *Phormidium luridum* with sodium dodecyl sulfate. The complex contains 70% of the chlorophyll *a* of the organism, is homogeneous upon gel electrophoresis and ultrafiltration, and contains four subunits (mol wt ca. 35,000; complex mol wt ca. 160,000). Per subunit there are five chlorophyll molecules plus traces of β-carotene and 4-keto-β-carotene. It appears that one-fifth of the complexes contain P700; a quinone is also present (175). Ogawa et al. (597), having disrupted lamellae from *Anabaena variabilis* with Triton X-100, found a dense particle containing P700 and a less dense particle with myxoxanthophyll. Whether the latter particle is related to photosystem II (597) is unclear, but the presence of P700 in complexes prepared by the two groups of workers indicates the association of those complexes with photosystem I.

Pigments, lipids, and elements of electron transport chains. The only chlorophyll found in blue-green algae is chlorophyll *a* (e.g., 544, 556, 691, 692; Fig. 2). It has been confirmed that the chlorophyll from *Phormidium luridum* contains phytol (728). In vivo, the absorption peak is shifted to a wavelength about 13 nm higher than the absorption peak in methanol (209, 703). Representative values of chlorophyll as percent of algal (dry weight) are 2.2 (677) and 0.2 to 1.0 (741).

Tabulations of the quantities of individual carotenoids found in a large variety of blue-green algae are presented in the papers of Stransky and Hager (741) and Hertzberg et al. (375). Suffice it here to say that β-carotene (i), echinenone (ii), myxoxanthophyll (xi), and sometimes zeaxanthin (viii) are most frequently the major carotenoids present, although in exceptional cases canthaxanthin (iii), caloxanthin (ix), nostoxanthin (x), oscillaxanthin (xii), and a glycoside (xiii) have been found to account for 10% or more of the total carotenoid present. The structures of the carotenoids are as follows.

(i) β-Carotene (Fig. 3i) is the only carotene

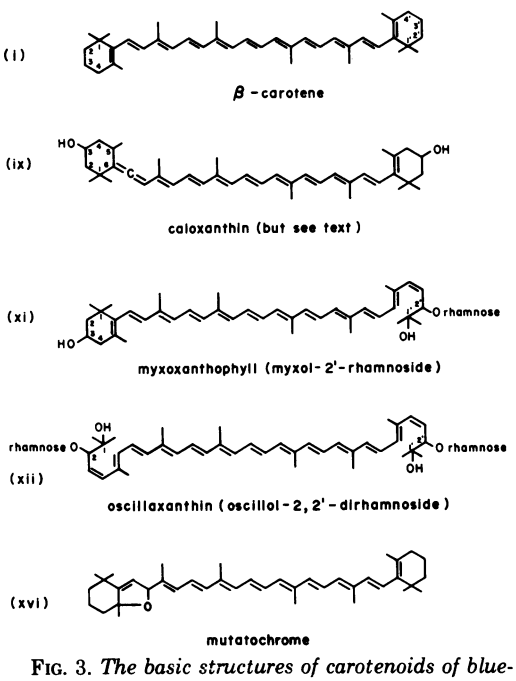

FIG. 3. *The basic structures of carotenoids of blue-green algae.*

which has been found in blue-green algae (e.g., 120, 320, 363, 447, 479, 763).

(ii) Echinenone (myxoxanthin; aphanin; 4-keto-β-carotene), "myxoxanthin" (363), and "aphanin" (763, 764) have been shown to be identical to 4-keto-β-carotene ("echinenone") (319, 321, 370).

(iii) Canthaxanthin (aphanacin; 4,4'-diketo-β-carotene; reference 370).

(iv) 4-Keto-4'-hydroxy-β-carotene (741).

(v) 4-Keto-3'-hydroxy-β-carotene (369).

(vi) Cryptoxanthin (3-hydroxy-β-carotene; reference 741).

(vii) Isocryptoxanthin (4-hydroxy-β-carotene; reference 361a).

(viii) Zeaxanthin (3,3'-dihydroxy-β-carotene). Originally identified as lutein ("leaf xanthophyll"), an intensely orange compound in extracts of *O. rubescens* was subsequently shown to be zeaxanthin (369, 447), and the presence of zeaxanthin and absence of lutein have been confirmed for other blue-green algae (320, 741).

(ix) Caloxanthin, as also (x), was first observed in *A. nidulans* (379, 741). The structure 3,3' - dihydroxy - 5 - hydro - 7 - dehydro - β - carotene (Fig. 3ix) was assigned by Stransky and Hager (741). The validity of this structure, however, has been questioned (375).

(x) Nostoxanthin (3,3'-dihydroxy-5,5'-dihydro-7,7'-didehydro-β-carotene) (see ix).

(xi) Myxoxanthophyll (1',2'-dihydro-3',4'-didehydro-3,1'-dihydroxy-γ-carotene≡"myxol," with rhamnose or, as a minor compound, hexose in glycosidic linkage at the 2' position; Fig. 3xi). Myxoxanthophyll, a major xanthophyll in most blue-green algae examined, has not been detected in other members of this group (375). Its structure was established by Hertzberg and Jensen (372).

(xii) Oscillaxanthin (1,1'-dihydroxy-2,2'-di-β - L - rhamnosyl - 1,2,1',2' - tetrahydro-3,4,3',4' - tetradehydrolycopin≡2,2'-dirhamnosyl - "oscillol"; Fig. 3 xii; reference 373).

(xiii) Myxol-2'-*O*-methyl-methylpentoside, as also xiv and xv, was isolated from *O. limosa* and assigned this structure by Francis et al. (238).

(xiv) Oscillol-2,2'-di-(*O*-methyl-methylpentoside) (see xiii).

(xv) 4-Keto-myxol-2'-methylpentoside (see xiii).

(xvi) Mutatochrome (flavacin; Fig. 3 xvi; reference 371).

(xvii) Aphanizophyll has spectral properties very similar to those of myxoxanthophyll. Nonetheless, the two pigments are not identical (370). Aphanizophyll may be 4-hydroxymyxoxanthophyll (374).

(xviii) Unknown carotenoids have been found in trace amounts in several blue-green algae (361a, 741).

The principal water-soluble pigments of blue-green algae are discussed below, under "phycobilisomes and biliprotein pigments."

Mono- and digalactosyl diglyceride, phosphatidyl glycerol, and sulfoquinovosyl diglyceride (Fig. 4), the four principal fatty acid-containing lipids found in chloroplasts, are also present in blue-green algae. Lecithin, phosphatidyl ethanolamine, and phosphatidyl inositol have not been found in these algae (567). Tabulations of the abundance of different fatty acids, principally C_{14}, C_{16}, and C_{18}, in a variety of blue-green algae may be found in a number of publications (399, 452, 567, 620).

The absence of α-linolenic acid (18:3 [3, 6, 9]) from *A. nidulans* and certain other blue-green algae (398, 452, 453, 567, 620, 729) shows that, although α-linolenic acid is common to eukaryotic photosynthetic plants, it cannot be a requirement for the photosynthetic production of oxygen. However, α-linolenic and (or) γ-linolenic acid (18:3 [6, 9, 12]) is present in other blue-green algae (452, 453, 512, 567, 568,

620, 729). The absence of α-linolenic acid is not restricted to unicellular blue-green algae: *Hapalosiphon laminosus*, which has a branched, filamentous habit, also lacks fatty acids with three double bonds (399, 568). Branched-chain fatty acids are almost completely absent from blue-green algae (620). Capric acid (10:0), elsewhere rare, can comprise as much as 50% of the fatty acids of *Trichodesmium* (620). (Distinctive lipids of heterocysts are discussed below.)

C_{15}-C_{19} hydrocarbons are found in blue-green algae (818), with n-C_{17} often predominating (295, 341), but with C_{19} constituting 98 to 100% of the hydrocarbons in three marine strains (818). Branched alkanes, principally 7- and 8-methyl heptadecane, have been detected in extracts of *Nostoc* (342).

Sterols have not been definitively demonstrated in blue-green algae (120, 511); where traces of sterols were detected (557, 648, 727), no adequate proof was presented that eukaryotic contaminants were wholly absent from the cultures extracted.

Elements of electron transport chains and other pigments are discussed here because they may be (but are not in each case necessarily) structurally or functionally associated with membranes.

The quinones of blue-green algae (see Fig. 5) include plastoquinones (PQ) A, also called PQ 9 (5, 100; see also 206, 510), B, and $C_{1\text{-}6}$ (742); the naphthoquinone, vitamin K_1 (also called phylloquinone), and (to date, found only in *A. nidulans*) a monohydroxy analog of vitamin K_1 (5, 115, 510, 742; see also 206); and membrane-bound α-tocopherolquinone (116). A tabulation of the amounts of PQ A, vitamin K_1, and α-tocopherolquinone in five blue-green algae has been presented by Carr et al. (115), who did not detect ubiquinone in any of the algae.

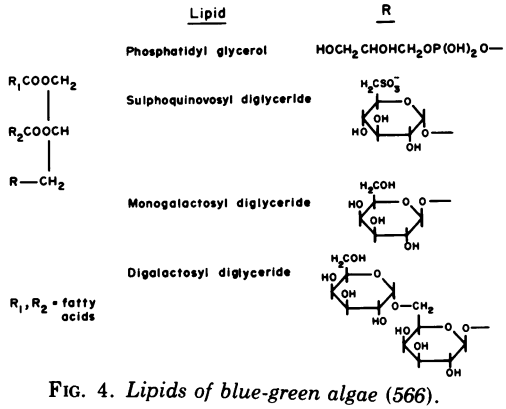

FIG. 4. *Lipids of blue-green algae (566).*

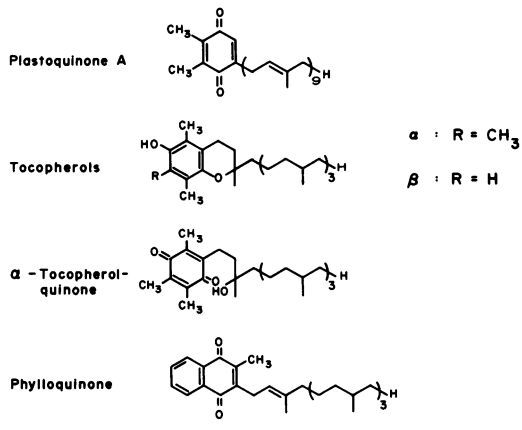

FIG. 5. *Quinones and tocopherols of blue-green algae (761a). Plastoquinones B and C are similar to plastoquinone A, and have the side chain hydroxylated. In plastoquinone B, the hydroxyl group in the side chain is acylated.*

Both α- and β-tocopherol are present in *A. variabilis*; neither is found in *A. nidulans*. Of the two, only α-tocopherol is found in *Nostoc muscorum* and *Fremyella diplosiphon*, and from <0.2 to 1.5 μg of α-tocopherol is found per g (dry weight) in several other blue-green algae (115, 169, 366, 636). Incorporation of label from tyrosine and methionine into quinones and tocopherols of *A. variabilis* has been demonstrated (79).

Cytochromes solubilized from blue-green algae by sonic treatment are briefly summarized in Table 4. These cytochromes are described extensively in a series of papers by Holton and Myers (400–402). A *c*-type cytochrome was purified from *Synechococcus*, and its amino acid composition was determined (162).

In addition to cytochromes solubilized by sonic treatment, *A. variabilis* contains two cytochromes, absorbing at 557 and 562 nm, which remained tightly membrane-bound (596 and cf. 62, 744). Diphenylamine markedly increases the cellular content of the 554- and 562-nm cytochromes (596).

After initial work with *A. nidulans* and other blue-green algae (71, 400), ferredoxin was crystallized from *Nostoc* (549; cf. also 28). Extensively purified ferredoxin from *A. nidulans* was characterized (835) as mol wt about 11,000 with two iron atoms and one labile sulfur atom per molecule (cf. also 212, 716, 744). Its amino acid composition has been determined (162, 835).

Smillie (716) found that extracts of *A. nidu-*

TABLE 4. *Cytochromes solubilized from blue-green algae*

Absorption bands reduced (nm)				Potential (E_o', V)	Comment	Reference
No.	α	β	Soret			
i	553	521	416	0.30	*c*-Type from *Tolypothrix tenuis*	448; and see 162
	554			0.35 ± 0.01	From *Anacystis nidulans*	400; and see 596, 716, 744
ii	549			−0.26 ± 0.02	*c*-Type; $\frac{\text{Chlorophyll}}{\text{(ii)}} = \frac{220}{1}$ Ferredoxin 0.86	400; and see 596, 716
iii	552				(iii)/(ii) ~ 1:100	400; and see 596

lans contain, in addition to ferredoxin, a flavoprotein—which he called phytoflavin—capable of efficiently mediating photosynthetic reduction of oxidized nicotinamide adenine dinucleotide phosphate (NADP), despite the fact (81) that its redox potential is greater than that of NADP. Phytoflavin lacks iron (716); its role may be to replace ferredoxin under conditions of iron deficiency (81). Ferredoxin-NADP reductase from *A. variabilis* is also a flavoprotein (744). An unidentified flavoprotein from *Synechococcus* has been purified, and its amino acid composition was determined (162).

A copper-containing protein capable of acting as a redox reagent was purified from *A. variabilis* by Lightbody and Krogmann (515) and was called "plastocyanin," the name given to similar proteins from photosynthetic tissues of other plants (see also 62).

From 0.05 to 0.1% of the dry weight of *A. nidulans* is a tetrahydrobiopterin glucoside tentatively identified as having a dehydrated side chain to which glucose is attached by an α-linkage (236, 530). The biochemical origin of the side chain has been studied (529). However, whether precisely this compound occurs and is the sole pteridine compound in *A. nidulans* is presently controversial (839). Pteridines were also found in members of the *Nostocaceae* (236).

A heat-stable water-soluble factor, apparently the same as one found in *P. luridum* and capable of stimulating photosynthetic phosphorylation of adenosine diphosphate (ADP), was isolated from spinach and found to be similar in spectral properties to an aromatic pteridine (72; cf. also 277, 530, 531).

Dangeard (166, 167) observed a zone of growth, or perhaps accumulation, of *Phormidium* and *Lyngbya* at 720 to 730 nm, whereas Nultsch and Richter (588) found a small peak in the action spectrum of $^{14}CO_2$ fixation at 719 nm. These phenomena are not understood.

A pigment capable of photooxidizing uric acid in vitro, and having an absorption maximum at 730 nm in 50% ethanol, was isolated from *A. nidulans* (33). This pigment is probably identical or closely related to a pigment purified from *Synechococcus cedrorum* (286), and is probably responsible for mediating the photooxidation (most effectively at 750 nm) of uric acid, imidazole, etc. by *A. nidulans* (33; cf. also 326, 327). Whether a similar pigment is involved in the slow, bleached growth of *A. quadruplicatum* on uric acid is unknown (40).

Gas vacuoles (pseudovacuoles). The ability of certain blue-green algae to float accounts probably for their biological success, and certainly for much of their contribution to air- and water-pollution problems (233). Early observations, recently reviewed (788; cf. also 226, 250), showed that, when suspensions of these algae are subjected to a sudden pulse of hydrostatic pressure, the algae can no longer float. At the same time, certain reddish vacuoles of low refractive index disappear. The principal finding that led Klebahn (457, 458) to conclude that the vacuoles are filled with a gas was that the total volume of algal suspension decreased upon disappearance of the vacuoles, and the change in algal buoyant density was consistent with substitution of liquid for gas in the vacuole volume. The interpretation that the contents are gaseous was tested directly by Jost and Matile (441), who made freeze-etch micrographs of *O. rubescens* frozen to −120 C, a temperature at which no water would sublimate. The vacuoles were empty, proving that they had contained a gas. Walsby (787) has analyzed carefully the pressure relationships involved in gas-vacuole rupture, and has shown

how the presence of gas vacuoles may be utilized to determine the turgor pressure of prokaryotic cells.

Fogg's prediction (226) that by diffusive interchange the content of the vacuoles would approach the gas mixture present in the aqueous milieu was definitively proven by Walsby (786), who showed that the membranes are quite permeable to nitrogen, oxygen, and argon.

Gas vacuoles of blue-green algae consist of packed arrays of cylindrical vesicles, 0.2 to 1 μm long and 70 to 75 nm in diameter, with conical ends. The vesicle boundaries—or membranes—, preserved after fixation with OsO_4 but not $KMnO_4$, are much thinner than a "unit membrane," and have a beaded substructure (83). The vesicles ("Hohlspindeln") are constituted of ribs, spaced about 40 Å apart, which in turn consist of closely appressed units of size 2.8 by 3.0 by 4.2 nm (438, 439). The ribs wind helically (145, 439), nearly perpendicular to the long axis of the vesicle. When the formation of gas vacuoles is induced in *N. muscorum* by transferring the cells to distilled water, the young vesicles are biconical, leading to the suggestion that new elements may be added midway along the length of the vesicles (784). However, the mechanism by which water can be excluded from a volume in the interior of a cell remains unknown. The kinetics of reformation in vivo of experimentally collapsed vacuoles have been followed (508). Of considerable interest is the finding that some reformation of vesicles appear possible in vitro (509).

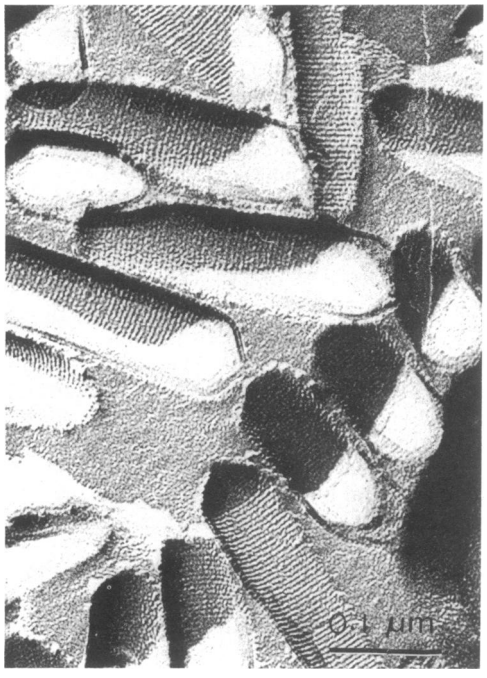

FIG. 6. *Electron micrograph of a frozen-etched preparation of isolated, highly purified, intact gas vesicles. The ribs comprising the vesicles are visible, and the protein monomers comprising the ribs can be discerned. Courtesy of D. D. Jones and M. Jost (431); with permission.* ×*149,000.*

Molisch (552) was the first to observe gas vacuoles expressed from cells; he found them to consist of a great number of smaller bodies. These can retain their in vivo shape and structure (790). Jones and Jost purified gas vesicles by osmotic rupture of cells and flotation (431; cf. also 101, 789; Fig. 6). The vesicles were shown to consist solely of protein and to account for 3.6% of the total cellular protein (431). The only N-terminal amino acid is alanine, and gel electrophoresis indicates the presence of only a single protein species, of mol wt 14,000 (432). This mass is close to the mass of an ellipsoidal protein having the dimensions found (439) for the morphological subunit of the gas vacuoles (cf. also 440). Fifty-two percent of the amino acids are nonpolar (Gly, Ala, Val, Leu, Ileu). Gas vacuole production, and recovery during isolation, could be followed by monitoring light-scattering eliminated by pressurization (431; cf. also 787). Exposure to the vapors of various organic solvents, e.g., chloroform, ethanol, and ether, results in collapse of the gas vesicles (431). Changes in "global" properties of isolated vesicles can be followed by electron paramagnetic resonance and by fluorescence, once the vesicles are reacted with appropriate "labels" (430).

The functions of gas-vacuole formation are as yet not wholly resolved. Gas vacuoles (e.g., those largely encircling the photosynthetic apparatus of *Trichodesmium erythraeum* [38]) may serve to scatter, and thereby to prevent absorption of, light when it is present at too high an intensity (cf., e.g., 785). Since the vesicles are often induced by ionic deficiency (e.g., 784) and may take up as much as 60 to 70% of the cell volume (38; and cf. 724), Jost (unpublished data) suggested that they may be a means for concentrating ions within cells by decreasing the intracellular solution volume. By determining buoyancy, gas vacuoles can regulate the light intensity, and other environmental conditions, to which algae are exposed (787, 788).

Other Intracellular Components

DNA. The deoxyribonucleic acid (DNA) of blue-green algal cells has been visualized by

the Feulgen reaction (88, 121, 180, 333), by acridine orange (837), Giemsa (121, 253), and other stains, and in the living cell by dark-phase-contrast microscopy (121). The position of the DNA, largely central but partially peripheral in the cells, has been confirmed by deoxyribonuclease (DNAse) treatment (188) and by ^{3}H-thymidine autoradiography in conjunction with electron microscopy (499). At the light microscope level, the appearance of the DNA is of many little blobs (837). In part, this appearance surely is due to distortion of the shape of the nuclear material by spatial constraints imposed by photosynthetic lamellae (412); some authors were unable to find more than one disjoint mass of nuclear material per cell (121). On the other hand, Fuhs (253, confirmed by 333) asserted that there are one, two, four, or eight "genomes" per cell, increasing in from the end of an *O. amoena* filament. He has suggested that many large-celled blue-green algae contain multiple copies of their genome per cell (257). Consistent with this view point are the observations that hair cells of *Calothrix braunii* appear to contain about one-fifth and two-fifths as much DNA as actively growing vegetative cells, according to quantitative fluorescent microscopy (776a), and that the average amount of DNA per cell of *A. variabilis* can vary 7.5-fold as a function of growth rate (804). Whereas Kellenberger fixation gives a picture of randomly oriented, 25 Å fibrils predominating within the centroplasm (654; and cf. Fig. 1), definite orientation of these fibrils is occasionally observed (500).

Blue-green algal cells lack a nuclear envelope (573). Glutaraldehyde fixation has failed to reveal any (microtubular) mitotic apparatus (201). Histones are absent (534; cf. also 171). In these ways, the blue-green algae reveal in part their prokaryotic nature (730).

Recent estimates are that DNA ranges from about 0.43 to 1.7% of the dry weight in blue-green algae (cf. 158 and 689 for tabulations), although much lower figures have been given (213). The amount of DNA per cell ranges from 0.6×10^{-14} to 10×10^{-14}g (29, 158, 192, 804). A variation of guanosine plus cytidine content from 39 to 51% was observed in filamentous blue-green algae and from 35 to 71% in the *Chroococcales*, and DNA densities vary correspondingly (203, 729; cf. also 70, 158, 213, 476, 521, 689). The presence of 6-methylaminopurine and 5-methylcytosine in DNA from *Plectonema boryanum* has been reported (450).

The isolation of deoxyribonucleoprotein (DNA-ribonucleic acid [RNA]-protein = 88:4:8) from *A. cylindrica* (534) may initiate biochemical study of the "chromosome" of blue-green algae (cf. 740).

Ribosomes and RNA. Observations with the light microscope showed that RNA is diffusely distributed in the centroplasm (88, 188), perhaps in part bound to granular inclusions (188). A concentration of ribosomes in the region of the centroplasm was confirmed by electron microscopy. It was shown in addition, that ribosomes are found throughout the cells, including between photosynthetic lamellae (255, 654). Jost (438) described series of up to 15 110-Å particles, presumably ribosomes, linked by a fine thread; these particles appeared to have a central cavity (compare 100- to 150-Å particles; references 204, 654).

The sedimentation coefficient ($s_{20,w}$) of ribosomes from *A. cylindrica* is 71.6 and from *A. nidulans* is 69.0 (755). The ribosomes of blue-green algae dissociate to 50*s* and 30*s* subunits (157; and cf. 659), as do bacterial ribosomes. Ribosomes from *A. variabilis* and their subunits are stable in 1 mM phosphate buffer, pH 7, containing 0.1 M KCl (157). RNA extracted from four genera of blue-green algae and analyzed by gel electrophoreis was principally of mol wt 0.55×10^6 to 0.56×10^6 (16*s*) and 1.06×10^6 to 1.07×10^6 (23*s*; 416, 518, 519).

Base compositions of RNA from blue-green algae have been reported (69, 151, 213, 689). 2-*O*-methyl ribose cytosine has been tentatively identified in *A. nidulans* RNA (69). Biswas and Myers (69) estimated that RNA accounts for 0.37 to 0.50% of the dry weight of *A. nidulans*, whereas Serenkov (689) gave estimates of 0.78 and 3.40% for two filamentous species.

Glycogen granules (α-granules). Granules found between the photosynthetic lamellae of many species of blue-green algae can appear, depending in part on sectioning, as 250 Å granules with a special affinity for lead hydroxide (654), 300 Å "α-granules" (616), crystals (541), rods, etc. (309; see Fig. 7). Similar structures in *O. rubescens* are up to 3,000 Å long and consist of 70-Å discs with globular subunits and a central pore (438; see Fig. 7, right inset).

That these granules are composed principally of glycogen, long known as a major product of photosynthesis by blue-green algae on the basis of iodine staining (250; cf. 124) and chemical analysis (see below), was proven by the following evidence. These granules as seen with the electron microscope, and periodic acid-Schiff (PAS)-positive material as detected in the light microscope, are located primarily at the periphery of the cell in the "chromatoplasm," and both are almost com-

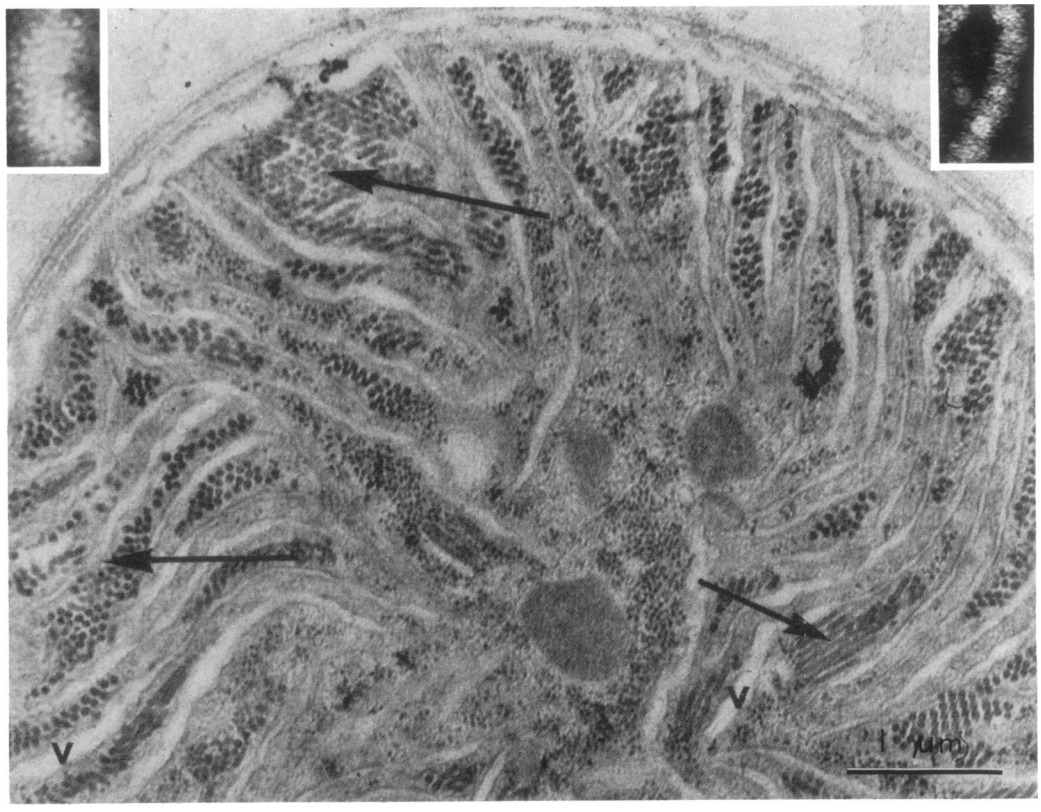

FIG. 7. *Glycogen granules (arrows) within a cell of Oscillatoria chalybia. Courtesy of R. M. Giesy (309); with permission. ×20,300. Left inset: Glycogen granule of Nostoc muscorum. Courtesy of L. Chao (124); with permission. ×400,000. Right inset: Glycogen granule of O. rubescens. Courtesy of M. Jost (438); with permission. ×192,000.*

pletely absent after 96 h of darkness and are largely absent following growth in the presence of excess nitrogen (as urea) (309). In addition, the granules are—specifically—dissolved by the action of diastase (255, 309), as is PAS-positive material also (309).

An amylopectin-like fraction from *Oscillatoria* sp. appeared to be a predominately 1:4-linked polyglucoside with an average of 23 to 26 glucose units per highly branched chain (415). Chao and Bowen (124) demonstrated directly the equivalence of the granules described above with just such a polysaccharide, by isolating 310- by 650-Å granules (Fig. 7, left inset) from *Nostoc muscorum* and by showing that they contain highly branched polyglucosyl units with short external chain lengths.

One-quarter of the polysaccharide of *Tolypothrix tenuis* (773) is composed of a series of glucofructan oligosaccharides, fructofuranosyl-(3 → 4)$_n$-fructofuranosyl-(2 → 1)-α-glycopyranoside (774), the cellular localization of which is unknown.

Cyanophycin granules (structured granules). Refractile granules called cyanophycin granules, present in vegetative cells and especially prominent in spores (akinetes) of blue-green algae, were characterized as soluble in dilute acid (614) and as showing certain staining reactions indicative of the presence of protein (e.g., Sakaguchi reaction for arginine: reference 229; and cf. 45) but not other such reactions (e.g., Millon's reagent, boiling concentrated nitric acid, for aromatic amino acids: reference 362).

A correspondence between cyanophycin granules and inclusions seen in the electron microscope and labeled "structured granules" (188) appeared probable because of the prominence of structured granules within spores (140, 486, 547, 660, 809). The correspondence was proven by the demonstration (488) that granules isolated by Simon (704) have the ultrastructural aspect of structured granules, and solubility and staining properties characteristic of cyanophycin granules.

The ultrastructure of cyanophycin granules is observed after fixation with OsO_4 (cf. Fig. 1); the granules appear to be dissolved by treatment with $KMnO_4$ (486, 500, 502, 505, 506). The granules have an irregular spheroidal form up to about 0.5 to 1.0 μm in diameter in vegetative cells and up to about 1.7 μm in diameter in spores. The average interval between their layers, as seen following fixation with OsO_4, is 150–160 Å (252, 438).

The granules isolated from nitrate-grown vegetative cells of *A. cylindrica*, where they account for up to 10% of the dry weight, consist of high molecular weight (25,000–100,000 d) copolymers of aspartic acid and arginine (1:1, mol/mol). This extremely unusual composition explains why the granules stain with certain protein-specific reagents but not with others, and reveals them as particularly well suited to serve as a nitrogen reserve (704, 705). The observation (421) that formation of these granules is stimulated by chloramphenicol suggests that the protein of cyanophycin granules is not made by ribosomes. Dense granules which form in rifamycin-treated *Anacystis montana* (657) are probably cyanophycin granules, which further suggests that the protein of these granules is not coded for by messenger RNA (cf. "nucleic acid metabolism and protein synthesis").

Phosphate granules (volutin, metachromatin). Large metachromatic granules generally located in or adjacent to the centroplasm of blue-green algae were identified as phosphate bodies on the basis of staining reactions and solubility properties (88, 188, 197–199). After culture in the absence of phosphate, few filaments have these granules, whereas, after the same period in the presence of phosphate, such granules are abundant (750, 765).

Electron-dense bodies up to ca. 0.5 μm in diameter and which tend to evaporate at high electron-beam intensities (Fig. 8) were taken (252, 333) to be phosphate bodies on the basis of comparable appearance and behavior of phosphate bodies from bacteria. This identification was made conclusive by Jensen (424; cf. also 425) on the basis of examination of adjacent thick and thin sections, acid extraction, and staining reactions.

Considered to consist of metaphosphate (e.g., the cyclic compounds trimetaphosphate and [or] tetrametaphosphate) by certain authors (88, 333), these granules were taken by other authors to be comprised of long, open-chain polyphosphates on the basis of acid solubility (188, 451) and on the basis of meta-

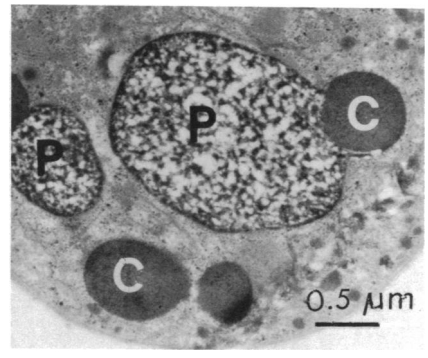

FIG. 8. *Phosphate granules (P) and cyanophycin granules (C) in a cell of Anabaena cylindrica. Courtesy of N. J. Lang (488); with permission. ×17,250.*

chromasia coupled with staining with lead nitrate-ammonium sulfide (197–199, 451, 750). Some authors have thought that these granules contain, in addition, nucleic acid (189, 250, 750).

All of these viewpoints can draw support from chemical studies. Niemeyer and Richter (570) found that ^{32}P rapidly labels polyphosphate and metaphosphate, especially trimetaphosphate, in *A. nidulans*. These could be separated from DNA and RNA, and could be fractionated by thin-layer chromatography. In addition, preliminary evidence has been presented that RNA and polyphosphate are complexed together in extracts of *Anabaena variabilis*, and may, therefore, be associated in vivo (151).

Poly-β-hydroxybutyrate granules. Poly-β-hydroxybutyrate is present in cells of *Chlorogloea fritschii* (113), apparently as granules which are slightly electron dense and are surrounded by a membrane ca. 3 nm thick (428; Fig. 9).

Polyhedral bodies. Structures termed "polyhedral bodies" by Pankratz and Bowen (616) and previously seen by other authors (333, 505, 506) have a polygonal outline, up to 0.5 μm in width. The validity of the statement (808), based on observation of serial thin sections, that polyhedral bodies are only about 0.1-μm thick, is doubtful since long, narrow cross-sections are not seen. The structures are homogeneously gray following OsO_4 fixation, whereas $KMnO_4$ fixation shows them to have a fibrillate interior and a bounding "membrane" (616). The ultrastructure of these inclusions is thought to include a periodic array of equal-sized subunits, revealed by negative staining (283; Fig. 10). Polyhedral bodies, although consistently present in the centroplasm of vege-

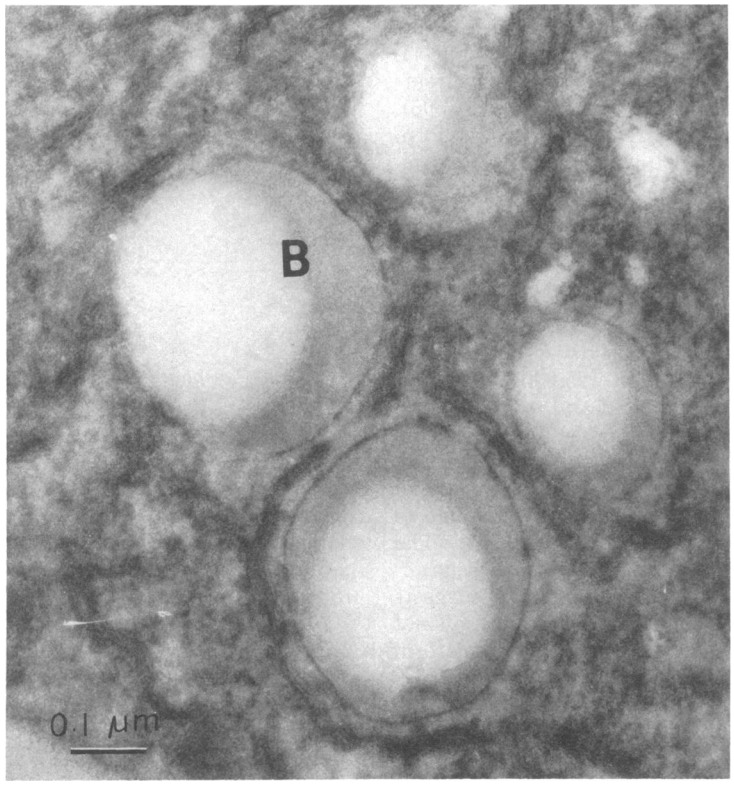

FIG. 9. *Granules (B) identified as containing poly-β-hydroxybutyric acid, within a cell of Chlorogloea fritschii. Courtesy of T. E. Jensen (428); with permission.* ×97,500.

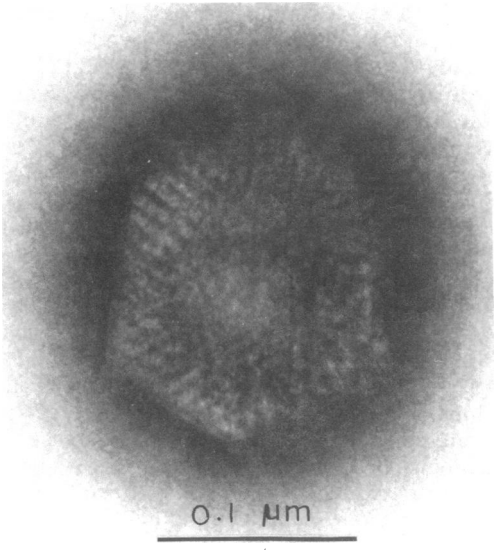

FIG. 10. *Polyhedral body from Anacystis nidulans, negatively stained with a 2% solution of sodium phosphotungstate. Courtesy of E. Gantt (283); with permission.* ×260,000.

tative cells, have not been identified chemically. Whether they correspond to inclusions observed by light microscopy (e.g., 188, 250, 765) is unknown (see also "sulfur metabolism" and Table 11).

Lipid deposits. Lipid deposits, although not a major feature of the cytology of blue-green algae, have been repeatedly reported (e.g., 250, 290, 291, 614). The ultrastructural aspect of these inclusions may possibly be the small, very osmiophilic β-granules of Pankratz and Bowen (616; Fig. 1).

Phycobilisomes and biliprotein pigments. Blue-green algae produce oxygen in response to illumination with yellow light with a quantum efficiency approximating the efficiency with which they produce oxygen when illuminated with red light (208, 210). That is, light absorbed by the major blue pigment, phycocyanin, of blue-green algae appears to be about as active as chlorophyll in "photosynthesis." If phycocyanin is photosynthetically active only by virtue of transferring the light energy it absorbs to chlorophyll, then the phycocyanin has to be localized in very close proximity to the

chlorophyll (27). Duysens (193) demonstrated such energy transfer directly: light absorbed by phycocyanin activates fluorescence of chlorophyll. In addition, although phycocyanin is water-soluble, its absorption spectrum is shifted about 10 nm to higher wavelengths in vivo than it is following isolation (209, 436), suggesting that its microenvironment in situ may not be wholly aqueous. Furthermore, when *S. cedrorum* is macerated in a solution of 4 g of dextrin per 10 ml of buffer, most of the phycocyanin remains associated with particles capable of being easily sedimented; the amount of phycocyanin solubilized is much greater at a lower concentration of dextrin (760; cf. also 743). Cohen-Bazire and Lefort-Tran (146) showed that exposure of intact cells of *Gloeocapsa alpicola* to 3% glutaraldehyde results in bonding of 30% of the phycocyanin to photosynthetic lamellae. Fujita and Tsuji (275, 772) were able to isolate, from *A. cylindrica*, a "chromoprotein," an aggregate containing about 2% of the phycocyanin of the alga together with a pigment which may be chlorophyll, that can photocatalyze a transfer of electrons from ascorbate to oxygen (phycocyanin alone cannot). It is unknown if this chromoprotein was initially soluble, or was detached from membranes during isolation. The photovoltaic effect of bileaflet membranes has been said to be affected by the presence of phycocyanin (418). All of these observations are consistent with the idea that there is a labile association between phycocyanin and thylakoids.

Gantt and Conti (282) found a regular array of particles—which they called "phycobilisomes"—on the outer surface of the photosynthetic lamellae of the red alga *Porphyridium cruentum*, and presented evidence that these particles correspond to aggregates of the major red pigment, phycoerythrin, of this alga.

A similar array of structures (Fig. 11) was subsequently found on the photosynthetic lamellae of various blue-green algae (204, 205, 283, 396). In view of the many similarities in the structure, chemistry, and function of the

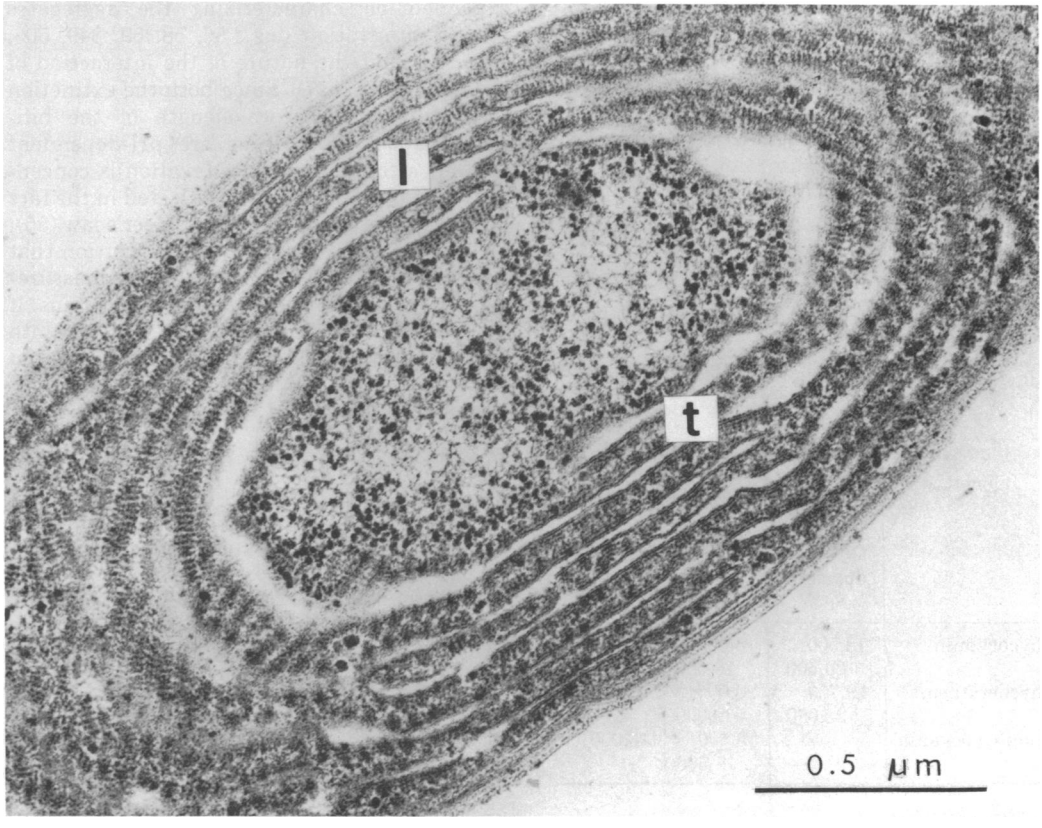

FIG. 11. *Arrays of "phycobilisomes" (l, cut in longitudinal direction; t, cut in transverse direction) on the thylakoids of Synechococcus lividus. Courtesy of M. R. Edwards and E. Gantt (205); with permission.* ×*60,600.*

photosynthetic apparatus of red and blue-green algae (see "origin of chloroplasts"), and in view of all of the above evidence suggesting proximity of phycocyanin to photosynthetic lamellae in blue-green algae, it seems very probable these phycobilisomes of blue-green algae are aggregates of biliproteins.

The best present proposal for the detailed structure of the phycobilisomes of a blue-green alga is that presented by Edwards and Gantt (205) on the basis of work with *Synechococcus lividus*. According to their view, these structures are rods, ca. 350 Å in diameter, consisting of close-packed heptamers of smaller rods, each of which is a stack of dimeric discs. Each disc of a dimer, about 30 to 35 Å thick by about 105 to 125 Å in diameter, might correspond to hexameric assemblages of phycocyanin, of diameter about 120 Å, seen in electron micrographs of negatively stained phycocyanin (56).

The chromophores of C-phycocyanin and phycoerythrin, the major blue and red water-soluble proteinaceous pigments of blue-green algae, are bile pigments, i.e., linear tetrapyrroles (598, 600). The pigments are therefore referred to as phycobiliproteins or simply biliproteins, and in vivo aggregates of biliprotein molecules as phycobilisomes. In vitro, the visible absorption peak of C-phycocyanin is at about 615 to 620 nm; that of C-phycoerythrin is at about 557 to 565 nm; and that of allophycocyanin, a light-blue biliprotein, is at about 650 nm, with a shoulder at about 600 nm (349, 350, 359). Several species of *Phormidium* contain, in addition, a phycoerythrin with two visible absorption peaks, at about 543 and 565 nm (359, 580); the two-peaked form may, however, be derived from C-phycoerythrin (600).

TABLE 5. *Subunit molecular weights of biliproteins isolated from various blue-green algae*

Biliproteins	Molecular wt		
	Nostoc punctiforme, *Anacystis nidulans*, *Anabaena variabilis*, *A. cylindrica*, *Calothrix* sp.[a]	*Synechococcus* and *Aphanocapsa*[b]	*Fremyella diplosiphon*[c]
Phycocyanin	18,500; 20,500	16,000; 20,000	16,300; 17,600
Phycoerythrin	19,700; 22,000	20,000; 22,000	18,300[d]; 20,000[d]
Allophycocyanin		15,500; 17,500	16,000

[a] Reference 591.
[b] Reference 312.
[c] Reference 51.
[d] Ratio—1:1, mole/mole.

Phycocyanin was crystallized from extracts of a blue-green alga first by Svedberg and Katsurai (745), who made use of ammonium sulfate precipitation. Hattori and Fujita (349) separated phycocyanin, phycoerythrin, and allophycocyanin from *Tolypothrix tenuis* by taking fractions precipitating at different concentrations of ammonium sulfate; purified the pigments with calcium phosphate gels (359); and crystallized them individually by using ammonium sulfate (see also 580).

In their pioneering study of phycocyanin, by using the ultracentrifuge, Svedberg and Katsurai (745) showed that in solution the pigment is present in different aggregation states, depending on the pH. Since the publication of their study, a great deal of effort has been expended on characterizing the aggregates present in solution (e.g., 56, 58, 59, 349, 503, 528, 783) and the nature of the interaction of the monomers (527). Since both the extinction coefficient and the wavelength of the biliprotein absorption peaks are pH-dependent and since the degree of aggregation is concentration dependent (560), as reflected in the fact that phycocyanin does not obey Beer's law (55), these studies have pointed to the caution that must be employed in interpreting measurements of light absorption by the biliproteins. If the proteins, in cells, are incorporated into phycobilisomes, the aggregation phenomena in vitro may, at least partially, reflect the aggregation phenomenon in vivo (compare 56 with 205).

One group of workers has produced much evidence that phycocyanin from *Plectonema calothricoides* and other blue-green algae has a monomer molecular weight of about 28,000 or 30,000 (60, 446; and see 258, 560). However, several groups of investigators have now found, by using sodium dodecyl sulfate-polyacrylamide gel electrophoresis, that each of the biliproteins from other blue-green algae is composed of pairs of subunits of molecular weight about 22,000 or less (see Table 5; 51, 312, 589, 591).

Amino acid (60, 64, 150) and end-group (64, 150) analyses have been published for biliproteins of blue-green algae and their subunits. Convincing evidence of protein homogeneity has, however, not been presented in all cases.

Glazer et al. (313; cf. also 51, 54) found no evidence of antigenic relationships between phycocyanin, allophycocyanin, and phycoerythrin of blue-green (or red) algae, whereas pigments of corresponding chromatic character from different blue-green (and red) algae were antigenically related.

The biliprotein subunits are pigmented. If there are one to two chromophores (molecular weight ca. 600) per subunit (51), the biliproteins would contain a weight percent of chromophoric group approximating the estimates (3.6–5.1%) that have been made (92, 163, 165, 600). The light and heavy subunits of *Fremyella* phycoerythrin may have one and two chromophoric groups, respectively (51). Biliproteins account for 14 to 18% of the dry weight of *T. tenuis* (349), about 19% of the dry weight of *A. cylindrica* (144), and up to 24 to 28% of the dry weight of *A. nidulans* (11, 556).

Cleavage of the chromophores, phycocyanobilin (present in phycocyanin and allophycocyanin), and phycoerythrobilin (present in phycoerythrin; 600) from their apoproteins without alteration of the chromophores appears possible with 12 N HCl at 25 C for 30 min or 20 min, respectively (598, 599), with enzymes (702), or by prolonged refluxing with methanol (128, 163, 590). The last-named procedure, in one of its several variations, appears to be the method of choice at present.

Cole, Chapman, and Siegelman (147, 148) determined the structure of phycocyanobilin to be that shown in Fig. 2b, and this structure has been corroborated (661). Crespi, Smith, and Katz (163) proposed a structure differing only in that the hydrogen on the nitrogen of ring A is transposed to the nitrogen of ring C.

A structure presented (127, 160, 661; but cf. 684) for phycoerythrobilin (Fig. 2c) differs from that of phycocyanobilin only around ring D.

Native phycoerythrin and phycocyanin lack metals, although allophycocyanin was reported to have a small (0.66%) ash content (349). Phycocyanobilin may be present in a co-planar ring configuration within the protein (490, 598). Such a configuration could account for the loss of the high absorbancy and fluorescence of the native protein upon denaturation (490). It has been argued (661) that both phycocyanobilin and phycoerythrobilin are linked to the apoprotein by one of the propionic acid side chains and by the nitrogen of ring A.

Studies of bile pigment formation in the blue-green pigmented eukaryote *Cyandium caldarium* (768–771) have not been extended to blue-green algae, with the exception that added protoporphyrin has been shown to increase phycocyanin production by *A. nidulans*, perhaps indirectly (314).

Other inclusions. "Cylindrical bodies" about 130 nm in outside diameter and up to 1 μm long were reported in *Symploca muscorum* (616). Similar structures were observed in *Trichodesmium erythraeum* (38; cf. also 107).

In addition, many unusual membranous, filamentous, crystalline, etc. structures were observed in 1, 2, or 3, of 60 other strains of blue-green algae (426).

Overall Chemical Composition

Analyses of overall cellular composition are summarized in Table 6. The differing compositions for *A. cylindrica* reflect the fact that extracellular mucilage can account for as much as 44% of the dry weight of cultures (C. P. Wolk, unpublished data). For a discussion of the differences in composition of *A. quadruplicatum*, see "chromatic variation." So long as nitrogen is available in abundant and easily assimilable form, and the algae are not produc-

TABLE 6. *Composition of various blue-green algae*

Organism	Percentage of dry wt								
	C	H	N	Ash	P	Protein (N × 6.25)	Carbohydrate	Lipid	Reference
Anabaena cylindrica	48	6.8	10.4	6.5–7	1.8–2	63			144
A. cylindrica (old culture)			6.8			43	25	4	149
Agmenellum quadruplicatum, nitrate-grown	46.64	6.58	9.70	10.7[a]		64	27	9	40
A. quadruplicatum, uric-acid grown	43.58	6.40	2.69			18	74	7	40
Microcoleus vaginatus (old culture)			5.6			35	66	6	149
Spirulina			10.3–11.6	5–7	0.9	64–73	12–17	5–7	141

[a] Reference 621.

ing copious amounts of mucilage, nitrogen accounts for about 10% of cell dry weight.

PHYSIOLOGY

Photosynthetic Light Reactions

Intact cells. Blue-green algae have often been favored for the study of photosynthesis because of the wide spacing of the absorption maxima of their principal pigments, and—for purposes of comparison—because they are the only known oxygen-producing prokaryotes.

The quantum efficiency of oxygen production by light absorbed by phycocyanin approximates the quantum efficiency for chlorophyll-absorbed light. Light absorbed by carotenoids is also utilized, but less efficiently (averaged over the carotenoids, ca. 20% as efficiently; 208–210). In fact, biliprotein-absorbed light can be more active in eliciting oxygen production than is chlorophyll-absorbed light (357; and cf. 607). Moreover, the quantum efficiency of oxygen production by light absorbed by chlorophyll drops rapidly above about 680 nm ("red drop"; 21); and light absorbed by phycocyanin yields fluorescence of chlorophyll *a*—thus directly demonstrating energy transfer from phycocyanin to chlorophyll—with a quantum efficiency greater than that by which chlorophyll fluorescence is excited by chlorophyll-absorbed light (193). The proportionality between the action spectra for fluorescence and for oxygen production led to the suggestion that light absorbed by biliproteins is photosynthetically active only via transfer of excitation energy to chlorophyll (194), whereas the red drop in photosynthetic oxygen production and the existence of "weakly fluorescent chlorophyll *a*" implied that part of the chlorophyll was somehow different, functionally, from the rest (193). (There are many other papers on the phenomenon of fluorescence in blue-green algae [e.g., 136, 168, 307, 315, 316, 618, 619, 766]. Photosynthetic activity of phycoerythrin in a blue-green alga was shown [358] in *Phormidium ectocarpii*, the only detectable biliprotein of which is a two-peaked phycoerythrin [359].)

Synergistic effects of light of different wavelengths in production of oxygen by blue-green algae were first observed in *Phormidium persicinum* (539). This enhancement phenomenon was given more detailed and exhaustive study by Jones and Myers, working with *A. nidulans*: the decrease in the quantum efficiency of oxygen production above about 680 nm could be offset by simultaneous irradiation with light absorbed by biliproteins (435). A related phenomenon was studied in a marine *Anabaena* (73; and cf. 538). Thus, in blue-green algae as in other algal divisions, photosynthesis involves a photosystem ("II") primarily responsible for production of oxygen, and an additional photosystem ("I") which enhances the oxygen production by photosystem II. System II embodies much of the biliprotein pigments, plus—presumably—that chlorophyll *a* rendered fluorescent by light absorbed by the biliproteins more efficiently than by light absorbed by chlorophyll.

Kok (462) found that *Nostoc*, as well as all other chlorophyll *a*-containing plants tested, shows a temporary (about 10 ms), dark-reversible decrease in absorption at about 700 nm, following exposure to a flash of high-intensity light. This peak was interpreted as due to a pigment (P700) not the same as chlorophyll A "in its normal status" (462), present in a ratio P700-chlorophyll *a* of about 1:400 and with a potential, E'_o, of about 0.46 V (464). Bleaching of P700 (in $<3 \times 10^{-4}$ sec) is activated principally by chlorophyll-absorbed light, and also by light absorbed by carotenoids. Regeneration of the pigment, on the other hand (time constant, ≥ 5 ms), is activated by light absorbed by biliproteins and by a small fraction of chlorophyll *a* and is very sensitive to 3-(3,4-dichlorophenyl)-1,1-dimethyl urea (DCMU, an inhibitor of photosynthetic evolution of oxygen; 464). These data suggested that P700 serves as a "trap" for energy assimilated by a photosystem (I) associated primarily with chlorophyll and, under the influence of light absorbed by that photosystem, donates an electron to the primary oxidant of photosynthesis, and is thereby bleached; and that reductants generated by photosystem II by the oxidation of water reduce oxidized P700 in a subsequent dark reaction.

(Other papers concerning P700 include those relating P700 to a light-induced electron paramagnetic resonance signal [463, 795] and attempts to purify P700 [e.g., 595]. Krey and Govindjee [468] found evidence of a trap, fluorescing maximally at 693 nm, for photosystem II of *Anacystis*.)

Thus was found one means of looking, within intact cells, at a component of the electron transport chain of photosynthesis. Other such means were also found. Upon illumination with red light, *A. nidulans* exhibits an increased, blue fluorescence which has the emission (196) and excitation (604) spectra of reduced pyridine nucleotide. Light-stimulated absorption changes attributable to cytochrome oxidation can also be observed (21; see also 464).

Amesz and Duysens (21) found that the action spectra for phosphopyridine nucleotide reduction and cytochrome oxidation by intact cells of *A. nidulans* are proportional, with chlorophyll *a* and phycocyanin being about equally active. Light absorbed by phycocyanin reduces cytochrome, by a DCMU-sensitive system (II), with about sixfold higher efficiency than does light absorbed by chlorophyll *a*.

The general scheme of electron transport in photosynthesis emerging from these studies with intact cells is illustrated in Fig. 12a (21, 195, 378, 464).

X, the primary electron acceptor for NADP photoreduction, has not yet been identified with certainty (277, 381).

Arnon and co-workers (459, 540), however, have proposed a quite different interpretation of electron transport during photosynthesis. According to their concept, rather than have phosphorylation (adenosine triphosphate [ATP] generation) coupled to a single noncyclic pathway of electron flow, systems I and II operate independently with a cyclic electron flow in system I resulting in generation of ATP, and system II, itself embodying two light reactions, resulting in NADP reduction and ATP production (Fig. 12b). Arnon and coworkers have observed that, in vitro, O_2 production accompanying CO_2 fixation is enhanced but NADP reduction is not enhanced when short-wavelength (system II) light and long-wavelength (system I) light are combined (540). To date, none of this work has been done with blue-green algae.

Teichler-Zallen and Hoch (756) have presented evidence that cyclic electron transport occurs in *A. nidulans*, that it is an important circuit for electron flow, and that it is probably coupled with ATP formation. There is also evidence that cytochrome *f* and P700 are not on the same electron transport chain in *P. boryanum* (380).

It remains to be seen whether the parallel (Arnon) or series version of photosynthesis, or perhaps some synthesis of the two incorporating some mechanism for excitation transfer from one photosystem to another, will prove to be correct for blue-green algae.

Cell-free systems. Preparations of *A. variabilis* ground with alumina were found to catalyze a substrate-independent phosphorylation of ADP at a rate of 200 to 500 μmol of P_i per mg of chlorophyll per h; this reaction is dependent on a mediator such as phenazine methosulfate (PMS; 631). All of the photophosphorylating activity of the crude extracts is recoverable in a membranous fraction sedimenting in 1 h at 105,000 × *g* (693). Activity is not lost when almost all phycocyanin is removed (631). Rates as high as 710 μmol of ATP per mg of chlorophyll per h were observed in a similar system, under nitrogen (190; cf. also 71, 743). Plastoquinone A restores activity following isooctane extraction (514). Cyclic photophosphorylation is increased 5- to 10-fold in cell-free preparations made from *A. variabilis* grown in the presence of diphenylamine (562). Light-dependent or light-initiated hydrolyses of ATP may represent a reversal of the photophosphorylation mechanism (514, 631).

Cyclic photophosphorylation was also observed with resuspended, lyophilized *Anacystis* (300) and with a similar suspension which was, in addition, treated with lysozyme (297, 299). In this latter sort of preparation, cyclic photophosphorylation is catalyzed by the natural cofactor, ferredoxin, with rates up to 80 μmol per mg of chlorophyll per h (80). In this reaction, ferredoxin can be replaced by phytoflavin (81).

Cyclic photophosphorylation was observed in lysed protoplasts of *P. luridum*. Washing of membranes with very dilute buffers leads to loss of activity. Activity can be restored by readdition of a soluble protein which is neither cytochrome 554 nor plastocyanin, and may be a coupling factor (62; see also 504). This alga also contains a heat-stable water-soluble factor which stimulates photophosphorylation of ADP (72).

Photosystem I, supplied with electrons from ascorbate and a carrier such as 2,6-dichlorophenol-indophenol (DCPIP; 555), can supply reducing power for many in vitro reductions, e.g., of (i) O_2, (ii) methyl viologen (MV), (iii) "cytochrome reducing substance (CRS)," and (iv) ferredoxin.

a. $H_2O \rightarrow II \rightarrow Q \rightarrow$ cytochrome $\rightarrow P \rightarrow I \rightarrow XH \rightarrow PNH$
b. $H_2O \rightarrow II_b \rightarrow C550 \rightarrow$ cytochrome $\rightarrow$ plastocyanin $\rightarrow II_a \rightarrow Fd \rightarrow PNH$

FIG. 12. *Alternative models for the electron transport chain of photosynthesis, simplified. In the "series" model (a), Q is the quencher for fluorescence of photosystem II, and may be quinone; P may be P700; X is the primary photooxidant of photosystem I; and PN is pyridine nucleotide. In the parallel model (b), photosystem II is visualized to involve two photoreactions, IIa and IIb; Fd is ferredoxin; and C550 is unidentified, but is not a cytochrome. According to this model, photosystem I operates in parallel with photosystem II and is active only in cyclic photophosphorylation. Photophosphorylation coupled to noncyclic electron transport is considered to occur in both (a) and (b).*

(i) Photoreduction of MV was used (340) to observe photosystem-I activity in glutaraldehyde-fixed cells of *A. nidulans*.

(ii) Photoreduction of O_2 to H_2O_2 (the "Mehler reaction") is rather little stimulated by MV, and is not reduced by removal of ferredoxin. This reduction is, however, inhibited by antibodies (presumably against "X") which inhibit reduction of ferredoxin (403). In the presence of cyanide to inhibit catalase, the consumption of O_2 by this reaction is an easily assayable measure of photosystem I activity (555). The Mehler reaction of blue-green algae has been studied. Of five species tested, only *A. flos-aquae* proved to be deficient in catalase (139).

(iii) CRS present in *A. cylindrica* is reduced by photosystem I in the light and subsequently reduces exogenously supplied cytochrome *c* in the dark (267). Since the CRS electron pool is equivalent to about one-fifth of the chlorophyll present (272) and is unaffected by petroleum ether extraction, CRS cannot be cytochrome *f*, plastocyanin, or plastoquinone (269). CRS is tightly bound to photoreactive lamellar fragments prepared by sonic treatment and is heat-stable but apparently of large molecular size (270; cf. also 271). There appears to be a competition between reduced CRS and reduced ascorbate to donate electrons to cytochrome 553. In the presence of DCPIP, tetramethylphenylenediamine (TMPD), or MV, ascorbate is favored (265).

(iv) Ferredoxin reduced by photosystem I can in turn donate electrons to (a) NADP via ferredoxin-NADP reductase (which has been purified from *A. variabilis;* reference 744), (b) substrates of nitrogenase (see "nitrogen fixation"), (c) nitrate and nitrite (see "reduction of nitrate and nitrite"), and probably additional oxidants. In reactions (a) and (b) and in nitrite reduction, ferredoxin can be replaced by phytoflavin (81, 82). Since reaction (a) is reversible, it provides an alternative route for reduction of ferredoxin, by reduced NADP (NADPH). Ferredoxin may also be reduced by dithionite.

Yet another source of electrons for reduction of ferredoxin is hydrogen gas. The in vivo photoreduction of nitrite by H_2 (347) is slow presumably because of ineffective coupling of ferredoxin to the hydrogenase reaction, since NADP photoreduction and hydrogenase-coupled reduction of PMS are much more rapid than ferredoxin-coupled reduction of NADP via hydrogenase. The last-named reaction, in a particulate fraction with hydrogenase and NADP photoreduction activities, is not affected by light (266). Hydrogenase from *A. cylindrica* has been characterized by Fujita and co-workers (266, 273), who could also solubilize the enzyme (273). *Synechococcus* and *Synechocystis* photoreduce CO_2 in an atmosphere of hydrogen, with stoichiometric uptake of hydrogen and CO_2 (245–247; cf. also "reduction of nitrate and nitrite").

Oxygen production by cell-free preparations of a blue-green alga was observed first by Thomas and de Rover (760), using *S. cedrorum* ground with carborundum and suspended in a solution of 4 g of dextrin/10 ml of buffer. Benzoquinone was the Hill reagent. Benzoquinone can also be used as an electron "shuttle" in an in vivo Hill reaction with *Anacystis* (133). Isolation of membranous particles from *A. variabilis* in 20% Ficoll permits Hill reactions with NADP, ferricyanide or trichlorophenol-indophenol as Hill reagents. The Hill reactions are inhibited 50% by 0.6 μM DCMU (743). Sucrose-washed particles containing only a trace of phycocyanin retain a high specific Hill reaction activity, although in the presence of phycocyanin, higher rates were found under light-limited conditions (190, 743). Corresponding particles from *A. nidulans*, prepared with dextran or carbowax, lose Hill reaction activity (with ferricyanide, indophenol dyes, or cytochrome *c*) upon extraction with water, and regain that activity upon readdition of the extract. The active component is a protein, but not phycocyanin or ferredoxin (244; and cf. 117). Photochemical reduction of NADP by cell-free preparations of the same alga is completely inhibited by 20 μM *p*-chloro-1,1-dimethylurea (CMU), and the inhibition reversed by DCPIP plus ascorbate (71). To achieve Hill reactions with cell-free preparations of *A. cylindrica* requires use of concentrations of sucrose or polyethylene glycol much greater than those required for similar work with *A. variabilis* (274; cf. also 266–269). A photosystem II-mediated photoreduction of DCPIP is observed with aldehyde-fixed *Anacystis* (340, 522).

The first demonstration of noncyclic photophosphorylation, i.e., of ATP formation coupled to a Hill reaction, in a cell-free preparation of a blue-green alga was achieved by Gerhardt and Trebst (300) using *Anacystis* which had been lyophilized in 5% sucrose and resuspended in 0.04 M $MgCl_2$. Ferricyanide, quinones, and NADP (even CO_2 (617)) would serve as Hill reagents (oxidants). Rates, and the effects of inhibitors, including DCMU and NH_4Cl (an uncoupler of phosphorylation), were

generally similar to those that had been found with isolated chloroplasts. The ratio of ATP formed to NADPH was 1:1 (300). The same activities were found when the lyophilized preparations were treated with lysozyme, which led to release of much of the cellular muramic acid and phycocyanin (297, 299; cf. also 99). When protoplasts of *P. luridum*, suspended in an osmoticum, were diluted into reaction mixtures, the protoplasts instantly ruptured. With cell-free preparations obtained in this manner, Biggins (62) obtained NADP Hill reactions with P:2e (i.e., ATP-NADPH) ratios of about unity, but with rates (ca. 150 μmol per mg of chlorophyll per h) about 10-fold greater than the rates which had been obtained with lyophilized *Anacystis*. The Hill reaction appears to require plastoquinone (514) and, at least in the presence of fluoride, CO_2 (782).

Carbon Metabolism

Pathways of CO_2 fixation and carbohydrate breakdown. It was established by means of $^{14}CO_2$ fixation (445, 576) and enzymatic studies (34, 649, 813; Fig. 13) that the initial pathway of photosynthetic carbon dioxide fixation by blue-green algae is the Calvin cycle. Citrulline is also formed (see "amino acid metabolism"). The initial product of dark fixation of $^{14}CO_2$ observed in *N. muscorum* is aspartic acid (554). The activities of the Calvin cycle enzymes have been recorded for *T. tenuis* (489).

Although initially not detected (649, 650), a "type II" fructose diphosphate aldolase is present in four blue-green algae tested (34, 811-813). This aldolase, from *A. nidulans*, has a molecular weight of about 137,000, requires a

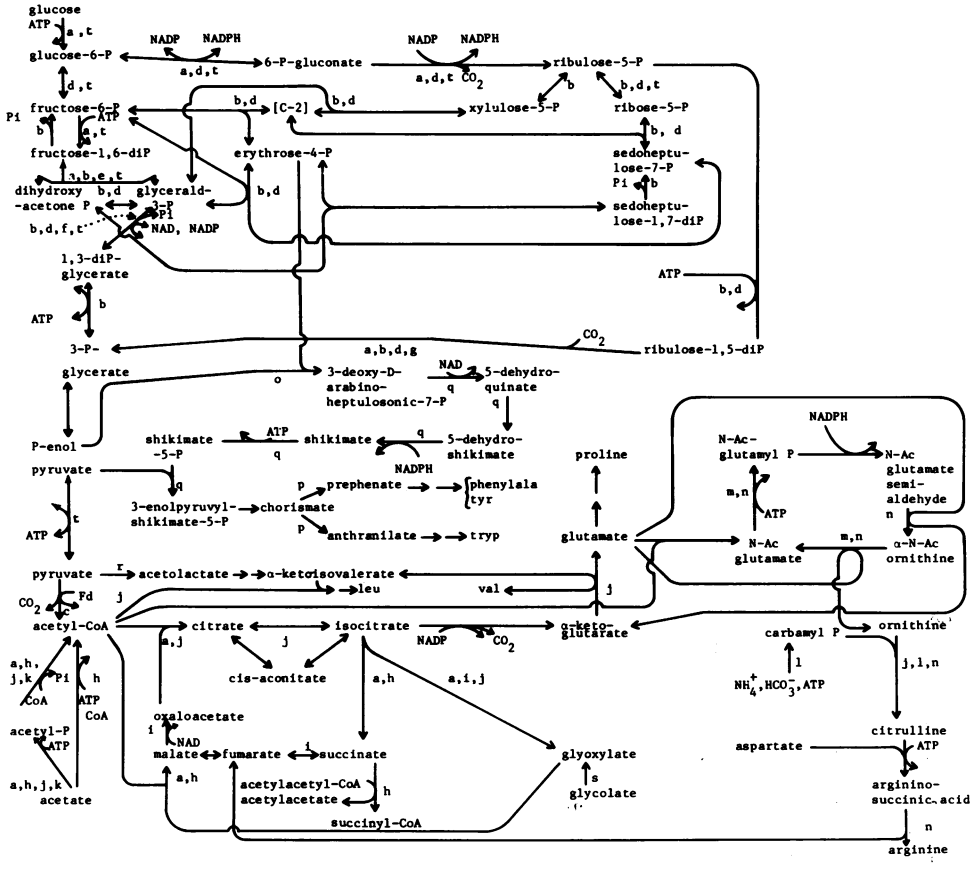

FIG. 13. *Enzymatic pathways, in blue-green algae, for which there are supporting data from in-vitro assays. References for the individual reactions are indexed: a, 118; b, 489; c, 498; d, 649; e, 811, 812; f, 278, 406, 408; g, 23, 300; h, 626; i, 717; j, 383; k, 386; l, 392; m, 382; n, 409; o, 796; p, 797; q, 53; r, 407; s, 330; t, 626a. Additional details of the tryptophan biosynthetic pathway are presented in reference 419a.*

divalent metal (Fe^{+2} is optimal) and thiol acid for activity, and with a 50-fold greater K_m also cleaves sedoheptulose diphosphate (812).

Both NAD- and NADP-dependent glyceraldehyde-3-phosphate (GAP) dehydrogenases are present in *A. nidulans* with an activity ratio about 1:6 (278). Evidence has been presented that in *A. variabilis* a single enzyme of molecular weight 200,000 to 300,000 links dehydrogenation of GAP with both NAD and NADP (406, 408).

Carboxydismutase (ribulose diphosphate carboxylase) from *A. nidulans* is a 19.5*s* enzyme (23). Unlike enzymes of acetate metabolism, the activities of which are unchanged in acetate-grown *A. variabilis*, the activity of this enzyme is decreased (118).

Pyruvate kinase from *A. variabilis* is activated by fructose-1,6-diphosphate, fructose-6-phosphate, and glucose-6-phosphate, and inhibited by citrate. Inhibition of phosphofructokinase by ATP levels above 1.2 mM is annulled by adenosine monophosphate (AMP); citrate, phosphoenolpyruvate, and octanoate also inhibit this enzyme (626a).

Neither pyruvate oxidase nor pyruvate dehydrogenase has been detected in *A. variabilis*, but rather an ATP-activated oxido-reductase which results in the formation of acetyl-coenzyme A (AcCoA) with concomitant reduction of ferredoxin (498).

On the basis of "label-chasing" experiments with glucose labeled with ^{14}C at either C-1, C-2, or C-6, ribose-*1*-^{14}C and fructose-*6*-^{14}C, insensitivity of respiration to high concentrations of arsenite and iodoacetamide, and other evidence, Cheung and Gibbs (135) proposed that the major pathway of carbohydrate breakdown in *T. tenuis* is the oxidative pentose-phosphate cycle (cf. also 810). The same proposal was made for *A. variabilis* (626a).

Enzymatic studies on sugar- and uronic acid-nucleotide metabolism in *A. flos-aquae* have been conducted (24, 25). Enzymes (phosphorylase, branching enzyme) involved in polyglucan biosynthesis in *Oscillatoria princeps* have been studied (e.g., 242, 243).

The discussions of amino acid metabolism and of acetate metabolism are relevant to the present topic.

Acetate metabolism. AcCoA formation from acetate (Ac) is mediated by acetate thiokinase ($Ac + CoA \xrightarrow{ATP} AcCoA$) in *A. nidulans* and *C. fritschii* (383, 386, 626), but by acetate kinase ($Ac + ATP \rightarrow$ acetyl phosphate) and phosphotransacetylase (acetyl phosphate + $CoA \rightarrow AcCoA + P_i$) in *A. variabilis* (626; see Fig. 13).

When ^{14}C-acetate is supplied, it is incorporated extensively into lipid (17, 386). Some information on the metabolism of long-chain fatty acids by blue-green algae has been published (26, 211, 566, 567). Label from acetate-*2*-^{14}C and oleate-*1*-^{14}C (18:1) appears primarily in monogalactosyl diglycerides, and principally (among the fatty acids) in oleic (18:1) and linoleic (18:2) acids plus (for acetate-*2*-^{14}C only) palmitic acid (16:0). These findings were interpreted as signifying that monogalactosyl diglyceride (MGDG) is the lipid primarily involved in linoleic acid synthesis in *A. variabilis* and that oleic acid is not first broken down and then resynthesized (26; cf. also 567). Although comparable labeling of MGDG is obtained with acetate-*2*-^{14}C in *A. nidulans*, phosphatidyl glycerol is more highly labeled than MGDG in *A. cylindrica* (565).

Label from acetate-*1*-^{14}C and acetate-*2*-^{14}C has been found in proteins of blue-green algae essentially only in the four amino acids glutamic acid, proline, arginine, and leucine (17, 383, 386). Of label in glutamic acid derived from acetate-*1*-^{14}C, more than 90% is in the γ-carboxyl group (383, 384). Partial degradation of the ^{14}C-leucine also supported the operation of established pathways for its biosynthesis (383). Glutamate can be formed from AcCoA by the first three enzymes of the citric acid cycle, citrate synthase, aconitase, and isocitrate NADP dehydrogenase, followed by transamination to the α-ketoglutarate thereby formed; glutamate dehydrogenase activity has not been observed (383). Low malic and succinic dehydrogenase activities have been detected (717), but neither α-ketoglutarate dehydrogenase (627, 717; cf. also 625) nor succinyl-CoA synthetase (627) has been detected in cell-free extracts. Together with the fact that ^{14}C-acetate does not significantly label aspartic acid (17, 383, 386), these observations indicate that blue-green algae have only an incomplete citric acid cycle. The lack of an intact citric acid cycle may explain the inability of some blue-green algae to grow heterotrophically (717; but see "organic nutrition"). Succinate, presumably required for porphyrin biosynthesis (chlorophyll, cytochromes) can presumably be made by the glyoxylate cycle, since low levels of isocitrate lyase and malate synthase have been detected in *A. nidulans* and *A. variabilis*, as has also an enzyme capable of transferring CoA to succinate specifically from acetyl-acetyl-CoA (626). Glyoxylate can also be derived from glycolate (330).

The mechanism by which the relative incorporation of ^{14}C into glutamate is enhanced

about 40% when saturating red light is supplemented with blue light, or is replaced with saturating white light (356), is unknown.

The discussion of the section on "organic nutrition" is also pertinent to the present topic.

Respiration

Intact cells. Endogenous levels of respiration, as microliters of O_2 per hour per milligram (dry weight), are 1.96 ± 0.10 for *A. variabilis* at 25 C, 1.05 ± 0.06 for *N. muscorum* G at that same temperature, and 28.9 ± 0.28 for *A. nidulans*, by far the fastest-growing alga of the three, at 39 C (466). Respiratory quotients ($-\Delta CO_2/\Delta O_2$) of 0.92 ± 0.03 (798) and 1.00 to 1.10 (466) have been reported. Respiratory rates are independent of the K^+-Na^+ ratio and of the pH, between pH 4.6 and 9.0, of the suspension medium (466).

Endogenous respiration of *Anabaena* is inhibited 20 to 30% by 10^{-5} M HCN, 70 to 75% by 10^{-3} M, and only 75 to 80% by 10^{-1} M, whereas an atmosphere of about 96.7% CO–3.3% O_2 inhibits respiration by only about 50% (798; cf. also 63). Moreover, azide is inhibitory at less than 10 mM, exogenously added cytochrome *c* stimulates oxidation of hydroquinone and ascorbate, and light reverses the CO inhibition of glucose oxidation by yellow (dark-incubated) cells (798). These facts point to participation of cytochrome oxidase in respiration of *Anabaena*, but simultaneously indicate that a significant fraction of respiratory oxygen uptake does not involve cytochrome oxidase (see also following section).

Respiration is stimulated by the uncoupling agents dinitrophenol and carbonyl cyanide *p*-trifluoromethoxyphenylhydrazone (FCCP; 63). Added substrates do not stimulate respiration (63), or stimulate maximally about two- (466), four- (836), or sixfold (798). However, the level of dark respiration of *P. boryanum* is increased 11-fold, from 5 to 55 nmol of O_2 per min per mg of protein, by 8 to 10 h of prior illumination (609; cf. also 177). The level of viral synthesis in the dark is simultaneously increased 10^3-fold to near the level in the light (609), suggesting that the endogenous substrate(s) for enhanced respiration can serve effectively as substrate(s) for anabolic activities in the dark.

NADH and NADPH (etc.) oxidation. Blue-green algae have both NADH (413, 495–497) and NADPH (495–497) oxidase activities under conditions where transhydrogenase activity is not detected. Phosphorylation (0.4 nmol per min per mg of protein) which was observed to be associated with NADPH oxidation (2.0 nmol per min per mg of protein), is absolutely dependent upon the presence of oxygen and is inhibited 25% by 5 μM FCCP (497). Levels of NADH oxidation (495–497) and of associated phosphorylation (496) in vitro are below comparable levels for NADPH, even if isocitrate is included together with the NADH (497). NADH and NADPH oxidase activities are associated with particulate fractions from *A. nidulans* and *A. variabilis* (413, 497).

In concord with the observations of phosphorylation-coupled oxidation of pyridine nucleotides, it was found that on transition from aerobic steady state to anaerobic steady state, the level of NADP of *Anacystis* cells decreases from 1.04 to 0.60 μmol per g (dry weight) with a corresponding increase in NADPH. The ATP level decreases from 3.02 to 1.20 μmol per g (dry weight) (cf. also 391), with a corresponding increase in AMP (difference = +0.44 nmol/g) and ADP (difference = +1.24 nmol/g). The level of NAD, however, stays constant (63).

Oxidation of succinate, malate, and ferricytochrome *c* by membrane fragments has also been observed (63). The cytochrome oxidase from *A. variabilis* has been studied. It is strongly inhibited by cyanide, little inhibited by carbon monoxide, and not inhibited by azide (754).

Interactions of respiration with photosynthesis. The phenomenon noted by Brown and Webster (93), that light can both inhibit and stimulate oxygen uptake by blue-green algae, was studied extensively by Hoch and co-workers (387, 607) by use of ^{18}O-labeled oxygen gas and mass spectrometry. Whereas oxygen production is strictly proportional to the intensity of illuminating (red) light, O_2 uptake first decreases as intensity increases, and then increases to a rate greater than in the dark. Hoch et al. (387) suggested that the acceleration of O_2 uptake at medium and high intensities ("photorespiration") is due to oxidation of a reductant formed photosynthetically. They further suggested that the inhibition of oxygen uptake at low intensities, an inhibition unaffected by DCMU, can be explained as follows. Electrons generated by respiration, rather than flowing to oxygen, flow to oxidized P700. Measurements of net oxygen exchange have been reported (434; cf. also 587) which confirm the more detailed measurements of Hoch and co-workers. Whereas dark respiration is saturated by about 0.05 atm of O_2, photorespiration increases linearly with O_2 to at least 0.2 atm. Moreover, photorespiration is very sensitive to the partial pressure of CO_2,

and is completely inhibited by 0.02 atm of CO_2 (513).

Association of the products of the reduction of tellurite and tetranitroblue tetrazolium with the "chromatoplasm" area of *Nostoc* cells, as viewed with the electron microscope, led to the suggestion that respiratory sites are present on photosynthetic lamellae (67). The possibility of deposition near the thylakoids following reduction elsewhere in the cells (765) has, however, not been excluded. Similarly, no clear interpretation is now possible of the association with intracellular granules, of the products of other oxidation-reduction reactions (188, 189, 252, 765).

Nitrogen Metabolism

Nitrogen (N_2) fixation. Because fixation of nitrogen gas by blue-green algae, like that by photosynthetic bacteria, is generally not limited by the availability of exogenous carbohydrate, these algae—where they occur—probably fix much more nitrogen than do heterotrophs (735). In particular, blue-green algae have been historically of prime importance as an agent of nitrogen fixation in agricultural economies based principally on rice (170, 709, 793).

It has been known since 1901 that elective cultures for organisms capable of fixing gaseous nitrogen under aerobic conditions in the light select for blue-green algae (50; cf. also 14, 239). Long afterward, fixation of elemental nitrogen by axenic cultures of blue-green algae, species of *Nostoc* and *Anabaena*, was first demonstrated (15, 182, 817; cf. also 227). Nitrogen fixation under aerobic conditions has subsequently been demonstrated in other members of the order *Nostocales* (e.g., 792), and in members of the orders *Chroococcales* (*Gloeocapsa:* 653, 834; cf. also 592 and 729) and *Stigonematales* (e.g., 229a). *Gloeocapsa* lacks heterocysts. Of the filamentous blue-green algae which do not form heterocysts, *Plectonema* has been shown capable of fixing nitrogen, but only in the absence of added oxygen (738), whereas there is presumptive but inconclusive evidence that *Trichodesmium* (104), and possibly members of other genera (e.g., 31), can fix nitrogen under aerobic conditions.

The elements molybdenum (76, 235, 819), calcium (7), and sodium (97) were shown to be especially important for growth of blue-green algae on nitrogen gas. Inhibition of nitrogen fixation by carbon monoxide and hydrogen together with a K_m of 0.02–0.10 atm of N_2 are in-vivo characteristics shared with the nitrogen-fixing systems of other organisms (106, 815). The ability of nitrogen-fixing blue-green algae to reduce acetylene is also ascribed to the nitrogen-fixing enzyme system, nitrogenase (736).

Schneider et al. (680) first reported high—but very variable—fixation of ^{15}N-labeled nitrogen gas by cell-free extracts of blue-green algae. Extracts of *Mastigocladus laminosus* had the highest activity. Reproducibly high rates of nitrogenase activity in extracts of blue-green algae were first reported by Smith and Evans (721), who were able to increase the in vivo nitrogenase activity by means of a prior incubation under nitrogen plus carbon dioxide, and then argon plus carbon dioxide (cf. also 559). In vitro activity requires ATP and a reductant (721, 737). Dithionite ($Na_2S_2O_4$) as reductant supports higher rates of acetylene reduction than does ferredoxin, including ferredoxin from *Anabaena* (722), although photochemically reduced ferredoxin appears likely to function in nitrogen fixation in vivo (723). Phytoflavin from *A. nidulans* can also serve as electron source for the nitrogenase from *A. cylindrica* (82). In the presence of ferredoxin and ferredoxin-NADP reductase, NADP reduced by a reaction with isocitrate can also serve as electron donor to nitrogenase (723). Pyruvate, too, can serve as electron source for the activity of nitrogenase (156, 723), but the pathway of electron transfer is unclear. In vitro, nitrogenase is labile to oxygen and cold (360).

Nitrogenase can be separated into two components which are active in acetylene reduction only in combination (725). At low extract concentrations, the acetylene-reducing activity of nitrogenase from *A. cylindrica* is proportional to the cube of the extract concentration (830; cf. also 82). Approximate linearity may be restored by addition of extract of algae starved for molybdenum in the presence of tungstate, suggesting that in vitro the acetylene-reducing unit is a dissociable trimer, one of the three units of which is molybdenum dependent (830). Nitrogenase from *M. laminosus* and *A. cylindrica* remains in the supernatant liquid following (i) centrifugation at 40,000 $\times$ *g* for 10 to 20 min (680, 722), and (ii) centrifugation at 144,000 $\times$ *g* for 3 h once the enzyme has been partially purified (361). *Gloeocapsa* nitrogenase may perhaps be much more easily sedimented (280).

Since photosynthesis generates reducing power and ATP, both of which are required for nitrogen fixation, it is natural to expect some sort of a relationship between these two pro-

cesses. Indeed, up to 450 $\mu W/cm^2$ of monochromatic light (625 or 675 nm) acetylene reduction increases linearly with intensity (218; cf. also 155). However, both *A. cylindrica* and *C. fritschii* can fix limited quantities of nitrogen gas in the dark. *C. fritschii* can do so continuously if fed sucrose (153, 215). Light stimulation of nitrogen fixation by nitrogen-starved algae is virtually unaffected by concentrations of CMU—an inhibitor of photosystem II—which almost completely inhibit carbon dioxide fixation (156). Although no such simple relationship holds for algae not starved for nitrogen, it has been observed with such algae that DCMU is much more inhibitory to acetylene reduction under conditions stimulating photorespiration than under conditions inhibiting photorespiration. That is, photorespiration and nitrogenase activity may compete indirectly for "reducing power" (513). The details of the relationship between photosynthesis and nitrogen fixation remain to be determined.

Reduction of nitrate and nitrite. Under anaerobic conditions in the light, intact filaments of *A. cylindrica* reduce NO_3^-, NO_2^- and NH_2OH to ammonia, with the production of extra oxygen. The stoichiometry was shown to be (345):

$$HNO_2 + H_2O = NH_3 + 1.5\ O_2$$

$$NH_2OH + H_2O = NH_3 + 0.5\ O_2 + H_2O$$

and probably

$$HNO_3 + H_2O = NH_3 + 2O_2$$

Nitrate reductase activity increases adaptively in response to the presence of nitrate (235, 345, 346, 533, 601). Nitrite reductase is induced by nitrite, but is neither induced nor repressed by nitrate (601). In *A. flos-aquae*, nitrate induces nitrite-assimilating activity (75), perhaps indirectly.

Cell-free preparations derived from acetone powders of *A. cylindrica* and by cavitation can reduce nitrate to nitrite (353). The enzyme responsible, nitrate reductase, can be solubilized with the detergent, Triton X-100 (348). With cell-free preparations, it could be shown that electrons for nitrate reduction may be derived from NADH, via a diaphorase which is labile to cavitation; from NADPH, in the presence of ferredoxin or an artificial carrier such as MV; from dithionite in the presence of MV; or from photoreduced ferredoxin (353, 354). Since photoreduced ferredoxin can, but dithionite-reduced ferredoxin cannot, donate electrons to nitrate, it was postulated that an electron carrier between ferredoxin and nitrate reductase is inactivated by dithionite (354).

In vivo photoreduction of nitrite by *A. cylindrica* is reduced 40% by 0.6 μM CMU, a concentration which inhibits the Hill reaction and CO_2 uptake by 60 and 50%, respectively (345), and an action spectrum of the photoreduction of nitrite shows that photosystem II is principally active (264). "Emerson enhancement" occurs: reduction with light of 695 nm is enhanced best by 620-nm light, whereas reduction with 623-nm light is enhanced maximally by light of wavelength 700 nm (264). Anaerobically, and in the presence of sufficient CMU to suppress O_2 evolution completely, nitrite is reduced by H_2 in a light-dependent reaction (347). An action spectrum of the anaerobic, H_2-dependent photoreduction shows that photosystem I is principally active but that there is extensive participation by biliproteins (264).

In vitro, nitrite can be reduced with the following hydrogen donors: ferredoxin, reduced chemically (dithionite) or photochemically (81, 354); phytoflavin, reduced photochemically but not reduced with dithionite (81); NADPH, in the presence of ferredoxin or MV; and dithionite and MV (354). NADH (352) and dithionite-reduced flavins (flavin-adenine dinucleotide [FAD], flavin-mononucleotide [FMN]: reference 355) are unable to serve as electron sources for nitrite reduction. Nitrite reductase was shown to be a soluble enzyme (353), of molecular weight approximately 68,000, which reduces nitrite stoichiometrically to NH_4^+. The enzyme was partially separated from NH_2OH reductase and showed no sulfite reductase activity (355). Since the partially purified enzyme does not appear to show a requirement for ATP, it is unclear why, under anaerobic conditions in vivo in the presence of CMU, reduction of NO_2^- by H_2 is light dependent (347), or why in crude extracts, cyanide, dinitrophenol, and arsenate inhibit the reduction (352).

Incorporation of ammonia. Magee and Burris (533: cf. also 814), having administered ^{15}N-labeled N_2, NO_3^- and NH_4^+ to *N. muscorum* strain G for periods of 1.5, 1.5, and 1 h, respectively, examined the atom percent excess ^{15}N in products of the hydrolysis of proteins and nucleic acids.

Their results suggest that glutamic acid and, to a lesser extent, aspartic acid are major early products of the fixation of NH_4^+. Comparatively high labeling of nucleic acid bases following application of $^{15}NO_3^-$ is at present not understood. Extensive incorporation of NH_4^+ into arginine via carbamyl phosphate (cf. fol-

lowing section) may have been masked, in their data, by the presence of three less heavily labeled atoms of nitrogen in each arginine residue.

Enzymatic analysis has revealed a transaminase capable of forming glutamate from α-ketoglutarate, but glutamic dehydrogenase was not found (383). Thus, the major initial reaction for incorporation of NH_3 has not yet been identified.

Amino acid metabolism. When *N. muscorum* photosynthesizes in the presence of $^{14}CO_2$, the carbamyl group of citrulline is heavily labeled (517, 576) by the coupling to ornithine of carbamyl phosphate formed from NH_3 and $H^{14}CO_3$ (392; cf. also 394). ^{14}C-urea introduces label into citrulline less markedly (18). Citrulline is an intermediate in the pathway of arginine biosynthesis in blue-green algae (Fig. 13; 382, 409; and cf. 673). Although arginine inhibits the activity of *N*-acetyl glutamate phosphokinase (382, 409), an enzyme early in this pathway, externally added arginine (2.5 mM)—which is partially incorporated—fails to repress any of the enzymes of arginine biosynthesis which have been assayed, and also has little effect on the activities of arginine-breakdown enzymes (409, 410).

Acetolactate synthetase in *A. variabilis*, by analogy to other organisms, the first enzyme in the biosynthetic pathway to valine and leucine, is inhibited 50% by valine, and may be present as two isozymes. Repression has not been observed (407). Threonine deaminase, the first enzyme in the pathway to isoleucine, is inhibited by isoleucine (174, 407); the inhibition is relieved by valine (407).

The usual microbial pathways of aromatic amino acid biosynthesis are present in blue-green algae (53, 419a, 796, 797). The first step, condensation of phosphoenolpyruvate and erythrose-4-phosphate to form 3-deoxy-D-arabinoheptulosonic acid-7-phosphate, is feedback-inhibited by L-tyrosine and, at 100-fold higher concentrations, by L-phenylalanine (796). Whereas anthranilate synthase of *A. nidulans* is inhibited 50% by 1.7 μM tryptophan, the activity of chorismate mutase is unaffected by tyrosine, phenylalanine, or tryptophan (797; and cf. 419a). In *A. quadruplicatum*, tryptophan represses enzymes of the tryptophan biosynthetic pathway (419a).

Nucleic acid metabolism and protein synthesis. "Polynucleotide phosphorylase," a DNA-independent polymerase utilizing ribose diphosphates (111, 652), and DNA- dependent RNA polymerase (111, 112, 376, 652), both from *A. nidulans*, have been purified and characterized. The RNA polymerase contains subunits of molecular weight 147,000 and 125,000 (β and β'), 39,000 (α), and 86,000 (σ) (376). Rifamycins inhibit the DNA-dependent RNA polymerase of *A. montana* (658), with consequent accumulation of "dense bodies" within the cells (657). An enzyme from *A. nidulans* capable of photoreactivating transforming DNA from *Hemophilus* (668; cf. also 801) has also been purified and characterized. It requires light for activity (668; cf. also 548). Photoreactivation has also been studied in *A. quadruplicatum* (37, 41). Other enzymes of nucleic acid metabolism in blue-green algae have not been investigated.

In the presence of puromycin and labeled methionine, *A. nidulans* synthesizes *N*-formyl-methionyl puromycin suggesting that *N*-formyl methionine acts as chain initiator in this organism (42; cf. also 22). Formation of *N*-formyl-^{14}C-methionyl puromycin by "washed" ribosomes from *Nostoc* is greatly stimulated by initiation factors from *Escherichia coli* (669). Cell-free preparations capable of polypeptide synthesis and apparently RNA-dependent have been reported (47; and cf. 279).

Sulfur Metabolism

The sulfur metabolism of blue-green algae has been studied little. There is preliminary evidence that sulfate induces sulfate-reducing activity (637). Reduced MV can donate electrons to sulfite in cell-free supernatants from several blue-green algae (667). One strain of thermophilic *Synechococcus* shows a light-stimulated production of hydrogen sulfide (694).

H_2S (10^{-4} M) does not decrease photoassimilation of CO_2 by *Oscillatoria* but decreases O_2 evolution 99%; 4×10^{-4} M Na_2S totally prevents O_2 evolution (558). Even higher concentrations of Na_2S (0.1%, ca. 1.25×10^{-3} M) are tolerated, and the sulfide is oxidized (739).

As of the present date, no particulate storage form of sulfur has been identified for sulfate-grown blue-green algae, although 20-fold growth without added sulfur has been reported (474). The availability of sulfur does not affect qualitatively the frequency of appearance of polyhedral bodies in thin sections of cells of *A. cylindrica* (C. P. Wolk and M. Jost, unpublished data). Since cells starved for sulfur become markedly yellowed, it may be that the "auxiliary" photosynthetic pigment, phycocyanin, serves as a sulfur reserve as well as a nitrogen reserve (see "chromatic variation").

Genetics

Variants, presumed to be genetic mutants,

have been described of spontaneous origin (e.g., 803; cf. also 444, 713, 802); have been selected for, as resistant, in the presence of antibiotics and other poisons (470–472, 634, 713); have resulted from treatment with X rays and ultraviolet (UV) light (220, 367a, 714); and have been induced by chemical mutagens. Chemical mutagens used include 8-azaguanine (46) and alkyl sulfonates (473, 699), although the greatest success has been with use of *N*-methyl-*N'*-nitro-*N*-nitrosoguanidine (NTG). First applied to blue-green algae by van Baalen (35; and see 95), NTG has resulted in variant strains of many types, such as those defective in reduction of sulfate, nitrate or nitrite (367a, 733); filamentous variants of coccoid organisms (e.g., 367a, 419, 420, 477); a short-trichome variant of the filamentous alga, *Plectonema* (611); and variants auxotrophic for acetate, biotin, methionine, phenylalanine (367a), and tryptophan (419a). Repair of NTG mutagenesis has been studied (732).

Genetic transfer has been claimed, on the basis of what appear to be satisfactory supporting data, by means of both recombination (46) and transformation (699). Anastomosis of cells and filaments has been stated to occur in *N. muscorum* (494; cf. also 762).

It has proven possible to map certain genes crudely by means of determining the rate of mutation of those genes as a function of time during synchronous growth, since for a given gene that rate should double at the time of its replication, if all genes are co-linear (29, 368).

Cyanophage

A virus capable of reproducing in, and lysing, blue-green algae was first discovered by Safferman and Morris (663, 664). The virus, called a "cyanophage," was designated LPP-1 because of its host range: *Lyngbya*, *Phormidium*, *Plectonema*. Other viruses with the same host range have since been isolated (164, 612 [cf. 525], 665). The LPP viruses thus far isolated form two serological groups (665; and cf. 613). Other cyanophage have also been reported (Table 7). LPP-1 has been by far the most thoroughly studied.

The best present description of LPP-1 is that it is probably icosahedral, with a short tail (679), from which tail fibers protrude (700). The short diameter of the head is 586 ± 20Å (the outer coat is 80 to 100 Å thick), and the tail is about 200 to 225 Å long and 150 Å in diameter. The tail is joined to the head by a "capital" about 100 Å long and 250 Å in diameter (523, 524). The virus contains only DNA, which is linear, with a contour length of 13.2 ± 0.5 μm as measured by the Klein-Schmidt technique, and a sedimentation coefficient $s_{20,w}^{\circ}$ = 33.4 ± 0.7*s*, values which are consistent with a molecular weight of 27 × 10^6 (this much DNA would just fill the viral head). The density and the temperature denaturation profile of the DNA indicate that it is composed 53% of guanylic and cytidylic acids (523; for additional determinations of the molecular weight of the intact virus and of its DNA, cf. 317). The virus is hydrated to the extent of 0.37 *g* of water per *g* of virus (317). The molecular weights and number per virion of the structural proteins of LPP-1M have been determined; about 80% of the total protein is comprised of about 310 copies of a protein of mass 44,000 daltons and about 450 copies of a protein of mass 14,000 daltons (3).

TABLE 7. *Viruses known for blue-green algae, and their hosts*

Virus	Host range	Reference
LPP-1, 2	*Lyngbya*, *Phormidium*, *Plectonema*	663, etc.; see text
SM-1	*Synechococcus elongatus* and *Microcystis aeruginosa*	666
C-1	*Cylindrospermum* sp.	712
AR-1	*Anabaenopsis raciborskii*, *A. circularis*, and *Raphidiopsis circularis*	712
AS-1	*Anacystis nidulans* and *Synechococcus cedrorum*	662
N-1	*Nostoc muscorum*	1

The viruses appear to affix themselves to host cells by their tails and are presumed to inject their DNA through the host walls (718–720). There have been several studies of the kinetics of one-step growth of LPP-1 and related viruses (317, 608, 695). After adsorption (92% complete in 1 h:317) there is a 3-h eclipse period (608) during which intracellular, infective viruses are not found. Synthesis of the proteins of the host is shut down within 5 h after infection (697). Virus particles appear extracellularly after a latent period of 7 h following infection (317). Viral growth is essentially complete at 14 h after infection (317, 608, 695). The complete cycle of vegetative growth of the virus, including replication of DNA and inclusion of the DNA within coats, appears to take place within a "virogenic stroma" between the plasmalemma and displaced thylakoids (695; and cf. 719), but there is controversy on this point (96). About half of the host DNA is broken down to provide acid-soluble precursors of viral DNA (696). Viral proteins synthesized at "very early," "early," and "late" times during infection, and corresponding (at 3 nu-

cleotides per amino acid encoded) to 65% of the viral genome, have been revealed by elegant pulse-label experiments with ^{35}S (697). The final burst size is about 100 particles per cell (317). Although LPP-1 and LPP1-G fail to grow at 35C, in contrast to other LPP isolates, initial symptoms of infection, including invagination of photosynthetic lamellae, do take place (610).

LPP1-G grows well in *Plectonema* in the light, or in the dark after 10 to 12 h in the light, but grows very poorly in dark-adapted cells. In the light, 1 μM DCMU completely inhibits CO_2 fixation by intact *Plectonema* for at least 13 h, but delays viral growth by only 1 h. Viral growth in light or dark is completely inhibited by 10^{-4} M carbonyl cyanide *m*-chlorophenylhydrazone, an uncoupler of oxidative phosphorylation. These results suggest that if viral growth requires, in addition to ATP formation, reduced pyridine nucleotides, the reduced nucleotides can be generated from a substance formed in the light and used up in the dark (609, 698; and cf. 2).

Lysogeny has been observed in *Plectonema* (110, 613). Data demonstrative of genetic transduction have not yet been reported.

Movement

Mechanism. A long succession of investigators (see 105, 250) has implicated the secretion of mucilage as an important factor in the gliding movement of blue-green algae. The following types of observations were made. (i) Filaments, during movement, deposit a trail of mucilage (344) which can even remain as "bridges" when filaments descend from the overhanging portion of a grain of dirt (675). (ii) Tiny particles which touch *Oscillatoria* filaments stick to a layer of slime and are conducted in a spiral path along the filaments (e.g., 224). In the case of the *Oscillatoria* species studied by Hosoi (414) and Schulz (685), when an organism moves, the slime substance remains motionless relative to the substratum, whereas, when a filament is held motionless (and not rotating) by micromanipulation, the slime substance moves spirally around the filament at a rate approximating the rate of movement of unhindered filaments. (The "oscillatory" path of the end of an *Oscillatoria* filament is the two-dimensional, microscopic projection of its motion, which is actually spiral [105].) (iii) The direction of flow of microfibrils in mucilage parallels the direction of filament movement (481).

However, certain facts are inconsistent with the idea that slime secretion plays a critical role in the motility of blue-green algae. Certain species of *Oscillatoria* secrete an extremely small amount of mucilage or none at all and yet can move actively so long as they touch either particles of dirt or other filaments (571). Hormogonia of *O. rubescens* lack slime, as determined by electron microscopy, but move actively (438). Burkholder (105), and other investigators cited by him, have observed—albeit, infrequently—free swimming of algal filaments, but this cannot be due to propulsion "powered" by extrusion of mucilage.

Rhythmic contractions were advocated to be of primary importance in motility (e.g., 676, 777, 778). The existence of such contractions has, however, been contested (685) both on the basis of detailed measurements of photomicrographs of *O. tenuis* in motion and the observation that certain unicellular blue-green algae and single- or few-celled hormogonia can glide. An apparent relative movement of the end walls of cells was observed in photographs but was ascribed to an up-and-down movement of the filament (685). Proof of the existence of "surface waves" in motile *Oscillatoria* filaments has been presented by Ambrose (20), although with a regrettable lack of details, using a novel type of illumination which permits observation specifically of those parts of an organism that make contact with the surface of a microscope slide.

Propulsion is effected throughout a filament, as is shown by the following facts. If the front of a filament is killed or is blocked in its movement, the rear of the filament continues to move forward; different parts of a filament can move in independent directions; and, if a filament is dissected, each of the pieces continues to move (344, 674).

Halfen and Castenholz (334, 335) have sought to explain the mechanism of motility in *O. princeps*. They have shown that in the L_{III} region of the cell wall, as demonstrated both in fixed and stained and in freeze-etched material, is a layer of fibrils in parallel array pointing in the (helical) direction of motion, and found pointing in the mirror-image direction of motion of a different alga. Observations of inversion and curling of cell fragments were interpreted as implying that the fragments—and perhaps the fibrils—are under torsion (cf. 423). The thick L_{II} layer of the wall of *O. princeps* has a great many thin regions ("pockets") through which (for example) ATP might be delivered relatively easily to activate the fibrillar layer of the wall. Motility, the authors suggested, is produced by waves *in* L_{III} expressed *through* L_{IV} and acting against sheath or solid substratum. This model has the twin

virtues that it is consistent with the facts known about motility in blue-green algae and is amenable to further experimental testing.

Movement in the dark; effects of nonphotic parameters. Diverse blue-green algae move in the dark (cf., e.g., 335, 344, 578, 675). Movement of *Phormidium* in the dark is probably energized by respiration, since it is greatly decreased when ambient air is replaced by argon (587) and since uncouplers of respiratory phosphorylation inhibit dark movement at lower concentrations than they inhibit light-stimulated movement (583). Similarly, the movement of *O. princeps*, which moves at the same rate in the light as in the dark, appears to be dependent upon respiration since it is inhibited by cyanide and by dinitrophenol (335). The energy which this alga must expend for movement through a viscous medium has been calculated probably not to exceed 5% of the energy available from respiration (336).

Speeds of movement range up to about 11 μm/s (335). The speed of forward movement of *Nostoc* doubles, and that of *O. jenensis* doubles or triples with a 10° rise in temperature (344, 674), although as temperature continues to rise, movement eventually slows and stops (344; and see 105).

Oscillatoria formosa and other blue-green algae have been shown to move away from free acids, both inorganic and organic, and from other chemical stimuli (224, 675).

Effects of light on movement: changed speed of movement. Early observations (e.g., 344, 676) of an acceleration of the movement of blue-green algae by light ("photokinesis") have been criticized (105) on the grounds that heating effects and the incidence of scattered light may not have been adequately controlled. *O. princeps* shows no such acceleration (335).

Nultsch (578, 581, 582, 584-587) has systematically studied the photokinetic phenomenon that "point" inocula of *Phormidium* species spread more rapidly in the light than in the dark. The ratio, "R_K," of the average colony diameter in the light to the average colony diameter in the dark proved to be time independent and was, for that reason, chosen as a measure of the photokinetic effect of the incident light. For *P. autumnale*, R_K is positive between 2×10^{-2} and 3×10^4 lx, with a peak at about 2×10^3 lx, and is negative at 4×10^4 lx of white light (578). Intensities up to about 10^5 lx result in positive photokinesis in other species (586). In four species of *Phormidium*, chlorophyll *a* appears to dominate the visible part of the action spectral curve, and wavelengths in both the infrared and UV regions of the spectrum are also active (578, 581, 586; cf. the following two sections).

Since light of wavelengths absorbed by chlorophyll is much more active photokinetically in *Phormidium* than is light absorbed by biliproteins, it may be principally photosystem I of photosynthesis which energizes photokinesis. Considerable evidence has been presented consistent with the thesis that the photokinetic effect of light is mediated by ATP produced by cyclic and noncyclic photophosphorylation (582, 585, 587)—a reasonable thesis, since movement requires the expenditure of energy. However, if this hypothesis is correct, it is unclear why 50 μM DCMU should completely inhibit photokinesis, with that inhibition partially reversed by ferrocyanide (582); why infrared and UV light are photokinetically active; and why the action spectrum for photokinesis should be so different in *A. variabilis*. In the latter alga, the peak of the action spectrum corresponds closely to the peak of absorption of phycocyanin, whereas light absorbed only by the longer-wavelength absorption peak of chlorophyll is photokinetically active (586).

Orientation relative to the direction of light. Diaphototaxis, movement of filaments to a direction perpendicular to the direction of incident light, has been studied in *Oscillatoria* species (105). More thoroughly studied, in blue-green algae, is topophototaxis, movement toward or away from a light source.

Although individual germlings of *Nostoc* spores move toward a light source, except in the presence of a rich organic medium (343, 344), filaments of *A. cylindrica* and *A. variabilis* commonly move as a bundle, usually—but not always—with the individual filaments bent into U's, and with the centers of the U's directed toward the front of the bundle. Single filaments of *Anabaena* species have much less regular topotactic paths than have filament bundles and apparently cannot shift direction as rapidly (184, 185). *Cylindrospermum licheniforme* filaments move in similar, if less neat, bundles. Crude action spectra of topophototaxis appear to peak in the orange or red for both *A. variabilis* and *C. licheniforme* (183).

In contrast to those *Nostocaceae* tested, *Oscillatoria* and *Phormidium* appear to lack a steering mechanism. Thus, the paths of *O. sancta*, *O. formosa*, *O. mougeotii*, and *P. uncinatum* toward a light source consist of scalloped concatenations of a basic, hemicyclical "step," in which the direction of movement of the filament is reversed at the end of each step (105, 183, 185).

Algae inoculated as a streak onto a petri dish

spread differentially toward (a distance S_1) and away (a distance S_2) from a light source (185). This phenomenon was quantified by Nultsch (577, 581) in terms of the ratio $R_t = 100 (S_1 - S_2)/(S_1 + S_2)$. This ratio measures the topophototactic movement of the center of the ellipse of expansion, as a percent of the small radius of the ellipse (577). R_t is positive between 1 to 5 and 10^4 lx of white light in *P. uncinatum* and *P. autumnale*, with a peak at about 2×10^2 lx, but becomes negative at about 2×10^3 lx in *P. ambiguum* (see 586). Peaks at about 565 and 615 nm in the action spectrum of topophototaxis of *P. autumnale* are presumably due to the biliproteins, the peak at about 495 nm may be due to carotenoids, whereas the peak at ca. 400 nm may be due to the same unknown pigment that is active in photokinesis. Since wavelengths greater than about 640 nm are topophototactically inactive, and there is a trough in the action spectrum at 425 to 435 nm, chlorophyll appears not to be active in topophototaxis. Although the topophototactic responses of *P. uncinatum* closely resemble those of *P. autumnale* (185, 581), *O. mougeotii* is strongly topophototactic at 398 and 654 to 705 nm, and only weakly phototactic at 508, 557, and 740 nm (185). Thus, in topophototaxis as in photokinesis, there are large disparities between the pigments which are active in different algae.

Response to a gradient of intensity. A "positive photophobotactic" response to sharp gradients of light intensity is exemplified by unhindered passage of a filament from dark to light, but reversal of direction soon after the front of a filament passes from light into dark (183). Such reversals of direction can take place repeatedly when a filament, moving back and forth across a small, illuminated area, encounters the edge of that area (185). Although no such response was observed in *A. variabilis* and *C. licheniforme* (183), *Nostoc* germlings change direction upon moving from light to dark (344). Shading the rear of a filament of *Phormidium uncinatum*, the shade moving with the filament, elicits little reaction. When the rear 50% was shaded for 5 to 10 min, no filament was observed to reverse direction, and only 10 of 30 filaments reversed direction when the rear 75 to 95% was shaded. However, 26 out of 30 filaments reversed direction after about 1 min when the front 10% of the filament was shaded, and 15 out of 20 filaments soon reversed direction in response to shading of the front 5% of the filament (185). Since the whole of a filament is involved in propulsion, these observations that the front portion of the filament controls the direction of filament movement constituted the first experimental demonstration of physiologically important, intercellular interactions in a blue-green alga.

O. mougeotia and *P. uncinatum* accumulate in a 3- by 3-mm light field on an agar sheet in a petri dish (183), reaching a final concentration after about 5 h (579). The extinction of light by the field (3 by 3 mm) after 8 h, corrected for absorption by glass and agar, was taken as a measure, "R_p," of photophobotaxis (579; cf. also 183, 185). In all such measurements, however, it is unclear to what extent the final aggregation is due to the photokinetic and topophototactic effects of light scattered from the illuminated region. For two strains of *Phormidium*, R_p is positive from .1 lx to over 5×10^4 lx, with a peak at 5×10^3 to 10^4 lx (579, 581).

Action spectra of photophobotaxis show peaks at wavelengths corresponding to the peaks of the absorption spectra of the pigments active in photosynthesis, but with activity above 700 nm apparently too great to attribute to those pigments (579, 588). In fact, there is a striking parallelism between the visible-light action spectra of photophobotaxis and of $^{14}CO_2$ fixation, suggesting that there is a relationship between photophobotaxis and photosynthesis (588). A test for Emerson-type enhancement, however, has not been reported; redox reagents supposed to have a specific effect on photophobotaxis through interaction with the electron transport chain of photosynthesis have rather parallel effects on dark kinesis (584); and 10^{-3} M DCMU—a very high concentration—only partially inhibits photophobotaxis (582). Unfortunately, additional experiments with inhibitors have also not led to a further elucidation of the presumed relationship between photophobotaxis and photosynthesis (583).

Culture

Inorganic nutrition. Elements, other than H, C, N, O, S, and P, that are or may be expected to be required for the growth of blue-green algae are summarized in Table 8.

Media used up until about 1950 for autotrophic growth of blue-green algae have been described by Allen (6). With time, certain variations have been introduced, including the following. (i) As the phosphate concentration was increased to provide additional buffering action, the concentration of calcium was decreased to prevent precipitation during autoclaving (e.g., 465). With the advent of new buffers (see below), the concentrations of phosphorus and calcium may again change. (ii)

TABLE 8. *Requirements by blue-green algae for metals, boron, and chloride*

Element	References for demonstration of requirement[a]	Comments
B	214; cf. also 301	
Na	6, 7, 9, 31, 44, 209, 465	In the presence of NO_3^-, Na^+ deficiency results in increased activity of nitrate reductase and, thereby, production of toxic levels of nitrite (97). Na deficiency also results in decreased reduction of N_2 (7, 97).
Mg	304, 305	Constituent of chlorophyll, as well as a required cofactor for numerous biochemical reactions
Cl	Requirement not demonstrated (cf., however, 782)	
Mn	651	Required for O_2 production by intact *Anacystis* and for Hill reaction (134, 298, 645), and for structural stability (298) as well as for proper division of growing cells (651)
Fe	304, 305, 605	
Co	393, 635, 748	0.075 μg of vitamin B_{12}/liter completely eliminates the requirement for (optimally) 0.2 to 0.4 μg of Co/liter (393). Of ca. 0.63 μg of "B_{12}" per g (dry weight) of *Anabaena*, 65 to 70% is cobalamin (94; and cf. 561, 655).
Cu	Requirement not demonstrated	Presumably required for plastocyanin (515)
Zn	Requirement not demonstrated	
K	6, 78, 143, 209, 465, 532	
Ca	7, 209, 532	More Ca^{2+} appears to be required for growth on N_2 than for growth in the presence of nitrate (7).
Mo	76, 393, 748, 819, 820	Required for growth on nitrate and N_2; no requirement shown for growth on NH_3.

[a] The *rigorous* requirements for such a demonstration, as proposed by Holm-Hansen et al. (393), have rarely been satisfied.

Fixed nitrogen was omitted for nitrogen-fixing organisms. (iii) Microelements were included (e.g., 209). (iv) A chelating agent was provided (see below). Sometimes, quite dilute media have been used (e.g., 138, 303). Many laboratories now make use of the media of Allen and Arnon (8) and Kratz and Myers (465).

There are few publications detailing systematic efforts to optimalize concentrations of minerals in media for these algae. Representative results are presented in Table 9.

In addition to the elements shown in this table, Na is required at 1 to 5 (7, 8) or 4 to 40 (465) mg/liter; Mn at 0.01 to 0.5 mg/liter (298, 651); Mo at 0.1 mg/liter, for growth on nitrate, to 0.5 mg/liter, for growth on N_2 (76, 819); B at 0.1 mg/liter (214; 1 mg/liter is inhibitory); and Co at 0.2 to 0.4 μg/liter (393). Cu and Zn are often provided at about 0.02 and 0.05 mg/liter (e.g., 8) although determinations of optimal concentrations have not been reported; higher concentrations have been provided when EDTA is present as chelating agent (e.g., 465).

It has been proposed (306) that the growth response to any particular, required element saturates at a "critical" tissue concentration of the element which is essentially independent of other factors. For *Microcystis aeruginosa*, these concentrations were: N, 5% of dry weight; K, 0.5%; Mg, 0.3%; P, 0.2%; and Ca, 0.04%, as determined by a comparison of the ratio of element weight to dry weight and by the relative cell yield, as a function of the concentration of the element in the medium (302, 306). Unfortunately, the effect of other factors on the value of the critical concentration has yet to be thoroughly investigated (232). In particular, the great disparity in optimal elemental concentrations determined in different studies, as shown in Table 9, although determined with different organisms, may reflect the very different general level of salt concentrations.

Carbon dioxide is frequently supplied to cultures at concentrations in excess of the concentration (0.03%) in air (16: 1% and 5%; 465: 0.5%; 8: 5%), to overcome the rate-limiting process of diffusion of CO_2 into culture media. Alternatively, a rapid flow of air, well dispersed in a culture, can provide CO_2 sufficiently rapidly that its rate of dissolution is not limiting for algal growth.

In nature and in culture, blue-green algae grow best at alkaline pHs (231; and cf. e.g., 16, 465, 532, 639). Unusually high pH optima of pH 10 to 11 were determined (303–305; cf. also 838) for *M. aeruginosa* and *Coccochloris peniocystis*. *Spirulina* also grows best at an elevated pH (142). At the other extreme, *Aulosira fer-*

TABLE 9. *Optimal ranges of concentrations of inorganic nutrients, for autotrophic growth of blue-green algae*

Element	Optimal concn[a] ranges, calculated			
	References			
	532	304, 305	465	635; marine alga[c]
N	≤14-35	≥7	35-680	59
P	2-20	0.2-≥2	45-270	0.4-400
K	4-20	1-≥5	110-1260	5-240
Mg		0.1-≥3	15-50	50-1200
S		0.8-≥4	20-66	660
Ca	60-250[b]	0.25-≥10	1.7-8.4	10-400
Fe		0.03-≥0.6	0.88	4

[a] Milligrams per liter.

[b] May represent a requirement for a microelement contaminant.

[c] High NaCl required.

tilissima is stated to grow well in soil at pH 5.6 (671), and *M. laminosus* appears to grow in hot springs at pH values of 4.8 and above (89).

For many years, the only well-defined buffer added to cultures of blue-green algae was phosphate (e.g., 532). Tris(hydroxymethyl)-aminomethane (Tris) was used to buffer the medium for a marine *Phormidium* (635), but has been found to be toxic to *M. aeruginosa*, especially above pH 8 (536, 537). Alanyl-glycine and alanyl-alanine have been used to buffer phosphate-free suspensions of *A. cylindrica* (823). Glycyl-glycine, glycyl-alanine, and alanyl-glycyl-glycine were toxic, as were a number of other compounds capable of buffering in the pH range 7-9 (821). The Good buffers (318) are, however, satisfactory for buffering algal suspensions with *N*-tris(hydroxymethyl)-methyl-2-aminoethane sulfonic acid (TES) particularly good (C. P. Wolk, unpublished data).

Citrate (303, 465) and EDTA (8, 393, 465, 635) have been used as chelating agents to maintain iron and manganese in solution at the alkaline pHs at which blue-green algae normally grow. Since other polyvalent cations are also sequestered, the relative contents of various cations are important parameters of media containing chelating agents.

Organic nutrition. The first-culture experiments with bacteria-free blue-green algae (639) and extensive experiments with those blue-green algae which have been most frequently used for physiological studies, namely *A. nidulans*, *A. variabilis*, *N. muscorum* strain G (465), and *A. cylindrica* (C. P. Wolk, unpublished data), failed to elicit growth in the dark on organic substrates. However, there are now increasing indications that the ability to grow heterotrophically is widespread among these algae (365, 454). Table 10 summarizes some of the successful attempts to achieve heterotrophic growth of blue-green algae.

Fermentative growth has been observed with *C. fritschii*, with simultaneous fixation of nitrogen (215).

Numerous investigators have found that sugars increase growth of blue-green algae in the light (15, 16, 215, 639, 817; cf. also 6). This work culminated in the demonstration (39; cf. also 456) that *Lyngbya lagerheimii* and *A. quadruplicatum* grow, in the presence of glucose, in dim light which is itself insufficient to support growth; glucose supported only "marginal" growth in the dark. Glucose can contribute up to 46% of the dry weight of *A. variabilis* without, however, affecting the growth rate of that alga (626a).

A. variabilis, *N. muscorum*, and *A. nidulans* assimilate acetate and incorporate it into organic products (17) to a much greater extent in the light than in the dark. The assimilation is greatly stimulated by CO_2, and is very sensitive to DCMU (383, 386). Glycolate is rapidly taken up and respired to the extent of about 90% by *A. flos-aquae* and *Oscillatoria* sp. in the dark. Light increases the amount metabolized by about 40%, and greatly decreases the amount respired, so that about 50% of the glycolate can be assimilated in 1 h in the light (546).

Extracellular proteolysis, manifested by blue-green algae (6), is the most probable explanation of the ability of egg albumin, serum albumin, peptone, and casein to supply the nitrogen requirement for growth of these algae (639). By supplying "unlabeled" amino acids (Leu, Met, Phe, Ala, Val, and Tyr) to deuterated cultures of *P. luridum* and *Fremyella diplosiphon*, Crespi et al. (159) demonstrated the uptake of these amino acids and their incorporation into phycocyanin. Asparagine can serve as a nitrogen source for certain blue-green algae but not others (31, 639). It also improves the growth of nitrate-grown *Phormidium* (635), and—as does also glycine—yields a transient inhibition in the production of heterocysts by *A. cylindrica* (228). Arginine and glycine can serve as nitrogen sources for growth of four non-N_2-fixing blue-green algae and decrease the nitrogenase activity of three nitrogen-fixing strains (833). Methionine can satisfy the sulfur requirement of *A. nidulans* and *A. variabilis* (637). Exogenously supplied arginine, methionine, and tyrosine can act as biosynthetic precursors in the latter alga (79, 409). Exogenous threonine acts as a precursor

TABLE 10. *Representative examples of heterotrophic growth of blue-green algae*

Alga	Substrates for heterotrophic growth	Additional information	Reference
Nostococeae			
Nostoc punctiforme	Glucose, sucrose, lactose, maltose, starch, dextrin, inulin, (citrate)		343
N. punctiforme	Glucose, mannose, fructose	Fructose required for heterotrophic N_2 fixation	817
N. muscorum A	Glucose	N_2 fixed	16, 465; cf. also 6
Nostoc sp.	Glucose, sucrose, fructose	From coralloid roots of a cycad. Generation time 25 h in aerobic dark. Slower growth in anaerobic dark	385
Chlorogloea fritschii	Sucrose, maltose, glycine, glutamine, glucose, mannitol	Only with glucose and mannitol must nitrate be added. Very slow growth, with gradual adaptation to heterotrophy	215, 219
Anabaenopsis	Glucose, fructose, sucrose, maltose	Spores formed during dark growth	794
Anabaena cycadeae	10% Glucose + 2% casein hydrolysate	0.6 Doublings/day	710
Oscillatoriaceae			
Oscillatoria (2 strains)	0.2% Glucose + 5% yeast autolysate		6
Lyngbya	0.2% Glucose + 5% yeast autolysate		
Phormidium	0.2% Glucose + 5% yeast autolysate		
Lyngbya	Glucose	From marine habitat	31
Scytonemataceae			
Tolypothrix tenuis	Glucose + Casamino Acids	0.4 Doublings/day	455, 456
Plectonema boryanum	Glucose	Continuous flow-through of fresh nutrient required. Bleaches in dark, greens in light. Dark subculture possible	614a

in *A. nidulans* (529). *C. fritschii* can grow heterotrophically with glycine or glutamine (219). Amino acid auxotrophs (Phe, Tryp) have been isolated (367a, 419a).

The occurrence of urease in blue-green algae (57) explains the ability of various of these algae to utilize urea as a nitrogen source (6, 31, 144, 465, 833; cf., however, 65). The metabolic products of ^{14}C-urea resemble those of $^{14}CO_2$, except for lesser labeling of glutamate and aspartate and greater labeling of glutamine and asparagine (18), presumably due to concomitant incorporation of urea-derived NH_3.

Uric acid can supply the nitrogen requirement of certain blue-green algae, either as well as nitrate or (in the case of *A. quadruplicatum* PR-6) much less well (40). A wide variety of nucleic acid precursors are taken up and incorporated into nucleic acids by intact cells of *A. nidulans* (633).

Vitamin B_{12}, at 75 ng/liter, completely eliminates the Co requirement of *N. muscorum* (393). This vitamin, or an analogue of it, is required for growth of various marine blue-green algae (30, 31, 635).

Indole acid (IAA) was found to be a growth requirement for *Nostoc* sp. (102; cf. also 4). The form of the macrocolonies of some blue-green algae appears to depend on interactions with other microorganisms (593, 832).

Light and temperature. In autotrophic cultures of blue-green algae, availability of light limits growth in all but dilute suspensions. To circumvent this problem, algae have been grown on flat, shaken tables (159), in large volumes with lamps immersed (159, 526), with vessels completely surrounded with lamps (826), pumped through translucent pipes of relatively small diameter (442), in a special growth vessel in which the algal suspension flows in a thin film under a bell jar (478), or in flasks containing a relatively thin layer of suspension.

Both fluorescent and incandescent illumination can support maximum growth rates (465). High-intensity Lucalox lamps (G.E.) also sup-

port rapid growth, provided that the time-average light intensity to which individual cells are exposed is not excessive (C. P. Wolk, unpublished data). The spectrum of incident light can affect the pigmentation of the algae (see "chromatic variation").

Growth rates on the order of a 1- (478) or 2-day (305) doubling time have frequently been found for blue-green algae, but an approximate 6-h doubling time has been reported for *A. cylindrica* (144) and for *Nostoc* sp. (385), whereas coccoid blue-green algae double in as little as about 2 h (465). A summary of growth rates has been published (411). Cell densities achieved range from about 0.2 (304, 305) to 7 to 8 g (dry weight) per liter (8).

Temperatures appropriate for culture of thermophilic blue-green algae are discussed by Castenholz (122, 123). Many nonthermophilic blue-green algae are normally grown at "room temperature" (20–25 C), but show increased growth rates as the temperature is raised to 30 C and above (411, 465).

Synchronous growth. Three groups of workers have achieved a degree of synchronization of the growth of *A. nidulans*, by cycling between 8 h at 26 C and 6 h at 32 C, with dilution at the end of each cycle (520); by incubating for 12 h in the dark, and then exposing to continuous light (29); and by means of preliminary deprivation of both light and CO_2 (367, 368). The time course of chemical (781) and ultrastructural (780) changes have been followed during synchronous growth resulting from temperature cycling. A "division burst" starts 2 h after transfer to the higher temperature.

Means of obtaining pure cultures. Pure (unialgal, axenic, and preferably clonal) cultures of motile blue-green algae have often been obtained by sequential subculture of filaments which have migrated away from contaminants on solid media (84, 103, 182, 343, 635, 823). Variations on this practice include phototactic attraction of the contents of germinated spores (343) and migration through agar (103). Silica gel is sometimes used in place of agar so as further to reduce growth of contaminants on inorganic media (170, 639, 734). Spatial separation of algae from contaminants has also been achieved with pour plates (31).

Antibiotics (635, 734) have been used, but, since blue-green algae are prokaryotes, it is often difficult to kill contaminating bacteria selectively in the presence of these algae. Chlorine water was employed successfully by Fogg (227). Despite misgivings at use of a mutagenic agent (31), UV irradiation has been used repeatedly and successfully to isolate pure cultures of blue-green algae (e.g., 15, 31, 76, 303, 397). Use of gamma irradiation may also prove practicable (467).

Growth of single cells. Quantitative surface plating of unicellular blue-green algae has been achieved (i) if the formation of toxic concentrations of peroxides is prevented by addition of catalase, replacement of citrate by EDTA, or decrease in the concentration of manganic ion in the medium (32, 535; cf. also 36), and (ii) by the alternative approach of sterilizing the nutrient medium separately from the agar (10). Spores of the filamentous alga *Anabaena doliolum* give rise quantitatively to clones on the medium of Allen and Arnon (8) solidified with agar (706, 711). Sufficiently prolonged cavitation of suspensions of this alga in a "sonic cleaning bath" breaks the filaments into fragments which are close to one cell in average length. These fragments give rise to clones with high plating efficiency on the same medium (C. P. Wolk, unpublished data).

Substances Secreted; Toxins

A significant fraction of the carbon and nitrogen fixed by blue-green algae is subsequently excreted. For instance, of the nitrogen fixed by cultures of *Calothrix scopulorum*, about 40% is released to the outside of the cells (433). The only free amino acids found in culture solutions of *Calothrix brevissima* were aspartic and glutamic acids and alanine (792). Free amino acids, probably glutamic acid and alanine, accounted for at most 10% of the extracellular nitrogen in a culture of *A. cylindrica*. Hydrolysis of culture filtrates revealed, in addition, serine, threonine, glycine, tyrosine, and traces of valine and leucine, indicating that the alga releases peptidic material (230; cf. also 533 and 747). This material may complex with heavy metals, reducing the toxicity of—in particular—high concentrations of cupric ion (234). Water-soluble, nondialyzable extracellular products of several blue-green algae were found to contain 12 different amino acids (803).

Extracellular pentose has been found in cultures of *A. cylindrica* (230), and organic acids were found in the filtrate of *Oscillatoria* sp. (324, 325). Less than 1% of photosynthetically fixed carbon is secreted as glycolate (132, 176, 364).

In the presence of algal blooms, fish can die not only as a result of nocturnal suffocation, as microorganisms reduce the oxygen level in the water, but also by poisoning (638). A massive poisoning of mammals has been attributed to

Microcystis toxica (731). Poisonings have been blamed on *M. aeruginosa*, *M. flos-aquae*, *Anabaena flos-aquae* (including *A. lemmermannii*) and *Aphanizomenon flos-aquae*. In addition, *Nodularia spumigena*, *Coelosphaerium Kützingianum*, and *Gloeotrichia echinulata* have been incriminated in intoxications (322). A "very-fast death factor" from cultures of *Anabaena flos-aquae* kills in 1 to 2 min following application to mice of a minimum lethal dose (322). A "fast-death factor" from contaminated cultures of *M. aeruginosa* kills in 30 to 60 min. This factor was identified as one of five closely related peptides isolated from the cells (not the supernatant liquid) of these cultures. It is a cyclic oligopeptide, of molecular weight less than 2,600 (322). Three toxins from nonaxenic *Aphanizomenon flos-aquae* are structurally closely related to an unidentified, paralytic, shellfish toxin derived from *Gonyaulax catenella* (422). Associated with impure cultures of *Lyngbya majuscula* is a lipid-soluble, water-insoluble, dermatitic factor (550, 551). It would be desirable to know whether the toxic factors found in these mixed cultures would also be produced by axenic algal cultures.

Regulation And Development

Biochemical regulation. There is very little information available on the role of metabolic controls in the physiology of blue-green algae. In particular, the extent to which altered concentrations of enzymes are important in the differentiation of heterocysts and akinetes is unknown. Thus, the relatively high specific activity of nitrogenase in heterocysts under aerobic conditions (see "heterocysts") may result merely from inactivation, by oxygen, of nitrogenase in vegetative cells. The mechanism by which ammonium and, in *Anabaena flos-aquae* and *A. doliolum*, nitrate lead rapidly to loss of nitrogenase activity (75; C. P. Wolk, unpublished data) is unknown. As noted above, nitrate and nitrite induce nitrate and nitrite reductase, respectively. Also, wide variations in alkaline phosphatase activities of *A. flos-aquae* are found, as a function of growth conditions (74). A number of enzymes of amino acid anabolism are feedback-inhibited, and, at least in *A. quadruplicatum*, repression controls the concentrations of enzymes in the pathway of tryptophan biosynthesis. Growth in the presence of acetate or glucose has very little effect on the level of enzymes of acetate and glucose metabolism in *A. variabilis* (118, 626a). However, the activities of certain enzymes of carbohydrate metabolism (pyruvate kinase, phosphofructokinase) are inhibited or increased by metabolites (626a).

Chromatic variation. Nitrogen-deficient *A. nidulans* was found to contain normal levels of chlorophyll *a* and carotenoids, but to lack phycocyanin. Upon addition of nitrogen to such a culture, net protein synthesis begins almost immediately, and net RNA synthesis begins soon thereafter. Phycocyanin is first detected 3 to 4 h after addition of nitrogen. Net DNA synthesis is observed only after recovery of "normal" pigmentation is almost complete (13). Qualitative tests with other blue-green algae suggest that loss of phycocyanin is a characteristic feature of nitrogen deficiency in these organisms. This pigment presumably serves in part as a nitrogen reserve (13, 40, 705). The phycocyanin content of *A. nidulans* (as percent of dry weight) approximately doubles when air is supplemented with 1% CO_2 (207).

When *A. quadruplicatum* strain PR-6 is grown with uric acid as nitrogen source, it grows slowly (0.47 doublings per day; cf. 7.3 doublings per day with nitrate), with cell size slightly greater than when growing with nitrate, and with a grossly altered cellular composition (cf. Table 6) characterized by a low content of proteins (including pigments) and a high content of carbohydrate, particularly polyglucosides (40).

The color of certain blue-green algae is dependent on the intensity of incident light (250). Increasing the intensity of light incident on *A. nidulans* results in a decrease in the amounts of chlorophyll and phycocyanin per gram of cells, with much less change in the amount of carotenoids (11, 556).

In the presence of a single 10-W, clear, tungsten lamp to permit maintenance of a constant growth rate, *A. nidulans* responds to a high intensity of red light by sharply reducing its cellular chlorophyll despite an essentially unchanged phycocyanin content. Cells grow with one-fourth of the usual chlorophyll content (436; cf. also 177).

It was demonstrated in the early 1900's that certain members of the *Oscillatoriaceae* assume a color complementary to the color of the incident light. However, this work was in part subject to the criticism that light of constant intensity was not employed (see review and critique in 250).

Fujita and Hattori (260–263, 351), in a very penetrating series of investigations, studied chromatic adaptation in *T. tenuis*. They showed that a 6-min final illumination following a 20-h preillumination determines the proportions of phycocyanin and phycoerythrin

formed during a subsequent dark period, the sum of the two proteins being approximately constant. Final illumination with green light (action maximum, 541 nm) results in maximum production of the red pigment, phycoerythrin, whereas final illumination with red light (action maximum, 641 nm) results in maximum production of phycocyanin. If a sequence of alternating illuminations with red and green light terminates the light period, the pigment formed in the dark depends on the final illumination. The logarithm of the amount of phycoerythrin formed in the dark is proportional to the product of the time and intensity of illumination with green light, and is unaffected by a dark break of up to 3 h separating two parts of the green illumination. Energy requirements for half-maximal photoinduction of phycoerythrin and phycocyanin are on the order of 10^6 ERG/cm^2. The action spectra (Fig. 14) and other evidence make it appear that phycocyanin and phycoerythrin themselves are not the pigments which determine biliprotein formation in the dark following illumination. The authors hypothesize that the photoreceptors are precursors of the bile pigments. However, it may be that a single phytochrome-like absorber is functioning, with transformation from one form of the absorber to another during irradiation, and with pigment production in the dark a nonlinear function of the amounts of absorber in the two forms. Such a photoreversible pigment, with absorption maxima at about 520 and 650 nm, has been obtained from *Tolypothrix* (671a). The action spectra of chromatic adaptation in *T. tenuis* resemble the action spectra of *Nostoc* development.

Development of Nostoc muscorum strain A. Heterocyst-free hormogonia of *N. muscorum* strain A, derived by abscission of sequences of vegetative cells from heterocyst-containing filaments, develop as follows, forming an "aseriate stage": terminal cells differentiate as heterocysts; each intercalary cell is said to divide in a plane parallel to the axis of the trichome, forming a packet of cells (494). In complete darkness, slow growth occurs in the form of the aseriate stage. If the alga, grown in the dark, is exposed to moderate illumination with white light for a few minutes, such packets expand into long filaments containing intercalary heterocysts, in 3 to 4 days in the dark. An extract of light-grown cells has the same effect as does light (493). In the active region of the spectrum, the percent of microcolonies, seeded in agar, which later develops is proportional to the time and to the intensity of the incident light, 1.6×10^5 erg/cm^2 being sufficient to induce development of 50% of the aseriate microcolonies. The induction of development by red light is antagonized by simultaneous or subsequent exposure to green light (491, 492). The action spectra (Fig. 14), although not corresponding to the absorption spectra of phycocyanin and phycoerythrin, resemble the action spectra of chromatic adaptation by *Tolypothrix*. Photomorphogenesis in *N. commune* is essentially identical to that in *N. muscorum*, except for different relative quantum effectiveness of red and green light (656; and cf. 220).

Spores (akinetes). Spores of blue-green algae often have been observed to germinate, and have been taken to be resistant cells, but the nature and extent of their resistance have been studied little. Spores of species of *Nostoc* and *Cylindrospermum* survive heating to much higher temperatures than do vegetative cells (310).

Both phosphorus deficiency (296, 823; and cf. 310, 688) and nitrogen deficiency (172, 343, 707; and cf. 310) have been implicated as factors particularly important in the control of sporulation. The importance of other factors, including the light intensity, temperature, and culture density, has been documented (823; cf. also 109, 172, 343). Factors about which nothing is known appear to be involved in the very extensive differentiation of vegetative cells into spores in clonal colonies of *Anabaena doliolum* (706) and in the sporulation of *A. cylindrica* in the presence of high concentrations of phosphate (823). Heterocysts have been shown to play a role in the sporulation of *A. cylindrica*, in which akinetes normally form adjacent to heterocysts (823, 824; see following section).

Spores have been purified by destroying vegetative cells with a French press and then separating spores from heterocysts by means of centrifugation (217, 828). The isolated spores are capable of germination (217).

Spores of blue-green algae (Fig. 15) are to some extent similar to vegetative cells. Thus, the photosynthetic thylakoids can be retained during sporulation (140, 486, 502, 547). Spores of *A. cylindrica* have some or all of the pigments of vegetative cells (216, 828), and retain the capacity for photosynthetic CO_2 fixation and for respiration (217). Spores can contain glycogen (547, 837), polyhedral bodies (140, 547), presumed lipid granules (140, 547), and numerous large cyanophycin granules. Phosphate granules are apparently absent from

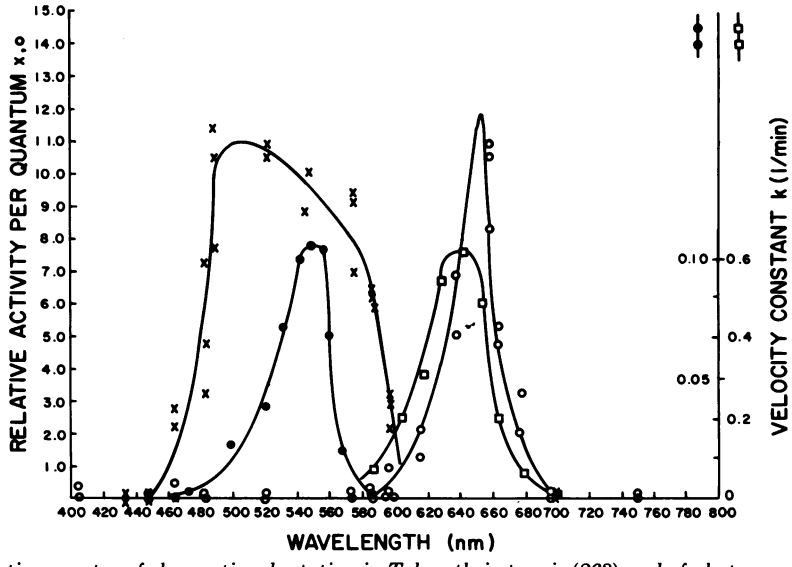

FIG. 14. *Action spectra of chromatic adaptation in Tolypothrix tenuis (263) and of photomorphogenesis in Nostoc muscorum (491). Red light results in enhanced formation of phycocyanin and diminished production of phycoerythrin during a subsequent dark incubation of Tolypothrix (□) and leads to the transition from an aseriate form of growth to filamentous growth in Nostoc (○). These effects are reversed by irradiation with green light (● and ×, respectively). Courtesy of Y. Fujita (263) and N. Lazaroff (491); with permission. The units of activity of light are defined in detail in the two publications cited.*

mature spores (750; and cf. 140, 486, 547). Spores of other species are unpigmented (294).

Spores are larger than vegetative cells. Unlike growth of vegetative cells, growth of spores is not accompanied by septation and is determinate in extent. The physical constraint imposed by the thick envelope surrounding the cell wall may determine the maximum size attained by spores of any given species. Deposition of the envelope is the only sporulation-associated process known which appears to differ qualitatively from processes of vegetative growth (140). The composition of a wall-plus-envelope fraction isolated from spores of *A. cylindrica* was found to be: 41% carbohydrate, 24% amino compounds, 11% lipid, 2% ash, and the balance unaccounted for. The composition of the carbohydrate moiety is 76% glucose, 17% mannose, 4% xylose, and 3% galactose (192; see "heterocysts"). Because the envelope is far thicker than the cell wall, the composition of the fraction isolated must approximate the composition of the envelope.

During germination, localized rupture of the envelope permits outgrowth of the germling before or after septation. The cell wall of the spore, internal to the envelope, is retained as the cell wall of the germling (547). Large spores of blue-green algae contain much more nuclear material than do vegetative cells (776a, 837). It seems probable that further replication of DNA need not precede septation during germination of these spores.

Use of a species such as *A. doliolum*, in which synchronous sporulation of vegetative cells can occur naturally (707), should permit biochemical study of the processes of differentiation and germination of spores of blue-green algae. The possibility of inducing synchronous sporulation of other species is suggested by the observation that *A. cylindrica*, which normally forms only short strings of spores adjacent to heterocysts, forms some long chains of spores in the presence of a salt of glucuronic acid (823).

Intercellular interactions; control of patternization. The end walls of intercalary cells of filamentous blue-green algae are sometimes much thinner than the side walls (e.g., 289), and supposed "pores" are seen in the end walls of these cells as well as in the end walls of heterocysts (485, 809). Intercellular chemical communication can occur, possibly via these pores: staining of members of the *Oscillatoriaceae* with methylene blue (86, 676) or ruthenium red (543) begins in the end cell of a filament, independent of whether the cell is apical or the result of cutting the filament, and proceeds slowly along the filament. The stains move more rapidly via a number of end walls

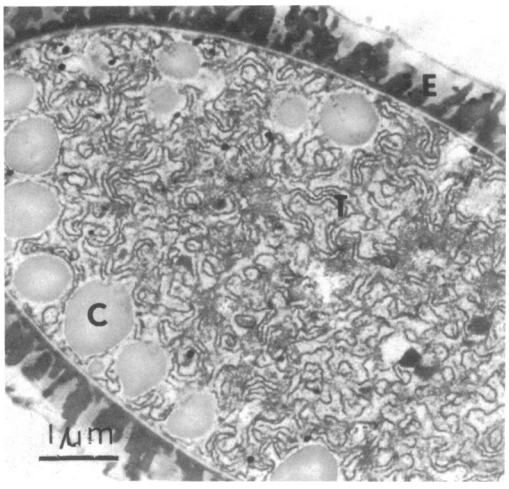

FIG. 15. *Maturing spore of Cylindrospermum sp. Thylakoids (T), the envelope (E), and cyanophycin granules (C) are indicated. Courtesy of R. L. Clark and T. E. Jensen (140); with permission.* ×*10,100.*

and membranes than they do through the single side wall and membrane of the cells of the filament. The studies of Drews (185) of photophobotaxis were the first to demonstrate intercellular interactions of physiological significance in blue-green algae (see "response to a gradient of intensity").

Cytophysiological gradients occur along filaments. For example, gradients of cell diameter and extent of vacuolization in the *Rivulariaceae* (294) DNA per cell (253, 776a; see also 333), accumulation of the fluorescent pigment uranina (404, 405), and biliprotein content during aerobic release of *A. cylindrica* from nitrogen starvation (323) have been observed. These gradients may result in part from unequal cell division. It appears likely, however, that intercellular interactions are responsible for some such gradients (cf. 222).

Evidence supporting a role of heterocysts in the sporulation of adjacent vegetative cells, a role suggested 110 years earlier (119), has been presented by Wolk for *A. cylindrica* (823, 824). The same author showed that heterocysts inhibit nearby vegetative cells, within the same filament, from becoming heterocysts, and thereby mediate the pattern of vegetative growth of *A. cylindrica* (825). The latter pattern consists of a semi-regular spacing of heterocysts along the algal filaments. Thus, the developmental patterns found in filaments of this alga—and probably the patterns found in related algae as well—are dependent on intercellular interactions called "inductions" and "fields of inhibition," well known but little understood in studies of the development of multicellular eukaryotes. To elucidate the interactions which control the development of the alga remains a challenging problem.

By means of pulse-label experiments in which the movement of ^{14}C was followed by autoradiography and by isolation of heterocysts, it was shown that part of the carbon fixed photosynthetically by vegetative cells moves through filaments into heterocysts, where it is incorporated into cellular constituents (826). In addition, the high specific activity of nitrogenase in heterocysts of aerobically grown *A. cylindrica* (829, 830) implies the occurrence of a flux of products of N_2 fixation from the nongrowing heterocysts to vegetative cells.

Carbohydrates—for which heterocysts may normally act as sinks—can inhibit sporulation of vegetative cells (343, 821). Sources of fixed nitrogen can mimic or stimulate the inhibition by heterocysts of heterocyst formation (see "heterocysts"). Thus, the movement of carbon-containing substances into, and of nitrogenous metabolites out of, heterocysts may be relevant to the control of the developmental patterns within algal filaments (222, 821). The identities of the moving C and N compounds are as yet unknown.

Heterocysts. Micrographs of thin sections of heterocysts presented by many authors (131, 221, 328, 329, 449, 469, 483, 485, 502, 654, 681, 805, 809, 816) may be summarized by the reconstruction in Fig. 16.

As is evident in the light microscope, one of the most prominent processes in heterocyst differentiation is formation of the thick outer envelope of the heterocyst. This envelope consists of a peripheral "fibrous" region, a thick "homogeneous" layer subjacent to it (and possibly of identical composition), and a laminated layer, which borders on a wall the structure of which is similar to the wall of a vegetative cell (485). Ultrastructural (483) and physiological (191) evidence implies that the wall of a vegetative cell, including its peptidoglycan-containing layer L_{II}, is largely retained during heterocyst differentiation. Based on the content of glucose and mannose, an envelope-plus-wall fraction was found to account for 52% of the dry weight of isolated heterocysts of *A. cylindrica* (192). This fraction contains 62% carbohydrate, 15% lipid, 4% amino compounds, and 2% ash (balance not accounted for).

Since the lipid content of this fraction probably corresponds largely to the laminated layer (see below), and the vegetative wall can account for the amino compounds and a very small percentage of the carbohydrate, the car-

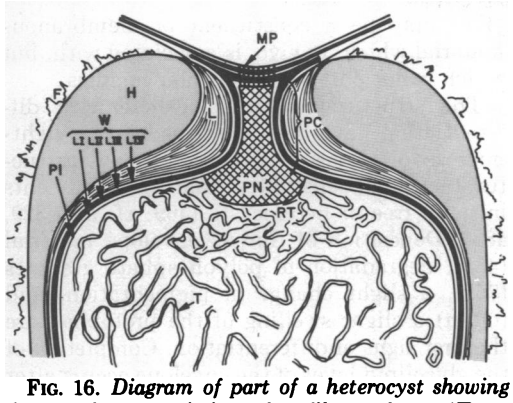

FIG. 16. *Diagram of part of a heterocyst showing the envelope consisting of a fibrous layer (F), a homogeneous layer (H), and a laminated layer (L); the subjacent wall (W), with its four layers (L_I-L_{IV}); the plasmalemma (Pl); microplasmodesmata (MP); a polar nodule (PN) in the pore channel (PC); and thylakoids appearing relatively "normal" near the center of the cell (T) and reticulated (RT) near the ends of the cell. The end wall (top) of the adjacent vegetative cell is also shown. The thicknesses of the wall layers L_I-L_{III} are exaggerated, for clarity. (After Lang and Fay [485].)*

bohydrate moiety appears to correspond principally to the "fibrous" and "homogeneous" layers of the envelope. The composition of the carbohydrate moiety, 73% glucose, 21% mannose, 4% xylose, and 3% galactose (192), is very similar to the composition of the polysaccharide in the wall-plus-envelope fraction isolated from spores. It will be interesting to find out whether the envelopes of heterocysts and spores have in common a polymer not found in vegetative cells. If so, it would provide support in chemical terms for Geitler's (288) hypothesis—based on morphological observations—that metabolic processes taking place in filaments call forth, at particular loci, changes which are equally favorable for the formation of spores or heterocysts, and that the decision as to which is to be formed comes late, or at least later. In that they have only three cell types, *Anabaena* and closely related organisms seem naturally suited for an inquiry into the relationship between alternative differentiation processes. Geitler's hypothesis has the merit that it associates two seemingly diverse processes, so that information learned about one may be applicable to understanding of the other.

The inner, laminated portion of the envelope appears to surround the heterocyst completely except at the junctions with adjacent vegetative cells (485, 816). At these junctions, the walls are traversed by structures which resemble plasmodesmata (485, 809). The laminated layer of the envelope apparently consists entirely of four lipids (480, 816) characteristic of heterocysts (569, 791, 828). (i) The least polar lipid is 25-hydroxyhexacosanoic acid (1-α-D-glycopyranose) ester (480; cf. also 791). (ii) Small amounts of a slightly more polar lipid ester are found. (iii) Yet more polar, and most abundant, is 1-(*O*-α-D-glycopyranosyl)-3,25-hexacosanediol. (iv) The most polar lipid is 1-(*O*-α-D-glycopyranosyl)-3,25,27-octacosanetriol. In lipids i, iii, and iv, the carbohydrate is glucose in about 90% of the molecules, and galactose in the remainder (98, 480). This hydrophobic layer may constitute a barrier to the movement of hydrophilic molecules between the growth medium and the interior of the heterocyst (816). Such molecules, for instance, the products of nitrogen fixation by heterocysts (737, 829, 830), may be able to pass readily out of and into heterocysts only via the polar regions of the heterocysts, where these cells are in contact with adjacent vegetative cells. To what extent the envelope layers restrict diffusion of gases into heterocysts is unknown.

Nonradioactive heterocysts are able to "expose" nuclear emulsion, an effect which has been attributed to leakage of an internal "reductant" (737). The normal pallor of heterocysts as seen with the light microscope is due to lack of absorption by phycocyanin (217, 737, 757, 758, 828; and cf. 816). However, phycocyanin is present under certain conditions (251, 628, 757, 758), and may possibly be present under all conditions, but sometimes bleached by a reductant present (259, 816). Heterocysts contain a large fraction of the amount of chlorophyll present per vegetative cell (217, 757, 828), and all carotenoids and lipids of vegetative cells in amounts approximately proportional to their content of chlorophyll (816; and cf. 828). There is no evidence for the presence of photosystem II in heterocysts, and this system is absent from heterocysts isolated by means of a French press (178). If heterocysts in situ lack photosystem II and if they respire actively (223; cf., however, 221), they may have a very low internal partial pressure of oxygen (222). An active photosystem I is present (178, 828), and physiological evidence suggests that heterocysts are capable of both photoreduction and photophosphorylation (829). Heterocysts fix little or no CO_2 (826). The membranes of heterocysts, especially in the polar regions of the cells, are often much more reticulate than those of vegetative cells (see, e.g., 483). It is as yet unknown if the difference in conformation

of the membranes is due to a difference in composition or to a difference in the intracellular milieu. It is also unknown what relation, if any, there is between the presence of a "reductant" in heterocysts (737), the apparent presence of an endogenous electron source for photoreduction of acetylene (829), and the fact that, under anaerobic conditions in the dark (C. P. Wolk, unpublished data), heterocysts are the major or sole site of reduction of triphenyltetrazolium chloride in algal filaments (181, 443, 737, 751, 765).

Further study of the nonstructural constituents of heterocysts would be greatly facilitated by (i) a nondamaging means of isolating heterocysts and (or) (ii) a means of achieving synchronous differentiation by all cells in a culture. Most methods (French press, cavitation, osmotic lysis) presently in use to isolate heterocysts lead to cytological damage to those cells (221), leakage of enzymes (830), and partial autolysis (816). A possible approach to (i) is to destroy vegetative cells with lysozyme, which appears to leave the ultrastructure of heterocysts unaltered (221). In particular, use of the lysozyme from cyanophage might permit isolation in a time sufficiently short to prevent degeneration of heterocysts detached from vegetative cells. Very rapid isolation might be unnecessary if the (unknown) nutritional requirements of detached heterocysts were satisfied. The rarely observed, apparently synchronous differentiation of all cells of a filament into heterocysts (821) suggests that approach (ii) may be possible.

Nothing is known about the chemistry of the nucleic acids or about the enzymes of nucleic acid metabolism in heterocysts. Since heterocysts normally do not germinate (see below), it is possible that enzymes which replicate DNA are absent. Polyhedral bodies disappear during the differentiation of heterocysts (483). Glycogen granules may remain for a long time, but are said eventually to disappear (483). It is unknown if the disappearance of these inclusions represents a cessation of synthesis, together with unchanged breakdown, or accelerated breakdown; and it is unknown how the products of their degradation are utilized.

Material frequently seen in the polar regions of heterocysts has the ultrastructural appearance (221), high arginine content (229), and property of solubility in dilute acid (1 N HCl; C. P. Wolk, unpublished data) common to cyanophycin granules (488; cf. also 45, 461), and may represent a storage form for nitrogen fixed by heterocysts (see below). Chlorophyll present together with isolated polar nodules (178) may be a constituent of membranous material which, in vivo, is associated with, but which is not part of, these polar nodules.

The structural features of heterocyst differentiation have been described at the light-microscopical level (229) and at the ultrastructural level, on cells differentiating in filaments initially free of heterocysts (469; cf. also 329, 483). Deposition of fibrous envelope material (485), degradation of polyphosphate granules (752), a slight change in pigmentation, and (often) a slight swelling of the protoplast are the first signs of differentiation. Completion of the glycolipid layer of the envelope occurs after deposition of the polysaccharide component of the envelope (469), and probably leads to a profound change in the interactions between the protoplast of the heterocyst and the milieu. Thus, the deposition of the envelope may have extensive, additional effects on the metabolism of the developing heterocyst. Morphological differentiation can take place in less than 5 h (191, 469).

Fogg (228; cf. also 687) showed that nitrate, ammonium, and other sources of fixed nitrogen inhibit heterocyst formation in *A. cylindrica*. Substances affecting heterocyst formation were found to do so only while growth was occurring. However, Neilson et al. (559) observed that when an *Anabaena* sp. with a heterocyst-vegetative cell ratio of about 0.01% is starved for nitrogen under an atmosphere of A-CO_2, that ratio can increase to about 12% without any apparent, significant change in cell concentration. In a number of blue-green algae, heterocyst formation is completely suppressed by about 26 mM nitrate (615), but nitrogen sources have been reported not to inhibit heterocyst formation in *Anabaenopsis raciborskii* and *Cylindrospermum majus* (475). Nitrate was found to inhibit heterocyst formation in chemostat cultures of an *Anabaena* sp. only below a certain dilution rate (759), suggesting that nitrate may act via a metabolic derivative. It has been argued that ammonium itself is not the in vivo "repressor" of heterocyst formation in one strain of *A. cylindrica*, since it does not completely inhibit heterocyst formation in that alga (827). Release from ammonium inhibition has been used as a means of quasi-synchronizing the formation of heterocysts (469, 753). (In studies of the effects of metabolic inhibitors on heterocyst formation controlled in this fashion, it is essential to ascertain whether any observed effect is an indirect consequence of effects on growth.) Other studies of the effects of nitrogen sources (545, 594, 707, 821) and of other substances (172, 173) on heterocyst for-

mation have not elucidated the intracellular control of this process.

Simultaneous formation of spaced sequences of heterocysts (686), e.g., upon transfer of filaments of *A. cylindrica* from ammonium-containing to nitrogen-free medium (827), has been interpreted by Wilcox (807) as implying the continuous existence of sequences of relatively closely spaced "proheterocysts" during growth in the presence of ammonium (cf. also 752). However, ultrastructural evidence for the occurrence of proheterocysts in ammonium-grown filaments has been sought in vain (469). Moreover, it is not easy to understand, on the basis of Wilcox's interpretation, why very widely spaced heterocysts continue to differentiate in the presence of ammonium, in a different strain of the same species (827). It appears instead that, upon release from ammonium inhibition as well as during normal growth (825), certain cells start to differentiate, and that very early in the differentiation process, i.e., before any morphological changes have occurred which are visible in the light microscope, these cells start to inhibit differentiation of nearby cells. Morphological differentiation then proceeds at the inhibitory foci. That is, morphological differentiation may amplify or stabilize the pattern-determining, inhibitory, intercellular interactions and should facilitate their analysis but is probably not a necessary prerequisite for those interactions.

Heterocysts with particular sorts of past history exposed to particular culture media can germinate (cf., e.g., 287, 822; and see also 715), but, in view of the infrequency with which germination has been observed (251), it now cannot be concluded that heterocysts function normally as resting cells. By stimulating spore formation in *A. cylindrica* (823, 824), heterocysts can indirectly control the proportion of resting cells.

Borzi (77) and many later workers have pointed out that the fragile junction between heterocysts and vegetative cells serves as a locus for breakage of filaments. Another "physical" function ascribed to heterocysts is that they serve as holdfasts (19, 644) whereby they can, in addition, act as buttresses, permitting the branching of ensheathed filaments (461; cf. also 690).

Suggestions that heterocysts are sites for storage of cyanophycin (377; see also 85, 249, 362), supply metabolites to adjacent cells undergoing sporulation (119; cf. also 823, 824), produce substances which stimulate growth and division of nearby cells (251, 686, 687, 767), and by their formation release nitrogenous substances to adjacent cells (229) conveniently may (but not necessarily!) be subsumed under a proposal of Fay and co-workers (222, 223; and cf. 641, 642). This proposal may be restated in emended form as follows: heterocysts are the sole site of nitrogen fixation in aerobically grown (738), heterocyst-forming (653, 834) blue-green algae. That they are a major site of fixation in such algae, an interpretation consistent with the indirect results of Fay and others (222, 323, 737: see 825, 830), has been directly demonstrated by Wolk and Wojciuch (829, 830). However, other results (478, 602) provide support for the view that vegetative cells in these algae are also able to fix nitrogen. It remains to be determined unequivocally whether such vegetative cells fix nitrogen. If so, it is possible that under certain conditions, such as early stages of reversion from nitrogen deficiency (323) of heterocyst-forming species, nitrogenase activity will prove to be localized (virtually) exclusively in heterocysts.

EVOLUTION

Blue-green Algae and Other Prokaryotes.

Blue-green algae and bacteria have three characteristics, namely, presence of peptidoglycan in the cell wall, absence of a membrane delimiting the nuclear material, and nonmitotic division of the nuclear material, which distinguish prokaryotes from other living organisms (730; for additional shared characteristics cf. also 114, 202). The structure and composition of the walls of blue-green algae are typical of gram-negative bacteria. Whether these algae should be considered bacteria (419, 419a) is thus merely a matter of definition.

Two principal, possible affinities with other groups of bacteria have been suggested. (i) Certain filamentous, nonphotosynthetic, gliding bacteria, such as *Beggiatoa*, have been considered to be closely related to blue-green algae, principally on morphological grounds (e.g., 640, 726). (ii) Certain purple photosynthetic bacteria resemble blue-green algae in that they have capacities for photosynthesis and nitrogen fixation, and have membranous photosynthetic structures which can arise from the plasmalemma, and glycogen granules (202, 603). However, unlike the blue-green algae, they cannot photoooxidize water. Gliding, filamentous, photosynthetic prokaryotes with bacteriochlorophylls have recently been discovered (632). They combine features of groups (i) and (ii).

Paleontological evidence indicates that the blue-green algae are an ancient group of orga-

TABLE 11. *A comparison of cytochemical and physiological characteristics of blue-green algae and of the chromatophores of the lower red algae*

Entity or function	Blue-green algae	Chromatophores from *Bangiales*	Reference	Comment
Boundary other than membranes	Wall present	Absent	91, 281, 284	
Division	By median constriction	By median constriction	281	
Circumferential membranes	1+1	2	281, 284	
Thylakoid structure	Disjoint disks	Disjoint disks	282, 284	
Thylakoid ultrastructure	Controversial	Apparently similar to that in blue-green algae	563, 564	
Chlorophyll	*a* only	*a* only	125, 647	
P700	Present	Present	464	
Carotenoids	Numerous, including β-carotene, zeaxanthin, cryptoxanthin	β-Carotene, zeaxanthin, cryptoxanthin	741	Keto-carotenoids and glycosylated carotenoids characteristic of blue-green algae have not been found in red algae
Lipids	Monogalactosyl diglyceride, digalactosyl diglyceride, phosphatidyl glycerol, sulphoquinovosyl diglyceride	The four found in blue-green algae, plus glycerides, phosphatidyl choline, phosphatidyl inositol and phosphatidyl ethanolamine	52	Refers to intact *Porphyra* and *Porphyridium*. In other eukaryotes from which chromatophores have been isolated, the lipids characteristic of blue-green algae are the sole or major lipids found in the chromatophores (566)
Quinones	Plastoquinone A, etc., vitamin K_1, tocopherol, α-tocopherol quinone	Plastoquinone A, vitamin K_1, α-tocopherol quinone, ubiquinone	749	Refers to intact *Porphyra*
Cytochromes	*c* (or *f*-) types, and two membrane-bound cytochromes	*c* or *f*; *b* (physiological evidence)	195, 574	
Ferredoxin	Present	Not determined		Present in all photosynthetic organisms where sought
Pteridines	Present	Not reported		
DNA	Present, 2.5 nm, deoxyribonuclease digestible	2.5 nm, deoxyribonuclease-digestible fibrils present	66	Refers to chromatophores of *Laurencia* (*Florideae*)
RNA (especially ribosomal)	Present, 70*s*, containing RNA of molecular weight 0.56×10^6 and 1.06×10^6	RNAs of molecular weight 0.58, 0.68, 1.00 and 1.21×10^6 present	416	Refers to intact *Porphyridium*. 70*s* ribosomes present in chromatophores of other photosynthetic eukaryotes (114)
Glycogen granules	Present	Not observed		Starch is present outside of the chromatophores
Cyanophycin granules, phosphate granules, poly-β-hydroxy-butyrate	Present	Not observed		

Polyhedral bodies	Present	Absent		Pyrenoids, of somewhat similar form, are found in the *Bangiales*[a]
Lipid deposits	Sometimes present	Possibly present	91; cf. also 308	
Phycobilisomes	Present on thylakoid surface	Present on thylakoid surface	87, 281, 282, 284	Gantt and Conti (282) have presented the most direct evidence that phycobilisomes contain biliproteins. Biliproteins of the *Cryptophyceae* appear to be present *within* the thylakoids (285, 799)
Biliproteins	C-Phycocyanin, C-phycoerythrin, and allophycocyanin	C-Phycocyanin, of amino acid composition similar to the blue-green algal phycocyanin, or R-phycocyanin; R- or B-phycoerythrin; and allophycocyanin	60, 437, 600	Blue-green algal biliproteins cross-react immunologically with their chromatic counterparts from red algae (but not from *Cryptophyceae*) and the reaction appears not to be due to the chromophore (313)
Chromophores	Phycocyanobilin and phycoerythrobilin	Phycocyanobilin and phycoerythrobilin	126, 129, 130, 630	
Photosynthetic light reactions	Transfer of energy from biliproteins to chlorophyll; coordinate functioning of two photosystems; oxygen production (DCMU sensitive)	Transfer of energy from biliproteins to chlorophyll; coordinate functioning of two photosystems; oxygen production (DCMU sensitive)	193, 195, 574, 575	Major differences in the paths of electron transport have not been demonstrated
Pathway of photosynthetic CO_2 fixation	Calvin cycle (and probably, to a much lesser extent, carbamyl phosphate formation)	Consistent with Calvin cycle	48, 576	Refers to intact *Iridophycus* (*Florideae*) and *Porphyridium*
Assimilation of organics, nitrogen metabolism, genetics, culture		Not determined		
Chromatic adaptation	Occurs	Occurs	90	

[a] In the green alga *Eremosphaera viridis*, the pyrenoid appears to be a quasi-crystalline array of molecules of carboxydismutase, with lesser amounts of other Calvin cycle enzymes (389). It is interesting to note that polyhedral bodies are absent from heterocysts, which fix little or no CO_2 (826), whereas structurally similar inclusions are present in chemosynthetic bacteria, which can fix CO_2 (701).

nisms, at least 10^9 to 2×10^9 years old (311, 746). If, as seems possible, they were the first oxygen-evolving organisms on earth, they were probably responsible initially for producing the oxygen in the earth's atmosphere, a prerequisite for the evolution of eukaryotes whose energy requirements are normally dependent on mitochondrial respiration (603, 647).

Origin of Chloroplasts

One can hope that the advent of new analytical procedures will permit a probable evaluation of the validity of Mereschkowsky's hypothesis (542) that the photosynthetic plastids of eukaryotic plant cells are the evolutionary descendants of endosymbiotic blue-green algae. The greater are the differences between such plastids and contemporary blue-green algae, the greater would appear to be the difficulty of demonstrating such an evolutionary derivation: it may yet be discovered that prokaryotes exist, or have existed, which have (or had) chlorophylls *a* and *b*, like the *Chlorophyta* and *Euglenophyta*, or chlorophylls *a* and *c*, like the *Chrysophyta* and *Phaeophyta* (647). The question is therefore most properly put as follows (647). Did the chromatophores (chloroplasts) of one algal division, the *Rhodophyta*, arise from blue-green algae? (The alternative hypothesis, according to which a blue-green alga assimilated all of the organelles and functions necessary to evolve into a rhodophyte appears immeasurably less probable.)

The validity of such a possibility could be tested by determining: (i) whether such a process of endosymbiosis can occur, and, if it can occur, then by examination of the differences and similarities of the presumptive endosymbiont and contemporary blue-green algae (ii) whether the endosymbiont would probably have been identified as a blue-green alga. An affirmative answer to (ii) would require such an extensive array of similarities as to render extremely unlikely the alternative possibility of parallel evolution of the chromatophores and the prokaryotic algae.

It remains to be seen whether man can incorporate a blue-green alga into a eukaryotic cell in such a way that the two replicate in synchrony, with the eukaryote deriving nutrition from the prokaryote. A particularly salutary effect on human nutrition might follow if this could be achieved with a nitrogen-fixing blue-green alga and a nonleguminous crop plant, so that the plant could derive all of its nitrogen from the atmosphere.

A major difference between blue-green algae and photosynthetic plastids is the presence of cell walls in the former and their absence in the latter. *Geosiphon pyriforme* (460, 681) illustrates the inclusion of a *Nostoc*, complete with its walls, topologically within hyphae of a fungus (but surrounded by a membrane derived from the fungal plasmalemma). Intracellular "cyanelles" (293, 622), similar in morphology and pigmentation (125) to blue-green algae, were supposed to have walls (rather than merely circumferential membranes) on the grounds that they do not become disorganized following removal from a host, and this supposition is supported by the finding that the cyanelle from *Cyanophora paradoxa* has a lysozyme-sensitive envelope (672). However, no boundary other than a membrane was observed around the cyanelles in electron micrographs of *C. paradoxa* (338) and *Glaucocystis nostochinearum* (507; cf. also 339, 682, 683, 776).

It is unfortunate that intact chloroplasts of red algae have not as yet been isolated and their cytochemical and physiological characteristics determined following isolation. Known similarities of, and differences between, blue-green algae and the chromatophores of members of the *Bangiales*, or lower red algae, especially *Porphyridium*, are summarized in Table 11.

It may be concluded from this table that there is a striking but incomplete degree of similarity between the cells of blue-green algae and the chromatophores of the lower red algae. If such chromatophores were found free-living (as some halobacteria lack a peptidoglycan wall), they would probably be considered blue-green algae, albeit highly atypical ones. However, it is far from clear just what degree of metabolic autonomy is characteristic of such chromatophores. It also remains to be seen how closely related are the amino acid sequences of, and corresponding genetic codes for, the proteins common to the blue-green algae and to the chromatophores of members of the *Bangiales*. Nonetheless, the information available at the present time appears to justify use of the Mereschkowsky hypothesis as a "working hypothesis" for the origin of the chloroplasts of red algae.

ACKNOWLEDGMENTS

I thank Michael Jost, Anton Lang, David Krogmann, and Jack Myers and his colleagues, who read all or parts of the manuscript, and made helpful suggestions. I thank also the authors and publishers who generously permitted me to reproduce their figures. Support by the U.S. Atomic Energy Commission under contract AT(11-1)-1338 is gratefully acknowledged.

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