Plant Physiol. (1989) 91, 770–774
0032-0889/89/91/0770/05/$01.00/0

Received for publication February 2, 1989
and in revised form June 6, 1989

Functional Analysis of the Photosynthetic Apparatus of *Prochlorothrix hollandica* (Prochlorales), a Chlorophyll *b* Containing Procaryote[1]

Tineke Burger-Wiersma* and Anton F. Post

Laboratory for Microbiology, University of Amsterdam, Nieuwe Achtergracht 127, 1018 WS Amsterdam, The Netherlands

ABSTRACT

Light-shade adaptation of the chlorophyll *a/b* containing procaryote *Prochlorothrix hollandica* was studied in semicontinuous cultures adapted to 8, 80 and 200 μmole quanta per square meter per second. Chlorophyll *a* contents based on dry weight differed by a factor of 6 and chlorophyll *b* by a factor of 2.5 between the two extreme light conditions. Light utilization efficiencies determined from photosynthesis response curves were found to decrease in low light grown cultures due to lower light harvesting efficiencies; quantum requirements were constant at limiting and saturating irradiances for growth. At saturating growth irradiances, changes in light saturated oxygen evolution rate originated from changes in chlorophyll *a* antenna relative to the number of reaction centers II. At light-limiting conditions both the number of reaction centers II and the antenna size changed. The amount of chlorophyll *b* relative to reaction center II remained constant. As in cyanobacteria, the ratio of reaction center I to reaction center II was modulated during light-shade adaptation. On the other hand, time constants for photosynthetic electron transport (4 milliseconds) were low as observed in green algae and diatoms. The occurrence of state one to two and state two to one transitions is reported here. Another feature linking photosynthetic electron transport in *P. hollandica* to that in the eucaryotic photosynthetic apparatus was blockage of the state one to two transition by 3-(3,4-dichlorophenyl)-1,1-dimethylurea. Although chlorophyll *b* was reported in association with photosystem I, the 630 nanometer light effect does not exclude that chlorophyll *b* is the photoreceptor for the state one to two transition.

Cellular pigment levels and photosynthesis in phytoplankton are tuned to the ambient light field, and the adaptive patterns show great similarities between algae and cyanobacteria (9, 20). Two strategies of light-shade adaptation based on the concept of PSU[2] have been described (10); either the PSU changes in size due to changes in the amount of light harvesting antennae relative to the reaction centers of PSI and PSII, or PSU numbers change due to an altered number of reaction centers. Green algae and diatoms are reported to increase PSU size and/or number during shade adaptation (8–10, 19), whereas cyanobacteria showed enlarged PSU sizes only (11, 15). The main features in which the photosynthetic apparatus of the cyanobacteria differs from that of the green algae are: (a) the thylakoid membranes are located in the cytoplasm and not in chloroplasts; (b) the main light harvesting antennae are the phycobilisomes which are extrinsic to the thylakoid membrane; (c) absence of Chl *b* in the light harvesting Chl-protein complexes.

Prochloron didemnii, an endosymbiont in tunicates, was the first reported procaryote with a pigment combination resembling that of green algae (17). Chl *a/b* ratios ranged from 3.8 to 6.9 (26, 28), and PSU sizes were reported as 240 (28) and 800 (25) Chl/P_{700}. A light-harvesting Chl *a/b* protein of 34 kD apparent molecular mass was found, but the observed phosphorylation of this protein could not be related to state 1→2 transitions (26). Significant amounts of Chl *b* were found associated with PSI (13). The lack of state 1→2 transitions was related to *P. didemnii's* occurrence at depths of 12 to 80 m, an environment from which far red light needed for the state 2→1 transition is permanently absent (26).

A second, but free-living procaryote containing Chl *b* was isolated from a shallow freshwater lake, where it maintains itself as one of the dominant species (4, 5). The first thylakoid membrane analyses of this prochlorophyte, *Prochlorothrix hollandica*, were performed by Bullerjahn *et al.* (3). A 30 to 33 kD Chl *b* binding protein was detected along with the presence of Chl *b* antenna molecules functionally coupled to the PSI reaction center. In contrast, the bulk of Chl *b* in green algae and higher plants is found in the light harvesting complexes of PSII (LHC II), where it is bound to apoproteins of 20 to 29 kD apparent molecular mass (2, 16, 27). This complex is shown to be directly involved in state 1→2 transitions (16). In *Dunaliella*, changes in Chl *a/b* ratios during light-shade adaptation were related to changes in Chl *b* binding to LHC II (27). In parallel with higher plants and green algae (*e.g.*, 2, 16), one would expect the Chl *b* binding LHC to be involved in the regulation of energy (re)distribution between PSII and PSI. However, the procaryotic nature of *P. hollandica* would predict energy distribution by spillover regulation directed by respiratory and photosynthetic electron

[1] This research was performed under auspices of the Department of Public Housing, Physical Planning and the Environment of the Netherlands. A. F. P. was supported by a special research grant from the Royal Dutch Academy of Sciences.

[2] Abbreviations: PSU, photosynthetic unit; RCI, reaction center of PSI; RCII, reaction center of PSII; LHC, light harvesting complex; σ_{Chl}, Chl *a* specific optical cross-section; σ_{cells}, optical cross-section of cells; α, light utilization efficiency; $1/\phi$, minimum quantum requirement; P_{max}, light saturated oxygen evolution rate; τ, time constant for the rate of linear electron transport; LL, HL, and HHL, 8, 80, and 200 μmol quanta $m^{-2}s^{-1}$.

transport (*e.g.*, 18). Here we report on a study on the light-shade adaptation in *P.hollandica* with respect to Chl *a/b* ratios, photosynthetic activity, PSU size and number, as well as to the occurrence of state transitions.

MATERIALS AND METHODS

Growth Conditions

Cultures of *Prochlorothrix hollandica* CCAP 1490/1 (4) were grown at 20°C in 2 L cylindrical vessels using a mineral medium (4). Continuous illumination was provided by circular fluorescent lamps (Philips TLEM 40W/33 and TLE 32W/33). Cultures were constantly mixed by aeration with sterile pressurized air. Cultures were operated in a semicontinuous mode, *i.e.*, culture density was kept low by daily dilution with fresh medium: $A_{750nm} = 0.10 \pm 0.02$, equivalent to 0.2 to 1.7 μmole Chl *a* per L, depending on growth condition. These conditions ensured a shallow light gradient over the 3.5 cm radius of the culture vessel. At all growth conditions, cultures were considered to be fully adapted after 30 d of growth. Irradiance values were measured in the center of the culture flasks using a spectroradiometer (type LI 1800, Li-Cor Inc, Lincoln NE).

Dry Weight

Dry weights were determined on washed samples, pelleted on Whatman GF/F filters and dried at 80°C for at least 16 h.

Chl

Chl *a* and *b* were calculated from absorption spectra of 90% acetone extracts of whole cells (14).

Photosynthesis Measurements

Photosynthetic oxygen evolution was measured in a well defined light field using an incubator chamber with flat face optics, and a multigain operational amplifier (7). This device was also used for the measurement of oxygen flash yields, allowing the estimation of the PSU size of RCII (19). Trains of saturating light flashes from EG&G FX-279 xenon flash tubes (<6 μs duration) were provided at various frequencies (0–40 Hz). Continuous far red illumination (710 ± 8 nm, 6 μmol quanta $m^{-2}s^{-1}$) ensured sufficient PSI activity and elimination of the "Kok" effect.

P_{700}

P_{700} content was determined in thylakoid membranes pelleted at 110,000*g* after several washes in 50 mM Tricine·NaOH buffer (pH = 8.0). Oxidation and reduction using 1 mM $K_3Fe(CN)_6$ and 5 mM Na-ascorbate, respectively, was traced with an Aminco dual wavelength spectrophotometer (type DW2000, SLM Instruments Inc., Urbana IL) at 703 nm using a 730 nm isobestic wavelength (11).

Optical Cross-Section

Chl *a* specific optical cross-sections (σ_{Chl}) were determined using a newly designed integrating sphere (Fig. 1). Light from an Osram HLX 64640 xenon lamp was collimated through a set of lenses and narrowed by a diaphragm to a beam with 0.6 cm diameter. Before entering the sphere through an opening 1.6 cm in diameter, the light beam passes a 1 cm sample cuvette with a 3 × 3 cm surface area. Once in the sphere light is diffused by a $BaSO_4$ layer with 100% reflectance in the PAR range. Light is detected with a Licor LI-195 SB quantum sensor mounted at an angle of 120° to the sphere's opening. This system allows for detection of forward scattering up to 30°. Most forward scattering occurs at a less than 10° angle and back scattering is less than 1% (12). This device allows to determine optical cross-sections in the PAR wavelength band as described previously (8).

Fluorimetric Determinations

Variable yields of PSII fluorescence were measured according to Post *et al.* (22). Light 1 and 2 were obtained using Schott double band interference filters of 714 and 630 nm, respectively, both with a half bandwidth of 8 nm (23).

Calculations and Statistics

The data given in the figures and tables are the average of at least triplicate measurements. All calculations were performed using standard methods (8). Student's *t*-test was used for statistical analyses.

RESULTS

Light Intensity Adaptation

Cultures of *P. hollandica* were grown at 8 (LL), 80 (HL) and 200 (HHL) μmol quanta $m^{-2}s^{-1}$ of which only LL light was limiting growth. Table I shows that lower irradiances invoked increased levels of Chl *a* and *b*. In contrast to a previous report (5), we observed a marked change in the Chl *a/b* ratio. The absorption spectra of thylakoid preparations of LL- and HHL-grown cells illustrate the increased contribution of Chl *b* relative to Chl *a* in HHL cells (Fig. 2). LL cells

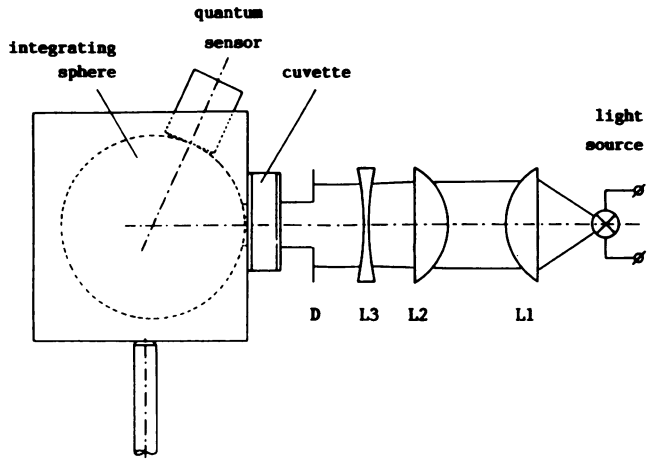

Figure 1. Experimental setup for the determination of optical cross-sections of suspended phototrophic microorganisms. *D* = diaphragm; *L1*, *L2*, and *L3* = lenses to collimate the light from the Osram HLX 64640 lamp.

Table I. *Effect of Culture Irradiance on Growth Rate, Pigment Contents, and Parameters of Light-Limited Photosynthesis in P. hollandica*

Culture	I[a]	μ[b]	Chl a[c]	Chl a/b[d]	α[e]	σ_{Chl}[f]	σ_{cells}[g]	$1/\phi$[h]
LL	8	0.003	40	18	33	6.4	0.26	11.6
HL	80	0.020	12	15.5	51	10.1	0.12	11.8
HHL	200	0.020	7	7	59	19.0	0.13	19.3

[a] Culture irradiance, μmol quanta m^{-2} s^{-1}. [b] Specific growth rate, h^{-1}. [c] Chl a, μmol·g dry weight^{-1}. [d] Chl a/b ratio, mol·mol^{-1}. [e] Light utilization efficiency, nmol O_2·μmol Chl a^{-1}·min^{-1}/μmol quanta m^{-2} s^{-1}. [f] Chl a specific optical cross-section, m^2·mmol Chl a^{-1}. [g] Optical cross-section of cells, m^2·g dry weight^{-1}. [h] Minimum quantum requirement, mol quanta·mol O_2^{-1}.

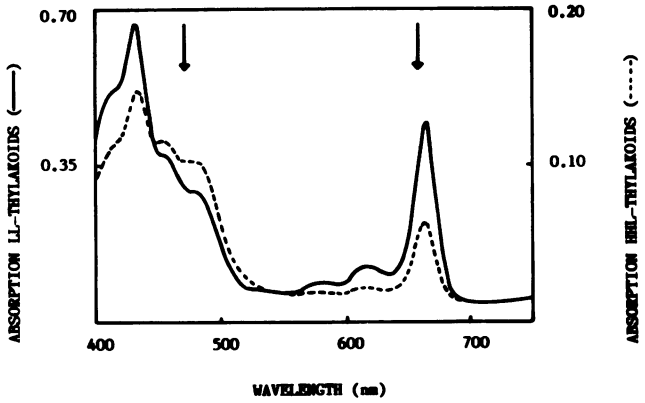

Figure 2. Absorption spectra of thylakoid preparations of *P. hollandica* cells grown at 8 (——) and 200 (- - - -) μmol quanta $m^{-2}s^{-1}$, respectively. Thylakoid isolation as described for P_{700} assay (see "Materials and Methods"). Arrows indicate Che *b* absorption maxima.

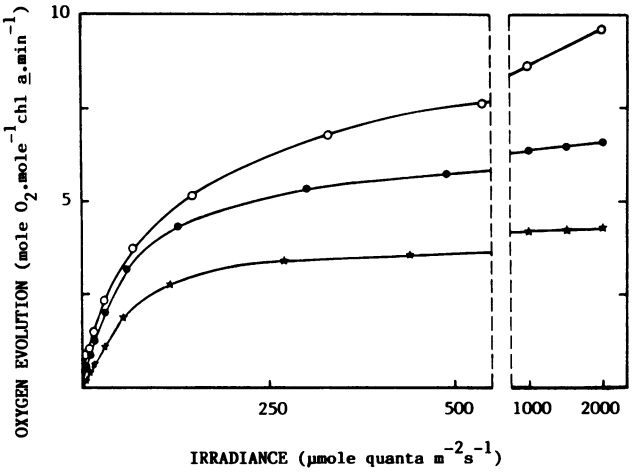

Figure 3. Photosynthesis response curves for cultures of the chlorophyll a/b containing procaryote *P. hollandica* adapted to 8 (★), 80 (●), and 200 (○) μmol quanta $m^{-2}s^{-1}$.

contained 2.5 times more Chl *b* as compared to HHL cells, whereas Chl *a* contents increased 6 times (Table I). The induced changes in photosynthetic potential are shown from the saturation curves for oxygen production *versus* irradiance (Fig. 3). The light utilization efficiency (α), which was calculated from the initial slope of the photosynthesis *versus* light intensity curves, increased with growth irradiance (Table I). However, the difference between HL and HHL cells, both growing at light saturation, was only significant at the 95% confidence level. The Chl *a* specific optical cross-section (σ_{Chl}) of LL-adapted cells was low compared to HL cells, although σ_{cells} increased considerably in the LL situation. Changes in σ_{Chl} may be caused by packaging of Chl molecules leading to self-shading effects in, or between, thylakoid membranes. Besides this, relative changes in levels of pigments other than Chl *a* contribute to total absorption and may induce changes in σ_{Chl} (8). The quantum requirement for photosynthesis ($1/\phi$), which was derived from α and σ_{Chl}, remained unchanged for LL and HL cells. Growth in HHL caused a considerable increase in $1/\phi$, possibly due to energy dissipation in order to avoid photoinhibition.

The light-saturated oxygen evolution rate (P_{max}) was substantially lowered in LL cells (Fig. 3), suggesting that at least part of the increased Chl contents served to enhance the light-harvesting antenna. One way to determine this is by assaying the PSU sizes for LL-, HL-, and HHL-adapted cells. The PSU can be defined either as the number of Chl *a* molecules per electron transferred after a saturating light flash (Chl *a*/RCII) or as the number of Chl *a* molecules present per molecule of P_{700} (Chl *a*/RCI). The PSU size reflected by Chl *a*/RCII increased as cells became more shade adapted (significant at the 99.5% confidence level) (Table II). However, the increase in PSU size could not account for the almost sixfold increase in Chl *a* in the LL cells. From this it follows that the number of RCII in LL cells had doubled as compared to HL and HHL cells. Apparently, *P.hollandica* cells change both antenna size and PSII number in response to low light conditions. Besides of being determined by the RCII number, P_{max} is also dependent on the rate at which RCII can reopen after performing the primary reactions. This is related to the capacity of electron flow and thus by the rate at which electrons are transferred in linear electron transport. The time constant (τ) for this process is obtained from P_{max} and Chl *a*/RCII (8). For all growth conditions τ was constant at 4 ms suggesting that the rate of photochemistry is not affected by light limited growth.

Chl *a*/RCI increased by approximately 50% when LL and HHL cells are compared (Table II). This implies that the ratio

Table II. *Parameters of Light-Saturated Photosynthesis, Photosynthetic Unit Size, and Reaction Center Ratios for P. hollandica*

Culture	P_{max}[a]	Chl a/RCII[b]	n RCII[c]	Chl b/RCII[d]	τ[e]	Chl a/RCI[f]	RCI/RCII[g]
LL	4.2	868	$28 \cdot 10^{15}$	50	4.3	380	2.3
HL	6.4	521	$14 \cdot 10^{15}$	35	4.4		
HHL	9.2	335	$13 \cdot 10^{15}$	43	4.2	246	1.4

[a] Photosynthetic capacity, μmol O_2·μmol Chl a^{-1}·min^{-1}. [b] RCII-based photosynthetic unit size, mol Chl a·mol RCII^{-1}. [c] Number of RCII, g dry weight^{-1}. [d] Chl b per RCII, mol Chl b·mol RCII^{-1}. [e] Minimal turnover time of a photosynthetic unit, ms. [f] RCI-based photosynthetic unit size, mol Chl a·mol RCI^{-1}. [g] Reaction center ratio, mol·mol^{-1}.

RCI/RCII increased by 70% in the LL grown cells. Chl *b*/RCII did not significantly change with growth irradiance suggesting that *P. hollandica* has no adaptive response to LL resulting in an increased light harvesting of single PSII units. Based on this observation and a Chl *a*/*b* ratio of 3.2 (HCP Matthijs, personal communication), we calculated that the Chl *a*/*b* binding complex is constant at approximately 190 Chl *a* + *b* per RCII.

Light Quality Adaptation

Since Chl *b* contents relative to Chl *a* contents were very low in all light conditions, the question arose as to whether energy (re)distribution between PSII and PSI could occur as it does in green chloroplasts and cyanobacteria. Regulation of energy (re)distribution is routinely studied from changes in PSII fluorescence. The highly fluorescent state 1 is reached after overexcitation of PSI, preferably using light of 690 nm or higher. State 2 is established by overexcitation of PSII, most conveniently accomplished by excitation of the accessory pigment system. In this study we used 714 nm light 1 and 630 nm light 2. The latter was chosen to excite both PSI and PSII Chl *a* and Chl *b* with a slight overexcitation of Chl *b* relative to Chl *a*.

State 1→2 transitions were observed in HL-grown *P.hollandica* after changing over from a 10 min. preillumination with light 1 to actinic light 2 flashes (Fig. 4A). Steady state fluorescence was established with 630 nm light suggesting that either Chl *b* is the photoreceptor of light 2 or, alternatively, that the PSII Chl *a* antenna is larger than its PSI counterpart. Superimposing light 1 immediately elevated PSII fluorescence before the actual state 2→1 transition (indicated by the arrow) took place. Since 714 nm light was not detected by the photomultiplier, the rapid first change suggests an immediate change in direct energy transfer from PSII to PSI. Removal of light 1 caused an instant drop in fluorescence followed by a state 1→2 transition (*arrow*). Repeating these experiments in the presence of DCMU elevated the fluorescence levels (Fig. 4B). Neither state 1→2 nor state 2→1 transitions were observed and, apparently, the addition of DCMU in the presence of light 1 fixed the cells in state 1.

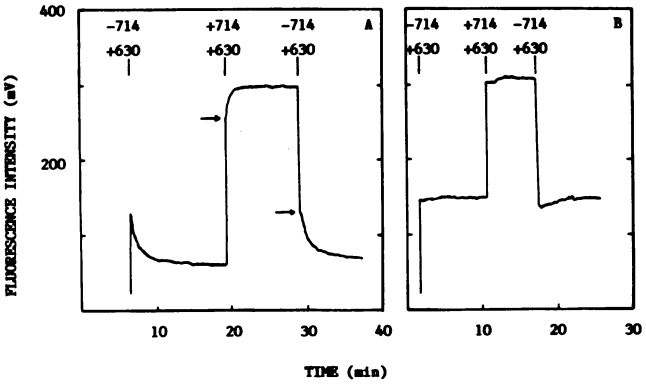

Figure 4. Changes in *in vivo* PSII fluorescence effected by continuous light 1 (714) and intermittent light 2 (630) for *P. hollandica* in the absence (A) and presence (B) of the herbicide DCMU. *Arrows* indicate start of state transition.

DISCUSSION

In essence, the experiments reported here confirm the intermediate status of *P. hollandica* between cyanobacteria and algae in light-shade adaptation phenomena. A striking feature is the increased Chl *a*/*b* ratio in LL adapted cells. In eucaryotic algae, Chl *a*/*b* and Chl *a*/*c* ratios usually decrease when cells become shade adapted (8, 10, 19, 21) due to enhanced accumulation of LHC II relative to PSI and PSII units (see, *e.g.*, Refs. 1 and 27). The amount of Chl *b* per RCII in *P.hollandica* did not change with culture irradiance, and assuming a constant Chl *a* + *b* number per binding protein, this would indicate a constant amount of the 30 to 33 kD Chl *a*/*b* binding protein per RCII. This would suggest a lack of light control on the transcription/translation in Chl *a*/*b*-protein biogenesis in *P.hollandica* whereas, among other factors, light level is a controlling factor in eucaryotic systems (1). Increase of the RCII number at LL then may be an alternative way to enhance PSII absorption (10). The relative contribution of PSI increased in LL-grown cells as was shown from the RCI/RCII ratios. This mode of adaptation is characteristic for cyanobacteria (15, 20) and a similar phenomenon is observed in chromatically adapting cyanobacteria (11, 23). In the latter case it could be directly related to balancing PSI and PSII reactions in monochromatic light (23). Its function in light-shade adaptation might be to guarantee the continuation of the ATP-generation by cyclic phosphorylation to meet energy needs for cell maintenance during periods of arrested growth.

Time constants for photosynthetic electron transport were well in the range found for green algae and diatoms (8), whereas for cyanobacteria longer time constants are reported (23). Another observation relating photosynthetic electron transport in *P.hollandica* to that in eucaryotic systems is the blockage of the state 1→2 transition after addition of DCMU. Since in cyanobacteria respiratory and photosynthetic electron transport intersect, thereby enabling state 1→2 transitions in the dark (6, 18), an apparent lack of such an interaction in *P.hollandica* is suggested by these results. The low abundance of Chl *b* in the Chl *a*/*b* protein complex in both HHL- and LL-adapted cells (this study) and the poor stacking of thylakoids (5) does not prevent light state transitions to occur to an extent known from other phototrophs. The state 2 situation is established by light absorption in accessory pigment complexes of PSII-like LHCII (2, 16, 24) or phycobilisomes (6, 18, 22, 23) which broadens the action spectrum of PSII extensively as compared to PSI. The accessory pigment of *P.hollandica*, Chl *b*, is located in a complex associated with PSI (3) (GS Bullerjahn, personal communication; GS Bullerjahn, T Jensen, D Sherman, L Sherman, submitted for publication). These observations suggest that the presence of an accessory pigment complex of PSII is not a prerequisite for light state transitions. If so, it might indicate that the process of energy (re)distribution evolved earlier than, or at least independent of, light harvesting complexes associated with PSII.

LITERATURE CITED

1. **Batschauer A, Mosinger E, Kreuz K, Dorr I, Apel K** (1986) The implication of a plastid derived factor in the transcriptional

control of nuclear genes encoding the light harvesting chlorophyll *a/b* protein. Eur J Biochem **154:** 625–634
2. **Bennett J** (1983) Regulation of photosynthesis by reversible phosphorylation of the light harvesting chlorophyll *a/b* protein. Biochem J **212:** 1–13
3. **Bullerjahn GS, Matthijs HCP, Mur LR, Sherman LA** (1987) Chlorophyll-protein composition of the thylakoid membrane from *Prochlorothrix hollandica*, a prokaryote containing chlorophyll *b*. Eur J Biochem **168:** 295–300
4. **Burger-Wiersma T, Stal LJ and Mur LR** (1989) *Prochlorothrix hollandica* gen. nov., sp. nov.: a filamentous oxygenic photoautotrophic procaryote containing chlorophylls *a* and *b*: assignment to *Prochlorotrichaceae* fam. nov. and order *Prochlorales* Florenzano, Balloni and Materassi 1986, with emendation of the ordinal description. Int J Syst Bacteriol **39:** 250–257
5. **Burger-Wiersma T, Veenhuis M, Korthals HJ, Van de Wiel CCM, Mur LR** (1986) A new prokaryote containing chlorophylls *a* and *b*. Nature **320:** 262–264
6. **Dominy PJ, Williams WP** (1987) The role of respiratory electron flow in the control of excitation energy distribution in blue-green algae. Biochim Biophys Acta **892:** 264–274
7. **Dubinsky Z, Falkowski PG, Post AF, Van Hes UM** (1987) A system for measuring phytoplankton photosynthesis in a well defined light field with an oxygen electrode. J Plankton Res **9:** 607–612
8. **Dubinsky Z, Wyman K, Falkowski PG** (1986) Light harvesting and utilization by phytoplankton. Plant Cell Physiol **27:** 1335–1349
9. **Falkowski PG** (1984) Kinetics of adaptation to irradiance in *Dunaliella tertiolecta*. Photosynthetica **18:** 62–68
10. **Falkowski PG, Owens TG** (1980) Light shade adaptation; two strategies in marine phytoplankton. Plant Physiol **66:** 592–595
11. **Fujita Y, Ohki K, Murakami A** (1985) Chromatic regulation of photosystem composition in the photosynthetic system of red and blue-green algae. Plant Cell Physiol **26:** 1541–1548
12. **Göbel F** (1978) Direct measurement of pure absorbance spectra of living phototrophic microorganisms. Biochim Biophys Acta **538:** 593–602
13. **Hiller RG, Larkum ADW** (1985) The chlorophyll-protein complexes of *Prochloron* sp. (Prochlorophyta). Biochim Biophys Acta **806:** 107–115
14. **Jeffrey SW, Humphrey GF** (1975) New spectrophotometric equations for determining chlorophyll *a*, *b*, c_1, and c_2 in higher plants, algae and natural phytoplankton. Biochem Physiol Pflanz **167:** 191–194
15. **Kawamura M, Mimuro M, Fujita Y** (1979) Quantitative relationship between two reaction centers in the photosynthetic system of blue-green algae. Plant Cell Physiol **20:** 697–705
16. **Kyle DJ, Kuang TY, Watson JL, Arntzen CJ** (1984) Movement of a sub-population of the light harvesting complex (LHC_{II}) from grana to stroma lamellae as a consequence of its phosphorylation. Biochim Biophys Acta **765:** 89–96
17. **Lewin RA** (1976) Prochlorophyta as a proposed new division of algae. Nature **261:** 697–698
18. **Mullineaux CW, Allen JF** (1986) The state 2 transition in the cyanobacterium *Synechococcus* 6301 can be driven by respiratory electron flow into the plastoquinone pool. FEBS Lett **205:** 155–160
19. **Myers J, Graham JR** (1971) The photosynthetic unit in *Chlorella* measured with repetitive short flashes. Plant Physiol **48:** 282–286
20. **Post AF** (1986) Transient state characteristics of adaptation to changes in light conditions for the cyanobacterium *Oscillatoria agardhii*. I. Pigmentation and photosynthesis. Arch Microbiol **145:** 353–357
21. **Post AF, Dubinsky Z, Wyman K, Falkowski PG** (1984) Kinetics of light intensity adaptation in a marine planktonic diatom. Mar Biol **83:** 231–238
22. **Post AF, Veen A, Mur LR** (1986) Regulation of cyanobacterial photosynthesis determined from variable fluorescence yields of photosystem II. FEMS Microbiol Lett **35:** 129–133
23. **Post AF, Zwart G, Sweerts J-P, Veen A, Rensman D, Van den Heuvel A, Mur LR** (1989) Chromatic regulation of photosynthesis in cyanobacteria. *In* Y Cohen, E Rosenberg eds, Microbial Mats, Physiological Ecology of Bentic Microbial Communities, American Society for Microbiology, Washington, DC, pp 305–312
24. **Satoh K, Fork DC** (1983) State I–State II transitions in the green alga *Scenedesmus obliquus*. Photochem Photobiol **37:** 429–434
25. **Schuster G, Nechustai R, Nelson N, Ohad I** (1985) Purification of photosystem I reaction center of *Prochloron* sp., an oxygen evolving prokaryote containing chlorophyll *b*. FEBS Lett **191:** 29–33
26. **Schuster G, Owens GC, Cohen Y, Ohad I** (1984) Thylakoid polypeptide composition and light independent phosphorylation of the chlorophyll *a/b* protein in *Prochloron*, a prokaryote exhibiting oxygenic photosynthesis. Biochim Biophys Acta **767:** 596–605
27. **Sukenik A, Wyman KD, Bennett J, Falkowski PG** (1987) A novel mechanism for regulating the excitation of photosystem II in a green alga. Nature **327:** 704–707
28. **Withers N, Alberte RS, Lewin RA, Thornber JP, Britton G, Goodwin TW** (1978) Photosynthetic unit size, carotenoids and chlorophyll-protein composition of *Prochloron* sp., a prokaryotic green alga. Proc Natl Acad Sci USA **5:** 2301–2305