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# Community photosynthesis of aquatic macrophytes

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## *Abstract*

We compared 190 photosynthesis–irradiance (*P-E*) experiments with single- and multispecies communities of macroalgae and vascular plants from freshwater and marine habitats. We found a typical hyperbolic *P-E* relation in all communities and no sign of photosaturation or photoinhibition of photosynthesis at the highest irradiances of about 2,000 $\mu$mol m$^{-2}$ s$^{-1}$. Macrophyte communities displayed much higher maximum gross production (GP$_{max}$), respiration, and light compensation point than separate phytoelements because of the multilayered structure and extensive self-shading in the communities, whereas light use efficiency at low irradiance ($\alpha$) was the same. Although GP$_{max}$ and $\alpha$ varied extensively among the 190 communities, their upper limits increased linearly and predictably with community absorption reaching 26.3 $\mu$mol m$^{-2}$ s$^{-1}$ O$_2$ and 0.090 mol mol$^{-1}$ photon at 100% absorption. The upper limit of $\alpha$ is close to a realistic limit of O$_2$ of 0.10 mol mol$^{-1}$ photon. The upper limit of GP$_{max}$, however, is markedly below the theoretically attainable 180 mol m$^{-2}$ s$^{-1}$ O$_2$, reflecting a suboptimal three-dimensional structure and light distribution. Indirect measures supported this explanation as GP$_{max}$ increased fourfold from communities with a very uneven to a more even light distribution. Photosynthetic characteristics of communities are strongly influenced by plant density, absorption, and distribution of light and cannot be interpreted from the photosynthetic behavior of phytoelements. Thus, many examples of carbon and nutrient limitation in experiments with separate phytoelements may not withstand at the relevant ecological scale of communities where light almost always constrains photosynthetic production.

Photosynthetic production is the key process in food production and carbon cycling in virtually all ecosystems and the process has been extensively studied both on land and in water. Light is the single most important factor for photosynthetic production, providing the energy for electron transport that ultimately leads to energy formation and carbon fixation. Understanding how photosynthesis responds to light at the proper ecological scale is therefore essential for our knowledge of ecosystem processes (Jarvis 1995; Englund and Cooper 2003). However, few measurements of aquatic community production are available in the literature (Van der Bijl et al. 1989; Middelboe and Binzer 2004; Binzer and Middelboe 2005) and those that exist frequently lack key information on plant density and photosynthesis for the entire range of irradiances (photons, 0–2,000 $\mu$mol m$^{-2}$ s$^{-1}$) expressed in relevant units per square meter.

Studies on photosynthesis of aquatic macroalgae and vascular plants, hereafter collectively referred to as macrophytes, have traditionally been made on separate phytoelements such as thallus pieces or leaves. Measurements of photosynthesis of phytoelements in relation to light have been used to determine interrelations between photosynthetic parameters, physiological status, or acclimatization to depth or depth strata in the communities (e.g., Huppertz et al. 1990; Markager and Sand-Jensen 1992; Necchi 2005). Ecological constraints are, however, experienced by whole individuals or communities and not solely by selected tissues. Thus, a leaf or a thallus piece can experience favorable or unfavorable conditions for growth and survival, whereas individuals or communities experience the opposite conditions. Measurements on phytoelements may, therefore, be irrelevant or even misleading at the proper ecological scale of entire individuals and communities.

Production of macrophyte communities can be regarded as a summation of production by all phytoelements in the community (Ceulemans and Saugier 1991). Community production is therefore determined by the physiological status as well as the local light climate of each phytoelement (Beyschlag and Ryel 1998). Because light diminishes through the canopy and the angles of phytoelements to the sun strongly influence the local light climate (Forseth and Teramura 1986; Russel et al. 1990; Binzer and Sand-Jensen 2002*b*), the production–irradiance relation is markedly different for the community and the phytoelements themselves (Ceulemans and Saugier 1991; Beyschlag and Ryel 1998). Canopies can, for example, effectively utilize light up to very high irradiances because an unused photosynthetic potential is available below the upper layers of phytoelements (Jarvis and Leverenz 1983; Ruimy et al. 1995). Consequently, photosynthesis of phytoelements may not tell much about photosynthetic production, light demands, and overall performance of entire individuals or communities.

Several essential community responses can be deduced directly from knowledge on photosynthesis–irradiance

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relations and local light regimes of the phytoelements. The fact that most communities have a much higher leaf or thallus area than ground area (leaf/thallus area index [LAI] $>> 1$) implies that communities will have either the same or a higher gross production (GP) per unit ground area than phytoelements per unit surface area. The quantum efficiency ($\phi$) should be the same in communities as for the phytoelements when all irradiance ($E$) is absorbed in the community, since all photosynthetic activity ($P$) thus takes place on the initial linear part of the $P$-$E$ curve ($\alpha$) where efficiency remains constantly high. Moreover, since communities are expected to have a higher respiration rate ($R$) per unit of ground area than the respiration rate of phytoelements per unit of surface area, the compensation point of photosynthesis ($E_c = R\alpha^{-1}$) for communities will exceed that of phytoelements. Respiration should also constitute a much higher percentage of gross production in the community than for separate phytoelements because most phytoelements in the community are not light-saturated even at the highest incident irradiances.

Photosynthetic parameters not only change from the scale of phytoelements to the scale of communities. They also change with density of the communities. In open communities, where not all irradiance is absorbed in the canopy, GP and the efficiency of light use at low irradiance ($\alpha$) will be low. As density increases, GP should increase hyperbolically toward an upper boundary while $\alpha$ should approach the values set by the phytoelements in the community. Respiration may be expected to increase more or less linearly with increasing macrophyte density and respiring biomass, implying that net production (GP–respiration) will reach a maximum at intermediate density (de Wit et al. 1970). At even higher density, net photosynthesis is expected to decline because of greater increase of respiration than GP due to extensive self-shading. Acknowledging that GP, $R$, and $\alpha$ increase with community density, it can be predicted that community $E_c$ and $E_k$ change less than the before-mentioned parameters.

To reach a high community production it is essential that all light is absorbed in the canopy. It is also essential that all photons are well distributed between the phytoelements and they mostly experience low irradiance and avoid excessive absorption of photons leading to photosaturation (Kuroiwa 1970; Liu et al. 2003). Photosynthetic parameters are thus dependent on the structure of the community. Theoretical models (e.g., Kuroiwa 1970; Sands 1995*a,b*; Binzer and Sand-Jensen 2002*b*) and experimental tests (Monsi et al. 1973; Ishii 1998; Binzer and Sand-Jensen 2002*b*) show that if light is distributed evenly among phytoelements, irradiance on each phytoelement is low and can be used efficiently for photosynthesis. This situation is achieved when most available light is absorbed in the canopy and absorbed irradiance per biomass is low. Measuring photosynthetic characteristics, absorption properties of phytoelements, and community biomass are thus not sufficient to describe community production, since three-dimensional (3-D) structure and distribution of light in the canopy also contribute to determine photosynthetic production (e.g., Ceulemans and Saugier 1991; Binzer and Sand-Jensen 2002*a*; Middelboe and Binzer 2004).

Table 1. Overview of the species and communities used in this analysis.

| Species | *n* | Source |
|---|---|---|
| Marine macroalgae | | |
| *Fucus serratus* | 9 | Binzer and Sand-Jensen (2002*a*) |
| *Enteromorpha* sp. | 3 | Binzer and Middelboe (2004) |
| *Chordaria flagelliformis* | 3 | Binzer and Middelboe (2004) |
| *Ahnfeltia plicata* | 3 | Binzer and Middelboe (2004) |
| Mixed macroalgal communities* | 15 | Binzer and Middelboe (2004) |
| Natural macroalgal communities† | 72 | This study |
| Freshwater macroalgae | | This study |
| *Cladophora glomerata* | 10 | |
| Freshwater plants | | This study |
| *Vallisneria americana natans* | 3 | |
| *Vallisneria americana gigantea* | 2 | |
| *Sagitaria subulata* | 2 | |
| *Sagitaria platyphyla* | 2 | |
| *Cabomba caroliniana* | 4 | |
| *Egeria densa* | 3 | |
| *Myriophyllum aquaticum* | 3 | |
| *Hygrophila corymbosa aroma* | 2 | |
| *Hygrophila corymbosa stricta* | 2 | |
| *Potamogeton pectinatus* | 4 | |
| *Potamogeton crispus* | 8 | |
| *Sparganium emersum* | 8 | |
| *Callitriche* sp. | 8 | |
| Marine seagrasses | | This study |
| *Zostera marina* | 24 | |
| | 190 | |

* The mixed macroalgal communities were different combinations of *Fucus serratus, Enteromorpha* sp., *Chordaria flagelliformis*, and *Ahnfeltia plicata*.

† Natural macroalgal communities were allowed to establish and grow for at least 1 yr in the field on an artificial substratum. Communities included *Fucus vesiculosus, Scytosiphon lomentaria, Enteromorpha* sp., *Cladophora* sp., *Polysiphonia fucoides, Ceramium rubrum*, and *Ectocarpus siliculosus* with 1–6 species present in each sample.

Our first four objectives here were to evaluate (1) differences in magnitude and interrelations between photosynthetic parameters in aquatic macrophyte communities, (2) changes in photosynthetic parameters with density and absorption in the communities, (3) differences in photosynthetic parameters between macrophyte communities and separate phytoelements, and (4) the effect of canopy structure on community photosynthesis. To make this evaluation, we compiled 190 data sets of macrophyte community production in relation to light for marine and freshwater species of macroalgae and rooted plants (Table 1). Because of the large collection of different communities, we anticipate substantial variations in photosynthetic and respiratory characteristics. On the other hand, we also anticipate clear constraints on maximum GP, net production, and photosynthetic efficiency related to photon absorption in the community and to maximum theoretical photon yield of photosynthesis. Here our final two objectives were to establish the upper boundaries for: (5) maximum gross and net production at high irradiance in aquatic macrophyte communities, and (6) photosynthetic efficiency at low irradiance in the communities.

## Methods

*Macrophytes and collection sites*—We compiled 190 data sets of plant community production versus irradiance. To measure only metabolism of macrophyte communities, sediments were rinsed off plant roots and incubation water was filtered (Whatman GF/C filters) to remove free-living algae, bacteria, and animals such that only firmly attached biofilms of microorganisms on macrophyte surfaces and on rock surfaces in the case of attached macroalgal communities remained.

Data sets were from 103 experiments with 19 different species in monoculture and 87 experiments with multispecies (2–6) communities (Table 1). Multispecies communities were either artificially constructed (15 experiments) by mixing freshly collected detached species in the incubation chamber or were natural macroalgal communities (72 experiments) that had been growing on stony substrata in shallow coastal waters for at least a year before being transferred to the laboratory for measurements. Density of the communities varied depending on species, type of experiment, and time of year. Density in terms of LAI (one-sided macrophyte surface area per unit ground area) and percentage absorptance of irradiance through the community relative to incident irradiance was varied systematically in the experiments. Each data set included 6–7 measurements at different irradiances from 0 to 2,000 $\mu$mol m$^{-2}$ s$^{-1}$.

The present contribution presents mainly new data, but because the aim was to provide an integrated view, we also included data from published studies using the same experimental setup and methods (Binzer and Sand-Jensen 2002*a*; Middelboe and Binzer 2004). Freshwater plants, a marine seagrass, and natural and constructed marine macroalgal communities were used in the 190 experiments. We selected species and communities to ensure that (1) they were in active growth and (2) as many species and growth types were included in the entire data set. A total of 61 experiments was made with 9 species of subtropical and 4 species of temperate freshwater plants and one freshwater macroalga, *Cladophora glomerata*. The selection included ramifying species with apical growth (e.g., *Potamogeton pectinatus*), species with basal growth (e.g., *Sagittaria* spp.), species very efficient at using $HCO_3^-$ (e.g., *Potamogeton crispus*), and a few species apparently unable to use $HCO_3^-$ (e.g., *Sparganium emersum*; Sand-Jensen 1983). Subtropical freshwater plants were supplied from a commercial aquarium facility TROPICA as fully developed specimens of a shoot length less than 40 cm and a restricted root development (<20% of total plant biomass) in vermiculite. Plants were acclimated in a laboratory growth facility for at least 1 week in a 16-h light (ca. 300 $\mu$mol m$^{-2}$ s$^{-1}$ photon) and 8-h dark cycle at the same temperature (20°C) as applied during the photosynthetic experiments and in the same type of water (i.e., alkaline groundwater as tap water containing ca. 5.0 mmol L$^{-1}$ dissolved inorganic carbon [DIC]). Vermiculite was removed and the roots exposed during experiments. Temperate freshwater species were collected during summer in shallow alkaline (4.3–5.5 mmol L$^{-1}$) and slightly $CO_2$-supersaturated streams from North Zealand, Denmark (daytime average about 0.15 mmol L$^{-1}$ $CO_2$; Sand-Jensen and Frost-Christensen 1998) and directly used for experiments. All freshwater species were carefully rinsed in running tap water and dead roots and rhizomes were removed. Photosynthetic experiments were made at 20°C for subtropical and 15°C for temperate freshwater species in alkaline tap water (ca. 5.0 mmol L$^{-1}$), which was pH adjusted during photosynthesis by injecting small aliquots of HCl so that the water contained about 0.15 mmol L$^{-1}$ $CO_2$.

A total of 24 experimental series was made with the temperate seagrass *Zostera marina* (eelgrass) collected during early summer in a nutrient-rich estuary Roskilde Fjord, Denmark from a site where water depth is 1.5 m, salinity is 14–15, and DIC is 2.3–2.5 mmol L$^{-1}$. The site was selected so that eelgrass shoots were well developed and maximum leaf lengths about 40 cm. Leaves and belowground parts were carefully rinsed before experiments and old rhizome segments and roots were removed. Leaves constituted 80% and roots and rhizomes the remaining 20% of the biomass during experiments. Photosynthetic experiments were made at 10°C and 20°C in filtered water (GF/C filters) from the collection site that was kept close to $CO_2$ equilibrium with atmospheric air by adjusting pH to 8.0–8.2.

Experiments with each macrophyte species were made at 4–5 different densities typically ranging from about 2 up to 12–16 LAI. Macrophyte surface area was determined on two subsamples of each species by first placing the tissue between water-sucking paper and measuring the wet weight and then measuring surface area by an area meter (Li-Cor) for species with wide leaves or thalli (>2 mm) and by microscopic determination of dimensions for fine-textured species. LAI during experiments was calculated from added wet weight and established conversion factor describing surface area per unit wet weight.

A total of 72 experimental series were made with natural macroalgal communities that had colonized and grown on cement tiles (30 × 30 cm) for more than a year in shallow waters (1 m) on a boulder reef in Kattegat off the coast of Ålsgårde, North Zealand, Denmark. Perennial *Fucus vesiculosus* was most common in the community, but other annual or perennial species and different growth forms dominated for shorter periods (e.g., *Ceramium rubrum, Cladophora* sp., *Ectocarpus siliculosus, Scytosiphon lomentaria*, and *Polysiphonia fucoides*). About nine communities were collected every 1 to 2 months from the reef, transferred submerged to the laboratory, and examined over the next few days in photosynthetic chambers in filtered seawater from the locality (2.2 mmol L$^{-1}$ DIC) at ambient temperature (2–22°C). Free $CO_2$ was kept close to air equilibrium by maintaining pH at 8.0–8.2. LAI of these natural communities was determined by removing the macroalgae, dividing them up into species, and measuring their wet weight and thallus surface area. Details on the restricted (1.8-fold) seasonal variability of maximum community production and on abundance and photosynthetic characteristics of individual macroalgal species will be given elsewhere (Middelboe et al. unpubl. data).

*Photosynthetic experiments and calculations*—Photosynthetic production of the communities was measured during the daytime period in a 36–38-liter glass chamber (40 cm tall and 30 × 30 cm in ground area) immersed in a 200-liter thermostatically controlled aquarium to maintain constant temperature. Detached plant shoots were placed evenly distributed in the chamber and with their roots and basal parts close to the bottom by weighing them down with small pieces of stainless steel. Natural macroalgal communities that had colonized cement tiles directly fitted into the chamber. Chambers were made of glass and the sides had reflecting mirrors to ensure that light did not vanish through them and they optically imitated the natural situation in large canopies with neighboring macrophytes. Stirring was provided by 2–3 submersible pumps. Two high-pressure sodium lamps (600 W, Hortilux) were used as light source because they can supply high irradiances (ca. 2,000 $\mu$mol m$^{-2}$ s$^{-1}$) and have a light spectrum resembling all colors like natural sunlight, albeit higher proportions of yellow and orange light. We regard differences from the natural sunlight spectrum as relatively unimportant for the photosynthetic characteristics also because quantum efficiency changes relatively little across the light spectrum for plants and thick macroalgae (Larcher 1995). It is more important for comparative purposes to use the same light source in all experiments. Variable irradiances were obtained by inserting neutral density filters above the chamber. Irradiance through macrophyte canopies was measured in 9 depth profiles in different positions with 5-cm depth intervals through 40-cm-tall canopies and 1–3-cm intervals through shorter canopies applying a 3-mm-diameter Spherical Micro Quantum Sensor (US-SQS, Heinz Walz GmbH). As a control, nine depth profiles were measured through water without macrophytes. Absorptance due to the canopy was normalized to the control and averaged for all depth profiles.

Experiments were performed at different temperatures, depending on time of the year for natural communities transferred from the field, but the majority of them (~80%) were made between 14°C and 18°C. Photosynthesis and respiration were measured as oxygen evolution and consumption rates, respectively, by means of a Clark-type oxygen sensor (YSI 5905) and logged every 5 s on a computer via an AD-converter (ADC-16, Picotech) or on a data logger (Li-Cor 1000). In some experiments, oxygen was measured with a Clark-type oxygen microsensor connected to a picoamperometer (Unisense A/S). Experimental series started by measurements of respiration in the dark and proceeded by photosynthetic measurements at 5–6 gradually higher irradiances (typically about 35, 70, 140, 350, 500, 750, and 1,800 $\mu$mol m$^{-2}$ s$^{-1}$). An experimental series lasted 4–7 h because of long equilibration periods following shifts in irradiance and low rates of oxygen change requiring long incubation periods to ensure accuracy compared to traditional photosynthetic experiments with detached leaves or thalli in small chambers. Oxygen concentrations were allowed to decline in the dark to 80% of air saturation and to increase to 130% in the light. To avoid oxygen effects on metabolic rates, oxygen concentrations were adjusted back to air saturation, if needed, by replenishing the water. DIC reduction during photosynthesis was negligible (<0.1 mmol L$^{-1}$) relative to the large DIC pools (i.e., 2.2–5.0 mmol L$^{-1}$). pH was measured with a combination electrode connected to a PHM 9 (Radiometer).

Net production in light (NP) and dark respiration ($R$) were calculated from the linear slope of the oxygen concentration versus time after rates had remained constant for at least 10 min when photosynthetic rates were high and for at least 30 min when rates were low. Gross production (GP) was calculated as the sum of net production and dark respiration (GP = NP + $R$; $\mu$mol m$^{-2}$ s$^{-1}$ of ground area) assuming that mitochondrial dark respiration continues unaltered in the light following conventions. Photosynthetic efficiency at low irradiance ($\alpha$, mol mol$^{-1}$ incident photon) was calculated from the linear slope of photosynthesis versus irradiance at light limitation by regression for four points between 0 to 175 $\mu$mol m$^{-2}$ s$^{-1}$. The light compensation point was calculated as respiration divided by $\alpha$ ($E_c = R\alpha^{-1}$). The irradiance at which production begins to saturate ($E_k$) was calculated as gross production divided by $\alpha$ ($E_k = \mathrm{GP}_{\max}\alpha^{-1}$). Because few of the communities were actually fully saturated by light, a fitted GP$_{\max}$ was used to estimate $E_k$.

Nonlinear and linear fits were performed using Graphpad prism, based on minimized least-square regression. Upper boundaries were determined using floating 99th percentiles for blocks of 10 measurements located at gradually higher irradiances to estimate nonlinear boundaries (GP$_{\max}$ and NP$_{\max}$ as function of $R$) and using the PC program "Blossom" (U.S. Geological Survey) to estimate linear boundaries (GP$_{\max}$ and $\alpha$ as a function of absorbtance).

We characterized the density of macrophyte communities in three different ways. First, open or closed communities provided a crude distinction of the percentage of light absorbed and the density of plant communities. Communities were classified as closed when they either absorbed more than 80% of the incident irradiance or had an LAI exceeding 4. Second, photon absorptance in the canopy was used as a measure of macrophyte density when data were available. Absorptance cannot provide information as to what happens when additional biomass is added after virtually all light is absorbed. For that purpose, the third measure, community respiration, is more suitable as an index of community density, because it was available for all 190 experiments and it should increase with the respiring plant biomass and with LAI. We acknowledge, however, that different species and life forms may have different respiration rates when normalized to biomass or LAI. Nevertheless, community respiration is a measure of

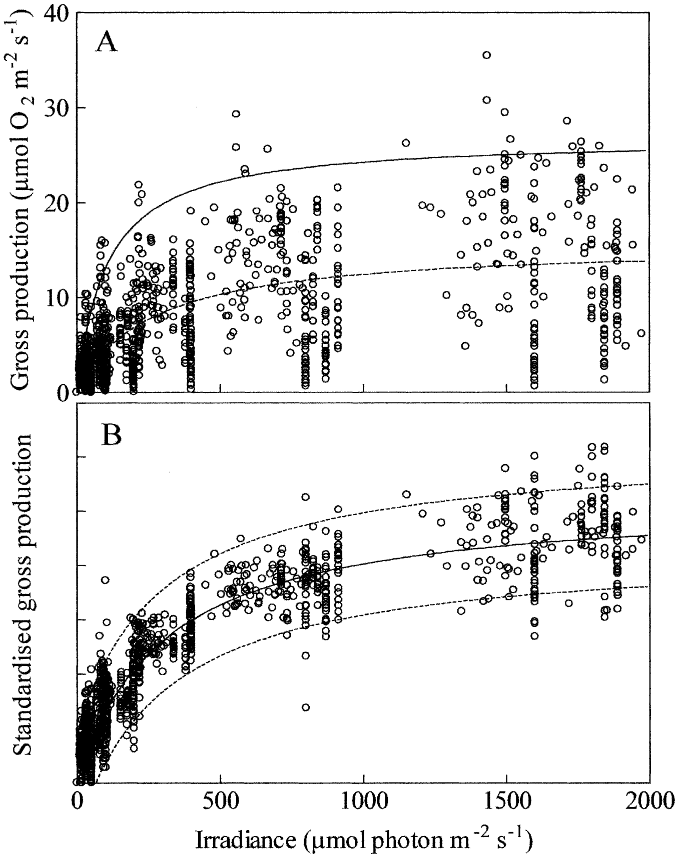

Fig. 1. (A) Gross production (GP) as a function of irradiance ($E$) for all communities in this study. (B) GP standardized to mean GP. The solid lines represents the average GP fitted to the hyperbola GP = $\alpha E\mathrm{GP}_{\max}(\alpha E)^{-1}\mathrm{GP}_{\max}{}^{-1}$ as proposed by Ledermann and Tett (1981). The dotted line represents the upper prediction limits that include 95% of all data.

metabolic activity of the community that should be tightly coupled to photosynthetic performance as well.

To evaluate the influence of the 3-D structure on photosynthetic production, we calculated how much of the incident irradiance was absorbed per unit of respiratory activity. This measure can also be used as a proxy of light absorptance per unit of biomass assuming that total community respiration is positively related to biomass. If each unit of respiratory activity and biomass absorbs only a small proportion of available light a higher potential production is expected in the community than if each unit absorbs a high proportion of available light.

## Results

*Community production at high and low irradiance*—Community production followed the well-known hyperbolic form with increasing irradiance in all experiments (Fig. 1A). The hyperbolic relation became more apparent when photosynthesis was standardized to the mean production in each experiment, thereby correcting for differences in community density and production capacity among experiments (Fig. 1B). Maximum gross production ($\mathrm{GP}_{\max}$) of $O_2$ at high irradiance averaged 14.2 $\mu$mol m$^{-2}$ s$^{-1}$ for all data sets (Table 2) and 8.6 and 16.8 $\mu$mol m$^{-2}$ s$^{-1}$ for open and closed communities, respectively.

The comprehensive data set was used more directly to determine the upper production limit in aquatic macrophyte communities. The upper prediction limit of the production–irradiance data (Fig. 1A) showed a maximum $O_2$ production rate of 25.5 $\mu$mol m$^{-2}$ s$^{-1}$. Using instead the frequency distribution of GP in all experiments yielded a 95th percentile of 25.2 $\mu$mol m$^{-2}$ s$^{-1}$ (Fig. 2). The frequency distribution confirmed that $\mathrm{GP}_{\max}$ values were significantly higher for closed than open communities, with the upper 95th percentile reaching 26.1 $\mu$mol m$^{-2}$ s$^{-1}$ for closed and 17.6 $\mu$mol m$^{-2}$ s$^{-1}$ for open communities (Fig. 2, Mann–Whitney, $p < 0.0001$).

Photosynthetic production at low irradiances showed that $\alpha$-values ranged from 0.003 to 0.095 mol mol$^{-1}$ photon with a median of 0.035 mol mol$^{-1}$ and an upper 95th percentile of 0.076 mol mol$^{-1}$ photon for all communities together (Fig. 2, Table 1). Closed communities had significantly higher $\alpha$ values than open communities (Fig. 2, Mann–Whitney, $p < 0.0001$).

Comparing photosynthetic production at high irradiance ($\mathrm{GP}_{\max}$) with the efficiency at low irradiance ($\alpha$ values) showed a positive relation (Fig. 3). The relation followed more closely a hyperbola ($r^2 = 0.63$) than a straight line ($r^2 = 0.46$). Thus, communities that are efficient at utilizing low irradiances are also more efficient at utilizing high irradiances.

Respiration rates in the communities, on average, constituted 28% ± 2% (95% confidence limit) of $\mathrm{GP}_{\max}$ (Table 2).

Table 2. Photosynthetic parameters of aquatic macrophyte phytoelements (Phyt) and communities (Comm). (Data for phytoelements are from Dring and Brown 1982, Madsen and Sand-Jensen 1994, Frost-Christensen and Sand-Jensen 1992, Kirk 1994, Olesen et al. 2002, Binzer and Sand-Jensen 2002*a*, Necchi 2005, and Plus et al. 2005)

| | Average | | Median | | 5–95th percentiles | | $n$ | | |
|---|---|---|---|---|---|---|---|---|---|
| | Phyt | Comm | Phyt | Comm | Phyt | Comm | Phyt | Comm | Unit |
| $\mathrm{GP}_{\max}$ | 8.80 | 14.2 | 8.90 | 14.4 | 2.92–13.6 | 3.15–25.2 | 31 | 190 | $O_2$, $\mu$mol m$^{-2}$ s$^{-1}$ |
| $\alpha$ | 0.048 | 0.036 | 0.042 | 0.035 | 0.014–0.096 | 0.007–0.076 | 61 | 190 | $O_2$, mol mol$^{-1}$ photon |
| $E_c$ | 21.7 | 119 | 16.3 | 106 | 5.0–52 | 40–226 | 75 | 190 | Photon, $\mu$mol m$^{-2}$ s$^{-1}$ |
| $E_k$ | 151 | 455 | 128 | 407 | 57–308 | 203–795 | 151 | 190 | Photon, $\mu$mol m$^{-2}$ s$^{-1}$ |
| Saturation | 337 | Not sat. | 250 | Not sat. | 82.0–700 | Not sat. | 35 | 190 | Photon, $\mu$mol m$^{-2}$ s$^{-1}$ |
| $R:\mathrm{GP}_{\max}$ | 0.098 | 0.279 | 0.048 | 0.273 | 0.023–0.267 | 0.106–0.503 | 134 | 190 | |

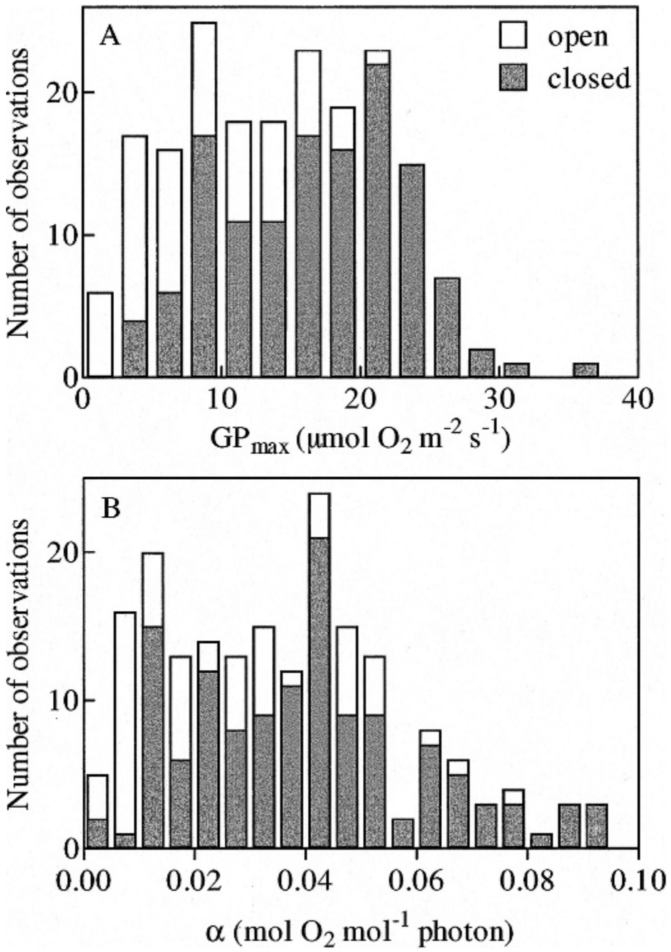

Fig. 2. Frequency distributions of (A) maximum gross production ($GP_{max}$) and (B) photosynthetic efficiency at low light, $\alpha$ in open and closed aquatic macrophyte communities.

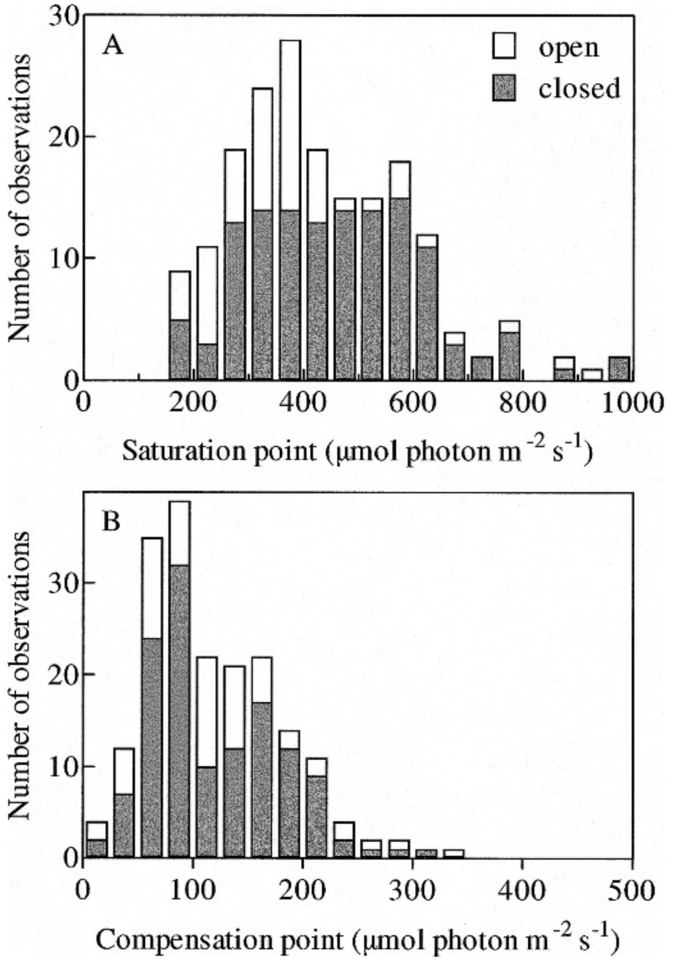

Fig. 4. Frequency distributions of (A) the saturation point of photosynthesis ($E_k$) and (B) the compensation point of photosynthesis ($E_c$) for open and closed aquatic macrophytes communities.

*Light demands are higher for communities than phytoelements*—Irradiance at the beginning of saturation ($E_k$, defined as $GP_{max}\alpha^{-1}$) averaged 455 $\mu$mol m$^{-2}$ s$^{-1}$ in the 190 experiments and there were no significant differences between open and closed communities ($t$-test, $p = 0.066$, Figs. 4, 5). The shape of the photosynthesis curves in Fig. 1B demonstrates, however, that community photosynthesis was usually not saturated even at a maximum attainable irradiance of 2,000 $\mu$mol m$^{-2}$ s$^{-1}$. Fitted maximum production was therefore significantly higher than the observed maximum production (Mann–Whitney, $p < 0.001$). Fitted $GP_{max}$ increased almost linearly with observed $GP_{max}$ and yielded a slope of 1.21, suggesting that community production could, on average, increase by 21% if irradiances higher than 2,000 $\mu$mol photon m$^{-2}$ s$^{-1}$ were available. In fact, only 12 of 191 experiments had an observed $GP_{max}$ exceeding the fitted $GP_{max}$, suggesting that in these 6% of the experiments, communities were either photosaturated or photoinhibited. If they were photoinhibited, the maximum decline of production at the highest irradiance only amounted to 5% of $GP_{max}$.

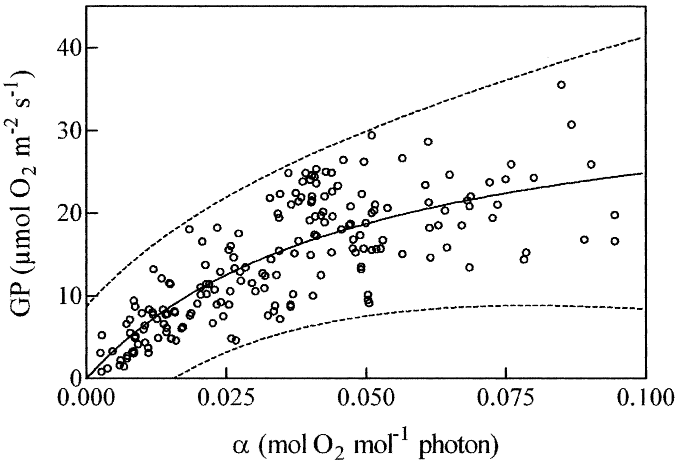

Fig. 3. Maximum gross production ($GP_{max}$) as a function of photosynthetic efficiency at low light ($\alpha$). Solid line represents the average; dotted lines represent the 95% prediction limit.

The light compensation point ($E_c$) was relatively high for the communities (median of 106 $\mu$mol m$^{-2}$ s$^{-1}$, 5–95th percentiles of 40–226 $\mu$mol m$^{-2}$ s$^{-1}$, Table 2). The values were not significantly different for open and closed communities (Mann–Whitney, $p = 0.56$, Figs. 4, 5).

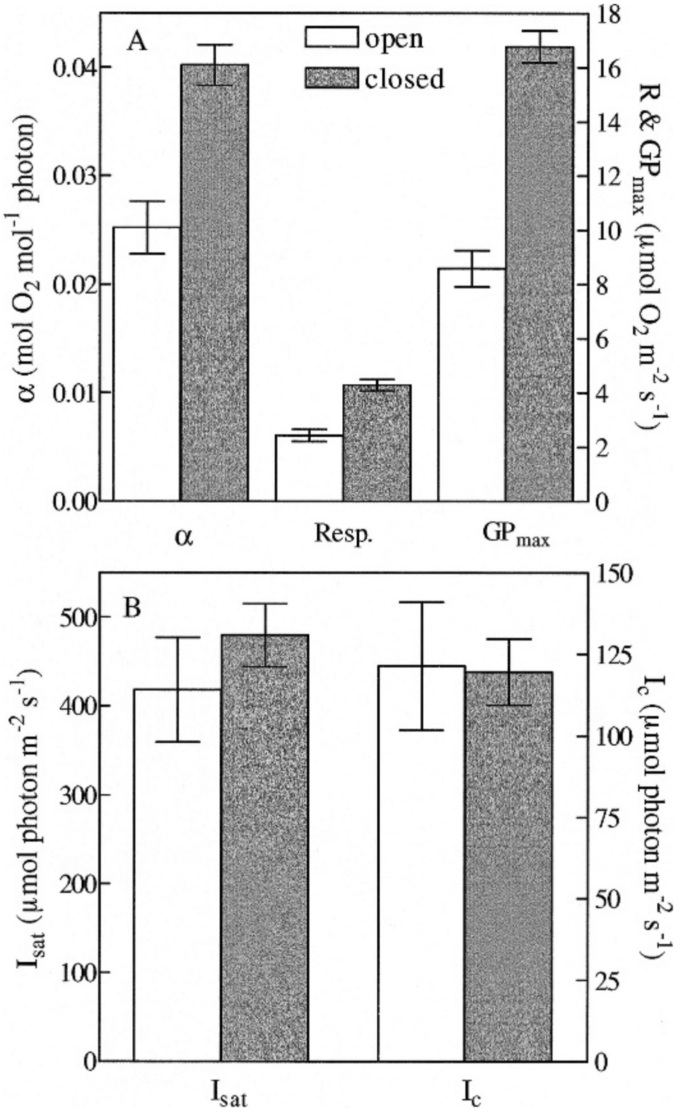

Fig. 5. Photosynthetic parameters for open and closed aquatic macrophytes communities. (A) Photosynthetic efficiency at low light (α), respiration ($R$), and maximum gross production ($\mathrm{GP_{max}}$). (B) Saturation point ($E_k$) and compensation point ($E_c$) of photosynthesis.

*Community production at increasing plant density*—Both $\mathrm{GP_{max}}$, α, and $R$ increased significantly from open to closed communities (Fig. 5). The fractional increase of each parameter was almost the same, implying that the derived parameters, $E_k$ and $E_c$, were almost the same in open and closed communities as described previously. Mean values for $E_k$ and $E_c$ were about 450 $\mu$mol m$^{-2}$ s$^{-1}$ and 120 $\mu$mol m$^{-2}$ s$^{-1}$, respectively (Table 1).

Community absorptance gradually approached 100% at higher macrophyte densities and $\mathrm{GP_{max}}$ and α increased significantly (Mann–Whitney, $p < 0.001$, Fig. 6). Variations in $\mathrm{GP_{max}}$ and α were still substantial among communities absorbing the same percentage of light. Absorptance, therefore, defines the upper limit of production and efficiency of light use and not the actually realized production in most cases. The upper limit of $\mathrm{GP_{max}}$ and α both formed a distinct boundary that increased linearly with absorptance in the canopy (Fig. 6). The upper limit of α was estimated at 0.0015 + 0.0885 × absorptance and, thus, reached a maximum at 0.090 mol mol$^{-1}$ photon at 100% absorptance. The upper limit of $\mathrm{GP_{max}}$ was estimated at 3.3 + 22.9 × absorbtance and reached a maximum $\mathrm{GP_{max}}$ of 26.3 $\mu$mol m$^{-2}$ s$^{-1}$.

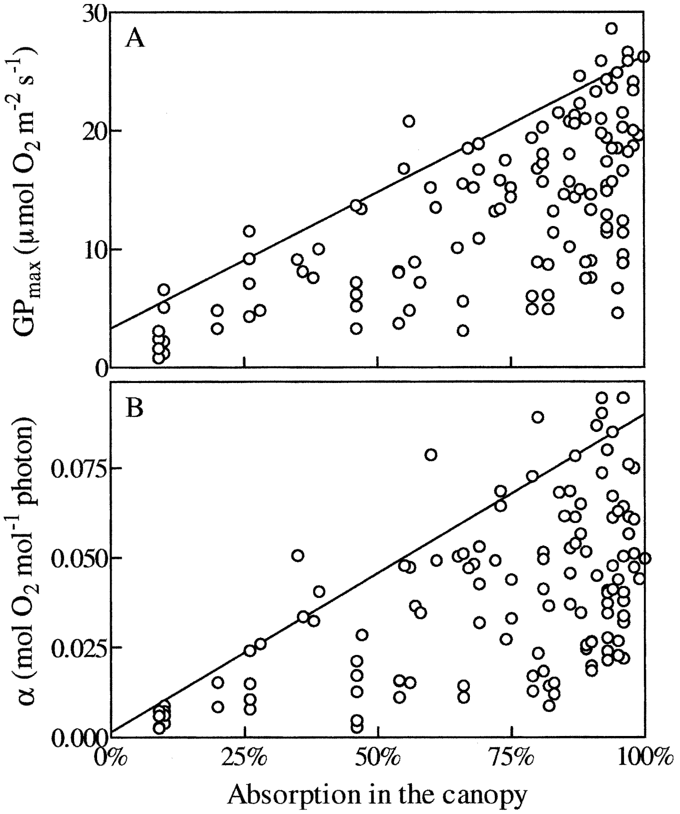

Fig. 6. (A) Maximum gross production ($\mathrm{GP_{max}}$) and (B) photosynthetic efficiency at low light (α) as a function of absorptance in the canopy. Lines represent the upper limits. The upper limit of $\mathrm{GP_{max}}$ was estimated at 3.3 + 22.9 × absorptance, reaching a maximum $\mathrm{O_2}$ of 26.3 $\mu$mol m$^{-2}$ s$^{-1}$. The upper limit of α was estimated at 0.0015 + 0.0885 × absorptance and reached a maximum at 0.090 mol mol$^{-1}$ photon at 100% absorptance.

$E_k$ was independent of community absorptance (Fig. 7), and although $E_c$ decreased significantly with absorptance, the decrease was very small (from 145 to 110 $\mu$mol photon m$^{-2}$ s$^{-1}$, $r^2 = 0.08$).

As respiration increased in communities of higher density, $\mathrm{GP_{max}}$ increased significantly with a slope on 3.3 ± 0.1 at low respiration rates (Mann–Whitney, $p < 0.0001$, Fig. 8A). However, a distinct upper boundary of $\mathrm{GP_{max}}$ was reached at increasing respiration rates, resulting in a hyperbolic relation of $\mathrm{GP_{max}}$ to $R$ for the entire range. The upper boundary of $\mathrm{GP_{max}}$ was attained at a respiration rate of about 3.8 $\mu$mol m$^{-2}$ s$^{-1}$.

Net production also increased with respiration rates in the communities, following an initial linear increase, saturation, and a subsequent decline at high community densities, where the increase in respiration was not counterbalanced by an increase in GP (Fig. 8B). The

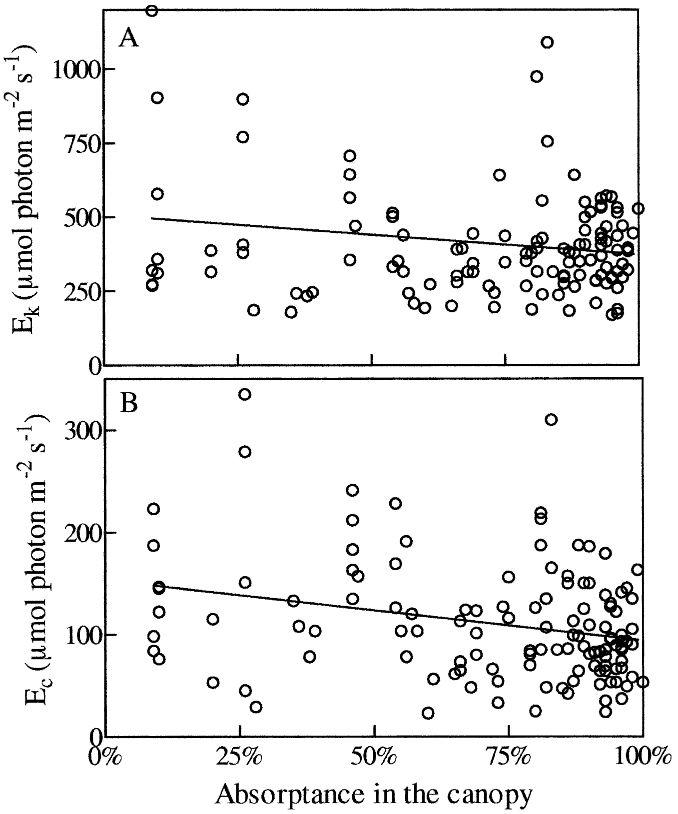

Fig. 7. (A) Saturation ($E_k$) and (B) compensation ($E_c$) point of photosynthesis as a function of absorptance in the canopy. Linear fits were not significant for $E_k$, but significant for $E_c$.

optimal community density of maximum net production was thus attained when respiration rates reached about 3.75 $\mu$mol m$^{-2}$ s$^{-1}$. Above this threshold, the upper limit of net production decreased with higher respiration at a rate of $-0.97$, not significantly different from a slope of $-1.0$ anticipated when GP remains constant as $R$ continues to rise.

The light use efficiency at low light also increased with respiration rate as community density rose (Fig. 8C). A distinct upper boundary was not apparent, but when $R$ exceeded 2 $\mu$mol m$^{-2}$ s$^{-1}$ values up to 0.1 mol mol$^{-1}$ photon were observed. Moreover, $\alpha$ values were significantly higher at high than low $R$ values ($p < 0.001$). Variations in $\alpha$ values were substantial at all $R$ values.

*Community production is affected by structure*—The 3-D structure and light distribution of macrophyte canopies can affect photosynthetic production. As predicted, we observed that GP$_{\text{max}}$ was significantly higher when absorption per unit of respiratory activity (and presumably respiring biomass) were high rather than low (Fig. 9, $p < 0.0001$). It could be postulated that the negative relation is controlled by the relatively few low values located above 0.5 $R^{-1}$ on the $x$-axis. However, there was also a significant decrease when only values below 0.5 $R^{-1}$ were included in the regression ($p < 0.001$). The relation therefore suggests that communities have a higher GP$_{\text{max}}$ when they distribute irradiance more evenly among phytoelements in the canopy.

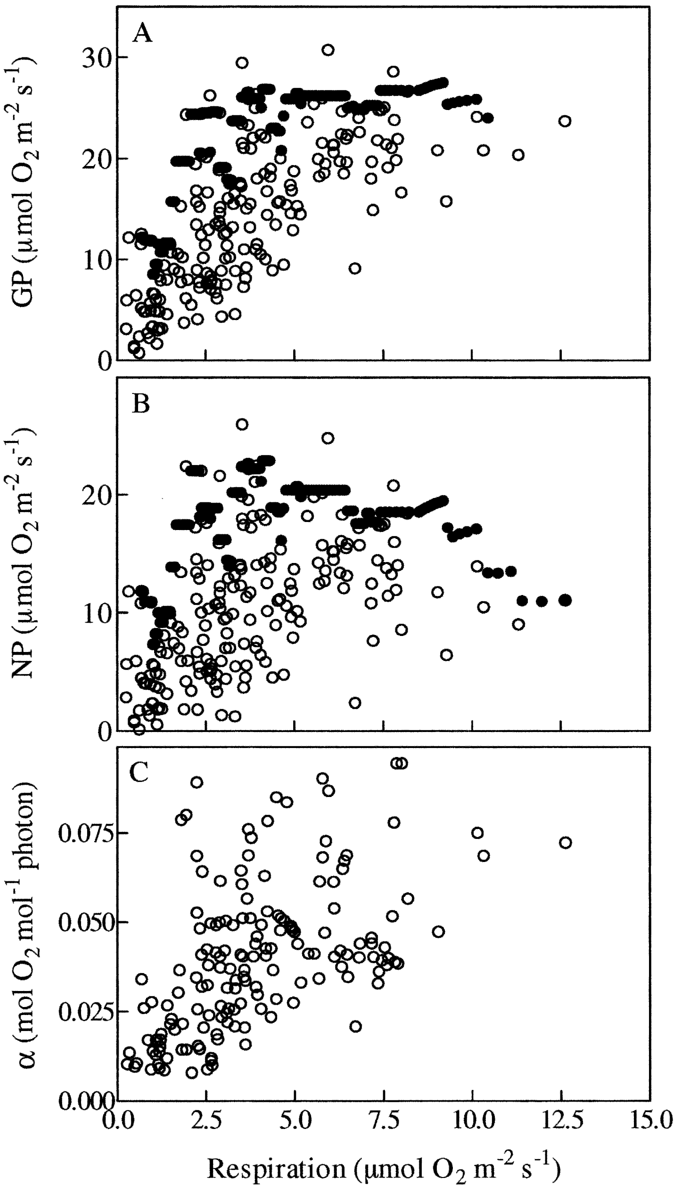

Fig. 8. (A) Maximum gross production (GP$_{\text{max}}$), (B) maximum net production (NP$_{\text{max}}$), and (C) photosynthetic efficiency at low light ($\alpha$) as a function of respiration ($R$). Closed circles represent the moving 95th percentiles of 10 consecutive data points.

## Discussion

*No saturation, high light demands, and no photoinhibition*—Measurements of photosynthetic parameters for phytoelements exposed to different incident irradiances in their local light climate can provide useful information on physiological status and light and shade adaptation with depth in the water column or in the plant canopy. However, this information is not useful for characterizing photosynthetic parameters of dense communities. Our study revealed that aquatic macrophyte communities were never fully saturated by high irradiances (2,000 $\mu$mol m$^{-2}$ s$^{-1}$) resembling those observed at noon on clear summer days.

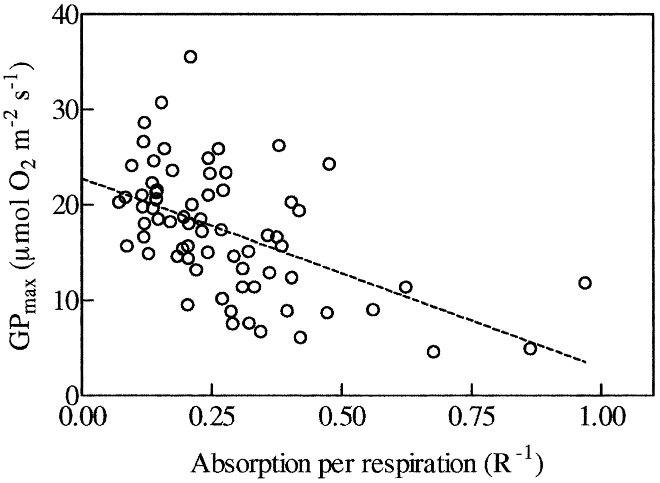

Fig. 9. Maximum gross production as a function of absorptance per respiration unit in the community. Only data for communities absorbing more than 80% of incoming light are included. A linear regression line is shown ($p < 0.0001$).

High irradiances were also needed for photosynthesis to balance respiration (mean $E_c$ of 119 $\mu$mol m$^{-2}$ s$^{-1}$) and to initiate photosaturation (mean $E_k$ of 455 $\mu$mol m$^{-2}$ s$^{-1}$). The $E_k$ values for community photosynthesis should not be confused with a measure of the true saturation of photosynthesis, because this was rarely achieved even at the highest irradiances. The estimated maximum photosynthetic rates were in fact 21% higher, on average, than rates at the maximum natural irradiances. Still, calculations of $E_k$ values for communities are useful because they allow comparison with those of the phytoelements measured under unshaded conditions separated from the communities. Phytoelements have mean $E_c$ and $E_k$ values that are about sixfold and threefold lower, respectively, than community values (Table 2). Thus, as initially predicted, photosynthetic parameters of the phytoelements do not add much information on photosynthetic performance of aquatic communities because internal self-shading and 3-D structure of the canopy generate a completely different integrated picture where high light demands of the community prevail and no photoinhibition is apparent.

It can be concluded that dense macrophyte communities are strongly limited by light most of the time because light continues to limit photosynthetic production up to the highest irradiances at noon on clear summer days. The importance of light limitation is in fact enhanced because the incident irradiance is much lower than this maximum level both before and after noon, during all hours on overcast summer days, and during most daylight hours outside the summer. A few previous field studies, using continuous open water measurements of oxygen in streams (Kelly et al. 1983; Uehlinger et al. 2000) or model estimations on the basis of measured light conditions within canopies of stream plants in the field and *P-E* relations in laboratory experiments (Van der Bijl et al. 1989), support the conclusion of light limitation of community photosynthesis under all seasons and most daylight hours. In contrast, many of the popular experiments on separate leaves and thallus pieces have given the false impression that photosynthesis is saturated by light at relatively low irradiances and that, consequently, other production-regulating factors such as inorganic carbon and inorganic nutrients might be more important than light. Many of the experiments on phytoelements of aquatic macrophytes suggesting carbon and nutrient limitation of photosynthesis and growth may lose their strength and relevance when repeated for individuals and communities, which is the proper scale for ecological evaluations. A challenge therefore exists, testing and re-evaluating inorganic carbon and nutrient limitation of community growth and metabolism.

Low irradiance on phytoelements in dense communities reduces the influence of variable inorganic carbon and temperature on community production because light-limited photosynthesis is usually regarded as being relatively independent of the two parameters. Temperature should, nonetheless, enhance respiratory rates of phytoelements and communities and inorganic carbon and temperature may stimulate community production by increasing the onset of light saturation ($E_k$) and, thereby, restrict the need for an optimal 3-D structure of the canopy to attain high rates of production. Experiments in DIC-rich waters (2–5 mmol L$^{-1}$) of the types used here have shown no or small effects on maximum community production of efficient $HCO_3^-$ users (e.g., *Fucus serratus* and *Potamogeton* pectinatus) upon elevating free $CO_2$ to supersaturated conditions (ca. 250 $\mu$M), whereas significant positive effects were observed for the few sole $CO_2$ users among freshwater plants (e.g., *Callitriche cophocarpa* and *Sparganium emersum*; Binzer and Sand-Jensen 2002*a*; Sand-Jensen et al. unpubl. data). Higher temperatures within the ambient range (2–22°C) for natural attached communities of macroalgae also stimulated metabolism, but the temperature influence was weak for maximum community production ($Q_{10}$ of 1.15) and higher for community respiration ($Q_{10}$ of 1.65; Middelboe et al. unpubl. data). Thus, temperature effects on production and respiration of macrophyte communities should be considered in future evaluations of effects of season, latitude, and global warming.

The absence of light saturation implies that none of the aquatic macrophyte communities as a whole is photoinhibited. So in an ecological perspective, photoinhibition of aquatic macrophyte communities in their natural habitat should not be very important. It is, however, possible that the upper phytoelements in the canopy can be inhibited (e.g., Huppertz et al. 1990; Hanelt et al. 1993), whereas the unused photosynthetic potential of the lower layers of phytoelements compensates for this inhibition such that the overall community production continues to rise up to the highest incident irradiances. Bleaching of the upper leaves in tropical seagrass canopies exposed to high temperatures in shallow lagoons under the burning sun shows that photodamage must occasionally be considered. Field measurements of fluorescence in temperate field populations of most aquatic macrophytes confirm, however, that photoinhibition is indeed rare (Witt 2003). Also, when leaves or thalli of aquatic macrophytes are tested at high irradiances in the laboratory, they rarely show signs of photoinhibition (Binzer and Sand-Jensen 2002*a*; Middelboe and Binzer 2004), though a small (10–15%) depression of maximum photosynthesis may develop after prolonged exposure to high irradiances (Van der Bijl et al. 1989; Witt 2003).

*Upper limits of photosynthetic production*—It has previously been suggested that the upper limit of $O_2$ production in aquatic photosynthetic communities of phytoplankton, microphytobenthos, or macrophytes is about 22 $\mu$mol m$^{-2}$ s$^{-1}$ (Sand-Jensen and Krause-Jensen 1997). This finding is in broad agreement with our study, although the upper limit of macrophyte production found here was somewhat higher at 25.2 $\mu$mol m$^{-2}$ s$^{-1}$ when calculated as the 95th percentile of all $GP_{max}$ values (Table 2). In this study we had access to more experiments and communities and can be more confident that the typical upper limits of aquatic macrophyte production have been determined. An upper limit of about 26 rather than 35 $\mu$mol m$^{-2}$ s$^{-1}$, which is the highest GP observed, is in better correspondence with the upper limit predicted from the production–irradiance curves (25.3 $\mu$mol m$^{-2}$ s$^{-1}$, Fig. 1A), the production–respiration curves (26.0 $\mu$mol m$^{-2}$ s$^{-1}$, Fig. 8A), and the maximum level predicted from the $GP_{max}$-absorbtance relation at 100% absorptance (26.3 $\mu$mol m$^{-2}$ s$^{-1}$, Fig. 6). The upper production limit of $O_2$ of 26.0 $\mu$mol m$^{-2}$ s$^{-1}$ in relation to community respiration was reached when respiration exceeded 4 $\mu$mol m$^{-2}$ s$^{-1}$ (Fig. 8A). The minimum ratio of $R:GP_{max}$ at the upper limit of production was thus 0.16. Although this ratio is lower than the average $R:GP_{max}$ ratio of 0.28 for all community experiments, it is still high compared to previous measurements of $R:GP_{max}$ ratios for individual phytoelements of aquatic macrophytes (median 0.048, Table 2; Markager and Sand-Jensen 1992). As expected, respiratory losses were much higher in dense communities because of self-shading than for individual unshaded phytoelements. Even for less dense communities where respiration should account for a smaller fraction of $GP_{max}$, minimum $R:GP_{max}$ values were still about 0.10. Down-regulation of respiration under shaded conditions in the lower part of the community is, therefore, an important response to allow survival of shaded tissues and attain high densities in aquatic communities (Van der Bijl et al. 1989).

The upper limit of $GP_{max}$ was distinct and positively, linearly related to canopy absorptance (Fig. 6A). Also, the upper limits of $\alpha$ were highly predictable and increased linearly with absorptance to a maximum of 0.090 mol mol$^{-1}$ photon at 100% absorptance (Fig. 6B). This value is close to the maximum attainable limit observed for phytoelements under optimum conditions (Frost-Christensen and Sand-Jensen 1992) and only slightly lower than the theoretically maximum limit of 0.125 mol mol$^{-1}$ photon according to the Z-scheme of photosynthesis. This theoretical upper limit should never be reached, because there is always some photon absorption by nonphotosynthetic elements and loss of excitation energy by fluorescence due to suboptimal conversion in the bio-optical and biochemical pathways of photosynthesis. If the maximum observed $\alpha$ value could be maintained up to the highest irradiances of 2,000 $\mu$mol m$^{-2}$ s$^{-1}$, the upper limit of $GP_{max}$ would reach 180 $\mu$mol m$^{-2}$ s$^{-1}$ at 100% absorptance in the aquatic communities, or sevenfold more than actually recorded. Although community gross production usually does not photosaturate, the *P-E* curve, nonetheless, deviates markedly from linearity, reflecting the suboptimal 3-D canopy structure. More linear relations and higher upper limits of about 50–70 $\mu$mol m$^{-2}$ s$^{-1}$ are found in terrestrial forests and grasslands with a more suitable 3-D structure and a more even light distribution in their canopies (Ceulemans and Saugier 1991; Ruimy et al. 1995; Sand-Jensen and Krause-Jensen 1997).

To achieve high production rates, macrophytes can either distribute photons evenly by changing the structure or acclimate phytoelements to local light. In aquatic communities, optimal 3-D structures is not achievable because of the strong drag forces of moving water (Koehl 1983; Gaylord et al. 1994). Macrophyte movements furthermore result in a highly variable light climate (Schubert et al. 2001). High saturation points of photosynthesis of phytoelements should therefore be more important for aquatic than for terrestrial community photosynthesis. Nevertheless, aquatic phytoelements mostly resemble shade-acclimated terrestrial leaves having low saturation points (Reiskind et al. 1989; Bowes and Salvucci 1989). It has been suggested that constraints on the supply rate of inorganic carbon and nutrients in water contribute to these low saturation points (Nielsen and Sand-Jensen 1989). Also the fact that most aquatic phytoelements receive light on both surfaces, either because light is very diffuse or their phytoelements alternate between facing upward and downward in turbulent water, should make them less capable of optimizing their photosynthetic apparatus and capacity to the local light climate.

*Photosynthetic parameters change with density*—When aquatic macrophyte communities grow and develop during the seasons, succession leads to changes in composition and abundance of the dominant species, as well as continuous changes in total biomass and chlorophyll content of the community. As macrophyte density changes so do photosynthetic parameters. The situation is obvious when succession introduces new species, but photosynthetic parameters will also change in single species communities because of variations in physiological variables, macrophyte density, and structure (Middelboe and Binzer 2004; Hirose 2005).

Clear differences in photosynthetic parameters were observed between open and closed communities in the data set. This is self-evident for $GP_{max}$ and $R$, because metabolic rates will increase with community density. With community respiration used as a general measure of metabolic activity and a proxy of plant biomass, $GP_{max}$ increased with community respiration toward an upper boundary at 26.2 $\mu$mol m$^{-2}$ s$^{-1}$ (Fig. 8). The same saturation of GP as a function of plant density has been shown for terrestrial communities long ago (de Wit et al. 1970) Also, maximum NP was reached at an intermediate community respiration resembling the observations of maximum NP values in terrestrial communities at intermediate LAI (de Wit et al. 1970). At the highest community densities, net production declined almost linearly with increasing community respiration as GP was already close to the upper limit set by light absorptance.

The increase in all primary photosynthetic parameters ($GP_{max}$, $R$, $\alpha$) means that the derived parameters, $E_c$ and $E_k$, are almost constant with increasing density (Fig. 7). The very small significant decrease in $E_c$ as communities absorb more photons acts in the opposite direction than expected. Communities with a low plant density surprisingly do not have lower $E_c$ or $E_k$ values, which they could benefit from in deeper waters with low light. However, other studies on community production of selected species have shown that $E_c$ does decrease at low densities (Binzer and Sand-Jensen 2002*a*) and when $E_c$ is plotted against respiration a small decrease from 150 to 100 $\mu$mol m$^{-2}$ s$^{-1}$ was observed as density decreased. Although the results are not unequivocal, we feel safe to say that decreasing density has relatively small influence on light demands because the decrease in respiration is counteracted by reduced absorbtance in the canopy. To reduce $E_c$ substantially, a reduction in biomass should therefore be followed by structural changes so that all photons are absorbed in the canopy. Thus, different morphological types should replace each other as light decreases (Hay 1983).

*Structure influences maximum photosynthetic rate*—Influence of the 3-D canopy structure on community production has been studied intensively in terrestrial plants with special emphasis on agricultural crops (e.g., Monsi et al. 1973; Ishii 1998; Gratani and Bombelli 1999). Collectively, these studies confirm that high rates of photosynthetic production in dense terrestrial communities exposed to high irradiances are attained when leaves predominantly have a vertical orientation, a clumped rather than an evenly dispersed distribution, are located in several depth strata, and change from sun acclimatization in the upper to shade acclimatization in the lower parts of the canopy. Only a few studies have addressed these questions in aquatic macrophyte communities (Ikusima 1970; Van der Bijl et al. 1989; Binzer and Sand-Jensen 2002*b*), though a suboptimal 3-D structure is the most likely candidate for explaining the much lower maximum production rates in aquatic rather than terrestrial plant communities (Sand-Jensen and Krause-Jensen 1997). Because of the high physical forces in moving water and the lack of rigid plant stems and algal thalli it is difficult to envision an optimal 3-D structured aquatic canopy for light interception and photosynthesis (Koehl 1983; Sand-Jensen 1998). Theoretically the same principles for optimizing light utilization should apply to aquatic and terrestrial communities and experimental manipulation of thalli of macroalgae from a horizontal to a vertical structure did enhance community photosynthesis in accordance with model calculations and previous terrestrial results (Binzer and Sand-Jensen 2002*a*,*b*). The fact that $GP_{max}$ increased significantly with reduced absorptance per unit of respiratory activity in the 190 aquatic communities (Fig. 9), implying a more uniform light distribution among the tissues, also suggests that differences in 3-D structure and light distribution are important for their photosynthetic potential. However, determinations of canopy structure and light distribution are needed to verify this explanation. So far, measurements of the vertical light attenuation coefficient in marine macroalgal communities have confirmed that a more uniform distribution of tissues and irradiance with depth is indeed accompanied by greater production rates (Binzer and Sand-Jensen 2002*a*; Middelboe and Binzer 2004). These results and theoretical consideration can also explain the transition of morphological types of marine macroalgae with depth in the sea from erect vertical morphotypes of high density dominating in shallow water at high incident irradiances, where it is advantageous to be able to distribute light efficiently between phytoelements, to flat, sheetlike horizontal morphotypes of lower density dominating in deeper water at low incident irradiance, where it is advantageous to absorb all remaining light in a few thallus layers to ensure a positive metabolic output (Hay 1983).

In conclusion, this broad-scale study of aquatic communities with different morphological types and densities has shown that photosynthetic parameters are scale dependent. We therefore need to determine light demands and reevaluate inorganic carbon and nutrient limitation at the proper scale of entire communities. Canopy structure and morphological types are important to account for lower photosynthetic rates in aquatic communities than in terrestrial communities and changes in performance with depth.

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