

From thallus to communities: scale effects and photosynthetic performance in macroalgae communities

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ABSTRACT: Experiments on aquatic plant photosynthesis are often performed on spatial scales much smaller than natural systems. The photosynthesis-irradiance relationship (P-I curve) depends, however, on whether photosynthesis is measured on leaves, shoots, plants or entire communities, so that results cannot be reliably extrapolated from the limited spatial scale of experiments to the larger scale of natural systems. To evaluate how the photosynthetic response changes with spatial scale for aquatic plants, we measured the photosynthetic production as a function of irradiance for thallus pieces, single-species and multi-species communities of 4 different marine algae (*Fucus serratus*, *Chordaria flagelliformis*, *Enteromorpha* sp. and *Ahnfeltia plicata*). Thallus pieces followed the well-known hyperbolic shape of P-I curves; that is, the community P-I curves approached linearity. Thallus pieces, thus, saturated at irradiances below 160 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, while the communities started to saturate at values 4 times higher and never became fully saturated even at 1750 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. This increasing linearisation of the P-I relationship for communities influenced the photosynthetic parameters, as maximum gross photosynthesis and compensation irradiances increased 3 to 8 times. The increasing linearisation of the P-I curves is attributed to the 3-dimensional structure of the communities, since communities with a low extinction per unit leaf area, and thus an even distribution of irradiance among thallus parts, used their potential photosynthesis capacity more efficiently. Although not significantly different, multi-species communities had a slightly more linear response and a higher gross photosynthesis than single-species communities, suggesting a more efficient distribution and photosynthetic use of light among the photosynthetic tissue. An increase in spatial scale from thallus pieces to communities decreased variation in photosynthetic rates between species, implying that differences between species are much smaller on natural scales than experiments on single thallus pieces suggest. The findings imply that experiments on the thallus scale should be avoided or treated with caution when predicting the ecological performance of plants in their natural habitat.

KEY WORDS: Community · Photosynthesis · Production · Macroalgae · Irradiance

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INTRODUCTION

Ecological experiments are often performed on spatial scales that are much smaller than the natural systems of interest. As a consequence, the interpretation of results cannot be applied to natural systems without extrapolating from the limiting spatial scale of experi-

ments to the larger scale of natural systems (Englund & Cooper 2003).

Data from terrestrial plants suggests that the photosynthetic characteristics of plants change with scale so that the relation between photosynthetic production and irradiance (P-I) of a single thallus piece does not apply for whole plant communities (e.g. Beyschlag &

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Ryel 1998). Interpretations of experiments made on leaves or thallus pieces cannot, therefore, be easily extrapolated to a higher spatial scale (plant, stand or community). Nevertheless, in aquatic plant research, extrapolations are made vigorously in experiments on carbon acquisition, nutrient acquisition and light demand.

Changes in the P-I curves are caused by the complex distribution of irradiance in the foliage that influences light interception and can vary depending on the size, density and especially inclination of leaves (McMillen & McClendon 1979, Oker-Blom & Kellomäki 1983, Myers et al. 1997). This is well documented for terrestrial plants, but has received only little attention in aquatic plant communities. Such communities do not have the rigid structure of terrestrial plants and, thus, lack the ability to orientate leaves favourably in respect to light interception.

In aquatic plant research, the focus of photosynthetic studies has been mainly on leaves of rooted macrophytes or on single thallus parts of macroalgae, while there are surprisingly few measurements of photosynthetic production in aquatic macrophyte communities (e.g. Van der Bijl et al. 1989, Krause-Jensen & Sand-Jensen 1998, Binzer & Sand-Jensen 2002a). This is unfortunate, as the scale of interest for the plant is not performance of a single leaf or a part of the thallus, but the overall performance of the whole plant or plant community. Photosynthetic production of communities is, thus, an important determinant of plant growth rates, nutrient cycling, secondary production and carbon dynamics in ecosystems, and is not necessarily correlated with the photosynthetic production of leaves or thallus pieces.

The general hyperbolic form of photosynthetic production in relation to irradiance (P-I curves) for single leaves or thallus parts is well known from measurements on terrestrial plants, and aquatic plants and algae (Lüning & Dring 1985, Markager & Sand-Jensen 1994). The hyperbolic form implies that photons are utilised at maximum efficiency for photosynthesis at low irradiance, while the efficiency gradually decreases at higher irradiance. The efficiency of utilising incident and absorbed photons (quantum efficiency) at low irradiance and the maximum rate of photosynthesis at high irradiance have been extensively documented for both terrestrial and aquatic macrophytes (e.g. Frost-Christensen & Sand-Jensen 1992, Markager & Sand-Jensen 1994, Enriquez et al. 1996).

In stands or communities of plants, the variable positions and density of photosynthetic tissue result in a complex distribution of irradiance between the photosynthetic tissues, and the distribution of irradiance affects the P-I relationship. The maximum community photosynthesis is obtained when all photons are dis-

tributed and absorbed evenly among photosynthetic elements, so that each of them experiences irradiance below saturation. If this is achieved, an increase in irradiance will not saturate photosynthesis at the tissue level and there will be an almost linear relationship between community photosynthesis and incident irradiance up to a value of 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (Ceulemans & Saugier 1991, Ruimy et al. 1995). Every absorbed photon can, thereby, be converted to ATP production and carbon assimilation at high efficiency (Russel et al. 1990). However, if the irradiance is unevenly distributed, so that most of the photons are absorbed at high intensities in the upper layers of photosynthetic tissue, community photosynthesis will gradually saturate with increasing irradiance; even in this case, gross photosynthesis will not saturate, since the lower photosynthetic tissue in the community will have an unused photosynthetic potential (Binzer & Sand-Jensen 2002a,b). Whole communities of plants, thus, have a different photosynthetic response to increasing irradiance than the leaves or thallus parts that constitute them. Aquatic plants should generally saturate at lower irradiances than terrestrial plants due to lack of a rigid structure that can assure an even distribution of light among the photosynthetic tissue (Sand-Jensen & Krause-Jensen 1997, Beyschlag & Ryel 1998, Binzer & Sand-Jensen 2002b). Nevertheless, the different morphologies of aquatic plants lead to different abilities to utilise irradiance, depending on their absorption properties, photosynthetic potential and ability to distribute irradiance.

As the P-I relation changes from thallus to community, the parameters used to characterise the photosynthetic production of plants will change accordingly. In plant communities, an increase in respiration per unit ground area is expected with higher biomass. Since the light-use efficiency (α) for the community should be about the same as for all thallus pieces (or slightly higher if all photons are absorbed), the light compensation point for the community should increase with biomass. Maximum gross photosynthesis will increase with biomass, but the extent of this increase will depend on plant structure and light distribution in the canopy (Middelboe & Binzer 2004). The saturation point will also increase when measuring plants or communities instead of cells or thallus pieces, resulting in a P-I relation that approaches linearity in the relevant range of irradiances (0 to 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), as seen in many terrestrial crops and grasses in which the P-I relation is best described by a straight line up to maximum irradiance.

Combining species with different size and morphology may distribute irradiance more evenly between photosynthetic elements, than in single-species communities, where plants of the same size and morphol-

ogy may aggregate biomass in certain layers and, thereby, constrain the possibilities of an even distribution of photons. Multi-species communities may, thus, be able to use light more efficiently than single-species communities, resulting in a more linear P-I curve.

Our main hypothesis is that the photosynthetic characteristics change with spatial scale, so that photosynthetic production of whole plant stands or communities cannot be extrapolated from measurements on single leaves or thallus pieces without considering the plant structure, light distribution and plant density. To investigate this aspect, measurements on photosynthetic production as a function of irradiance were performed on single thallus pieces, single-species and multi-species communities.

Several explicit hypotheses were tested. Firstly, we predict that an increase in spatial scale causes P-I curves to approach linearity, so that P-I curves of single-species and multi-species communities can be better described with a linear expression than P-I curves of thallus pieces, implying that the saturation intensity (I_{sat}) increases. Secondly, we hypothesise that the parameters normally used to characterise photosynthetic performance of plants, such as the maximum photosynthesis rate (P_{max}), the light utilisation efficiency (α) and the compensation point of photosynthesis (I_c) change according to the linearisation of the P-I curves. Thirdly, we hypothesise that high photosynthetic production is caused by an even distribution of photons among the photosynthetic tissue in the canopies. Finally, we hypothesise that multi-species communities might improve light distribution, resulting in a more linear P-I curve than single-species communities.

MATERIALS AND METHODS

Four different species of macroalgae were collected by hand at a shallow boulder reef in Aalsgaard on the northern coast of Zealand, Denmark in October 2002. The 2 brown algae *Fucus serratus* and *Chordaria flagelliformis*, the green algae *Enteromorpha* sp. and the red algae *Ahnfeltia plicata* were chosen because of their different sizes and morphologies. Prior to experiments, they were kept in large aerated buckets with running seawater at 7°C. To resemble natural communities, epiphytes were left on the thallus, but specimens with many epiphytes were avoided in experiments.

Photosynthetic production of thallus pieces. A closed cylindrical glass chamber (78 ml) was used for measuring the photosynthesis-irradiance response of thallus pieces taken from the upper, middle and lower part of the specimens. Measurements were performed in natural seawater, kept close to 16°C by means of a

constant-temperature cooling jacket surrounding the photosynthesis chamber. To further minimise heating of the chamber at high irradiance, a petri-dish with 1 cm of water was inserted between the light source and the chamber to absorb long-wave thermal radiation.

Algae were fixed horizontally on a plastic net in the chamber and stirring was assured by a magnetic stirrer bar. Incident irradiance on the thallus surface was supplied from a 100 W halogen lamp. The maximum irradiance was 1600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and variable irradiances (0, 5, 30, 90, 380, 750 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) were obtained by inserting neutral density filters between the light source and the chamber. The temperature in the chamber was continuously recorded using a thermocouple (TC-08, Picotech) to avoid measurements during light-dark switches where temperature changed 0.5 to 0.7°C, or if necessary to be able to correct for the temperature-sensitivity of the electrode ($\sim 3\% \text{ } ^\circ\text{C}^{-1}$). Temperature changes were less than 0.1°C min^{-1} and had no significant influence on the calculated photosynthetic production rates.

Photosynthetic production and respiration were measured as oxygen evolution rates by means of a Clark-type microsensor (Revsbech & Jørgensen 1986) connected to a picoammeter (Unisense). The electrode output was logged on a computer using an analogue-digital converter (ADC-12, Picotech).

Net photosynthesis (NP) in the light and respiration in the dark (R) were calculated from the linear slope of the curve describing oxygen concentration versus time when constant rates had been attained (subscript 't' is used to denote measurements on thallus pieces; for communities, a 'c' is used). Linear regressions of oxygen concentration versus time were always highly significant ($r^2 > 0.99$) for all measurements. Gross photosynthesis (GP) was calculated as the sum of net photosynthesis and dark respiration ($GP_t = NP_t + R$), assuming that dark respiration continued unaltered in the light. Measurements were expressed per unit of thallus surface area. Surface area was determined by the computer program Image-J (freeware) on copied and scanned images of the thallus pieces, with a standard 1 cm^2 quadrat to avoid scaling problems during photocopying or scanning.

The photosynthesis versus irradiance curves (P-I curves) were characterised by the following photosynthesis parameters. The photosynthetic efficiency at low irradiance (α_i : $\text{mol O}_2 \text{ mol}^{-1} \text{ photons}$) was determined as the initial linear slope between photosynthesis and irradiance at light limitation. This was analysed by a linear regression at irradiances up to 90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, since determining α_i with nonlinear fits yields different values depending on the equation used. The photosynthetic efficiency was also used to calculate

the light compensation point ($I_{c,t} = R_t/\alpha_t$) at which gross photosynthesis and respiration are of equal magnitude and net oxygen exchange is zero. The maximum rate of gross photosynthesis ($GP_{\max,t}$) was determined at light saturation and the light-use efficiency at maximum irradiance (LUE : mol O₂ mol⁻¹ photons) was determined as $GP_{\max,t}$ divided by the maximum irradiance in the experiments ($LUE = GP_{\max,t}/I_{\max}$). The onset of light saturation ($I_{\text{sat},t}$) was estimated as $GP_{\max,t}/\alpha_t$.

Photosynthetic production in communities. The photosynthetic production in the algal communities was measured in 36 l glass chambers using the same principles as for thallus pieces. Intact specimens of the 4 different algae were placed in the chamber using sucker discs, or in the case of *Enteromorpha intestinalis* they were left on the original substrate (hand-sized stones), and placed on the bottom of the chamber. The maximum photosynthetic production at high irradiance was measured under a wide variety of plant densities (Middelboe & Binzer 2004) and P-I relations were then measured at the optimal plant density, where net photosynthetic production was highest. In the case of *Enteromorpha*, where the optimal density was not reached, we used the highest achievable density.

The photosynthesis chambers were immersed in a thermostatically controlled aquarium to maintain constant temperature and stirring was ensured by 2 submersible pumps.

The light source consisted of two 400 W high pressure sodium lamps yielding a maximum irradiance of ~1750 μmol photons m⁻² s⁻¹. Variable irradiances (~0, 40, 80, 180, 400, 840 μmol photons m⁻² s⁻¹) were obtained by inserting neutral filters. All experiments were performed at 16 ± 0.2°C and there was no significant change in temperature during light-dark switches.

Photosynthesis was measured and logged as described for thallus pieces. Community density was measured as the leaf area index (LAI , m² area surface m⁻² ground area). LAI was routinely measured as g wet weight (WW) after a correlation between WW and thallus surface had been established for all species. The conversions from WW to thallus surface area were *Fucus serratus* 14.4 ± 1.1 cm² g⁻¹ WW (mean ± 95% CL), *Enteromorpha intestinalis* 38.5 ± 3.2 cm² g⁻¹ WW , *Ahnfeltia plicata* 33.3 ± 1.2 cm² g⁻¹ WW and *Chordaria flagelliformis* 15.8 ± 0.5 cm² g⁻¹ WW .

The same terminology and methodology were used to determine the photosynthetic parameters for community photosynthesis as for thallus pieces. Since the P-I curves did not saturate in the community experiments, the maximum obtainable photosynthetic rates at infinite irradiance were estimated by a non-linear curve fit to a simple rectangular hyperbola ($GP_c = \alpha_c \times I \times GP_{\max,c} / GP_{\max,c} + \alpha_c \times I$) as originally proposed by Burk & Lineweaver (1935) (Lederman & Tett 1981). More complicated de-

scriptions of the P-I curve did not provide a better description.

Optical properties of communities. To estimate the irradiance extinction per LAI (K_{LAI}), irradiance below the canopy at different leaf area densities in single-species communities was measured with a Spherical Micro Quantum Sensor with a diameter of 3 mm (US-SQS, Heinz Walz) connected to a Diving-PAM Underwater Fluorometer (Heinz Walz). Measurements were calibrated in the laboratory set-up using a calibrated spherical quantum sensor (Biospherical Instruments). Measurements were performed at 9 fixed horizontal positions in the photosynthetic chamber. K_{LAI} was estimated for all 4 species to give an expression of how the irradiance was distributed through the foliage. This was done by fitting irradiance data to an adapted version of Beer's law, where the depth in meters is replaced by the optical depth in the community measured as the number of thallus layers (LAI) above the measuring point, $I_{LAI} = I_0 \times e^{-K \times LAI}$. A high K_{LAI} thus, corresponds to a community where most of the incident irradiance is absorbed in the upper layers of the canopy, while a low K_{LAI} corresponds to a community where irradiance is distributed to lower layers or not absorbed at all.

Theoretical calculations. To test the linearity of the P-I curves, we used the departure of the relationship from linearity (D), as proposed by Ruimy et al. (1995), $D = r^2(H) - r^2(L)$. To use the same equations as Ruimy et al. (1995), the r^2 for the nonlinear fit (H) was obtained using the relation $GP = \alpha \times I \times GP_{\max} / \alpha \times I + GP_{\max}$, while the linear r^2 (L) was obtained with a fit to the equation, $GP = \alpha \times I + b$. When D declines, it is thus stated that the photosynthetic response is 'more linear' or approaches linearity.

To compare variations in maximum photosynthesis for thallus pieces and single-species or multi-species communities, the coefficient of variation was used as a measure of the relative variation ($CV = SD/\text{mean}$).

To test whether an even light distribution between all the photosynthetic tissue in the communities increases utilisation of photons compared to an uneven distribution of light among the tissue, we calculated how large a production the communities had, compared to their optimum production ($GP_{\text{opt},c}$) when all photons are absorbed and utilised at maximum efficiency ($GP_{\max,c}/GP_{\text{opt},c}$). The optimum gross photosynthesis in a community with infinite LAI ($LAI \rightarrow \infty$) can be described by the quantum efficiency for the thallus parts (α_t) and the incoming irradiance (I_0): $GP_{\max,c} = \alpha_t \times I_0$, or in the case where all photons are absorbed in the community: $GP_{\max,c} = \theta \times I_0$, where θ is the quantum efficiency based on absorbed photons. At a certain community density, the maximum amount of irradiance that each thallus part can receive with an even

distribution of incident irradiance can be calculated as I_0/LAI . Inserting I_0/LAI in the equation describing the P-I relation for the thallus and multiplying by LAI , thus, yields the optimal photosynthesis rate at the actual community density ($GP_{opt,c}$). Comparing $GP_{opt,c}$ to the actual photosynthetic production rates ($GP_{max,c}/GP_{opt,c}$) gives an impression of how efficiently the stands or communities utilise photons at the LAI used in the experiments.

RESULTS

Thallus pieces

The P-I curves for all 4 different algal species followed the well-known hyperbolic relation (Figs. 1 & 2). The parameters describing the curves were nevertheless quite different in the 4 species. α_t ranged from 0.024 to 0.078 mol O₂ mol⁻¹ photons, while $GP_{max,t}$ ranged from 2.6 to 10.5 $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 1). *Ahnfeltia plicata* had a much lower photosynthetic activity in the thallus with an α value of 0.024 mol O₂ mol⁻¹ photons, and gross photosynthesis and respiration rates which were approximately 3 times lower than in the other species.

The onset of light saturation ($GP_{max,t}/\alpha_t$) ranged from 106 to 158 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and the light compensation point ($GP_t = R_t$) was between 29 and 48 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The differences in $GP_{max,t}$ among species resulted in an almost 4-fold difference in the light-use efficiency (LUE) at high irradiances (1200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) from 0.0018 mol O₂ mol⁻¹ photons in *Ahnfeltia plicata* to 0.0088 mol O₂ mol⁻¹ photons in *Chordaria flagelliformis* (Table 1).

The curvature of the P-I relation described by the D value yielded 0.474 for all species, implying that the P-I relation for thallus pieces is far from linear (Fig. 3).

Single-species communities

The curve of photosynthesis in relation to irradiance for communities with a single-species had a markedly different shape than for thallus pieces (Figs. 1 & 2). The LUE of the community at low irradiance (α_c) ranged from 0.037 to 0.047 mol O₂ mol⁻¹ photons and the maximum photosynthesis at 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ($GP_{1500,c}$) ranged from 19.7 to 24.0 $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 2). Since respiration increases at the community scale (Fig. 2), the compensation irradiance also increased so that $I_{c,c}$ ranged from 66 to 158 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ or 1.5 to 4 times higher than for thallus pieces. The irradiance at the onset of saturation ($I_{sat,c}$) was between 670 and 986 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and

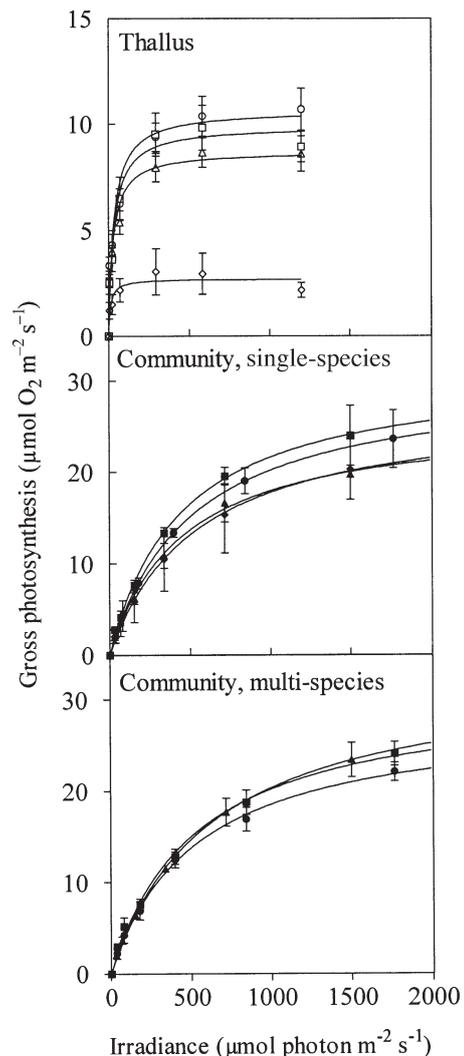


Fig. 1. Gross photosynthesis as a function of irradiance for thallus pieces, and single-species and multi-species communities. Lines represent data fitted to the equation: $\alpha \times I \times GP_{max} / (\alpha \times I + GP_{max})$ (Burk & Lineweaver 1935). Thallus pieces are open symbols, communities are closed symbols. *Fucus* (○/●), *Chordaria* (△/▲), *Enteromorpha* (□/■) and *Ahnfeltia* (◇/◆). For multi-species communities: 2 species (●), 3 species (▲) and 4 species (■). Note the different y-axis scale for thallus and community photosynthesis

was, thus, 4.4 to 9.3 times higher for communities than for thallus pieces. Nevertheless, photosynthesis was never saturated for any of the communities, so the maximum gross photosynthesis ($GP_{max,c}$) at very high irradiance was estimated as a non-linear curve fit, which showed that the theoretical $GP_{max,c}$ value at infinite irradiance ranged from 24.0 to 36.5 $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Table 2). Gross photosynthesis for *Ahnfeltia* at 150 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ only constitutes 56% of the photosynthesis that theoretically can be achieved at infinite irradiances, while the others attained 76 to 82% of their $GP_{max,c}$ at infinite irradiance (Table 2).

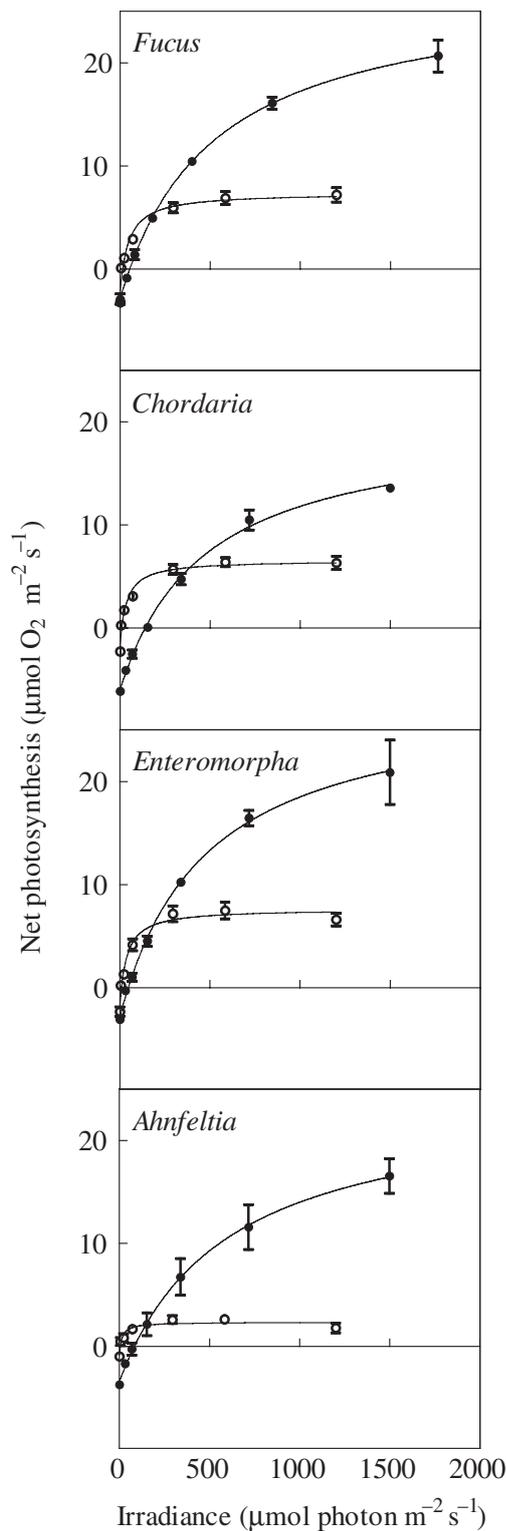


Fig. 2. *Fucus serratus*, *Chordaria flagelliformis*, *Enteromorpha* sp. and *Ahnfeltia plicata*. Net photosynthesis as a function of irradiance for the 4 species of algae. ○: thallus net photosynthesis (NP); ●: community net photosynthesis (NP_c). Error bars denote ±SE (n = 3)

Compared to thallus pieces, community *LUE* was markedly higher with an utilisation efficiency of 0.013 to 0.016 mol O₂ mol⁻¹ photons. This means that, at high irradiances, the communities utilised photons 2.0 to 2.5 times more efficiently than their corresponding thallus pieces for *Fucus*, *Chordaria* and *Enteromorpha*, while *Ahnfeltia* communities utilised irradiance almost 8 times more efficiently; however, at low irradiances, the α_c values for *Fucus*, *Chordaria* and *Enteromorpha* communities were lower than for thallus pieces.

The curvature of the P-I relation described by the *D* value yielded values for all single-species communities of 0.14. P-I curves for plant stands were, thus, significantly more linear than P-I relations for their corresponding thallus pieces ($p < 0.05$, ANOVA) (Fig. 3).

Multi-species communities

P-I curves for multi-species communities resembled those of single-species communities. α_c for multi-species communities ranged from 0.37 to 0.40 and $GP_{1500,c}$ at 1500 µmol photons m⁻² s⁻¹ ranged from 21.0 to 23.5 µmol O₂ m⁻² s⁻¹, although extrapolating to the maximum gross production for communities at very high irradiance ($GP_{max,c}$) showed that communities could reach values between 34.3 and 53.6 µmol O₂ m⁻² s⁻¹. The compensation points were higher for multi-species than for single-species communities, although not significantly ($p > 0.05$, ANOVA). Maximum gross photosynthesis at infinite irradiance and saturation points were higher but since these measures are based on extrapolated values from a curve fit, they are subject to high uncertainty. Multi-species communities had a lower *D* value than single-species communities, suggesting that they show a more linear response to increasing irradiance. This response is, however, also not significant.

P-I curves of multispecies communities are more similar to those of single species communities (Fig. 1) and their CV for maximum photosynthesis is smaller than for thallus pieces or single-species communities. Comparing the CV for thallus pieces, and single-species and multi-species communities reveals that the variation in photosynthetic production between species is larger on the thallus scale (45.0%) than on the community scale (16.9%). As more species are part of the communities, the CV declines further to 7.9% (Fig. 4).

Light extinction and photosynthetic production capacity

The optimum gross photosynthesis rate, based on an even distribution of light between the available thallus surfaces (*LAI*), was estimated to range from 28.7 to

Table 1. *Fucus serratus*, *Chordaria flagelliformis*, *Enteromorpha* sp. and *Ahnfeltia plicata*. Photosynthetic characteristics of the thallus from the 4 species of algae. Photosynthetic efficiency at low light, α (mol O₂ mol⁻¹ photons); maximum gross production: $GP_{\max,t}$ ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$); respiration: R_t ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$); onset of saturation: $I_{\text{sat},t}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); compensation point of photosynthesis: $I_{c,t}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); light-use efficiency at high irradiance: LUE_t (mol O₂ mol⁻¹ photons; at 1200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)

Species	α_t	$GP_{\max,t}$	R_t	$I_{\text{sat},t}$	$I_{c,t}$	$LUE_t(1200)$
<i>Fucus serratus</i>	0.069 ± 0.002	10.5 ± 0.3	3.2 ± 0.0	158 ± 5	48 ± 1.1	0.0088 ± 0.0002
<i>Chordaria flagelliformis</i>	0.062 ± 0.004	8.6 ± 0.4	2.3 ± 0.2	141 ± 5	37 ± 0.5	0.0072 ± 0.0004
<i>Enteromorpha intestinalis</i>	0.078 ± 0.007	9.4 ± 0.5	2.3 ± 0.3	124 ± 12	29 ± 0.9	0.0074 ± 0.0003
<i>Ahnfeltia plicata</i>	0.024 ± 0.003	2.6 ± 0.4	0.9 ± 0.3	106 ± 3	33 ± 5.8	0.0018 ± 0.0002

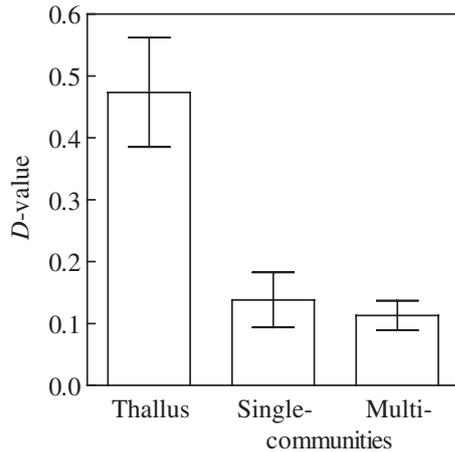


Fig. 3. The departure from linearity for thallus pieces, single-species communities and multi-species communities. The D values are expressed as r^2 for the hyperbolic fit minus r^2 for a linear fit ($r^2[\text{hyp}] - r^2[\text{lin}]$). Values for thallus pieces were significantly different from those of single-species or multi-species communities ($p < 0.05$, ANOVA)

118 $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ depending on thallus properties and LAI (Table 3). The values were used to estimate how much of the potential photosynthetic production

was attained in the communities. *Fucus serratus* and *Chordaria flagelliformis* only utilised between 17 and 31 % of their photosynthetic production capacity, while *Enteromorpha intestinalis* and *Ahnfeltia plicata* utilised more than 70 % of theirs. The greater utilisation of the photosynthetic production capacity was correlated with a lower extinction of irradiance per thallus area (K_{LAI}), so that a low K_{LAI} and deeper light penetration in the community, thus, results in a better utilisation of the community photosynthetic production capacity (Fig. 5).

DISCUSSION

Photosynthesis-light relationship change with scale

Photosynthetic production in a plant community is an integration of photosynthesis rates of all the thallus pieces in the community. It is, thus, an analogy to the leaf or thallus where photosynthesis can be regarded as an integration of photosynthetic processes in the different cell layers or chloroplasts in the leaf. While the uppermost parts of a community may receive high irra-

Table 2. *Fucus serratus*, *Chordaria flagelliformis*, *Enteromorpha* sp. and *Ahnfeltia plicata*. Photosynthetic characteristics of single-species and multi-species algal communities. Leaf Area Index: LAI (m^{-2} leaf m^{-2} ground area); photosynthetic efficiency at low light, α_c (mol O₂ mol⁻¹ photons); maximum gross production at 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$: $GP_{1500,t}$ ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$); compensation point of photosynthesis: $I_{c,c}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); maximum gross photosynthesis obtained by fitting a hyperbolic curve to the data: $GP_{\max,c}$ ($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$); onset of saturation: $I_{\text{sat},c}$ ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), light-use efficiency at high irradiance: LUE_c (mol O₂ mol⁻¹ photons; at 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$). LAI for multi-species communities is not listed since it depends on the combination of species

Species	LAI	α_c	$GP_{1500,c}$	$I_{c,c}$	$GP_{\max,c}$	$I_{\text{sat},c}$	$LUE_c(1500)$
<i>Fucus serratus</i>	9.9	0.043 ± 0.001	23.6 ± 1.1	68 ± 5	30.5 ^a	763 ^a	0.016
<i>Chordaria flagelliformis</i>	13.6	0.039 ± 0.001	19.7 ± 0.5	158 ± 3	24.0 ^a	615 ^a	0.013
<i>Enteromorpha intestinalis</i>	3.5	0.047 ± 0.002	24.0 ± 1.9	66 ± 3	31.5 ^a	670 ^a	0.016
<i>Ahnfeltia plicata</i>	13.5	0.037 ± 0.005	20.3 ± 1.1	112 ± 14	36.5 ^a	986 ^a	0.014
2 species	–	0.037 ± 0.001	21.0 ± 0.3	172 ± 7	34.3 ^a	927 ^a	0.014
3 species	–	0.040 ± 0.001	23.5 ± 0.6	192 ± 5	37.8 ^a	945 ^a	0.016
4 species	–	0.040 ± 0.001	22.9 ± 0.3	183 ± 8	53.6 ^a	1340 ^a	0.015

^aExtrapolated data

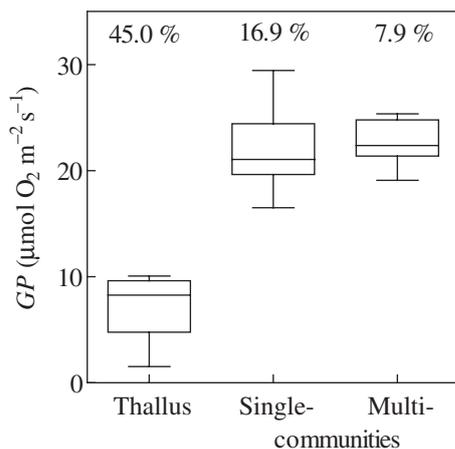


Fig. 4. Mean, 75% fractiles and range of gross photosynthesis for thallus pieces, and single-species and multi-species communities. Percentages above the boxes denote the coefficient of variation ($CV = SD/mean$) as a measure of relative variation at the different scales

Table 3. *Fucus serratus*, *Chordaria flagelliformis*, *Enteromorpha* sp. and *Ahnfeltia plicata*. Light extinction, potential optimal gross photosynthetic production and the realised photosynthesis relative to potential optimal gross photosynthesis in communities. $K_{LAI,c}$: LAI^{-1} ; $GP_{opt,c}$: $\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$

Species	$K_{LAI,c}$	$GP_{opt,c}$	$GP_{1500,c}/GP_{opt,c}$
<i>Fucus serratus</i>	0.43	75.0	31 %
<i>Chordaria flagelliformis</i>	0.62	118.2	16 %
<i>Enteromorpha intestinalis</i>	0.31	30.2	79 %
<i>Ahnfeltia plicata</i>	0.34	28.7	71 %

diances, shading will decrease irradiance through the canopy, as an analogy to the steep light gradients with depth in leaves. Acknowledging the well-known hyperbolic shape of the photosynthesis-irradiance relationship for leaves, it becomes apparent that the LUE will increase in the lower leaf layers when irradiance decreases and that an integration of all photosynthetic processes at a higher scale, thus, results in an increasing linearisation of the photosynthesis-light relationship.

Studies of terrestrial plant communities show a pronounced linearisation of the P-I curves compared to the hyperbolic relation for individual leaves. Compilations of data from Ruimy et al. (1995) show that communities of crops or forests begin to saturate at 1000 to 1200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, while grasslands saturate above 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. For some grassland communities, the photosynthesis-irradiance relationships are even better described by linear than hyperbolic fits. That P-I curves approach linearity at the community level is attributed to the distribution of irradiance among leaves in the foliage (Ceulemans & Saugier

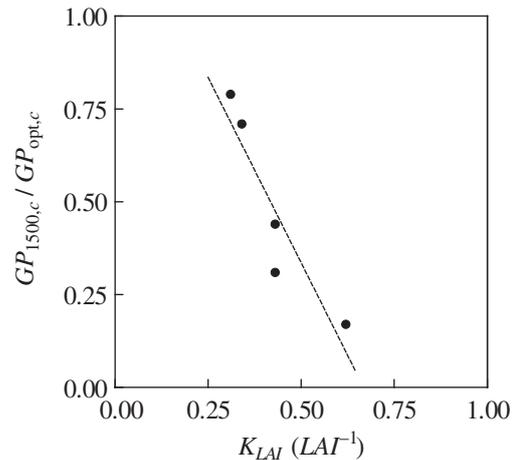


Fig. 5. The realised photosynthesis relative to potential optimal gross photosynthesis as a function of the light extinction (K_{LAI}) in the plant communities. The line has a slope significantly different from zero ($p < 0.05$, $r^2 = 0.85$)

1991), as leaves are positioned and inclined to the sun to minimise absorption of excess photons above light saturation (McMillen & McClendon 1979).

Although photosynthesis and distribution of irradiance might not be as efficient in aquatic as in terrestrial plant communities, due to lack of a rigid structure that can position leaves at optimal leaf angles to the sun (Binzer & Sand-Jensen 2002b), the differences from the thallus P-I curves are still pronounced (Fig. 1). The onset of photosaturation for the 4 algal communities is around 700 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, but none of the algal communities is fully saturated at the maximum irradiance of 1750 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. According to extrapolations, the algal communities could theoretically increase photosynthetic production by at least 20% if irradiance were increased 2-fold to extremely high irradiances above 3000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The onset of photosaturation for communities increases 5-fold compared to individual thalli and the deviation from linearity expressed as the D value decreases accordingly. Both saturation levels and the D value, thus, confirm the hypothesis that P-I curves are indeed more linear than thallus pieces and that plants do not become fully saturated by natural maximum irradiances at the community level.

Photosynthetic parameters change with scale

Following the linearisation of the P-I curves, the P-I parameters change with the spatial scale of the experiments. While the photosynthetic parameters describing the P-I curve for thallus pieces (Table 1) correspond to values from other studies (e.g. Lüning & Dring 1985, Markager & Sand-Jensen 1994), the parameters

describing community photosynthesis are different from those normally attributed to aquatic plants. These changes with scale are not related to the photosynthetic rates of the leaves. While photosynthetic rates of *Ahnfeltia* and *Chordaria* are markedly different at the thallus scale, with α and GP values for *Chordaria* being 3-fold higher than for *Ahnfeltia*, values are very similar at the community scale, although the communities have the same plant density (Table 2).

An assembly of leaves makes a canopy much more efficient in utilising incident irradiance than single leaves (Ceulemans & Saugier 1991). Maximum gross photosynthesis increased 2- to 3-fold from the thallus to the community scale for *Fucus*, *Chordaria* and *Enteromorpha*. For *Ahnfeltia*, photosynthetic production rates increased almost 8-fold. This result is interesting because the thalli of *Fucus*, *Chordaria* and *Ahnfeltia* are almost optically black, and the irradiance reaching a thallus piece is almost completely absorbed in the tissue. If communities had horizontally orientated thalli, no irradiance would be available for thallus pieces in the lower part of the canopy. The increase in gross photosynthesis from the thallus level to the community level reflects that the canopy has a structure that allows photons to reach the lower thallus layers. The increase in GP from thallus to community level is, thus, a function of canopy architecture.

The photosynthetic efficiency of the communities at low irradiance was expected to be about the same or perhaps slightly higher at the community scale than at the thallus scale, when the canopies are dense and absorb virtually all irradiance. Nevertheless, some of the α values were significantly lower for canopies than for thallus pieces (Tables 1 & 2). At low irradiances, canopy structure or self-shading should not have any effect when all irradiance is absorbed in the foliage, which is the case in our experiments where less than 1% of surface irradiance was present below the canopies (0.04 to 15 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, data not shown). It is, therefore, rather puzzling that α values are lower for communities than for thallus pieces. The result may be due to absorption in non- or less photosynthetically active tissues in communities relative to individual thalli. However, terrestrial studies have shown that despite the fact that α should theoretically be independent of scale when all light is absorbed in the canopy, there are no clear patterns in α with scale (Ruimy et al. 1995). Whatever causes the lowering of α_c relative to α_t is, therefore, not apparent. It is nevertheless striking that α_c is very similar among communities of different species (0.037 to 0.040 mol O₂ mol⁻¹ photons, Table 2) compared to the large differences of α_t observed between thalli of different species (0.024 to 0.078 mol O₂ mol⁻¹ photons,

Table 1). For α , it thus seems that the differences observed at the thallus scale disappear at the community scale.

Light compensation points measured on thallus pieces have been used to estimate depth distributions of algae and rooted macrophytes (e.g. Markager & Sand-Jensen 1992), but the light compensation point depends on plant density and plant structure (Binzer & Sand-Jensen 2002a). As plant density increases, respiration per unit ground area will increase accordingly (de Wit et al. 1970, Binzer & Sand-Jensen 2002a, Middelboe & Binzer 2004) and since α should theoretically be independent of scale, as long as all photons are absorbed, it is obvious that I_c will increase with scale and density. Community structure and density can, thus, influence the depth distribution of algae. While a flat sheet-like thallus with a low LAI is efficient at utilising light at low irradiances, multi-layered upright algae are better at utilising high irradiances (Binzer & Sand-Jensen 2002b). The fact that structure is a major controlling factor for depth distribution is supported by Hay (1983) who showed that mono-layered and flat algae have a deeper depth limit than multi-layered and terete algae which are well adapted to reach a high biomass and photosynthesis under high irradiances, but are unable to attain positive photosynthesis under low irradiance. In our study, the compensation point of photosynthetic production is significantly higher in communities than for thallus pieces. The light compensation point for whole plants is, therefore, dependent on the density and 3-dimensional structure and cannot be accessed by making experiments on individual thalli or leaves. It can be argued that plant density is often low near the depth limits of growth, implying that community respiration is low, self-shading is less pronounced and that measurements of I_c on single thallus pieces are, therefore, valid. This is, however, only the case when algae have a low density and a completely horizontal structure. If the photosynthetic tissue is vertically oriented, they will receive less photons per leaf area than available on the horizontal plane and incident irradiance should, thus, be higher to reach the compensation point. Compensation points are set by the irradiance that the plants experience and not by the irradiance present at the top of the canopy. It is, therefore, important to take the physical structure of the plant into account when measuring compensation points, and measurements should be made on plants or communities at the same density and structure as they are found near the depth limit.

In conclusion, an increase in spatial scale from the thallus level to the community level influences the parameters normally used to characterise the photo-

synthetic performance of plants. Using parameters determined on plant parts to predict ecological performance of whole plants or communities should, therefore, be avoided or treated with caution.

Light utilisation and light distribution

The photosynthetic production relative to the theoretical optimal gross photosynthesis ($GP_{opt,c}$) is correlated to how evenly the irradiance is distributed among the photosynthetic tissue. At a low K_{LAI} , where light is transmitted to the lower tissue in the community, a higher fraction of the photosynthetic potential is realised than when K_{LAI} is high and light is absorbed in the upper layers of the community (Fig. 5). This finding corresponds closely to the theories from terrestrial ecology where erectophile canopies utilise light more efficiently than planophile canopies (Russel et al. 1990, Myers et al. 1997). The high community photosynthesis of *Ahnfeltia* compared to its low thallus photosynthesis can only be caused by a better distribution and utilisation of light, which accords with the fact that *Ahnfeltia* has a rigid structure that can keep the individual thallus parts well apart, create penumbras and, thus, prevent direct shading (Stenberg 1998). High photosynthesis rates can, thus, only be achieved when irradiance is distributed evenly among the photosynthetic tissue, which supports the statement that the increase in GP from thallus to community level is a function of canopy architecture.

Comparing single-species and multi-species communities

There are no significant differences in the P-I curves of single-species and multi-species communities. Although the I_{sat} values are higher for multi-species communities, indicating a more linear P-I relation, these values are based on extrapolated values and, therefore, have larger confidence intervals. D values also tend to be smaller for multi-species than for single-species communities, but again the differences are not significant. We can, therefore, not conclude that multi-species communities are better at utilising irradiance than single-species communities, but the trends call for further investigation.

The variations between different combinations of multi-species communities are very small compared to single-species communities. Combining different species yields more predictable results since the variation decreases due to the averaging effect of adding more species (Doak et al. 1998). The coefficient of variation, thus, decreases as the spatial scale increa-

ses from thalli to communities and as single-species communities change to multi-species communities (Fig. 3).

Implications for light inhibition and afternoon depressions?

Photoinhibition and afternoon depression of photosynthesis have been extensively studied in aquatic plants (e.g. Huppertz et al. 1990, Hanelt et al. 1993). If the 3-dimensional structure of the communities and the inclination of photosynthetic tissue to the sun affect distribution of irradiance, this could suggest that photoinhibition is less important in natural plant communities than for individual photosynthetic tissues where experiments have often been performed on unshaded and horizontally oriented pieces of single thalli or leaves. A number of studies have shown that even at high irradiances, when the whole community photosynthetic response is considered, photoinhibition does not occur (Van der Bijl et al. 1989, Binzer & Sand-Jensen 2002a, Middelboe & Binzer 2004). Photoinhibition is, thus, probably not that important on larger spatial scales. Although photoinhibition will most likely occur in the uppermost leaves, if they are positioned perpendicular to the sun, it will only be a minor fraction of the photosynthetic tissue that is exposed to such high irradiances. Photoinhibition of a few leaves in the top of the canopy would probably not result in a decrease in photosynthesis at high irradiances at community scale, but rather influence the shape of the community P-I curve so it would curve more than if no inhibition was present. Hence, photoinhibition may be locally important for highly exposed photosynthetic tissue at the top of the canopy or for plants with a horizontal structure, as shown in many studies, but have less ecological importance for whole plants, stands or communities.

The spatial scale might also overestimate the degree of afternoon depression of photosynthesis, which is attributed to fatigue of the photosynthetic apparatus (e.g. Ramus & Rosenberg 1980). Plants in their natural habitat would experience markedly reduced irradiance due to their inclination to the sun and their location within the canopy. In addition, waves would move the plants back and forth, and distribute irradiance on both sides of the thallus. Further studies are needed to evaluate these aspects of photoinhibition and afternoon depressions of photosynthesis on a community scale.

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