

Light attenuation and photosynthesis of aquatic plant communities

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Abstract

We compiled 414 studies from the literature to test if general relationships exist between chlorophyll concentration, light attenuation, and gross photosynthesis across phytoplankton communities, macrophyte stands, and attached microalgal mats. We also evaluated the upper limit to photosynthesis in the various communities. Along with increasing chlorophyll concentration, the photic zone diminishes from >100 m in sparse phytoplankton communities to centimeters–meters in macrophyte stands to <1 mm in dense microalgal mats. This compression of the photic zone is paralleled by a marked increase in volumetric photosynthesis ($\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$). In contrast, integral photosynthesis ($\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) remains relatively constant, depending on both the photic zone and volumetric photosynthesis. A similar upper limit ($\sim 60 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) is attained in dense macrophyte and phytoplankton communities when most of the irradiance is captured by plants. Integral photosynthesis, however, is often far below this upper limit because background light attenuation by particles and dissolved organic matter restrict photosynthesis in many aquatic plant communities. Moreover, limitation of CO_2 and O_2 exchange may constrain integral photosynthesis in dense plant communities, which are often subject to severe CO_2 depletion and O_2 supersaturation.

Photosynthetic organisms in phytoplankton, macrophyte, and benthic microalgal communities have several functional traits in common. Chlorophyll *a* is the key photosynthetic pigment, and the photosynthetic machinery is quite similar (Stæhelin 1986) and requires the same environmental resources. Recent broad-scale comparisons among photosynthetic tissues of different organisms have revealed that light absorption and photosynthesis can be modeled as continuous functions of chlorophyll concentration and thickness of the photosynthetic tissues (Agusti et al. 1994; Enriquez et al. 1996). Nutrient uptake rates and growth can also be described as continuous functions of the relative surface area of different organisms (Nielsen and Sand-Jensen 1990; Niklas 1994; Hein et al. 1995). The success of these comparative studies makes it appealing to expand the comparative approach testing for broad-scale similarities in the regulation of light absorption and photosynthesis at the level of aquatic plant communities.

Having been inspired by Talling (1957a), who treated phytoplankton communities as compound photosynthetic systems, we here extend the analysis of chlorophyll concentration, light absorption, and photosynthesis to the community level. Phytoplankton communities tend to follow the same patterns as individual photosynthetic tissues in that increased chlorophyll concentration (mg Chl m^{-3}) is accompanied by increased light attenuation, thus resulting in narrow photic zones and increased volumetric photosynthesis ($\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$; e.g. Talling 1957a, 1971; Smith and Baker 1978; Smith 1979). In oligotrophic waters with low chlo-

rophyll concentrations and deep photic zones, light attenuation is strongly influenced by background attenuation due to the water itself, dissolved organic matter, and inorganic particles. As a consequence, a large fraction of the light incident at the water surface is unavailable for photosynthesis, and integral photosynthesis ($\text{mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) is low. Nutrient enrichment of oligotrophic waters tends to increase the fraction of light absorbed by phytoplankton, thereby enhancing integral photosynthesis (e.g. Smith 1979; Berman et al. 1984). In eutrophic waters, the dense phytoplankton community is often the major light-absorbing component, and nutrient enrichment enhances volumetric photosynthesis; however, because of the parallel reduction in the photic zone, integral photosynthesis may remain unchanged (e.g. Smith 1979).

With increasing phytoplankton biomass, integral photosynthesis gradually approaches saturation. The models of Vollenweider (1970), Bannister (1974), and Megard et al. (1979) predict that the upper limit of integral photosynthesis is approached hyperbolically as the chlorophyll concentration gradually becomes high enough to attenuate virtually all the photosynthetically active radiation. Background attenuation determines the fraction of light available to photosynthesis, and thereby acts as a competitive inhibitor of integral photosynthesis. Inter-system variation in background attenuation will therefore influence the relationship of light attenuation and integral photosynthesis to chlorophyll concentration. However, the form and precision of these relationships have not hitherto been tested on a large range of lakes and marine waters.

The concentration of chlorophyll increases several orders of magnitude from the sparse phytoplankton communities in oligotrophic waters, to macrophyte communities with intermediate chlorophyll concentration, to densely packed microbial mats. The increase in chlorophyll concentration between

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these different types of plant communities should lead to a parallel increase in volumetric photosynthesis and to a reduction in the thickness of the photic zone. However, the coupling between increased volumetric photosynthesis and compression of the photic zone may impose the same upper limit on integral photosynthesis across all types of aquatic plant communities (Sand-Jensen 1989; Krause-Jensen et al. 1996).

Comparison of the biomass and productivity of marine autotrophs in shallow temperate coastal waters reveals a shift from dominance by perennial macrophytes and benthic microalgae at low nutrient loading to dominance by ephemeral macrophytes and phytoplankton at high loading (Sand-Jensen and Borum 1991). This shift in plant community type is not accompanied by systematic changes in integral carbon photosynthesis (Borum and Sand-Jensen 1996), thus indicating the existence of a general limit to photosynthesis independent of the type of aquatic plant community.

The goals of this study are (1) to test the existence of a general relationship between Chl *a* concentration, light attenuation, and gross photosynthesis for all aquatic plant communities, and (2) to evaluate the regulation of maximum biomass and gross photosynthesis of different aquatic plant communities. Our analysis is based on 414 compiled datasets, mainly from temperate waters.

Theory

Light attenuation in aquatic plant communities—In optically homogeneous aquatic plant communities, monochromatic irradiance reduces exponentially with depth according to the equation

$$I_z = I_0 e^{-K_t z} \quad (1)$$

where I_0 and I_z are the values of downward irradiance at the upper boundary of the plant community and at depth z (m) into the plant community, respectively, and K_t (m^{-1}) is the total light attenuation of the community. The light-attenuating properties of plant communities can be conveniently characterized by a mean K_t value for the entire band of photosynthetically available radiation (PAR, 400–700 nm) rather than a series of K_t values for different wavelengths (Kirk 1994, p. 136).

The total light attenuation (K_t) is the sum of attenuation due to plants (K_c) and background attenuation (K_b). The attenuation due to plants is calculated as the product of chlorophyll concentration (c) and the chlorophyll-specific attenuation coefficient (k_c):

$$K_t = ck_c + K_b \quad (2)$$

With K_t in units of m^{-1} (based on the natural logarithm) and c expressed as $mg\ Chl\ m^{-3}$, the chlorophyll-specific attenuation coefficient (k_c) has the unit $m^{-1} (mg\ Chl)^{-1} m^3$ (i.e. $m^2 (mg\ Chl)^{-1}$). A parallel equation can be made with the concentration term expressed in dry weight (d , $mg\ DW\ m^{-3}$), and using a dry weight-specific attenuation coefficient (k_d , $m^2 (mg\ DW)^{-1}$). One obvious consequence of Eq. 2 is that provided k_c remains approximately constant, K_t will increase linearly with c in very dense plant communities, where $ck_c \gg K_b$.

The term photic zone (Z_{eu}) is intuitively easier to understand than the total light attenuation (K_t). For convenience, we define the photic zone as extending to 1% of the irradiance incident on the plant community, i.e. $Z_{eu} = \ln(100/I)/K_t = 4.6/K_t$.

Volumetric photosynthesis—The maximum volumetric photosynthesis (P_m , $mmol\ O_2\ m^{-3}\ h^{-1}$) is the product of the chlorophyll concentration (c , $mg\ Chl\ m^{-3}$) and the maximum chlorophyll-specific photosynthesis (p_{mc} , $mmol\ O_2 (mg\ Chl)^{-1}\ h^{-1}$):

$$P_m = cp_{mc} \quad (3)$$

Isolating c in Eq. 2 and inserting in Eq. 3 yields

$$P_m = K_t(p_{mc}/k_c) - p_{mc}(K_b/k_c) \quad (4)$$

In dense plant communities with light attenuation dominated by attenuation due to plants, the second term is small relative to the first term, i.e.

$$P_m \lim(ck_c \gg K_b) = K_t(p_{mc}/k_c) = (4.6/Z_{eu})(p_{mc}/k_c) \quad (5)$$

It follows that if the ratio between maximum chlorophyll-specific photosynthesis and chlorophyll-specific light attenuation (p_{mc}/k_c) is approximately constant in dense plant communities, then volumetric photosynthesis (P_m) is proportional to total light attenuation (K_t) and inversely proportional to the photic zone (Z_{eu}).

Parallel equations can be made with the concentration term expressed in dry weight (d , $mg\ DW\ m^{-3}$), and using the maximum rate of dry weight-specific photosynthesis (p_{md} , $mmol\ O_2 (mg\ DW)^{-1}\ h^{-1}$).

Integral photosynthesis—Talling (1957a,b) was the first to demonstrate the dependence of integral photosynthesis (P_a , $mmol\ O_2\ m^{-2}\ h^{-1}$) on chlorophyll concentration (c , $mg\ Chl\ m^{-3}$), total light attenuation (K_t , m^{-1}), incident photon flux (I_0 , $\mu mol\ photons\ m^{-2}\ s^{-1}$), and the irradiance at the onset of light-saturated photosynthesis (I_k):

$$P_a = (cp_{mc})[\ln(2I_0/I_k)/K_t] \quad (6)$$

The first term (cp_{mc}) is the maximum volumetric photosynthesis (see Eq. 3). The second term defines the depth that when multiplied by P_m yields the correct P_a . This formula has been verified in a range of freshwater environments (Talling 1965; Ganf 1975; Megard et al. 1979; Harris 1978), and similar formulae have been developed by Bannister (1974) and by Platt (1986) for marine environments based on the rectangular parabola for the P - I curve. The maximum integral photosynthesis in dense plant communities where $ck_c \gg K_b$ and $K_t \approx ck_c$ is

$$P_a \lim(ck_c \gg K_b) \approx (p_{mc}/k_c) \ln(2I_0/I_k) \quad (7)$$

This formula shows that the upper limit of P_a at maximum incident irradiance is determined primarily by the ratio of p_{mc} to k_c . Thus, provided that the communities have similar I_k , the same upper limit to integral photosynthesis can be reached by different plant communities if p_{mc}/k_c is constant. A compilation of I_k values shows high variability, but no systematic differences among different types of aquatic communities (table 10.1 in Kirk 1994).

By combining Eq. 6 and 7 it is possible to express the integral photosynthesis (P_a) relative to the maximum integral photosynthesis ($P_{a(\max)}$) achieved if all available light is absorbed by the plant community:

$$P_a = P_{a(\max)} [ck_c(K_b + ck_c)^{-1}]. \quad (8)$$

This expression is analogous to those presented by Bannister (1974) and Megard et al. (1979), and illustrates that background attenuation acts as a competitive inhibitor of P_a . The formula predicts the same kinetics as in one enzyme–one substrate reactions, with K_b/k_c representing the concentration of chlorophyll (c') at which half of the upper limit to integral photosynthesis is attained.

Methods

Collection and analysis of data—We compiled 414 datasets on light attenuation, chlorophyll concentration, and photosynthesis of different aquatic plant communities in both freshwater and marine areas (192 datasets for phytoplankton, 58 datasets for macrophytes, and 164 datasets for benthic microalgae). Most datasets originated from temperate waters. As we sought to evaluate the upper limits of photosynthesis in the communities, we mainly selected data from summer periods of high irradiance or from the spring maximum. Most values came from midday measurements in the field or from laboratory incubations at high irradiance in the case of some microalgal communities. Most measurements were located within the temperature range of 10–20°C. Temperature influences the maximum rate of photosynthesis, but it is not a major source of variation in this broad-scale comparison, where plant biomass varied up to 10⁵-fold within the communities, and comparisons were made among the different communities exposed to the same temperature range.

We chose to compare gross photosynthesis rather than net photosynthesis because gross photosynthesis is the pure photosynthetic process and therefore can be expected to reveal more precise information on the regulation of photosynthetic capacity among the communities. Net photosynthesis is by definition gross photosynthesis minus respiration, and if the plant community contains a high proportion of nonphotosynthetic biomass, its net photosynthesis may become negative. There are also serious methodological problems associated with measurements of net photosynthesis. Oxygen balance methods, for example, underestimate net photosynthesis because of respiration of heterotrophic organisms. Methods are more appropriate for calculating gross photosynthesis. With the microelectrode light/dark switch technique in benthic microalgal communities, gross photosynthesis is provided directly (Revsbech and Jørgensen 1983). With O₂ measurements in light/dark chambers or in open water (diel analyses in streams; Odum 1956; Kelly et al. 1983), gross photosynthesis is obtained by adding dark respiration to net photosynthesis. With ¹⁴C assimilation in short-term incubations at high irradiance, the values obtained are quite close to gross photosynthesis (Jespersen 1994).

We searched the literature for reports describing parameters for community photosynthesis, biomass, and light attenuation. All data and references are tabulated and available

Table 1. Parameters, symbols, and units used in presentation and analysis of the data.

Symbol	Parameter	Unit
Z_{cu}	Photic zone	m
K_t	Total light attenuation	m ⁻¹
K_b	Background attenuation	m ⁻¹
K_c	Attenuation due to plants	m ⁻¹
k_c	Chlorophyll-specific attenuation coefficient	m ² (mg Chl) ⁻¹
k_d	Dry weight-specific attenuation	m ² (mg DW) ⁻¹
c	Chlorophyll concentration	mg Chl m ⁻³
d	Dry weight concentration	mg DW m ⁻³
C_m	Maximum photic zone biomass of chlorophyll	mg Chl m ⁻²
P_m	Volumetric productivity (max.)	mmol O ₂ m ⁻³ h ⁻¹
P_a	Integral productivity	mmol O ₂ m ⁻² h ⁻¹
P_{mc}	Maximum chlorophyll-specific productivity	mmol O ₂ (mg Chl) ⁻¹ h ⁻¹
P_{md}	Maximum dry weight-specific productivity	mmol O ₂ (mg DW) ⁻¹ h ⁻¹
I_k	Onset of light saturated photosynthesis	μmol photons m ⁻² s ⁻¹

upon request. If needed, the original values were converted to the units specified in Table 1 to obtain comparable units. Rates of carbon fixation were converted to O₂ evolution by assuming that 1.2 mol O₂ is produced per mole of C fixed (Ryther 1956; Westlake 1963). The primary parameters of chlorophyll- and dry weight-specific attenuation coefficients (k_c , k_d) and maximum chlorophyll- and dry weight-specific photosynthesis (P_{mc} , P_{md}) in Tables 2 and 3 were all original values.

For the remaining datasets, partly lacking information on the relative contribution of plants to total light attenuation, chlorophyll concentration, or volumetric photosynthesis was calculated using the following simple and plausible assumptions. If lacking, the chlorophyll-specific attenuation coefficient (k_c) for phytoplankton and benthic microalgal communities was assumed to be 0.020 m² (mg Chl)⁻¹ (Talling 1960). For macrophytes we applied k_c values obtained in other studies of the same species. If light attenuation in open waters of lakes and coastal marine waters was only reported as Secchi depth (S), we used the approximation $K_t = 2.3/S$ (Højerslev 1978). If the vertical extension of the plant community, which is required to calculate chlorophyll concentration, was not specified, the following assumptions were made. For macrophytes in shallow streams (<0.8 m) and *Ruppia* spp. in shallow water (0.5 m), stand height was set at the water depth, since the plant stands usually reach to the surface. For *Zostera marina* we used a stand height of 30 cm (Borum 1980) and for *Halodule wrightii* a stand height of 10 cm (Den Hartog 1970). The thickness of epiphyte communities was set at 0.5 mm (viz. Sand-Jensen et al. 1985). Chlorophyll of benthic microalgal communities was assumed to be evenly distributed over the 1–5-mm-thick surface layer of sediment analyzed. When the chlorophyll content of macrophyte shoots was not available, we used the mean value of 9.6 mg Chl (g DW)⁻¹ attained in a compre-

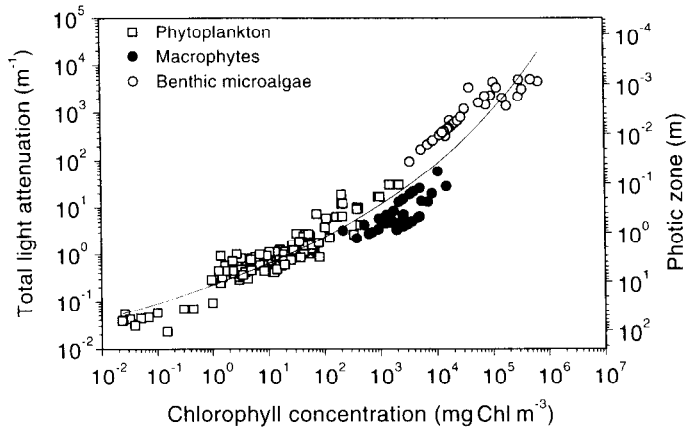


Fig. 1. Total light attenuation (K_t) and photic zone (Z_{eu}) vs. chlorophyll concentration (c) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. The double-log-transformed dataset ($n = 202$) fits the equation $y = (a + bx)/(cx + 1)$ with the following parameter values and 95% confidence intervals: $a = -0.65$ (-0.75 to -0.56), $b = 0.48$ (0.43 – 0.53), $c = -0.085$ (-0.099 to -0.072). The linear part of the curve, which represents chlorophyll concentrations > 10 mg Chl m^{-3} , fits a model I linear regression (predictive regression, line not shown): $y = 0.81x - 1.2$, $r^2 = 0.83$, $P < 0.001$, $n = 152$. Datasets in which high turbidity caused extreme background attenuation ($> 90\%$ of K_t) are excluded.

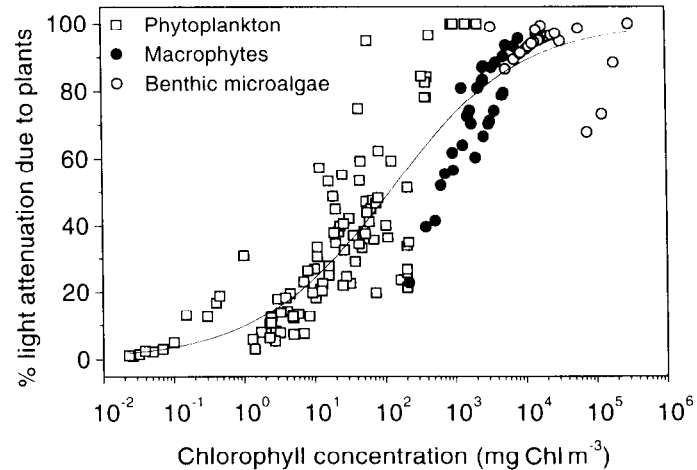


Fig. 2. Percentage of total light attenuation due to plants ($K_t/K_t \times 100\%$) vs. chlorophyll concentration (c) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. The dataset ($n = 176$) fits the sigmoid model $y = 100/(1 + a \exp(-bx))$, with the following parameter values and 95% confidence intervals: $a = 9.2$ (6.7 – 11.7), $b = 1.07$ (0.95 – 1.19). Datasets in which high turbidity caused extreme background attenuation ($> 90\%$ of K_t) are excluded.

hensive study of macrophytes from shallow Danish streams and lakes during peak development (Jørgensen 1990). Similar levels were reported in a comparative study by Madsen et al. (1993).

P_m represents the maximum volumetric photosynthesis at any depth within the photic zone. In some shallow macrophyte and benthic microalgal photic zones, P_m was estimated as integral photosynthesis (P_a) divided by the thickness of the photic zone (Z_{eu}). In some situations the maximum hourly integral photosynthesis at noon was estimated as 10% of the daily rate (viz. Keller 1988). The validity of this assumption for Danish localities in midsummer was tested by applying mean hourly irradiance data for July (corrected for surface reflection) and typical I_k values during summer of 200–300 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ (Harris 1978) to the equation of Talling (eq. 6, 1957a).

The data were log transformed to compensate for the very large variation in biomass and photosynthesis among different plant communities (i.e. up to 10^6 – 10^8 -fold) and to meet the requirements of parametric analyses. Linear regression was performed using model I regression (predictive regression). However, in cases in which the independent variable was not determined with greater accuracy than the dependent variable, we also present the slope obtained using model II regression (geometric mean functional regression) to account for the error in both regression variables (Ricker 1973). The slope (ν) of this model II regression is equivalent to the ratio between the slope of the model I regression (b) and the correlation coefficient (r) ($\nu = b/r$), and has the same error as b (Ricker 1973).

Results

Chlorophyll concentration and light attenuation—Chlorophyll concentration was found to increase $> 10^7$ -fold from sparse phytoplankton communities over macrophyte stands to benthic microalgal mats (Fig. 1). That of phytoplankton communities varied from 2×10^{-2} mg Chl m^{-3} in oceanic waters and clear lakes to 2×10^3 mg Chl m^{-3} in highly eutrophic lakes. The densest phytoplankton communities had chlorophyll concentrations within the range observed in macrophyte stands (2×10^2 – 15×10^3 mg Chl m^{-3}). Benthic microalgal communities were found to have the highest chlorophyll concentrations (up to 7×10^5 mg Chl m^{-3}). The 10^7 -fold increase in chlorophyll concentration from the most sparse phytoplankton communities to the most dense microalgal mats is accompanied by a 10^5 -fold increase in total light attenuation from ~ 0.02 m^{-1} to $\sim 5,000$ m^{-1} , with a corresponding reduction in the thickness of the photic zone from ~ 100 m to < 1 mm (Fig. 1).

The increase in light attenuation accompanying the increase in chlorophyll concentration is relatively small in phytoplankton communities in oceanic waters and oligotrophic lakes (Fig. 1), where the concentration of chlorophyll is low and its contribution to total light attenuation is limited relative to background attenuation (Fig. 2). The coupling between light attenuation and chlorophyll concentration becomes tighter at higher chlorophyll concentrations, where the plants are often responsible for most light attenuation (Figs. 1, 2). At chlorophyll concentrations ≥ 10 mg Chl m^{-3} , the relationship between light attenuation and chlorophyll concentration is almost linear in the double-log plot (Fig. 1), with a slope of 0.81 (SD of 0.029) in the model I regression and 0.88 in the model II regression.

At the same chlorophyll concentration, light attenuation

Table 2. Literature-based analysis of chlorophyll-specific attenuation coefficients (k_c) and dry weight-specific attenuation coefficients (k_d) for different aquatic plant communities. An extreme k_c value of 0.23 reported for a phytoplankton community dominated by *Coccolithus huxleyi* in the eastern Mediterranean (Megard and Berman 1989) was not included in the analysis (n represents the number of communities included in the analysis).

Mean(SE)	Min.–max.	Fractiles			n	Unit
		10%	50%	90%		
Phytoplankton						
0.0149(0.0011)	0.004–0.029	0.0081	0.0145	0.0246	32	m ² (mg Chl) ⁻¹
Macrophytes						
0.008 (0.0006)	0.0014–0.019	0.0041	0.0077	0.012	35	m ² (mg Chl) ⁻¹
0.024 (0.002)	0.006–0.077	0.011	0.021	0.042	59	m ² (g DW) ⁻¹
Benthic microalgae						
0.0264 (0.0039)	0.0066–0.0388	0.0156	0.0278	0.0366	7	m ² (mg Chl) ⁻¹
0.0635 (0.0060)	0.056–0.076	0.0567	0.059	0.072	3	m ² (g DW) ⁻¹

was higher in phytoplankton and benthic microalgal communities than in macrophyte communities (Fig. 1). This difference between community types is more clearly apparent from the mean chlorophyll-specific attenuation coefficient (k_c), which was 0.015 m² (mg Chl)⁻¹ for phytoplankton, 0.008 m² (mg Chl)⁻¹ for macrophytes, and 0.026 m² (mg Chl)⁻¹ for benthic microalgae (Table 2). Only few k_c values are available for benthic microalgae because most studies of light penetration in such communities lack data on chlorophyll content.

The percentage of light attenuated by plants was found to increase sigmoidally with increasing chlorophyll concentration (Fig. 2) and increasing total light attenuation (Fig. 3). The scatter of the relationship is considerable because of variation in the background attenuation and chlorophyll-specific attenuation coefficients. The fraction of light attenuated

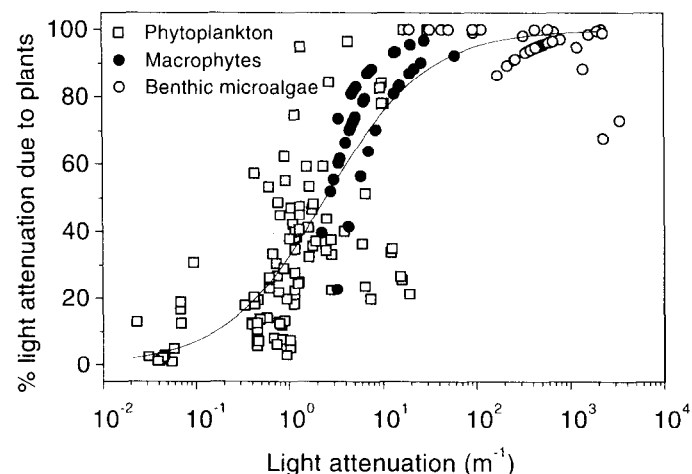


Fig. 3. Percentage of total light attenuation due to plants ($K_t/K_t \times 100\%$) vs. total light attenuation (K_t) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. The dataset ($n = 198$) fits the sigmoid model $y = 100/(1 + a \exp(-bx))$, with the following parameter values and 95% confidence intervals: $a = 2.05$ (1.68–2.41), $b = 1.84$ (1.55–2.13). Datasets in which high turbidity caused extreme background attenuation ($>90\%$ of K_t) are excluded.

by plants, $K_t/K_t = c(K_b/k_c + c)^{-1}$, increases sigmoidally with increasing chlorophyll concentration, but the exact fit of the curve depends on the K_b/k_c ratio, which represents the chlorophyll concentration (c') at which 50% of light is attenuated by the plants and hence half of the upper limit of integral photosynthesis is attained. This level varied >20 -fold (from ~ 10 to ~ 200 mg Chl m⁻³; Fig. 2) among phytoplankton communities (viz. Megard et al. 1979) and was ~ 10 -fold higher in macrophyte communities, mainly because k_c was lower than in the phytoplankton communities (Table 2).

The low chlorophyll-specific attenuation coefficient (k_c) found for macrophytes implies that they can develop a greater chlorophyll biomass (mg Chl m⁻²) than can microalgae before light is depleted within the community. The maximum chlorophyll biomass within the photic zone (C_{\max}) for each of the different plant communities can be simply calculated from the equation $C_{\max} = 4.6/k_c$, assuming that $K_b \gg K_c$ and that the photic zone extends to 1% of incident irradiance (Eq. 1). This calculation yields photic zone biomass values of 160–1,150 (mean of 310) mg Chl m⁻² for phytoplankton, 240–3,290 (mean of 600) mg Chl m⁻² for macrophytes, and 120–700 (mean of 177) mg Chl m⁻² for benthic microalgae. In the present datasets, chlorophyll biomass of phytoplankton communities was reported for the photic zone, while that of the benthic communities included the total chlorophyll biomass. Phytoplankton biomass ranged from 1 to 580 mg Chl m⁻² (mean of 85, $n = 139$). Macrophyte biomass ranged from 157 to 5,000 mg Chl m⁻² (mean of 1,750, $n = 48$), and the benthic microalgal biomass ranged from 1 to 900 mg Chl m⁻² (mean of 90, $n = 103$).

Volumetric photosynthesis—Maximum volumetric photosynthesis (P_m) was found to increase 10^7 – 10^8 -fold with increasing chlorophyll concentration and total light attenuation (Figs. 4, 5). Thus, P_m increased from 3×10^3 mmol O₂ m⁻³ h⁻¹ in the most sparse phytoplankton communities to 1×10^3 mmol O₂ m⁻³ h⁻¹ in the most dense. P_m in the macrophyte communities was intermediate, ranging from 20 to 4.4×10^2 mmol O₂ m⁻³ h⁻¹. Microalgal mats have the highest chlorophyll concentrations and the highest volumetric productivities between 1×10^2 and 1.8×10^5 mmol O₂ m⁻³ h⁻¹.

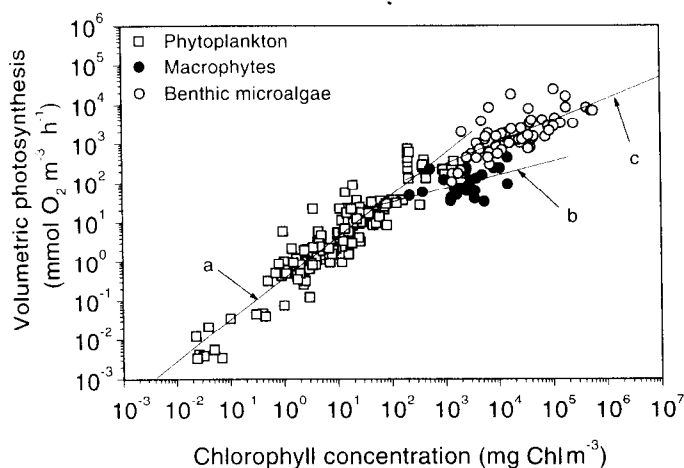


Fig. 4. Maximum volumetric productivity (P_m) vs. chlorophyll concentration (c) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. Data were log-transformed to compensate for the very large variation. The double-log-transformed dataset fits separate model I linear regression analyses for phytoplankton (line a), $y = 1.06x - 0.4$, $r^2 = 0.88$, $n = 140$, $P < 0.001$; benthic macrophytes (line b), $y = 0.35x + 0.81$, $r^2 = 0.22$, $n = 27$, $P < 0.05$; and benthic microalgae (line c): $y = 0.55x + 0.82$, $r^2 = 0.53$, $n = 63$, $P < 0.001$.

P_m was closely correlated to chlorophyll concentration across the different aquatic plant communities (Fig. 4). The slope of the linear regression for phytoplankton communities was 1.06 (SD of 0.034) in the model I regression and 1.13 in the model II regression, thus suggesting that photosynthesis normalized to chlorophyll increases slightly as the phytoplankton communities become more dense in highly eutrophic habitats. The slope of the regression for phytoplankton communities was markedly higher than for macrophyte stands (0.35 [SD of 0.13] in the model I regression and 0.75 in the model II regression) and benthic microalgal communities (0.55 [SD of 0.07] in the model I regression and 0.76 in the model II regression). In the region where chlorophyll concentration overlapped for benthic and planktonic communities, P_m tended to be higher for phytoplankton than for benthic communities of microalgae and macrophytes, a finding in concert with the chlorophyll-specific photosynthesis (p_{mc}), which averaged $0.52 \text{ mmol O}_2 (\text{mg Chl})^{-1} \text{ h}^{-1}$ for phytoplankton, $0.17 \text{ mmol O}_2 (\text{mg Chl})^{-1} \text{ h}^{-1}$ for macrophytes, and $0.15 \text{ mmol O}_2 (\text{mg Chl})^{-1} \text{ h}^{-1}$ for benthic microalgae (Table 3).

The relationship between maximum volumetric photosynthesis (P_m) also correlated positively with total light attenuation (K_t , Fig. 5). The regression for the phytoplankton communities was steeper (1.68 [SD of 0.065] in the model I regression and 1.82 in the model II regression) than that for the macrophytes (0.55 [SD of 0.15] in the model I regression and 0.90 in the model II regression) and benthic microalgae (0.97 [SD of 0.19] in the model I regression and 1.46 in the model II regression). At intermediate levels of light attenuation ($\sim 2\text{--}20 \text{ m}^{-1}$) the regression lines for the planktonic and macrophytic communities overlap. In this region, which encompasses both macrophytes and dense phytoplankton

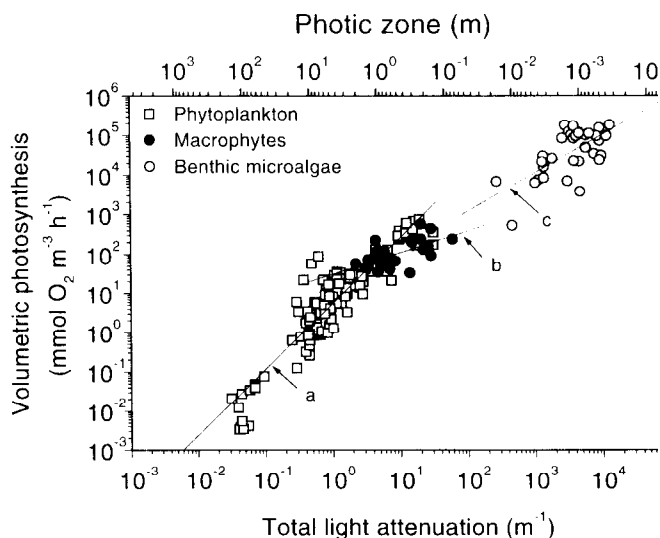


Fig. 5. Maximum volumetric productivity (P_m) vs. total light attenuation (K_t) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. Data were log-transformed to compensate for the very large variation. The double-log-transformed dataset fits separate model I linear regression analyses for phytoplankton (line a), $y = 1.68x + 0.74$, $r^2 = 0.85$, $n = 119$, $P < 0.001$; benthic macrophytes (line b), $y = 0.55x + 1.5$, $r^2 = 0.0$, $n = 26$, $P < 0.001$; and benthic microalgae (line c), $y = 0.97x + 1.14$, $r^2 = 0.44$, $n = 34$, $P < 0.001$. Datasets in which high turbidity caused extreme background attenuation ($>90\%$ of K_t) are excluded.

communities, integral photosynthesis should be highest because it is proportional to the P_m/k_t ratio (Eq. 6).

Integral photosynthesis—Integral photosynthesis at high midday irradiance peaked at $\sim 60 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ for dense phytoplankton communities and the macrophyte communities with chlorophyll concentrations in the range of $5 \times 10^4 \text{ mg Chl m}^{-3}$ (Fig. 6). The upper 90th percentile of integral photosynthesis was $55 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ for macrophyte and phytoplankton communities at a chlorophyll concentration $>10 \text{ mg Chl m}^{-3}$. Lower integral photosynthesis was recorded both in the more sparse phytoplankton communities with chlorophyll concentrations $<10 \text{ mg Chl m}^{-3}$ (upper 90% fractile, $18 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) and in dense communities of microalgae (upper 90% fractile, $38 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$; Fig. 6). Integral photosynthesis increased systematically with the percentage of available irradiance attenuated by phytoplankton and macrophyte communities (Fig. 6) plateauing at $\sim 60 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ over the light attenuation range 40–100%.

The higher maximum integral photosynthesis of phytoplankton and macrophyte communities compared to benthic microalgae is reflected in the p_{mc}/k_t ratio as predicted by Eq. 6. Thus, the ratio was $35 \text{ mmol m}^{-2} \text{ h}^{-1}$ for phytoplankton and 21 for macrophytes, but only 6 for benthic microalgae (Tables 2, 3). The lower maximum chlorophyll-specific photosynthesis (p_{mc}) found for macrophytes as compared to phytoplankton is thus compensated for by a lower chlorophyll-specific attenuation coefficient (k_t), thereby enabling a high productive biomass.

Table 3. Literature-based analysis of maximum chlorophyll-specific productivity (p_m) and maximum dry weight-specific productivity (p_{md}) of different aquatic plant communities (n represents the number of communities included in the analysis).

Mean(SE)	Min.–max.	Fractiles			n	Unit
		10%	50%	90%		
Phytoplankton						
0.52(0.02)	0.02–2.02	0.13	0.47	0.94	155	mmol O ₂ (mg Chl) ⁻¹ h ⁻¹
Macrophytes						
0.17 (0.02)	0.001–1.69	0.007	0.082	0.39	107	mmol O ₂ (mg Chl) ⁻¹ h ⁻¹
0.43 (0.04)	0.01–3.17	0.080	0.30	0.99	145	mmol O ₂ (g DW) ⁻¹ h ⁻¹
Benthic microalgae						
0.15 (0.03)	0.005–1.2	0.021	0.078	0.26	62	mmol O ₂ (mg Chl) ⁻¹ h ⁻¹
0.28 (0.04)	0.04–0.73	0.10	0.25	0.44	19	mmol O ₂ (g DW) ⁻¹ h ⁻¹

Discussion

Aquatic plant communities act as compound photosynthetic systems—Optical models predict that across the full scale of photosynthetic organisms, light absorption per unit weight of photosynthetic tissues increases with increasing pigment concentration and decreasing tissue thickness (Agusti et al. 1994). Because photosynthesis is directly related to light absorption (Björkman and Demmig 1987), the model predicts that photosynthesis per unit weight increases with increasing chlorophyll concentration and decreasing thickness of the photosynthetic tissue. This prediction has been confirmed by Enriquez et al. (1995, 1996) in broad-scale comparisons among different types of phototrophic organisms demonstrating that the maximum photosynthetic rate per unit weight is higher in thin photosynthetic tissue of high internal chlorophyll concentration among unicells

and thin macrophytic tissue than in thick photosynthetic tissue among large unicells and macrophytes many cell layers thick. A general relationship is therefore observed between the photosynthetic rate and the thickness of the photosynthetic tissue of phototrophic organisms from both aquatic and terrestrial habitats. The present study demonstrates that similar relationships also exist for chlorophyll concentration, light capture, and photosynthesis in aquatic plant communities. The same basic principles thus apply to the various types of plant communities as to photosynthetic tissues, with natural plant communities being amenable to treatment as compound photosynthetic systems (Talling 1957a). The reduced photosynthesis of oceanic communities with thick photic zones is thus comparable to the inefficiency of light capture and photosynthesis of thick macrophyte tissues low in chlorophyll concentration, where light absorption by non-photosynthetic structures have a major impact (Markager 1993; Agusti et al. 1994). The same scale-invariant laws thus describes light absorption and photosynthesis over the full

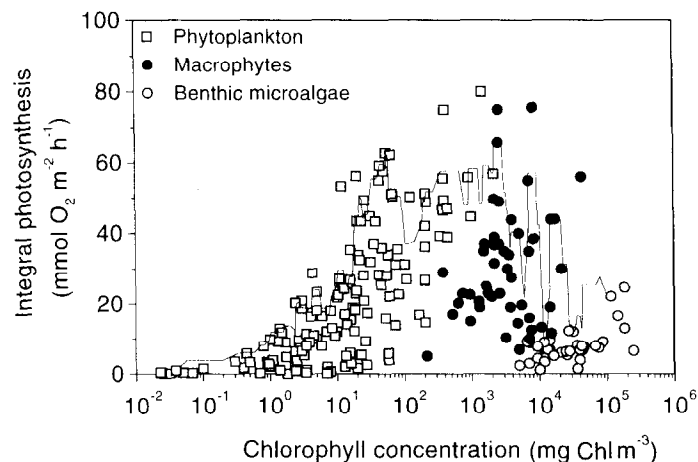


Fig. 6. Integral productivity (P_a) vs. chlorophyll concentration (c) within phytoplankton communities, macrophyte stands, and benthic microalgal mats. The dataset fits an envelope function representing gliding 90% fractiles of 10 consecutive data points. Integral productivity of epiphytic microalgae is not included because these communities do not achieve homogeneous cover and rates are consequently low. Exceptionally high phytoplankton productivities (>200 mmol O₂ m⁻² h⁻¹) of *Microcystis aeruginosa* (Robarts and Zohary 1992) were excluded here because of possible overestimation of productivity.

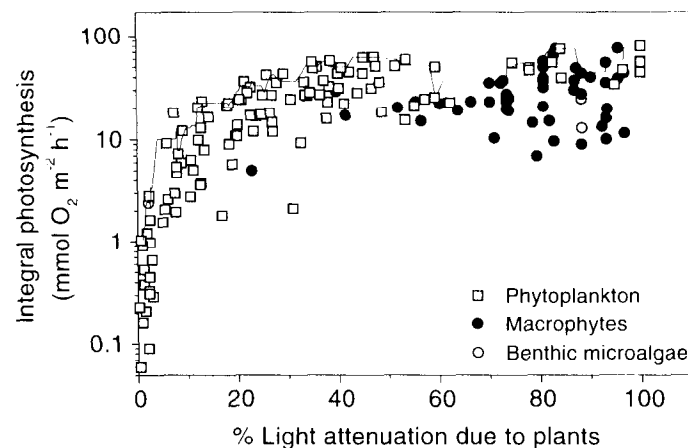


Fig. 7. Integral productivity (P_a) vs. the percentage light attenuation due to plants within phytoplankton communities, macrophyte stands, and benthic microalgal mats. The dataset fits an envelope function representing gliding 90% fractiles of 10 consecutive data points. Integral productivity of epiphytic microalgae is not included because these communities do not achieve homogeneous cover and rates are consequently low.

scale of photosynthetic systems from the smallest cells to the thickest aquatic plant communities.

Chlorophyll concentration and light attenuation—In the present study, light attenuation was found to increase across the entire 6–7 orders of magnitude range of chlorophyll concentration from thin oceanic plankton communities to dense microalgal mats (Fig. 1). Moreover, at high chlorophyll concentration, light attenuation increased more steeply with increasing chlorophyll concentration, and approached a linear relationship with a slope close to 1 (Fig. 1) owing to the increasing contribution of plants to total light attenuation (Figs. 2, 3). Similar relationships described previously for a narrow range of phytoplankton communities (e.g. Smith and Baker 1978) can thus be extended to encompass the full continuum of chlorophyll concentrations among plant communities. This pattern reflects a broad-scale relationship (Duarte et al. 1995), albeit that the variation in light attenuation for a given chlorophyll concentration is considerable due to interplant community variation in background attenuation (Fig. 2) and chlorophyll-specific attenuation coefficient (Table 2).

For a given chlorophyll concentration, light attenuation is generally higher in phytoplankton and benthic microalgal communities than in macrophyte communities (Fig. 1), this being mainly because the chlorophyll-specific attenuation coefficient (k_c) of microalgae is higher than of macrophytes (Table 2), as previously suggested by Westlake (1980a). That k_c is highest in the microalgae is mainly attributable to more efficient light exposure along the short path lengths within the unicells as compared to that in the multicellular tissue of macrophytes. The light absorbed per Chl *a* is reduced when the molecules are packed into chloroplasts, cells, and tissues relative to if they are in solution. This phenomenon is called the package effect, and it increases with increasing size and internal Chl *a* concentration of unicells (Duysens 1956; Morel and Bricaud 1986; Geider and Osborne 1992, fig. 6.2b; Kirk 1994). Although similar detailed empirical and theoretical evaluations have not been attempted for macrophytes, there is evidence for a decline in k_c with increasing chlorophyll concentration and increasing thickness of the photosynthetic tissue (Enriquez et al. 1994). Kirk (1994, fig. 9.2) calculated that for a constant intracellular pigment concentration, the chlorophyll-specific absorption coefficient at the red peak (670–680 nm) decreased ~5-fold as tissue thickness increased from <10 to 100 μm , corresponding to 10-fold size differences between microalgae and the photosynthetic structures of macrophytes. The higher intracellular chlorophyll concentration of microalgae compared to macrophytes (Sand-Jensen and Madsen 1991; Agustí et al. 1994) tends to reduce the differences in k_c between the two plant types.

Light scattering among unicellular algae in suspension and multiple scattering within and among multicellular plants also influence light attenuation in the plant communities. Scattering is difficult to correct for (Geider and Osborne 1992), and it is not known whether different scattering properties contribute to the differences in k_c described here. However, the differences between phytoplankton and macrophytes remain equally distinct when chlorophyll-specific

absorption coefficients are compared (Agusti 1991; Frost-Christensen and Sand-Jensen 1992). Higher proportions of accessory pigments to Chl *a* in some groups of microalgae would also increase k_c compared to higher plants. Calculations for model cells having the same Chl *a* content indicated that k_c for diatoms would be ~70% higher than for green algae because of the high proportion of fucoxanthin in diatoms (Kirk 1976).

The lower k_c found for macrophytes implies that, provided the lower boundary of the photic zone is located at 1% of surface irradiance, macrophyte communities can develop a larger chlorophyll biomass within the photic zone (mean of 600 mg Chl m^{-2}) than can phytoplankton communities (mean of 310 mg Chl m^{-2}). Light compensation points reported for both community types are highly variable (compilations in Enriquez et al. 1996; table 10.1 in Kirk 1994), but do not show systematic differences between the communities (Enriquez et al. 1996). The total chlorophyll biomass of the communities (i.e. the biomass of both the photic and the aphotic zone) is substantially higher and, apart from light, will also be constrained by losses due to respiration, senescence, and grazing. These loss processes are often more prominent in phytoplankton communities than in macrophyte communities (Sand-Jensen and Borum 1991; Enriquez et al. 1993; Duarte et al. 1995). Thus, the total chlorophyll biomass attained by integration with depth through the entire plant community (photic plus aphotic zones) should be higher for macrophytes, which accords with reported chlorophyll ranges of 200–5,000 mg Chl m^{-2} for macrophytes, 34–1,800 mg Chl m^{-2} for phytoplankton, and 30–1,650 mg Chl m^{-2} for benthic microalgal communities (Fenchel and Straarup 1971; Moss 1980; Rublee 1980; Westlake 1980b; Raven 1984).

Upper limits to integral photosynthesis—The increase in volumetric photosynthesis (Fig. 4) and the decrease in the thickness of the photic zone (Fig. 1) with increasing chlorophyll concentration tend to restrict the variation in integral photosynthesis by the different plant communities. Thus the upper limit of photosynthesis appears to be the same (~60 $\text{mmol m}^{-2} \text{h}^{-1}$) in both macrophyte and dense phytoplankton communities, where large fractions of the irradiance are captured by photosynthetic pigments (Fig. 7). The photosynthesis-to-attenuation ratio (p_m/k_c) regulates the upper limit of integral photosynthesis in the different plant communities, although it is also influenced by light acclimation as expressed in terms of the onset of light saturated photosynthesis (I_k , Eq. 7). I_k is highly variable, and no systematic differences among community types are evident in published reviews (e.g. table 10.1 in Kirk 1994). Even if differences did exist, a 50% difference in mean I_k would only lead to a 20% difference in integral photosynthesis at high incident irradiance because integral photosynthesis is proportional to $\ln(2I_0/I_k)$, not directly to $2I_0/I_k$. For a community to actually achieve its upper limit of potential photosynthesis requires that nutrients are available and grazing and other losses of biomass are sufficiently low to produce the maximum biomass of the photic zone.

Phytoplankton and benthic microalgae have higher k_c values (Table 2) and therefore lower chlorophyll biomass (g

m^{-2}) in the photic zone than do macrophytes. Thus, to achieve the same integral photosynthesis, maximum chlorophyll-specific photosynthesis of phytoplankton and benthic microalgae would have to be higher than in macrophytes. This is in fact the case for phytoplankton as p_{mc} was significantly higher than in macrophytes (Table 3), and integral photosynthesis of dense macrophyte and phytoplankton communities peaked at the same level (Fig. 6). In contrast, mean p_{mc} of benthic microalgae was similar to that of macrophytes and was markedly lower than that of phytoplankton. Kairesalo (1980) found a similar pattern, with the light-saturated photosynthesis-to-biomass ratio being ~ 3 -fold higher for phytoplankton than for epiphytic microalgae, and ~ 20 -fold higher than for epipelagic microalgae. The lower p_{mc} found for benthic microalgae might be partly due to methodological problems since it is typically calculated from the maximum integral photosynthesis divided by the chlorophyll biomass. This procedure tends to underestimate p_{mc} because the values are means for the photic zone, and because chlorophyll from below the photic zone (which does not contribute to photosynthesis) can be included in the calculation (Müller 1995). Nevertheless, independent data support the conclusion that integral photosynthesis of benthic microalgae does not fully attain the upper limit of $60 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ found for phytoplankton and macrophyte communities (Fig. 6). Measurements of integral photosynthesis of benthic microalgae based on O_2 fluxes in light and dark cores may be underestimates since they are based on the assumption that respiration during light exposure is similar to respiration in the dark, an assumption that is invalid because the increased O_2 penetration into illuminated sediments may increase respiration beyond that in the dark (Revsbech et al. 1981). However, because most microalgal photosynthesis data included in this study are based on the light/dark switch technique or on ^{14}C incorporation, we conclude that the photosynthesis of benthic microalgae is generally lower than that of well-developed communities of phytoplankton and macrophytes.

Light limitation by background attenuation—Integral photosynthesis is often far below the upper limit mentioned above (Figs. 6, 7). A main constraining factor is extensive light absorption by nonphotosynthetic components (background attenuation, Fig. 7). Background attenuation is often relatively high in the very sparse phytoplankton communities of oligotrophic waters (Fig. 2; Kirk 1994, table 10.2) due to attenuation by dissolved organic material, nonalgal particulate matter (Hobson et al. 1973), or the water itself ($\sim 0.04 \text{ m}^{-1}$). In a photic zone $\geq 57 \text{ m}$ in thickness, pure water alone will attenuate $>50\%$ of downward irradiance (Eq. 1). In such oligotrophic communities, lack of nutrients prevents biomass development, and the integral photosynthesis may be further restricted by nutrient limitation of the chlorophyll-specific photosynthesis (Malone 1980; Pedersen 1995).

Background attenuation also restricts integral photosynthesis in humic waters supplied with colored organic material from land, and in waters having a high concentration of mineral particles resuspended from the sediments or eroded from the catchment area. In numerous lakes in the northern

temperate forest regions of Scandinavia and North America, light attenuation due to dissolved organic material exceeds 1.0 m^{-1} (James and Birge 1938; Åberg and Rodhe 1942; Eloranta 1978; Jewson and Taylor 1978; Chambers and Prepas 1988). Assuming a mean k_c of $0.015 \text{ m}^2 (\text{mg Chl})^{-1}$ (Table 2), phytoplankton biomass will have to reach the high levels typical of highly eutrophic lakes ($\sim 45 \text{ mg Chl m}^{-3}$) just to compensate for background attenuation. To obtain such a high phytoplankton biomass requires much higher lake water nutrient levels than are natural for lakes in the nutrient-poor forested regions (Chambers and Prepas 1988). With increasing background attenuation, lake nutrient levels have to be higher to achieve the same level of integral photosynthesis. Thus, by analogy with the influence of deep vertical mixing below the photic zone (Sverdrup 1953; Talling 1957a, 1971), background attenuation will limit the maximum biomass and influence the time course of phytoplankton blooms. The importance of background attenuation for integral phytoplankton photosynthesis has been emphasized by Megard et al. (1979), who estimated that the chlorophyll concentration (c') necessary to attain half the upper limit of integral photosynthesis varied from 5 to $147 \text{ mg Chl m}^{-3}$ among the lakes included in their study. Interlake variability can be even higher, however. In the highly turbid Wuras Dam (K_t up to 22 m^{-1}) and Hendrik Verwoerd Dam (K_t up to 12 m^{-1} ; Grobbelar 1989), for example, c' was $\sim 1,200 \text{ mg Chl m}^{-3}$. Moreover, because chlorophyll concentration in the two dams remained low ($13\text{--}27$ and $0.7\text{--}7.9 \text{ mg m}^{-3}$, respectively), so did integral photosynthesis ($1.6\text{--}12.2$ and $0.06\text{--}1.2 \text{ mmol O}_2 \text{ m}^{-2} \text{ h}^{-1}$, respectively), despite high nutrient availability. Oscam (1978) proposed a simple formula to predict maximum chlorophyll concentration in German lakes as a combined function of mixing depth, background attenuation, and k_c . The overall importance of background attenuation for phytoplankton maximum biomass and integral photosynthesis and the interrelation with nutrient loading has largely been ignored, however.

Light attenuation in the water column shades the benthic macrophyte and microphyte communities, thereby regulating their depth distribution (Hutchinson 1975). When the plant communities are considered separately, background attenuation tends to be lower relative to attenuation due to plants in shallow macrophyte communities than in phytoplankton communities (Fig. 2). This is because macrophytes attain very high chlorophyll concentrations within the plant-filled water volume and attenuation due to plants thus reaches high levels ($>20 \text{ m}^{-1}$; Westlake 1964). Moreover, rooted macrophytes protect the sediment surface against resuspension, thereby restricting mineral turbidity (Sand-Jensen and Møbus 1996). In communities of benthic microalgae, on the other hand, light attenuation by mineral particles can be prominent (Fenchel and Straarup 1971; Jørgensen and Des Marais 1988). With almost pure microalgal mats, however, most irradiance incident on the community is attenuated by the microalgae (Lassen et al. 1992). That maximum integral photosynthesis is lower in benthic microalgal communities than in phytoplankton and macrophyte communities (Fig. 6) thus suggests that it is constrained by other factors than light. In fact, the upper limit of P_a in the various communities appears to be reached when the plants capture $\sim 50\%$ of the

irradiance, and P_a is not systematically higher when all light is captured by the plants (Fig. 7). This finding again suggests that at high plant densities, factors other than light contribute to regulate the upper limit of integral productivity.

Diffusion limitation—The supply rate of inorganic carbon to the photosynthetic layer and the removal rate of O_2 are regulated by diffusion and convective flow (Sand-Jensen 1989; Madsen and Sand-Jensen 1991). In dense plant communities volumetric photosynthesis is very high, and high exchange rates of inorganic carbon and O_2 are therefore required to avoid carbon depletion and O_2 accumulation (Fig. 4). The turnover time of a given O_2 pool in the water can be calculated by division with P_m . The highest P_m values within benthic microalgal mats yielded a turnover time of 6 s for a 0.3 mM O_2 pool (equivalent to the O_2 pool in air-saturated freshwater at 17.5°C), while the highest P_m values among phytoplankton communities corresponded to a turnover time of 10^3 s. This emphasizes the high intensity of O_2 production and the equivalent demands of inorganic carbon to support photosynthesis in the dense stands. Carbon dioxide is the ultimate substrate for photosynthesis, and insufficient CO_2 availability will restrict primary carboxylation and enhance secondary losses of CO_2 and already fixed photosynthetic energy via photorespiration and Mehler-type reactions (Bowes 1989). Inorganic carbon acquisition mechanisms are found among different aquatic phototrophic species and communities with the purpose of concentrating inorganic carbon internally and alleviating the constraints on the rates of carboxylation (Bowes 1993). The active use of inorganic carbon is particularly important in dense plant communities with strong depletion of inorganic carbon availability (Raven 1991). Oxygen accumulation increases photorespiration, thereby reducing photosynthesis (Bowes 1989). The exchange rates of carbon and O_2 are insufficient to saturate photosynthesis in many dense plant communities because they regularly experience high pH (>10), profound depletion of CO_2 (<20 nM), and consumption of large proportions of the inorganic carbon pool, while O_2 becomes grossly supersaturated (Talling 1966; Kolbe 1972; Revsbech et al. 1983; Pokorný et al. 1984). In dense phytoplankton communities, high inorganic carbon supply and O_2 removal are best achieved by convective flow in the water column and intense CO_2 invasion and O_2 evasion across the water surface. Carbon supply rates are particularly enhanced in hardwater localities, where pH is high for a given CO_2 level, and CO_2 invasion from the atmosphere is accelerated by direct chemical reaction with OH^- to form HCO_3^- rather than by normal hydration to H_2CO_3 (Emerson 1975; Portielje and Lijklema 1995). The procedures used to optimize phytoplankton yield in outdoor cultures also involve the use of shallow water of high alkalinity, bubbling with atmospheric or CO_2 -enriched air, and intensive stirring of the water to ensure high carbon supply and O_2 removal (Hartig et al. 1988; Avron 1989; Sukenik et al. 1991).

Photosynthesis is expected to be most curtailed in benthic microalgal communities because they have the highest chlorophyll concentrations and volumetric productivities, and thus require the fastest exchange of inorganic carbon and O_2 on a water volume basis (Fig. 4). The benthic microalgae

have no direct contact with the atmosphere, and have therefore to exchange gases and solutes with the water column by slow molecular diffusion across a laminar sublayer (often 50–1,000 μ m) offering appreciable resistance to transport (Revsbech 1989; Jørgensen and Revsbech 1990). With benthic microalgal mats on sediments, transport limitation is partly ameliorated by diffusive exchange with the anoxic carbon-rich sediment below the illuminated surface layer. This additional carbon source and O_2 sink does not exist in microalgal communities covering inert stones or macrophyte surfaces (Sand-Jensen et al. 1985), which are therefore subject to more profound inorganic carbon depletion and O_2 accumulation than any other plant community. Diffusion models and experiments verify that photosynthetic rates can be strongly limited by inorganic carbon supply rates (Ludden et al. 1985; Rasmussen et al. 1985). The most plausible explanation for why maximum integral photosynthesis is lower in surface mats of benthic microalgae than in dense phytoplankton and macrophyte communities (Fig. 6) thus seems to be limitation of inorganic carbon and O_2 exchange rates.

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