

## Production in aquatic macrophyte communities: A theoretical and empirical study of the influence of spatial light distribution

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### Abstract

Many terrestrial plant canopies regulate spatial patterns in leaf density and leaf inclination to distribute light evenly between the photosynthetic tissue and to optimize light utilization efficiency. Sessile aquatic macrophytes, however, cannot maintain the same well-defined three-dimensional structure because of the strong drag and shear forces of moving water. This difference in canopy structure has been suggested to account for the three- to fivefold higher gross production rates in terrestrial than aquatic communities. To evaluate the effect of community structure in aquatic habitats, we combined a simple mechanistic model and empirical measurements on artificially structured macroalgal communities (*Ulva lactuca*) with varying thallus absorptance and community density. Predicted and measured values corresponded closely and revealed that gross production in high-light environments was markedly enhanced by a vertical orientation of thalli when absorptance and community density were both high. This result implies that aquatic macrophytes of high thallus absorptance and community density exposed to high light are limited in attaining high gross production rates because of their inability to distribute photons evenly between the photosynthetic tissues. As scattering and attenuation in the water column increase, the effect of thallus structure on production declines and thin transparent macrophytes are more efficient at utilizing light than thick opaque macrophytes. The results confirm that inefficient distribution of light can account for the low community production rates in aquatic habitats and the depth distribution of form-functional groups of macroalgae with different canopy structure.

The spatial distribution and orientation of leaves is known to influence terrestrial community production by affecting the distribution of photons among leaves in the canopy (Riimy et al. 1995; Smith et al. 1997). Because of the universal rectangular hyperbolic response between production and incident irradiance for individual leaves or other photosynthetic elements, more photons are absorbed at high irradiance than are necessary to saturate photosynthesis, thereby reducing light use efficiency (Stenberg 1998). Maximum community production is obtained when all photons are distributed and absorbed evenly among photosynthetic elements, so that each element experiences irradiances below photosaturation. As a result, every absorbed photon can be converted to ATP production and carbon assimilation at high efficiency (Russel et al. 1990).

By regulating spatial patterns in leaf density and leaf inclination in the canopy, terrestrial plants are able to reduce light interception per unit of leaf surface and optimize light utilization efficiency. If a transect is taken from the upper to the lower part of the canopies of either broad-leaf trees or leguminous crops, there is often a gradual change from an almost vertical orientation of the leaves in the upper part of the canopy to a horizontal orientation in the lower part (McMillen and McClendon 1979; Ishii 1998). Vertical leaf orientation distributes the high irradiance received at a hor-

izontal surface at the top of the canopy to a large inclining leaf surface and permits large proportions of light to be transmitted down into the canopy. At low irradiance at the bottom of the canopy, leaves can maintain a horizontal orientation without risking photosaturation, thereby absorbing the maximum quota of remaining photons (Forseth and Teramura 1986; Ishii 1998). Furthermore, dividing photosynthetic tissue into many small leaves or needles and arranging them spatially facilitates bending, scattering, and transmission of light in the canopy, thereby attaining a relatively homogeneous light distribution among photosynthetic elements (Oker-Blom and Kellomäki 1983; Stenberg 1998). Spatial arrangement of leaves therefore makes the canopy more efficient than single leaves for converting high irradiances into photosynthetic production (Ceulemans and Saugier 1991).

Sessile aquatic macrophytes do not have the same well-defined spatial distribution of photosynthetic elements as terrestrial canopies and have developed flexible/elastic tissue to withstand the strong drag and shear forces in moving water (Koehl 1983; Gaylord et al. 1994). The resulting suboptimal distribution of light among photosynthetic elements in aquatic communities has been proposed to be the primary factor constraining maximum gross production to values three- to fivefold lower than those of terrestrial communities using a broad-scale comparison of most available data (Sand-Jensen and Krause-Jensen 1997). Understanding this fundamental differences in production rates between aquatic and terrestrial plant communities is essential to predict differences in ecosystem processes, including plant growth rates, carbon and nutrient fluxes, secondary production, microbial decomposition, and detritus accumulation between aquatic and terrestrial environments.

Other hypotheses—for instance, that strong light attenu-

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ation by surface reflection and absorption by particles or dissolved colored material might be primary factors preventing high aquatic production rates (Short 1980)—have been presented to explain the lower gross community production in aquatic than terrestrial communities. However, this explanation does not account for dense macrophyte communities in shallow water, where low community production is maintained despite high absorptance (>80%) of incident irradiance by photosynthetic tissue. For these communities, only a minor fraction of incident irradiances is lost from photosynthetic processes by the absorption of nonphotosynthetic matter (Krause-Jensen and Sand-Jensen 1998). Inorganic carbon availability could also constrain community production rates in dense aquatic communities because of the low diffusivity of carbon dioxide in water (Zimmermann et al. 1997). However, most macroalgae and flowering plants forming dense aquatic communities are able to use the rich pool of bicarbonate in water (often 0.5–5 mmol L<sup>-1</sup>) as a supplement to the carbon dioxide pool (~0.010–0.020 mmol L<sup>-1</sup> at air saturation, Boston et al. 1989; Reiskind et al. 1989). At low irradiance, the photosynthetic efficiency of the tissue of aquatic and terrestrial macrophytes are not markedly different (e.g., Markager and Sand-Jensen 1994; Ruimy et al. 1995; Enriquez et al. 1996). If light was optimally distributed in the aquatic communities, maximum production should not be three- to fivefold lower than that of terrestrial communities. Therefore, suboptimal spatial distribution of light in the canopy is likely to be the best explanation for low production rates in aquatic communities.

To evaluate this hypothesis, we took both a theoretical and an empirical approach. A simple model was constructed to permit determination of community production as a function of canopy structure, plant density, fractional absorptance, and the photosynthesis–light relationship for vertically separated layers of plant tissue. The model contains two sub-models: the first describes the light climate for each vertical layer in the community, and the second describes the photosynthetic output from each layer. Community production is then determined by integration of production across all layers in the community. The marine macroalga *Ulva lactuca* was used to test model predictions. The flat, sheetlike thallus of two cell layers can be cut into suitable sizes and shapes to construct communities of different density and orientation of thalli. Also, by using thalli of variable absorptance and placing neutral-density filters below thalli, it is possible to alter the fractional absorptance of photons for every layer.

Our primary goal was to test the hypothesis that a vertical arrangement of photosynthetic elements (i.e., thalli or leaves) in a plant community, by distributing light relatively evenly among the elements, will result in greater gross community production rates than a horizontal arrangement of photosynthetic elements with a steep attenuation of light with depth in the community. The second goal was to test the hypothesis that the advantage of an even distribution of light is highest in communities of high density and high absorptance of the photosynthetic elements. The second hypothesis derives from the idea that the effect of optimal light distribution should be highest when communities can distribute incident photons over a large surface of photosynthetic tissue and when community absorption capacity is high. A large

community absorption capacity in turn requires a dense community and a high absorptance of individual photosynthetic elements.

## Theory

Although mathematical models are a simplified representation of the reality they purport to describe, models are a mean of articulating ideas and formalizing them in an abstract way. Mechanistic models can thus synthesize an understanding of the complete system from knowledge of the behavior of its parts (Charles-Edwards et al. 1986). During the last 30 years, terrestrial ecologists have formulated models explaining how light distribution in canopies can affect community photosynthesis and have identified critical parameters (e.g., Kuroiwa 1970; Barnes et al. 1990; Ehleringer and Forseth 1990). However, applying these models to aquatic environments requires modifications because they differ dramatically from terrestrial habitats. In aquatic communities, light attenuation and scattering in the water column above the plant community lead to reduced light intensity and a more diffuse light field. Furthermore, aquatic macrophytes have a fractional light absorptance (i.e., a fraction of incident photons absorbed) ranging from 0.3 in thin thalli (e.g., *Enteromorpha* spp.) to 0.95 in kelps or other thick leathery algae (e.g., *Fucus* spp. or *Laminaria* spp., Frost-Christensen and Sand-Jensen 1992; Agusti et al. 1994). Optical models in terrestrial plant communities usually regard leaves as optically black with a fractional absorptance of 1.0 (Johnson et al. 1995).

To account for the variable light field and variable absorptance in aquatic macrophyte communities, we present a simple model on how the distribution of photosynthetic tissue affects community production.

*Light reaching the aquatic macrophyte community*—According to both Fresnel's equation and Snell's law sea surface reflectance (R) is low (<5%) at high solar angles >30° from the horizon (zenith angle < 60°), with a decrease of reflectance when waves are present (Kirk 1983). Direct measurements confirm that irradiance reflectance is less than 7% for solar zenith angles <60° when the surface is wind blown, and this holds true also for overcast skies (Preisendorfer and Mobley 1986; Mobley 1994). During measurements of maximum community production at high irradiance (i.e., at noon), reflectance is therefore of minor importance for light availability in communities.

Incident irradiance (E) will be attenuated by reflection at the sea surface, and light entering the water will be absorbed by the water itself, by dissolved substances, and by particulate matter. Irradiance (downwelling planar irradiance) at water depth z [E(z)] can be described as an exponential function of the subsurface irradiance [E(0)] and of the combined vertical attenuation coefficient (K), according to Beer's law (Eq. 1).

$$E(z) = E(0) \cdot e^{-Kz} \quad (1)$$

Distribution of light between thallus parts or leaves is only important when irradiance reaching the top of the canopy

[E(c)] exceeds the irradiance threshold for maximum photosynthesis of the individual photosynthetic tissue ( $E_{t,sat}$ ; where t is for thallus and c for community). As a consequence, community structure can only influence production when irradiances exceed  $E_{t,sat}$ . When  $z$  is the water depth at the top of the canopy we get Eq. 2.

$$E(c) = E(1 - R)e^{-Kz} \quad (2)$$

Defining the point of photosynthetic saturation from the maximum production rate ( $P_{t,max}$ ) and the light use efficiency at low light ( $\alpha_t$ ), we get Eq. 3.

$$E_{t,sat} = P_{t,max} \alpha_t^{-1} \quad (3)$$

We can thus define the optical situation in which plant structure influences community production as Eq. 4.

$$E(1 - R)e^{-Kz} > P_{t,max} \alpha_t^{-1} \quad (4)$$

Using  $P_{t,max} \alpha_t^{-1}$  as an estimate of the onset of photosaturation is a conservative choice because photosynthesis begins to saturate below that irradiance. Nonetheless, this parameter explains why plant structure does not have an effect on plant communities at low irradiances, where the photosynthesis–light relationship is linear.

*Distribution of light among plant parts in the community*—The attenuation of light in the plant community follows Beer's law as a function of the cumulative number of thallus or leaf layers ( $LAI_z$ ) from the top of the canopy to the relevant depth in the canopy ( $z'$ ) as a measure of optical depth.

$$E(z') = E(c)e^{-K_c LAI_z'} \quad (5)$$

$E(z')$  is the photon flux density at position  $z'$  in the canopy. The attenuation for each thallus or leaf layer in the community,  $K_c$ , can be calculated as a function of the leaf angle ( $\delta$ , angle between incident photons and the normal to the leaf) and the fraction of reflected and absorbed photons in each layer. Because reflectance is small at right angles and photons are reflected to other photosynthetic tissue at high leaf angles, the total reflectance from a community can be assumed negligible. However, reflected photons do not need to be considered if the assumption is made that absorptance (A) does not change with leaf angle. Derived from Beer's law, the attenuation ( $K_c$ ) for one layer of tissue is described in Eq. 6.

$$K_c = -\ln E(1)/E(0) \quad (6)$$

The fraction of transmitted light [ $E(1)/E(0)$ ] below one layer of tissue is described by Eq. 7.

$$E(1)/E(0) = 1 - \cos \delta \cdot A \quad (7)$$

The attenuation can therefore be calculated as in Eq. 8.

$$K_c = -\ln(1 - \cos \delta \cdot A) \quad (8)$$

This method of calculating  $K_c$  from leaf angle and absorptance by estimating the average irradiance in relation to depth in the community requires that the tissue is randomly distributed and does not account for penumbral effects (i.e., partially shaded areas) or sunflecks.

Combining Eqs. 1 and 5, we can express the irradiance at depth  $z$  and below a certain number of layers in the mac-

rophyte community defined by  $LAI_z$  [ $E(z')$ ]. The irradiance incident on a leaf/thallus surface ( $E_t$ ) can then be described using Lambert's cosine law, when the irradiance is regarded as a collimated light beam, as follows.

$$E_t = \cos \delta \cdot E(z') \quad (9)$$

$\delta$  is the angle between the light beam and the normal to the surface.

*Diffuse and direct light*—In aquatic environments, the distribution of light depends on the scattering and absorption properties of a body of water. If scattering is low compared to absorption, the light field can be regarded as a collimated beam. However, if the ratio of scattering to absorption is large, light will be more evenly distributed in all directions (Kirk 1983). In a diffuse light field, manipulating the angle to the sun will not change the irradiance received by a thallus part. For simplicity, if the light field in the water column can be assumed to be a fraction of downward collimated light ( $f_s$ ) and a fraction of diffuse light ( $f_d$ ) on a plane, then irradiance (E) can be expressed as in Eq. 10.

$$E = f_s E + f_d E = E_s + E_d \quad (10)$$

Irradiance for thalli/leaves ( $E_t$ ) with angle  $\delta$  to the sun can thus be described as in Eq. 11.

$$E_t = f_s E(z') \cos \delta + f_d E(z') \quad (11)$$

$E(z')$  is the photon flux density at depth  $z$  in the water and below  $LAI_z$  layers of tissue in the macrophyte community. For simplicity, we do not account for the increase in the fraction of diffuse light that occurs with depth in the community.

Equation 12 combines Eqs. 1, 5, and 6 to get the local irradiance incident on the surface of a photosynthetic element.

$$E_t = E(1 - R)e^{-Kz} e^{-\ln(1 - \cos \delta \cdot A) LAI_z'} \cos \delta \quad (12)$$

Accounting for the distribution of direct and diffuse light (Eq. 11) gives Eq. 13.

$$E_t = f_s E(1 - R)e^{-Kz} e^{-\ln(1 - \cos \delta \cdot A) LAI_z'} \cos \delta + f_d E(1 - R)e^{-Kz} e^{-\ln(1 - \cos \delta \cdot A) LAI_z'} \quad (13)$$

Reflectance can be ignored at high solar elevations. In shallow clear-water habitats with low scattering, the description of  $E_t$  can be simplified by regarding the fraction of diffuse light as zero.

*Light response of a single photosynthetic element*—Production in relation to irradiance incident on a single leaf or thallus follows a rectangular hyperbolic function with an eventual decline in production at very high irradiances because of photoinhibition. Several equations can describe the relationship between production and irradiance. A simple equation originally proposed by Smith and Talling (Lederman and Tett 1981) is used here to estimate gross production of single photosynthetic elements ( $GP_t$ , Eq. 14).

$$GP_t = \frac{\alpha_t E_t GP_{t,max}}{(GP_{t,max}^2 + (\alpha_t E_t)^2)^{0.5}} \quad (14)$$

$\alpha_i$  is the photosynthetic efficiency at low light,  $GP_{t,max}$  is the maximum rate of gross production for a single photosynthetic element, and  $E_i$  is the incident irradiance on the surface of the specific photosynthetic element calculated from Eq. 12 or 13. This equation does not account for photoinhibition. If thalli are inhibited at high irradiances, the model will underestimate the increase in production resulting from an even distribution of light among thallus parts.

Community gross production ( $GP_C$ ) can be described as a summation of photosynthetic rates for all elements in the community (Eq. 15).

$$GP_C = \sum_0^{LAI} GP_i \quad (15)$$

$GP_i$  denotes the photosynthetic rate of single thallus parts calculated from Eq. 14.

## Materials and methods

To test model predictions of the influence of community structure at varying community density and thallus absorbance, we constructed laboratory communities of *Ulva lactuca* with variable canopy structure.

*Ulva lactuca* was collected from a Danish estuary and acclimated in large aerated aquaria to 16°C and 300  $\mu\text{mol photon m}^{-2} \text{s}^{-1}$  for 2–4 d. Community production was measured in a 4.8-liter closed glass aquarium, contained within a large 200-liter thermostatically controlled aquarium to assure constant temperature ( $16 \pm 0.2^\circ\text{C}$ ).

Filtered seawater from the collection site was used as a medium for measurements, stirred by the oxygen electrode stirring rod. By pulsing oxygen-depleted water into the chamber, the time required to reach a new steady-state concentration of oxygen through complete mixing of the water was determined as 50 s.

Prior to experiments, the algae were cut into rectangular pieces of  $5 \times 14$  cm and fixed on Perspex net. The pieces were then mounted on a rack, where it was possible to manipulate the angle to the light source to obtain a horizontal community structure or a vertical structure with even photon distribution. In this way, community density (leaf area index, LAI,  $\text{m}^2$  thalli  $\text{m}^{-2}$  ground area throughout) could be varied from 2 to 8. Furthermore, absorbance per layer in the communities could be altered using neutral filters beneath the thallus pieces.

Production rates of oxygen were measured with a Clark-type temperature-compensating macroelectrode (YSI 5905). Oxygen concentrations were measured every 5 s, and mean values were logged every minute. A pen recorder followed continuous oxygen development in the chamber and production rates were measured when oxygen evolution rates had remained constant for at least 10 min. The production rate ( $\mu\text{mol O}_2 \text{s}^{-1}$ ) was calculated by linear regression using the slope of the oxygen concentration versus time ( $r^2 > 0.99$  in all measurements). Production measurements were standardized to square meters of ground area. Production rates were measured at seven irradiances from 0 to 1,600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , attained by using two 100-W halogen spots and inserting neutral filters between the light source and the

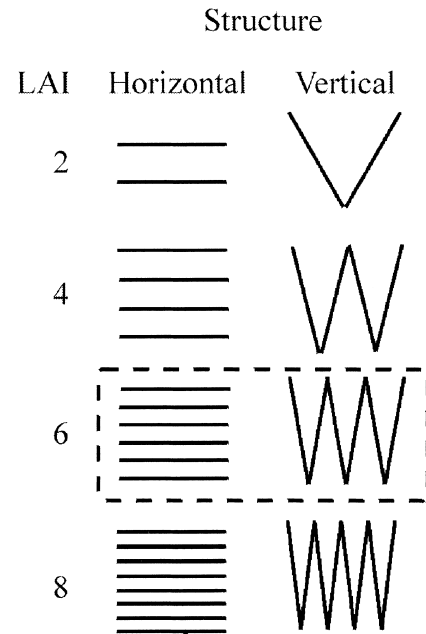


Fig. 1. Community structures used in the experiments. A horizontal structure and a vertical structure with an even distribution of photon flux density. For LAI = 6, experiments were made with varying absorbance in the thalli.

chamber. To decrease light attenuation because of increasing distance from the light source, mirrors were placed on the sides of the aquarium. Initial studies revealed that community production was highest at maximum irradiance and that no photoinhibition took place. Therefore, maximum gross production rates were calculated as net production at 1,600  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  plus respiration in the dark.

Two structural arrangements were compared: First, a horizontal structure and, second, a more vertical structure where all layers were illuminated evenly so that thallus angles increased as plant density increased ( $\delta = \cos^{-1} \text{LAI}^{-1}$ , Fig. 1). This vertical structure implies that not all photons will be utilized in the community because there are no additional thalli beneath to absorb the remaining fraction of light passing through the first layer. Nevertheless this set-up was chosen to avoid compensating for the increase in absorbance with thallus angle. In contrast, the horizontal community structure will absorb almost all incident light depending on LAI and absorbance.

The effect of variable absorbance was tested in a set-up with a LAI of 6 and a fractional absorbance varying from 0.4 to 0.99 for each stratum of the community. The effect of increasing community density was tested in a set-up with a fractional absorbance in the thalli of 0.73 and an increase in LAI from 2 to 8. The fractional absorbance was at a level where the theory predicts that canopy structure should influence community production. In contrast, communities with low LAI or low absorbance should have nonmeasurable differences in community production. The same thallus pieces of *Ulva lactuca* were used in consecutive experiments to avoid bias as a result of different photosynthetic rates in the thalli. Between experiments, the thalli were reacclimated to

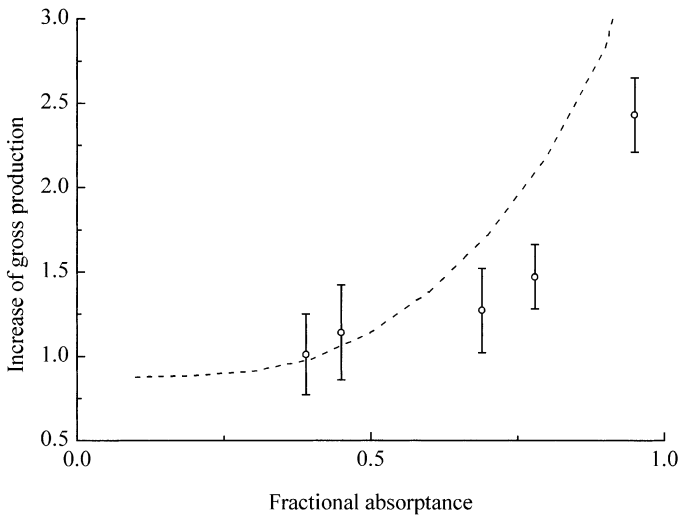


Fig. 2. Increase in gross production (mean  $\pm$  95% confidence limits) as a function of absorbance in the thalli in a vertical community relative to a horizontal community (LAI = 6). Values are  $GP_{\max}(\text{vertical})/GP_{\max}(\text{horizontal})$ . The dashed line represents model predictions.

the light conditions ( $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) in the large aquaria. All experiments were performed in triplicate.

Besides measuring community production, photosynthetic parameters of thallus pieces were measured as oxygen development in a small chamber exposed to a perpendicular light beam as described in Binzer and Sand-Jensen (2002). Assuming that reflectance is negligible when incident light is at right angles, thallus absorbance was estimated from the transmittance of a perpendicular light beam.

## Results

*Influence of canopy structure and thallus absorbance*—Calculations predict that community structure should have a greater influence on community production as absorbance per layer of leaves or thalli increases. Measured photosynthesis–irradiance parameters for *Ulva* thalli were used as input values in all predictions ( $\alpha_t = 0.018 \text{ mol O}_2 \text{ mol}^{-1} \text{ photons}$ ,  $GP_{t,\max} = 2.7 \mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ , and  $R_t = 0.2GP_{t,\max}$ ). A vertical canopy structure at a LAI of 6 should have a greater community production than a horizontal structure of the same LAI when fractional absorbance per layer exceeds 0.4, and it should attain a 2.5- to 3-fold higher production rate when fractional absorbance per layer approaches 1.0 (Fig. 2).

Our measurements on *Ulva* layers of variable absorbance, attained by inserting neutral filters below the *Ulva* pieces in a community with an LAI of 6, followed these predictions, though the measurements at high absorbance were slightly lower than predicted. Vertical and horizontal *Ulva* communities had similar production rates when fractional absorbance of each layer was 0.4. As absorbance increased, the vertical communities gradually showed higher production rates than the horizontal communities and reached 2.5-fold higher production rates when absorbance per layer was 0.95 (Fig. 2).

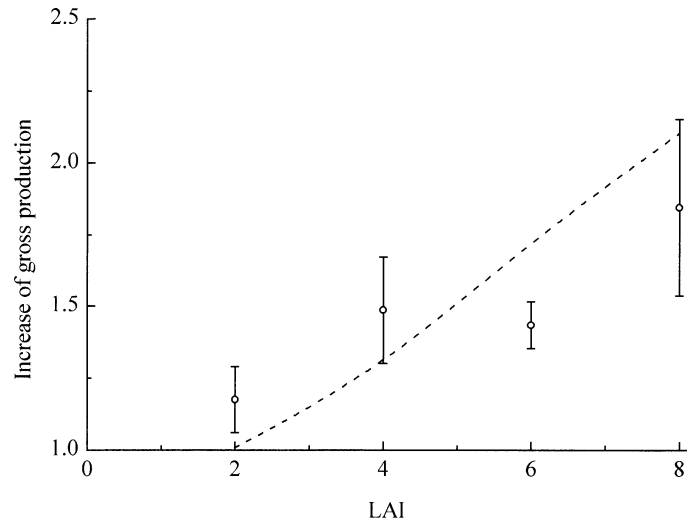


Fig. 3. Increase in gross production (mean  $\pm$  95% confidence limits) as a function of community density in vertical communities relative to horizontal communities (thallus fractional absorbance = 0.73). Values are  $GP_{\max}(\text{vertical})/GP_{\max}(\text{horizontal})$ . The dashed line represents model predictions.

*Influence of canopy structure and density*—For a fractional absorbance of 0.73, calculations predict a higher community production for a vertical than a horizontal canopy structure as community density (LAI) exceeds 2 (Fig. 3). The theory further predicts that the structural influence on community production gradually increases with increasing density and becomes twofold higher for a vertical than a horizontal structure at a LAI of 8. Measurements on *Ulva* communities with a fractional absorbance of 0.73 confirm these predictions, showing a 1.8-fold higher production rate for a vertical than a horizontal community at a LAI of 8.0 (Fig. 3).

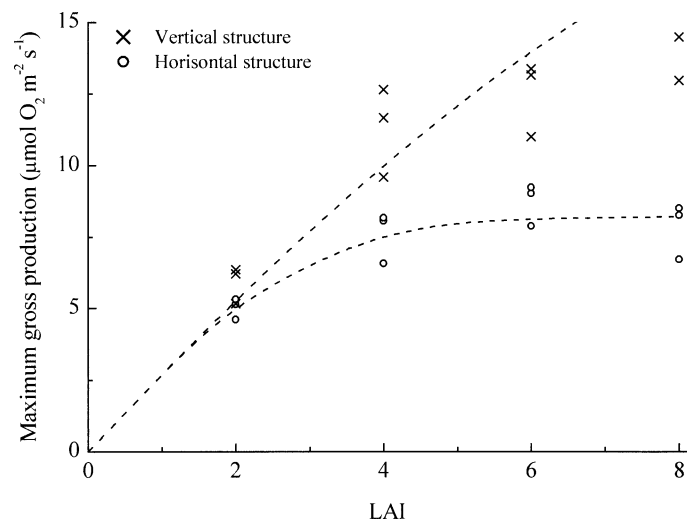


Fig. 4. Maximum gross production at increasing community density of *Ulva lactuca* with a thallus fractional absorbance of 0.73 and a horizontal or vertical structure. Dashed lines represent model predictions.

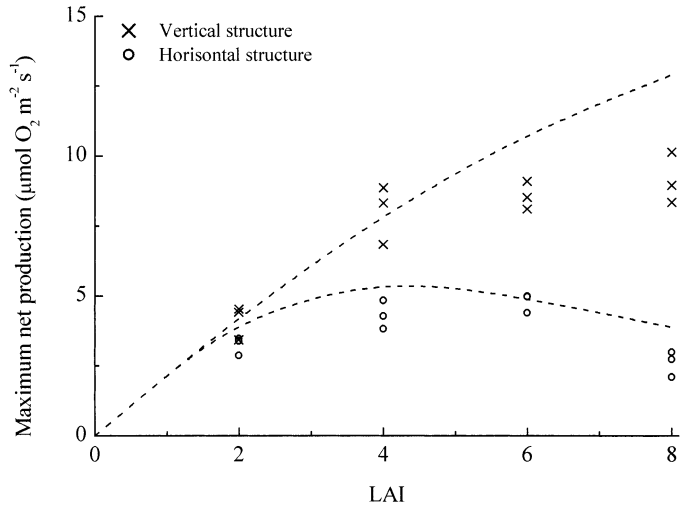


Fig. 5. Maximum net production at increasing community density of *Ulva lactuca* with a thallus fractional absorptance of 0.73 and a horizontal or vertical structure. Dashed lines represent model predictions.

*Gross and net community production as a function of canopy structure and LAI*—Measured rates of gross and net production were systematically higher for a vertical than a horizontal structure in *Ulva* communities at a LAI exceeding 2 (Figs. 2, 3). Gross and net community production for the vertical structure continued to increase as LAI values increased from 2 to 8, whereas gross community production for the horizontal structure reached a maximum at a LAI of 6, and net community production peaked at a LAI of 4–6 (Figs. 4, 5).

The relative benefit of having a vertical canopy structure was much higher for net than gross production. Thus, in dense communities with a LAI of 6–8, gross community production was 1.5- to 2.0-fold higher for the vertical than the horizontal orientation of *Ulva* layers (Fig. 4), whereas net community production was two- to threefold higher for the vertical than the horizontal orientation (Fig. 5).

*Modeling production in relation to irradiance*—The previous sections showed that an even distribution of light results in a pronounced increase in maximum production rates when community density and absorptance of photosynthetic tissue are high. From the measured values of the initial light response ( $\alpha_i$ ), maximum gross production ( $GP_{t,max}$ ), and respiration ( $R_i$ ) of single thallus pieces, it is possible to estimate net production in relation to irradiance for whole communities with different absorptance and community densities. For a fractional absorptance of 0.50, model estimates show that the increase in production as a function of photon flux density is almost independent of community structure when LAI ranges from 0 to 6, but also that the horizontal communities are most efficient at utilizing photons under low light conditions (Fig. 6A). At high absorptance (0.90), the vertical community can maintain high production rates, whereas horizontal communities absorb most of the light in the upper layers of the thalli, resulting in a net respiration in the lower layers and leading to lower community net production rates than for a single thallus piece (Fig. 6B). This pattern is less pronounced at lower community densities and model predictions agree that horizontal communities can only maintain high net production rates when absorptance or community density is low. The shape of the photosynthesis–irradiance curves and the relative increase or decrease in production as a function of community structure will depend on  $GP_{max}\alpha^{-1}$ , so that the difference in production resulting from the distribution of light is related to the irradiance for onset of photosynthetic saturation.

## Discussion

*Architecture and light utilization in aquatic communities*—The theoretical modeling approach and the empirical tests in this paper showed a close correspondence. They confirmed that gross production in aquatic communities in high-light environments is markedly enhanced by a vertical orientation of photosynthetic elements relative to a horizontal orientation, provided that absorptance by individual photosynthetic elements and community density are both high.

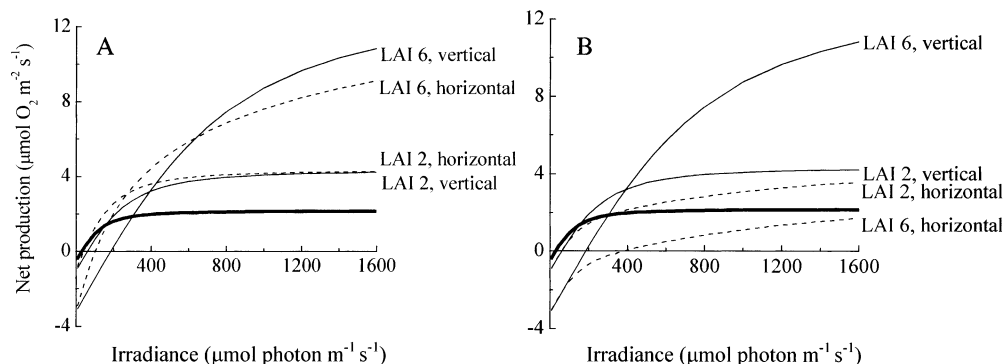


Fig. 6. Calculated net production in relation to irradiance for a horizontal community and a vertical community with LAI = 2 and 6 and a thallus fractional absorptance of (A) 0.5 and (B) 0.9. The measured photosynthetic parameters for *Ulva lactuca* are used as input photosynthetic parameters in the model ( $\alpha_i = 0.018 \text{ mol O}_2 \text{ mol}^{-1} \text{ photons}$ ,  $GP_{max} = 2.7 \text{ } \mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ ,  $R = 0.54 \text{ } \mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). The thick line represents net production of a single thallus piece.

The combination of high absorptance by photosynthetic elements and high community density implies that total community absorption capacity is high so that all incident photons are absorbed in the canopy. High community density is essential if a high irradiance incident on the community has to be distributed among all photosynthetic elements in such a way that none of them absorbs more light than needed for photosaturation. Only then can the maximum efficiency of converting photons into photosynthetic production be attained.

The vertical zone in marine coastal waters, in which the spatial distribution of photosynthetic tissues and light within macrophyte communities can influence photosynthetic production, is relatively deep. The canopy effect is therefore widespread and substantial. Equation 4 can be used to estimate the depth down to which incoming irradiance on the community can exceed the irradiance for onset of photosaturation, which is a prerequisite if canopy structure influences community production. The maximum solar irradiance at noon is about  $1,800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , the reflectance is negligible at noon, and the vertical light attenuation coefficient in clear coastal waters is about  $0.15 \text{ m}^{-1}$  (Kirk 1983). Assuming a threshold of  $80 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  for the onset of photosaturation in the low part of the range for algal thalli and flowering plants ( $83\text{--}208$  and  $50\text{--}160 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ; Kirk 1983), the relevant depth zone extends to 20.8 m in clear coastal waters. Assuming instead a high threshold of  $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$  for the onset of photosaturation, the vertical zone, where canopy structure can influence community production, extends to 14.6 m. This depth range from the surface down to 14.6 or 20.8 m includes much of the vertical zone covered by macrophyte communities and certainly the most productive part of it.

The macrophyte communities in coastal waters where these canopy effects on community production should be most substantial include the dense productive communities of seagrasses and kelps (Mann 1973). Seagrasses and kelps, on an average, extend down to water depths receiving about 20 and 2%, respectively, of surface irradiance (Markager and Sand-Jensen 1994; Pedersen et al. 1999). In clear coastal waters with an attenuation coefficient of  $0.15 \text{ m}^{-1}$ , the depth limits would be approximately 11 m for seagrasses and 26 m for kelps, so most of these communities are located within a vertical range receiving sufficient light to exceed the threshold of photosaturation. The other prerequisite for canopy structure to influence community production is a high photon absorption capacity, which is also met by seagrasses and kelp communities because they typically have high densities ( $\text{LAI} > 6$ ) and a high fractional absorptance of photosynthetic elements ( $>0.8$ , Frost-Christensen and Sand-Jensen 1992).

Despite the high density and high light absorptance of seagrasses and kelps, their community production rates are, nonetheless, markedly lower than in dense forest communities on land (Sand-Jensen and Krause-Jensen 1997). The most probable reason for the larger gross production in forest communities is that they have a multilayered rigid canopy structure of relatively small leaves that change orientation and photoacclimatization with depth in the canopy, whereas seagrasses and kelp communities have more unpredictable

structures, with leaves or thalli changing orientation depending on waves and currents. Seagrasses and kelp communities should therefore have greater difficulty attaining an optimal, even distribution of light among the photosynthetic elements, and the unpredictable nature of the light field should make photoacclimatization of the photosynthetic elements more difficult. Furthermore, photosaturation is typically reached at a two- to fourfold higher irradiance in terrestrial leaves ( $200\text{--}500 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , Ruimy et al. 1995) than in aquatic thalli or leaves ( $50\text{--}200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ , Kirk 1983). Because canopy structure only influences community production above the onset of photosaturation, terrestrial communities should be able to achieve an optimal canopy structure for light utilization more easily.

Macroalgal genera with a thin foliage, such as *Enteromorpha*, *Porphyra*, and weakly pigmented *Ulva*, have a relatively small thallus absorptance ( $0.2\text{--}0.6$ , Frost-Christensen and Sand-Jensen 1992; Markager 1993). Under these circumstances, structural differences between a vertical and a horizontal canopy have little influence on community production. We preferred to use *Ulva* in our experiments because it was exceptionally well suited for establishing the artificial canopy structure; by placing neutral filters behind the thalli, we were able to construct variable absorptances for experimental testing. However, in natural communities of thin-layered thalli of low absorptance, the benefit from a vertical instead of a horizontal orientation of the thalli is negligible unless the community is very dense ( $\text{LAI} > 8$ ). In nature, the thin sheetlike thalli are also so flexible that it is impossible for them to achieve a vertical structure, and they usually cover the seafloor in only one or a few horizontal layers. This is a situation where the horizontal structure has higher production rates and lower light demands than the vertical structure (Fig. 6A). *Ulva* can nevertheless form dense mats with a substantial biomass and gross production, but because the lower, shaded layers only contribute to respiration, net production is low (D. Krause-Jensen pers. comm.).

Crust-forming algae are a type of macroalga covering stone and rock surfaces in a thin layer. Although macroalgae with a thin foliage can grow down to 0.2% of surface irradiance in the sea, the thin crust-forming algae can survive at only 0.02% surface irradiance or less (Markager and Sand-Jensen 1992). These thin-crust and sheetlike algae mostly have low absorptance (Markager and Sand-Jensen 1992). A horizontal orientation of these thalli is actually beneficial in a low-light environment to optimize light absorption for the minimum investment in algal tissue (Markager and Sand-Jensen 1994). In a chronically low-light environment, there is only energy to form and maintain a low biomass. To optimize photon absorption per unit biomass, algae and plants must minimize self-shading in the community and package effects within the thalli or leaves. These features are best achieved by thin thalli or leaves in a single horizontal layer. In contrast, high-light environments have sufficient energy to form a community of high biomass and high absorption capacity that benefits from a complex spatial structure and allows for more even light distribution.

As irradiance decreases, the advantage of a vertical structure relative to a horizontal structure gradually diminishes.

Communities of low density will then have higher net production rates, and to maximize net production at low irradiance, the community would ultimately be reduced to a single horizontal layer. Thus, the main difference in selective forces between the low-light and high-light environments is relatively simple. In low-light environments, as large a proportion of available light as possible needs to be absorbed per unit biomass to ensure survival and growth. In contrast, as small a proportion of available light as possible needs to be absorbed per unit biomass to optimize gross production per unit vegetated area in the high-light environment. We would therefore expect multilayered species, with a high LAI and vertical organization of the thalli, to dominate in the upper part of the water column and single-layered foliose or crust-forming algae of low LAI to dominate in deep water where light is scarce. These predictions, based on bio-optical theory, accord with the overall depth distribution patterns of thick leathery, thin foliose, and crustose macroalgae in the sea (Markager and Sand-Jensen 1994). Likewise, detailed compilation of depth distribution data of marine macroalgae in the Caribbean by Hay (1983) showed that, for species of Chlorophyta and Rhodophyta, multilayered canopies were present only in the upper 15 m of the water column, whereas species with a single photosynthetic layer extended down 40–60 m. Moreover, the maximum blade width increased with depth of occurrence for seven species of *Sargassum*, suggesting that species living under high-light conditions have slender blades that facilitate an even distribution of light. The depth distribution of form-functional groups of macroalgae is thus affected by thallus structure and the ability to optimize photon use.

*Community production in relation to irradiance and community density*—Production in relation to increasing irradiance is highly dependent on the distribution of photons between thallus parts. When light is distributed evenly, communities have an almost linear response up to high irradiances, whereas horizontal communities with a high degree of self-shading begin to saturate at low irradiances. Multilayered communities with a horizontal orientation of layers will continue to have a photosynthetic gain at increasing irradiance because more photons are transmitted to the lower strata in the community where photosynthetic capacity is not utilized. The onset of photosaturation for natural communities of *Fucus serratus* is reached at low irradiances ( $<200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ), but they do not become fully saturated even at  $1,600 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Binzer and Sand-Jensen 2002), implying that these communities distribute photons unevenly. In contrast, efficient structures are observed in terrestrial forest vegetation where the gross production–light response curve is almost linear up to  $1,500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$  (Ceulemans and Saugier 1991; Ruimy et al. 1995). Thus, many forest stands respond to increasing incident light as predicted for a vertical community with a near-optimal distribution of light, whereas *Fucus serratus* communities respond much like horizontal communities with a nonoptimal distribution of light.

Community gross production will either increase or remain unaltered when plant density increases. However, gross production does not represent the excess energy available

for community growth, which is better represented by net production. In general, net community production will increase up to a certain threshold of LAI and then decrease above this value (de Wit 1970; Binzer and Sand-Jensen 2002). So entire plant communities do not benefit from a higher gross production in very dense stands because net production declines because of greater respiration than photosynthesis in the lower strata. This problem is solved in terrestrial plant communities by not allocating energy to leaves with a negative net production and subsequently shedding them, although there are examples of plants maintaining leaves below the light limit for net photosynthesis (Thomas and Sadras 2001). This solution is only possible, however, when photosynthetic tissues are arranged in discrete units with multiple growth zones for the same individual, and it is not possible in algae forming one entire thallus, as in many kelps, or in seagrasses producing long strap-formed leaves from a single basal meristem.

Vertical communities that distribute photons evenly between the photosynthetic tissue have maximum net production rates at higher LAIs than horizontal communities (Fig. 5), implying that communities can only maintain a high biomass and production if photons are distributed evenly so that all photosynthetic tissues receive photons at low flux densities (Russell et al. 1990). The large biomass, which can be sustained in vertically structured communities, however, does require high incident irradiances to compensate for high community respiration. Furthermore, the almost linear response in community production to irradiance results in a large reduction of production as irradiance decreases, whereas production in horizontal communities will be virtually unaffected because of a more hyperbolic response to irradiance. Vertically structured communities can thus attain high biomass and production, but they have higher light demands and are more susceptible to a reduction in irradiance. This could explain why marine seagrasses such as *Zostera marina* having a distinct vertical leaf orientation have high minimum light demands (20% of surface irradiance) and experience substantial reductions of biomass and depth distribution in turbid waters (Pedersen et al. 1999).

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