PERGAMON

Phytochemistry 61 (2002) 53–60

PHYTOCHEMISTRY

www.elsevier.com/locate/phytochem

Photosynthetic energy conversion under extreme conditions—II: the significance of lipids under light limited growth in Antarctic sea ice diatoms

Thomas Mock[a,*], Bernd M.A. Kroon[a,b]

[a]*Alfred-Wegener-Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany*
[b]*KroonAqa GmbH, Knurrhahnstraße 9, D-27572 Bremerhaven, Germany*

Received 14 December 2001; received in revised form 2 May 2002

Abstract

Low photosynthetic active radiation is a strong determinant in the development and growth of sea ice algae. The algae appear to have universal mechanisms to overcome light limitation. One important process, which is induced under light limitation, is the desaturation of chloroplast membrane lipids. In order to discover whether this process is universally valid in sea ice diatoms, we investigated three species coexisting in chemostats illuminated with 15 and 2 μmol photons m^{-2} s^{-1} at −1 °C. Growth under 2 μmol photons m^{-2} s^{-1} caused a 50% increase in monogalactosyldiacylglycerols (MGDG) thylakoid membrane related 20:5 *n*-3 fatty acids. This fatty acid supports the fluidity of the thylakoid membrane and therefore the velocity of electron flow, which is indicated by increasing rate constants for the electron transport between Q_A (first stable electron acceptor) and bound Q_B (second stable electron acceptor) (11.16±1.34 to 23.24±1.35 relative units). Two μmol photons m^{-2} s^{-1} furthermore resulted in higher amounts of non-lipid bilayer forming MGDG in relation to other bilayer forming lipids, especially digalactosydiacylglycerol (DGDG). The ratio of MGDG:DGDG increased from 3.4±0.3 to 5.7±0.3. The existence of bilayer thylakoid membranes with high proportions of non. bilayer forming lipids is only possible when sufficient thylakoid pigment–protein complexes are present. If more thylakoid pigment–protein complexes are present in membranes, as found under extreme light limitation, less bilayer forming lipids such as DGDG are required to stabilize the bilayer structure. Differences in protein contents between both light intensities were not found. Consequently pigment contents which nearly doubled under 2 μmol photons m^{-2} s^{-1} must be responsible in balancing the potential stability loss resulting from an increase in MGDG:DGDG ratio.

Keywords: Bacillariophyceae; Carbohydrates; Fluorescence induction; Lipids; Low temperature; Pigments; Proteins; Sea ice

1. Introduction

A number of sea ice diatom species coexist in the narrow space of brine channels (Krembs et al., 2000). This habitat is characterized by extreme conditions (low light intensities, low temperature, high salinities and limited supply of nutrients) which are strong selection factors for diatom species. Thus, only those species persist in this polar ecosystem which are able to acclimate or adapt (Kirst and Wiencke, 1995). The species probably all have the same mechanisms, which govern their success and differ from those in temperate or even tropical species. Species specific dominance in sea ice is probably related to small intraspecific differences (Huisman and Weissing, 1999) in e.g. salinity and temperature tolerance. In order to find universal mechanisms of regulation underlying these small intraspecific differences, we studied three dominant coexisting Antarctic sea ice diatoms by growing them in chemostats at −1 °C and two subsaturating light intensities. Low light acclimation is a universal physiological process, dependent on the structure and function of the photosynthetic apparatus. Photosystems and their subcomplexes, e.g. LHC (light harvesting complex), D1 (reaction center protein of photosystem II), D2 (reaction center protein of photosystem II), are anchored within the thylakoid membrane through lipids which are exclusively present in the chloroplast. This close connection between lipids and photosystem subcomplexes indicate an interdependence between both, which supports the concept of photo-

* Corresponding author. Tel.: +49-471-48-31-18-93; fax: +49-471-48-31-425.

E-mail address: tmock@awi-bremerhaven.de (T. Mock).

0031-9422/02/$ - see front matter
PII: S0031-9422(02)00215-7

Nomenclature

RC	reaction centre
PS II, I	photosystem II, I
LHC	light harvesting complex
D1/D2	PS II reaction centre proteins
Q_A	quinone A, first stable electron acceptor of PS II
Q_B	quinone B, second stable electron acceptor
F	fluorescence. Subscripts o, v, m represent the fluorescent level during light induction at the origin, variable and maximum levels, respectively
F_v/F_m	quantum yield
q	reaction centers
p	connectivity between PS II units
Φ_f	fluorescence yield
Φ_P	quantum yield
$q1$	open reaction centres
$q0$	closed reaction centres
σ	effective cross section of PS II
A	fraction of PS II characterized by a fast fluorescence decay after turnover saturation flashes at a rate of K_A
B	fraction of PS II characterized by a middle fluorescence decay after turnover saturation flashes at a rate of K_B
C	fraction of PS II characterized by a slow fluorescence decay after turnover saturation flashes at a rate of K_C
P vs I	photosynthesis (P) versus irradiance (I)
α	light limited slope of the P vs I curve/light utilization effiziency
Ik	light level at which photosynthesis saturates
P_{max}	maximum rate of photosynthesis
K	rate constant for fluorescence decay measurements
A,B,C_{comp}	amplitudes of fluorescence decay rate constants (K)
J_{con}	connectivity between reaction centres (PS II)
FA	fatty acid
PUFA	polyunsaturated fatty acid
MGDG	monogalactosyldiacylglycerol
DGDG	digalactosyldiacylglycerol
PC	phosphatidylcholine
PG	phosphatidylglycerol
PE	phosphatidylethanolamin
PI	phosphatidylinositol
TAG	triacylglycerol
SQDG	sulfoquinovosyldiacylglycerol

synthesis regulation by changes in the thylakoid membrane structure or the entire chloroplast. Thus, lipids have to be included into our concept of light acclimation of photosynthesis. An increase in membrane fluidity at low temperatures is essential to sustain diffusivity of gases, mobile electron and proton carriers like plastoquinone (PQ) and to repair low-temperature photoinhibition damage (e.g. Russel, 1997; Saruwatari et al., 1999; Reay et al., 1999). Apart from temperature, the strong seasonality of irradiance in polar regions plays an important role in photoautotrophic life, particularly in marine habitats where water turbulence determines the supply of photons. Some investigators have observed changes in lipid or fatty acid (FA) quality during light acclimation of algae and plants in addition to quantitative changes in chloroplast lipids (Pohl and Zurheide, 1979; Harwood and Jones, 1989; Sewon et al., 1997; Klyachko-Gurvich et al., 1999). This change is more distinct in combination with low temperatures (Tasaka et al., 1996). Ice diatoms are therefore well suited to study regulation of photosynthesis on the basis of lipid metabolism which is expected to be similar for the dominant diatom species. Special attention is therefore given to lipids as structural modulators of photosystem II efficiency as well as regulators of energy flow in three Antarctic sea ice diatoms.

2. Results

2.1. Physiology

The maximum attainable algal growth rate was strongly influenced by photon flux density. At 2 μmol photons m^{-2} s^{-1} the algae grew at a rate of 0.17 day^{-1} whereas the exposure to 15 μmol photons m^{-2} s^{-1} lead to a rate of 0.55 day^{-1}. The strong light limitation at 2 μmol photons m^{-2} s^{-1} resulted in an exceptional photophysiological acclimation, which was indicated by photosystem (PS) II related parameters as well as pigment concentrations. Fluorescence measurements were based on DCMU (3-(3,4-dichlorophenyl)-1,1-dimethylurea, 20 μmol l^{-1} final concentration) induction kinetics, which reveal the potential maximum of photosynthetic performance and not the in situ kinetics. Basic analysis of PS II related parameters (Table 1) resulted in an increase in connectivity between reaction centres of ca. 50% under 2 μmol photons m^{-2} s^{-1}. Relative values for energy trapping by open reaction centres were higher under 2 μmol photons m^{-2} s^{-1} than under 15 μmol photons m^{-2} s^{-1}. Reoxidation of Q_A (primary electron acceptor) increased at 2 μmol photons m^{-2} s^{-1} for the fast (K_A), middle (K_B) and slow (K_C) component of fluorescence decay measurements after

Table 1
Fluorescence variables for growth under 15 μmol photons m^{-2} s^{-1} (0.55 day^{-1}) and 2 μmol photons m^{-2} s^{-1} (0.17 day^{-1}): connectivity (J_{con}) between reaction centres (RC), open (K_{open}) RC and quantum yield are based on DCMU induction measurements

Variable	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}
J_{con}	0.341±0.010	0.663±0.008
K_{open}	0.408±0.0 15	0.539±0.023
Fv/Fm (yield)	0.337±0.009	0.398±0.010
K_A (ms^{-1})	11.16±1.34	23.24±1.35
K_B (ms^{-1})	0.42±0.12	0.96±0.22
K_C (ms^{-1})	0.02±0.02	0.07±0.03
r^2 (n=5)	0.966	0.978

Fluorescence decay rate constants for fast K_A, middle K_B and slow K_C component. Values are given as relative units; n=5; r^2=model fit.

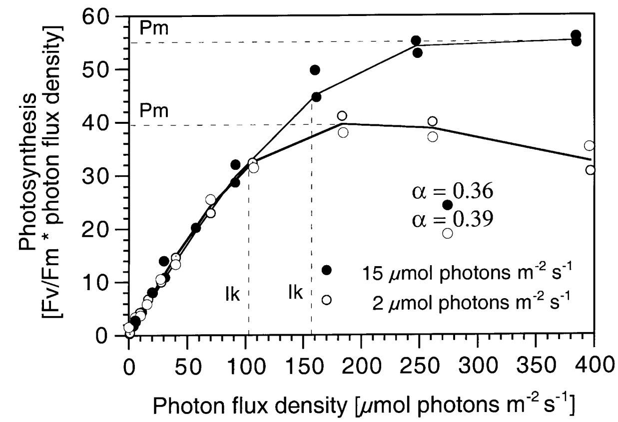

Fig. 1. Photosynthesis as F_v/F_m* photon flux density vs irradiance in ice diatoms under 15 μmol photons m^{-2} s^{-1} (μ=0.55 day^{-1}) and 2 μmol photons m^{-2} s^{-1} (μ=0.17 day^{-1}) are based on DCMU induction measurements. Photosynthetic parameters α (light utilization efficiency), Ik (quantum flux of PAR at onset of light saturation), Im (quantum flux of PAR for maximum of photosynthesis), Pm (maximum photosynthetic rate) were calculated after Eilers and Peeters (1988); n=2.

saturating light flashes. The fast (<10 ms) phase is attributed to electron transport from Q_A to Q_B (second electron acceptor) in PS II reaction centers that possess bound Q_B. The middle phase (10–50 ms) is thought to represent those reaction centers that had no bound Q_B before the saturating light flashes. Thus this phase may indicate the kinetics of equilibration of PQ binding to the Q_B site of D1 protein of PS II. The third, very slow component (>50 ms) seems to represent the decay of PS II centres that are unable to transmit electrons to the PQ pool. The slow Q_A reoxidation apparent from this phase is thought to result from recombination between Q_A and the water oxidation system in the S_2 state. Thus, electron transport is faster under 2 μmol photons m^{-2} s^{-1} and this is not caused by increasing amounts of Q_B bound to Q_A, which is indicated by the fluorescence amplitude of K_A (A_{comp}) the most important process for electron flow. A_{comp} remains relatively constant for both photon flux densities (0.012 and 0.011 for 15 and 2 μmol photons m^{-2} s^{-1}, respectively). Whereas B_{comp} increased under 2 μmol photons m^{-2} s^{-1} (Table 2). These amounts of bound Q_B were not influenced by dark adaptation of samples for 30 min, which revealed the comparison to measurements made only 90 s after sampling. The differences between PS II related parameters for both light intensities lead to differences in quantum yield and thus low light acclimation (Fig. 1). Maximum attainable photosynthetic rate (55–40 relative values) as well as the light level at which photosynthesis saturates (159–101 μmol photons m^{-2} s^{-1}) decreased whereas α (light utilization effiziency defined as the slope of photosynthesis vs irradiance curve; Fig. 1) increased (0.36–0.39) under 2 μmol photons m^{-2} s^{-1}. This typical photosynthetic response under low light acclimation is also supported by changes in relative pigment concentration (Fig. 2).

Pigments constituted a large proportion (±70%) of total cell carbon under 2 μmol photons m^{-2} s^{-1}, resulting in a carbon:chlorophyll (chl) *a* ratio of 3.5. However, only 30% of total algal carbon was represented by pigments in the 15 μmol photons m^{-2} s^{-1} incubation resulting in a carbon:chl *a* ratio of 7.4. No significant change in relative pigment ratios was observed compared to the major other lipids with exception of diadinoxanthin. Diadinoxanthin concentrations were reduced under 2 μmol photons m^{-2} s^{-1}, which caused a strong reduction in pigment ratios. Diadinoxanthin:chl

Table 2
Amplitudes of fluorescence decay rate constants for fast K_A (A_{comp}), middle K_B (B_{comp}) and slow K_C (C_{comp}) component for growth under 15 μmol photons m^{-2} s^{-1} (0.55 day^{-1}) and 2 μmol photons m^{-2} s^{-1} (0.17 day^{-1})

Variable	15 μmol photons m^2 s^{-1}		2 μmol photons m^2 s^{-1}	
	90 s	30 min	90 s	30 min
A_{comp}	0.011	0.012	0.016	0.011
	0.012	0.012	0.012	0.012
B_{comp}	0.006	0.004	0.017	0.018
	0.010	0.006	0.017	0.013
C_{comp}	0.001	0.001	0.004	0.001
	0.001	0.001	0.006	0.001

They were determined 90 s and 30 min after sampling; n=2.

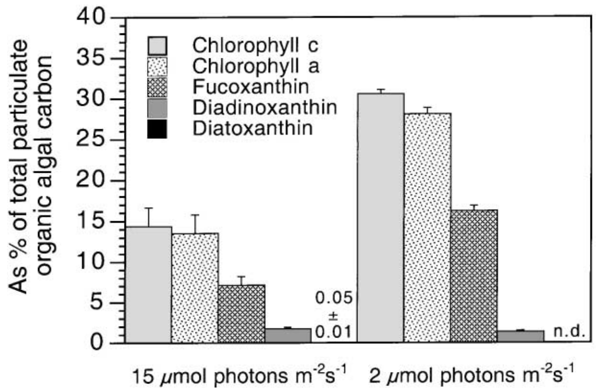

Fig. 2. Pigment composition of sea ice diatoms as % at total particulate organic algal carbon under 15 and 2 μmol photons m^{-2} s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively. Carotene was always below detection limit. Error bars denote standard deviations; n.d. = not detectable; $n=3$.

a ratio was 0.14 at 15 μmol photons m^{-2} s^{-1} and 0.04 at 2 μmol photons m^{-2} s^{-1}. Diatoxanthin as well as β-carotene represented less than 0.5% of total algal carbon.

2.2. Biochemistry

Macromolecular composition of diatoms was influenced by the availability of light (Fig. 3). Carbohydrates, as primary assimilates were reduced at 2 μmol photons m^{-2} s^{-1} whereas proteins and lipids remained unaffected under both applied photon flux densities. This is also the case for the membrane lipid fraction as well as for storage lipids of which the latter only represented a small proportion of total algal lipids (17%) (Fig. 4). The dominant membrane lipid class of ice diatoms under light limitation was MGDG, which is exclusively present in chloroplasts, particularly in thylakoid membranes (Fig. 5). DGDG as well as SQDG are also restricted to chloroplasts, whereas phospholipids also occur in non-chloroplast membranes.

The dominance of MGDG indicates that chloroplast membranes were the most abundant membranes in the cell. The most obvious effect of the reduction in irradiance on membrane lipid composition was an increase in MGDG:DGDG ratio to the unexpectedly high ratio of 5.6 at 2 μmol photons m^{-2} s^{-1} (Fig. 6). Fatty acid composition of the different membrane lipid classes as well as storage lipids was influenced by photon flux density. The proportion of polyunsaturated fatty acids (PA) (PUFA) at 2 μmol photons m^{-2} s^{-1} increased for all lipid classes with a concominant decrease of monounsaturated FA (MUFA) and saturated FA (SAFA), except for DGDG. Here, the fatty acid composition remained unchanged for both photon flux densities (Fig. 7). The strongest reduction of saturated FAs in all lipid classes except DGDG could be observed for 14:0 and 16:0 FAs at 2 μmol photons m^{-2} s^{-1}. The PUFA 20:5 increased by at least 38% in phosphatidylcholine (PC), phosphatidylglycerol (PG), sulfoquinovosyldiacylglycerol (SQDG), MGDG and triacylglycerol (TAG) at the same photon flux density. The relative proportion in phosphatidylethanolamin (PE) and DGDG remained more or less constant (Table 3).

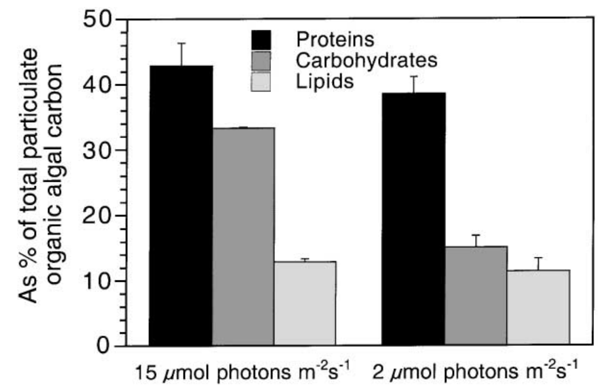

Fig. 3. Macromolecular composition of sea ice diatoms as % of total particulate organic algal carbon under 15 and 2 μmol photons m^{-2} s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively. Error bars denote standard deviations; $n=3$.

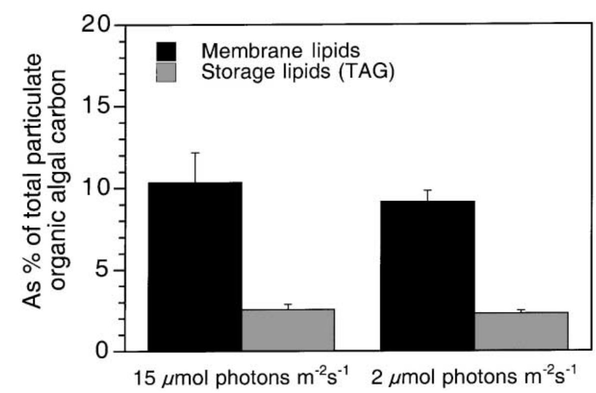

Fig. 4. Polar membrane lipids and storage lipids (triacylglycerol TAG) as % of total particulate organic algal carbon under 15 and 2 μmol photons m^{-2} s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively. Error bars denote standard deviations; $n=3$.

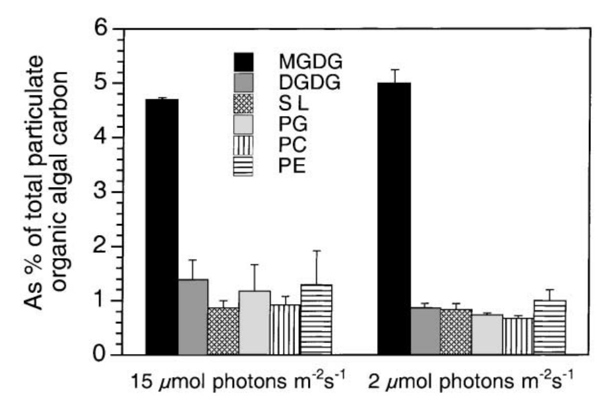

Fig. 5. Glyco- and phospholipid classes of sea ice diatoms as % of total particulate organic algal carbon under 15 and 2 μmol photons m^{-2} s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively. Error bars denote standard deviations; $n=3$.

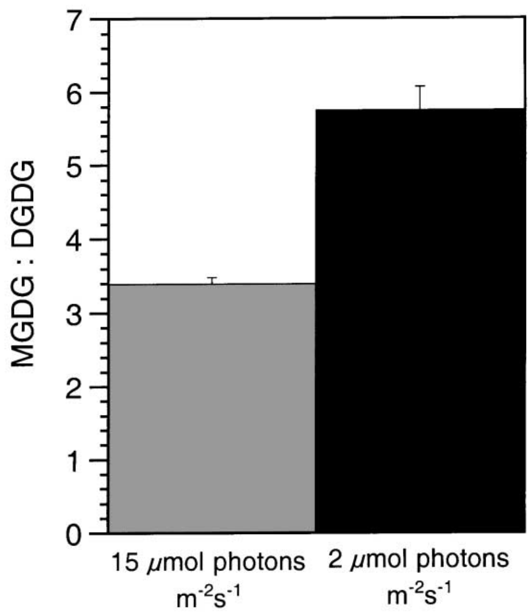

Fig. 6. Ratio of monogalactosyldiacylglycerol (MGDG) to digalactosydiacylglycerol (DGDG) under 15 and 2 μmol photons m^{-2} s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively. Error bars denote standard deviations; $n=3$.

3. Discussion

Low photosynthetic active irradiance is one of the strongest determinants in the development and growth of ice algae. The efficiency of light utilization is expressed by high chl *a* content, more so under 2 μmol photons m^{-2} s^{-1} than under 15 μmol photons m^{-2} s^{-1} (e.g. Falkowski and Owens, 1980). At 2 μmol photons m^{-2} s^{-1} almost all carbon and organic nitrogen produced in the cell is converted into pigments and proteins for photosynthesis (Geider et al., 1996, 1998). Thus the flux of excitation energy into carbohydrates is strongly reduced under extreme low light conditions (Fig. 3). However, the pool of lipids, particularly the storage lipid triacylglycerol remained constant. This may be due to a minimum requirement for these lipids. The increase in cell chl *a* under 2 μmol photons m^{-2} s^{-1} was related to changes in photophysiology of PS II. α increased whereas photosynthesis was saturated at 102 μmol photons m^{-2} s^{-1} in contrast to 158 μmol photons m^{-2} s^{-1} at 15 μmol photons m^{-2} s^{-1}. Consequently, maximum attainable photosynthetic rate was reduced under 2 μmol photons m^{-2} s^{-1} (Fig. 1).

The increase in photon trapping and generation of electrons at PS II under 2 μmol photons m^{-2} s^{-1} was regulated by an increase in connectivity (J_{con}) between reaction centres. The number of PS II and/or the LHC cross section probably increased in conjunction with an increase in chl *a*. One consequence, is a stronger probability of exciton capture by the reaction centres and thus a more efficient generation of electrons. Furthermore, the electron transport from reaction centres through the plastoquinone pool is faster under 2 μmol photons m^{-2} s^{-1} which is indicated by rate constants K_A, K_B, K_C and their amplitudes. The fluorescence amplitude for A_{comp} remained relatively constant under both photon flux densities indicating a similar amount of Q_B bound to D1, but the rate constants at 2 μmol photons m^{-2} s^{-1} increased by about 50% compared to 15 μmol photons m^{-2} s^{-1}. Such an increase in electron transport velocity between bound Q_A and Q_B can be explained by increasing FA desaturation of typical chloroplast FAs (MGDG, SQDG, PG), particular by increasing 20:5 *n*-3 of MGDG and SQDG. These fatty acids support the Q_A and Q_B interactions and thus the velocity of electron flow (Horvath et al., 1987). In contrast, amplitudes for the B_{comp} increased at 2 μmol photons m^{-2} s^{-1} which is revealed by a larger amount of bound Q_B and consequently a faster electron transport. Nevertheless, the major FA 20:5 *n*-3 of the chloroplast lipid class MGDG increased by ca. 50% in total fatty acids under 2 μmol photons m^{-2} s^{-1} (Table 3) as well as pigments like chl *a*/*c* (Fig. 2). This also supports the argument that chlorophyll molecules are associated with PUFA (Kates and Volcani, 1966; Cohen et al., 1988; Thompson et al., 1990). We suggest that diatoms use pairs of 20:5 to accommodate the phytol side chain of chl *a*. The desaturation of MGDG-FAs to 20:5 *n*-3 was correlated with a shift to low photon flux densities and the activity of PS I. This adaptive response which provides alterations to lipid–protein interactions in the membrane may be important for the self-assembly of active chlorophyll–protein complexes for photosynthetic apparatus of PS I (Klyachko-Gurvich et al., 1999) and perhaps also for PS II.

Not only the presence of PUFAs in thylakoid membranes is important for structure and function of PS I and II, but the composition of lipid classes also significantly influences membrane structure (Block et al., 1983). Under 2 μmol photons m^{-2} s^{-1}, the concentration of non-bilayer forming MGDG increased in relation to other bilayer forming lipids, especially DGDG (Fig. 5). The ratio of 5.8 between both glycolipid classes is much higher than the critical ratio of 2.5, above which transition to non-bilayer structures begins in MGD/DGD mixtures (Sprague and Staehelin, 1984). We assume that the existence of thylakoid bilayers is required in sea ice diatoms just like in all other photosynthetic organisms. The existence of bilayers with such high proportions of non-bilayer-forming lipids is only possible when sufficient thylakoid pigment–protein complexes are present (Webb and Green, 1991). If more thylakoid pigment–protein complexes are present in the membranes, as found under light limitation, less bilayer-forming lipids such as DGDG are required to stabilize the bilayer structure. Differences in protein content between both photon flux densities could be neglected due to insignificant changes in protein concentrations

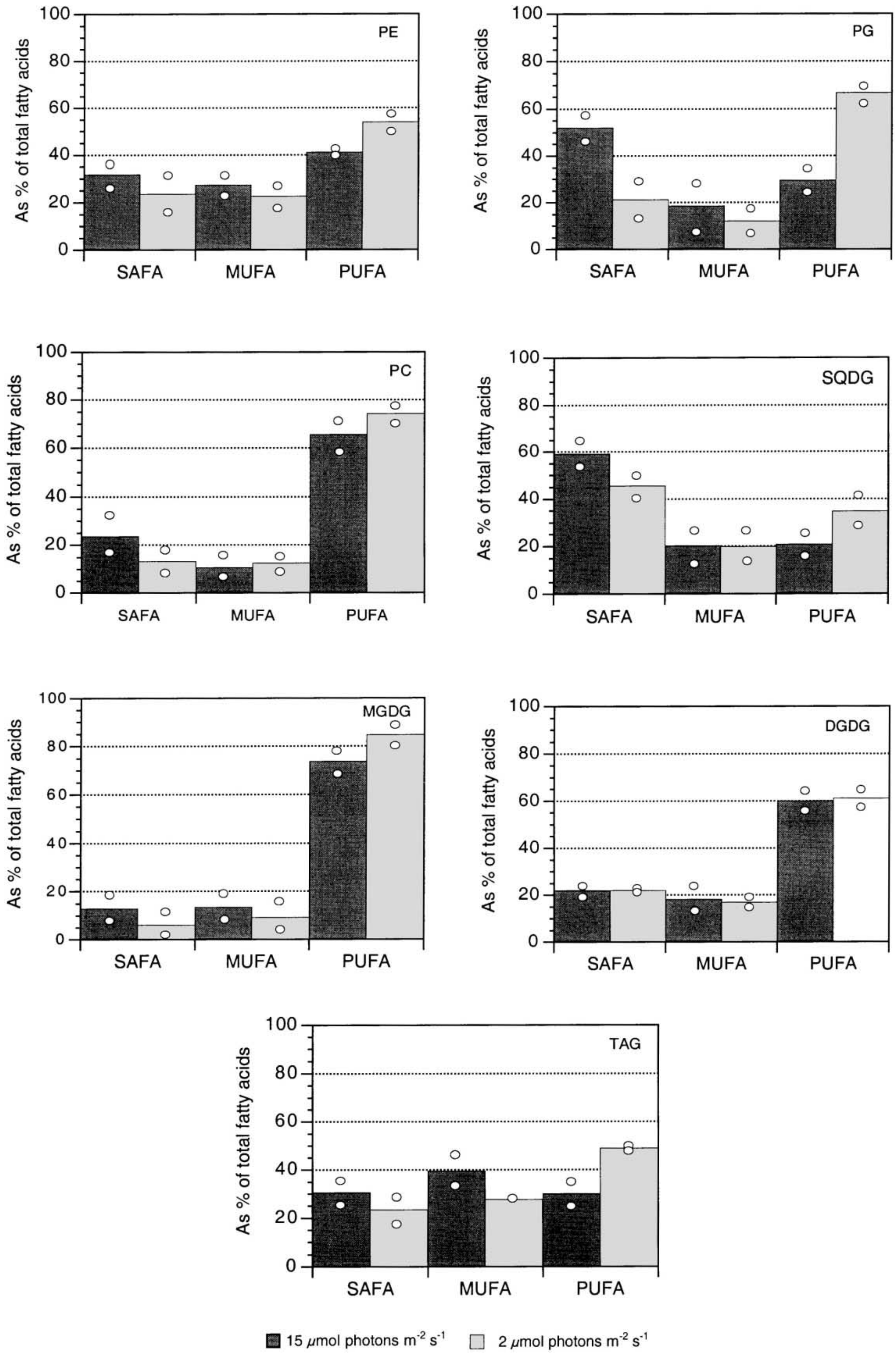

Fig. 7. Distribution of saturated (SAFA), monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) in lipid classes of sea ice diatoms as % of total particulate organic algal carbon under 15 and 2 μmol photons m^2 s^{-1} with corresponding growth rates of 0.55 and 0.17 day^{-1}, respectively; $n=2$.

Table 3
Fatty acid composition in lipid classes of sea ice diatoms at 15 μmol photons m^{-2} s^{-1} (growth rate 0.55 day^{-1}) and at 2 μmol photons m^{-2} s^{-1} (growth rate 0.17 day^{-1})

Fatty acid	PC		PE		PG		SQDG		DGDG		MGDG		TAG	
	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}	15 μmol photons m^{-2} s^{-1}	2 μmol photons m^{-2} s^{-1}
14:0	7.46	3.44	8.40	11.65	21.37	2.43	22.80	8.87	8.17	13.48	4.66	3.07	9.65	11.00
15:0	–	0.27	1.24	0.58	–	–	–	–	–	0.34	3.32	0.95	0.43	4.10
16:0	14.12	8.95	21.02	10.81	30.60	16.94	28.58	15.84	10.81	7.63	3.50	1.70	19.34	7.10
18:0	2.04	0.54	0.95	0.48	–	1.77	7.67	20.92	2.89	0.52	1.37	0.33	1.11	1.30
16:1*n*-7	7.30	8.69	23.53	20.11	11.88	6.31	20.21	19.74	8.45	13.30	8.72	6.23	36.02	24.76
18:1*n*-9	1.66	1.52	–	–	–	0.95	–	–	6.37	1.65	0.96	0.43	3.02	2.96
18:1*n*-7	1.82	1.92	3.77	2.50	6.60	4.95	–	–	–	1.08	0.83	0.73	–	–
20:1*n*-9	–	0.52	–	–	–	–	–	–	3.30	0.92	2.96	1.89	0.50	–
16:2*n*-?	2.87	0.40	–	1.00	–	0.85	–	–	10.59	3.11	2.48	1.03	1.69	–
16:3*n*-?	–	0.40	–	1.00	–	–	–	–	–	2.17	8.45	4.87	1.12	–
16:4*n*-1	–	0.50	–	–	–	0.52	9.46	12.63	4.45	9.10	35.41	33.84	1.57	2.08
18:2*n*-6	5.55	4.53	0.80	1.21	–	1.03	–	–	–	1.27	1.84	1.03	2.18	3.24
18:3*n*-3	2.98	0.63	–	–	–	–	–	–	–	0.60	2.38	–	0.91	–
18:4*n*-3	7.6	1.94	–	–	6.65	–	–	–	11.81	8.72	–	0.73	6.38	2.3
20:2*n*-?	–	–	13.36	18.48	–	–	–	–	–	–	–	–	1.47	–
20:4*n*-6	–	3.58	–	0.55	–	9.72	–	–	–	1.01	–	1.95	–	–
20:4*n*-3	1.62	1.08	3.20	11.12	–	1.18	–	–	–	2.81	–	–	1.08	2.27
20:5*n*-3	37.16	51.16	20.56	18.91	22.91	50.68	11.28	22.00	33.19	30.96	23.10	40.71	12.49	33.56
22:6*n*-6	7.82	9.92	3.15	1.62	–	2.66	–	–	–	1.31	–	0.79	1.04	5.38

Results are reported as % of total fatty acids. PC = phosphatidylcholine; PE = phosphatidylethanolamin; PG = phosphatidylglycerol; SQDG = sulfoquinovosyldiacylglycerol; DGDG = digalactosyldiacylglycerol; MGDG = monogalactosyldiacylglycerol; TAG = triacylglycerol. – Not detected; $n = 2$.

(Fig. 3). Pigment contents which nearly doubled under 2 μmol photons m^{-2} s^{-1} must therefore be responsible for an increase in the MGDG:DGDG ratio.

Consequently, photon flux density as an important determinant for growth in polar diatoms, influences the amount of chl *a* in the choloroplast, leading to biochemical changes of the chloroplast membranes in order to sustain intact bilayers and thus photosynthesis. Besides this influence of light on structural regulation of thylakoid membranes, light also regulates the fluidity of the thylakoid membrane.

4. Experimental

Material and methods which were applied in this investigation are identical to those in part I, described in: Photosynthetic energy conversion under extreme conditions: I. Important role of lipids as structural modulators and energy sink under *N*-limited growth in Antarctic sea ice diatoms (Mock and Kroon, 2002). Only the basic experimental conditions were changed as follows: two different photon flux densities were adjusted within continuous cultures: a total of 15.0 ± 5.0 μmol photons m^{-2} s^{-1} resulted in a growth rate of 0.55 day^{-1} with a optical density (OD) of 0.11 ± 0.01. A photon flux density of 2.0 ± 1.0 μmol photons m^{-2} s^{-1} lead to an algal growth rate of 0.17 day^{-1} with an OD of 0.037 ± 0.006. The algal composition in the first culture was $66 \pm 11\%$ of *Navicula gelida* var. *antarctica*, $20 \pm 7\%$ of *Fragilariopsis curta* and $14 \pm 9\%$ of *Nitzschia medioconstricta* after ca. one week under steady state growth. At 2 μmol photons m^{-2} s^{-1} and a growth rate of 0.17 day^{-1} *Navicula gelida* var. *antarctica* constituted $65 \pm 6\%$, *Fragilariopsis curta* $15 \pm 6\%$ and *Nitzschia medioconstricta* $20 \pm 7\%$ to the total community.

Acknowledgements

We are grateful to the crew of the RV *Polarstern* for their assistance during the expedition. We thank Gerhard Kattner and Martin Graeve for valuable discussions and for kind assistance with the lipids. Gerhard Dieckmann is thanked for reviewing an earlier version of the manuscript, and making suggestions for its improvement.

References

Block, M.A., Dorne, A.J., Joyard, J., Douch, R., 1983. Preparation and characterization of membrane fractions enriched in outer and inner envelope membranes from spinach chloroplasts. II Biochemical characterization. J. Biol. Chem. 258, 13281–13286.

Cohen, Z., Vonshak, A., Richmond, A., 1988. Effect of environmental conditions on fatty acid composition of the red alga *Porphyridium cruetum*: correlation to growth rate. J. Phycol. 24, 328–332.

Eilers, P.H., Peters, J.C.H., 1988. A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. Ecol. Model. 42, 199–215.

Falkowski, P.G., Owens, T.G., 1980. Light shade adaptation: two strategies in marine phytoplankton. Plant Physiol. 66, 632–635.

Geider, R.J., MacIntyre, H.L., Kana, T.M., 1996. A dynamic model of photoadaptation in phytoplankton. Limnol. Oceanogr. 41, 1–15.

Geider, R.J., MacIntyre, H.L., Kana, T.M., 1998. Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll a: carbon ratio to light, nutrient-limitation and temperature. Limnol. Oceanogr. 43 (4), 679–694.

Harwood, J.L., Jones, A.L., 1989. Lipid metabolism in algae. Adv. Bot. Res. 16, 1–53.

Horvárth, G., Melis, A., Hideg, E., Droppa, M., Vigh, L., 1987. Role of lipids in the organization and function of photosystem II studied by homogeneous catalytic hydrogenation of thylakoid membranes in situ. Biochim. Biophys. Acta 891, 68–74.

Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillations and chaos. Nature 402, 407–410.

Kates, M., Volcani, B.E., 1966. Lipid components of diatoms. Biochim. Biophys. Acta 116, 264–278.

Kirst, G.O., Wiencke, C., 1995. Ecophysiology of polar algae. J. Phycol. 31, 181–199.

Klyachko-Gurvich, G.L., Tsoglin, L.N., Doucha, J., Kopetskii, J., Ryabykh, I.B.S., Semenenko, V.E., 1999. Desaturation of fatty acids as an adaptive response to shifts in light intensity. Phys. Plant. 107, 240–249.

Krembs, C., Gradinger, R., Spindler, M., 2000. Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. J. Exp. Mar. Biol. Ecol. 243, 55–80.

Mock, T, Kroon, B. M., 2002. Photosynthetic energy conversion under extreme conditions: I. Important role of lipids as structural modulators and energy sink under N-limited growth in Antarctic sea ice diatoms. Phytochemistry 61.

Pohl, F., Zurheide, 1979. Fatty acids and lipids of marine algae and the control of their biosynthesis by environmental factors. In: Hoppe, H.A., Levring, T., Tanaka, Y. (Eds.), Marine Algae in Pharmaceutical Science. Walter de Gruyter, Berlin, pp. 473–523.

Reay, D.S., Nedwell, D.B., Priddle, J., Ellis-Evans, C., 1999. Temperature dependence of inorganic nitrogen uptake: reduced affinity for nitrate at suboptimal temperatures in both algae and bacteria. Appl. Environ. Microbiol. 65, 2577–2584.

Russell, N.J., 1997. Psychrophilic bacteria-molecular adaptations of membrane lipids. Comp. Biochem. Physiol. 118A (3), 489–493.

Saruwatari, M., Takio, S., Ono, K., 1999. Low temperature-induced accumulation of eicosapentaenoic acids in *Marchantia polymorpha* cells. Phytochemistry 52, 367–372.

Sewon, P., Mikola, H., Lehtinen, T., Kallio, P., 1997. Polar lipids and net photosynthesis potential of subarctic *Diapensia lapponica*. Phytochemistry 46, 1339–1347.

Sprague, S.G., Staehelin, L.A., 1984. Effects of reconstitution method on the structural organization of isolated chloroplast membrane lipids. Biochim. Biophys. Acta 777, 306–433.

Tasaka, Y., Gombos, Z., Nishiyama, Y., Mohanty, P., Ohba, T., Ohki, K., Murata, N., 1996. Target mutagenesis of acyl-lipid desaturases in synechocystis: evidence for the important roles of polyunsaturated membrane lipids in growth, respiration and photosynthesis. EMBO J. 15, 6416–6425.

Thompson, P.A., Harrison, P.J., Whyte, J.N.C., 1990. Influence of irradiance on the fatty acid composition of phytoplankton. J. Phycol. 26, 278–288.

Webb, M.S., Green, B.R., 1991. Biochemical and biophysical properties of thylakoid acyl lipids. Biochim. Biophys. Acta 1060, 133–158.