

Growth rates and photon yield of growth in natural populations of a marine macroalga *Ulva lactuca*

Ole Geertz-Hansen, Kaj Sand-Jensen

Freshwater-Biological Laboratory, University of Copenhagen, Helsingørgade 51, DK-3400 Hillerød, Denmark

ABSTRACT: We examined the photon yield of growth of free-floating *Ulva lactuca* L. in a eutrophic Danish estuary by exposing discs in mesh cages to 10, 40, and 100 % of ambient light in shallow water. Growth per incident or absorbed photon was much higher at 10 than at 100 % of ambient light. Growth was linearly related to photon flux density in low light and *U. lactuca* adapted to the shade by increasing the chlorophyll concentration and thus the photon absorbance in the tissue. Maximum yields at high temperatures in August–September ranged from 16.0 to 21.7 mmol C mol⁻¹ incident photon and 40 to 61 mmol C mol⁻¹ absorbed photon at 10 % of ambient light. These values show that light-limited growth of *U. lactuca* proceeds at the maximum attainable photon yields when *in situ* temperature and nutrient supply are suitable. Such high photon yields for growth are perhaps common among fast-growing species resembling *Ulva*.

INTRODUCTION

Growth rate determinations of aquatic microalgae and macrophytes are few and difficult to perform in nature. This is unfortunate, because growth determinations are important for evaluation of many central ecological aspects such as regulation of plant abundance by environmental resources and grazing, and rates and efficiencies of energy and material flow through plant communities.

Photosynthesis per incident and absorbed photon (photon yield) has frequently been determined for microalgae and terrestrial leaves in laboratory experiments under light limitation (e.g. Björkman 1981, Geider et al. 1985). However, photon yield of growth has rarely been determined for natural aquatic plant populations (see however Ramus 1990). This property is of utmost importance for the success of an organism in low light and more relevant for examining phenotypic light adaptation and interspecific differences than the more frequent measurements of photosynthetic performance. Growth rates are easy to measure in *Ulva* (Vermaat & Sand-Jensen 1987) and *U. lactuca* has a sheet-like thallus with well-defined light absorbance properties (Ramus 1978, Sand-Jensen 1988a).

In this study we examined the natural seasonal variation of *Ulva lactuca* L. growth rate and photon yield of

growth. We compared the maximum photon yield of net growth of *U. lactuca* in the field with reported values in photosynthetic experiments with phytoplankton, terrestrial leaves, and *U. lactuca* in laboratory culture.

MATERIALS AND METHODS

We measured growth rates from April to November in the eutrophic Roskilde Fjord, Denmark (Borum 1985). Measurements were made in shallow water (40 to 70 cm) at 4 locations along the estuary (tidal amplitude < 10 cm), but only results from 1 location in the mid-part (Stærgård) are presented here. This location had large shallow sediment flats and had slightly higher growth rates of *Ulva lactuca* than at the other localities, presumably due to high nutrient release from the sediments. Extensive N limitation was only observed from late June and through July (Geertz-Hansen 1989).

Growth rates (μ_a) were measured as changes in surface area (A) of *Ulva lactuca* discs of uniform size. Discs were incubated in mesh cages over 7 d, or longer when μ_a was small. The *U. lactuca* discs (17 mm in diameter) were punched from large free-floating specimens with a sharpened perspex tube (Vermaat & Sand-Jensen

1987). Twelve discs were placed in every cage. Growth rates (μ_a) were calculated as

$$\mu_a = (\ln A_t - \ln A_0) t^{-1} \quad (1)$$

where A_0 is the initial and A_t the final surface area after t days of incubation. *U. lactuca* discs stayed circular, unless grazed, and A was calculated from 2 diameter measurements perpendicular to each other. Heavily grazed discs were discarded, whereas the diameter of slightly grazed discs was measured in unaffected regions (grazing was usually from the margin). The data presented here were based on 7 to 12 surviving discs. The 95% CL ranged from 5.6 to 25.5% of the mean at ambient light and 4.5 to 39.5% at 10% of ambient light.

Incubations were made in cages at approximately 100, 40, and 10% of ambient light in shallow water. Percentage of surface light reaching the cages at the mean depth of 50 cm was $64 \pm 8\%$ (\pm SD, $n = 24$). Nutrient effects on growth were assessed by placing a plastic vial filled with Na_2HPO_4 or NH_4Cl (about 20 g vial⁻¹) in the cages. Nutrients were slowly released through small holes in the vial. We made no attempt to quantify the elevation of nutrient loading by this procedure, and only examples of N-stimulation of growth during certain periods are presented here (see Fig. 2). Phosphate addition did not affect *Ulva lactuca* growth.

Cages were made of perspex and nylon net (1.5 mm mesh size) and were fixed to the sediment by coiled stainless steel pegs (Geertz-Hansen 1989). About 70% of their outer surface (the sides and the bottom) was covered by net, maintaining good exchange with the surrounding water and the sediment. Shading was provided by black neutral density plastic sheets firmly attached to the perspex roof and black mesh gauze replacing the clear nylon net. Cages without shading received 99 to 100% of ambient light.

Continuous underwater light measurements on location were impossible to perform due to lack of reliable instrumentation that could work without daily supervision. Instead, we obtained measurements of the integrated daily surface photon flux density (400 to 700 nm) from the Hydrotechnical Laboratory 30 km away, and we measured weekly attenuation in the water column above the cages, and light transmittance through the cages. All *in situ* light measurements were with a 2π photon sensor (Licor 183a). Using a conservative 10% estimate for daily surface reflection (Wetzel 1983), we calculated the mean incident photon flux density for *Ulva lactuca* (mol photon $\text{m}^{-2} \text{d}^{-1}$; 1 mol photon = 1 Einstein) during every incubation period. We acknowledge that water attenuation may vary during incubation because of changes in water depth (<10 cm) and turbidity. Though this will affect the weekly estimates of photon yield of growth, this should

not lead to systematic errors (over- or underestimates), and the overall patterns should be correct.

Areal growth rates from Eq. (1) [m^2 produced (m^2 of *Ulva lactuca* surface)⁻¹ d^{-1}] were transformed to carbon specific growth rates [mol C produced (m^2 of *U. lactuca* surface)⁻¹ d^{-1}] by first multiplying μ_a by the mean dry weight density [g dry wt (m^2 of *U. lactuca* surface)⁻¹] of 10 initial and all *U. lactuca* discs retrieved from each cage after incubation, and then by converting dry weight to carbon. The carbon content of 161 discs was measured on a Perkin Elmer CHN-analyzer and showed a constant value of 26.5 ± 2.0 mmol C g^{-1} dry wt, independent of season and shading level. Dry weight was measured by freeze-drying to allow subsequent chlorophyll analysis.

Carbon-specific growth rates and photon flux density are both expressed on an areal basis and directly comparable. The photon yield of growth was calculated by expressing carbon-specific growth rates relative to incident photons (α_g , mol C fixed during growth per mol incident photon) and absorbed photons (ϕ_g , mol C per mol absorbed photon).

The proportion of incident photons being absorbed by the *Ulva lactuca* was estimated by measuring the chlorophyll content of all *U. lactuca* discs (Vermatt & Sand-Jensen 1987), and using the relationship to absorbance previously described (Sand-Jensen 1988a). In this relationship absorbance was calculated as incident minus transmitted light, thus including reflection. Later measurements in an integrating sphere (Frost-Christensen & Sand-Jensen unpubl.) confirmed that reflection was insignificant and yielded almost the same relationship.

RESULTS AND DISCUSSION

Chlorophyll content and growth rates

Chlorophyll content ranged from 1.3 to 15.5 μg chlorophyll cm^{-2} (Fig. 1). Chlorophyll content was usually several-fold higher at 10 relative to 100% of ambient light, and both N-limitation and sporulation reduced chlorophyll markedly. The highest chlorophyll content was found in April. A strong positive relationship between total N and chlorophyll content of *Ulva lactuca* was also observed (Geertz-Hansen 1989).

The relationship of growth rate (μ_a) to incident light is shown for several weekly periods in April, August, and early October, in which there was little effect of N-addition and zoospore formation on growth (Fig. 2, upper panel). The maximal growth rate was much faster at high temperature in August (ca 0.3 d^{-1}) than at lower temperatures in early October (ca 0.2 d^{-1}) and April (0.1 d^{-1}). A comparison of μ_a at a high light level of

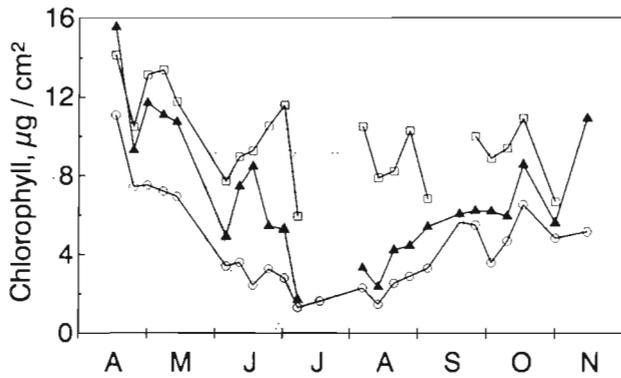


Fig. 1. *Ulva lactuca*. Seasonal variations of chlorophyll content at (○) 100%, (▲) 40%, and (□) 10% of ambient light. Shading indicates periods with strong N-limitation and/or sporulation

10 mol photon $m^{-2} d^{-1}$, common for the 3 periods, was consistent with a Q_{10} value for growth of about 2.0. The growth rate was only saturated by ambient light at low temperature (6 °C) in April. The rest of the year, increasing light continued to have a growth enhancing effect in shallow water. Growth rates declined markedly during periods of nutrient limitation and during zoospore formation (Fig. 2, lower panel). Nitrogen addition enhanced growth significantly during these periods.

The rapid growth rates of *Ulva lactuca* corresponded to previously reported growth rates of subtropical *U. fasciata* in outdoor flow-through tanks (Lapointe & Tenore 1981). Growth rates of *U. lactuca* exceeded several-fold the reported maximal growth rates of large and structurally complex *Fucus* and *Laminaria* species (0.01 to 0.03 d^{-1} ; Mann 1972, Guterstam et al. 1978, Nielsen & Sand-Jensen 1990). The rapid growth rate of *Ulva* is well explained by its favourable morphology for uptake of nutrient and use of light (i.e. 2-layered thallus, high surface area to volume ratio, all cells photosynthetically active; Rosenberg & Ramus 1984, Nielsen & Sand-Jensen 1990).

Photon yield of growth

Growth per incident photon, α_g , varied from 1 to 22 mmol C (mol incident photon) $^{-1}$, depending on time of year and shading level (Fig. 3). The α_g was high under nutrient saturation and high temperature in August–September and low during nutrient limitation and sporulation (Fig. 3). The α_g was always highest at 10% of ambient light. At this low light level, the relationship of μ_a with incident light was linear (Fig. 2) and *Ulva lactuca* showed the highest chlorophyll content (Fig. 1) and thus the highest light absorbance. At 40

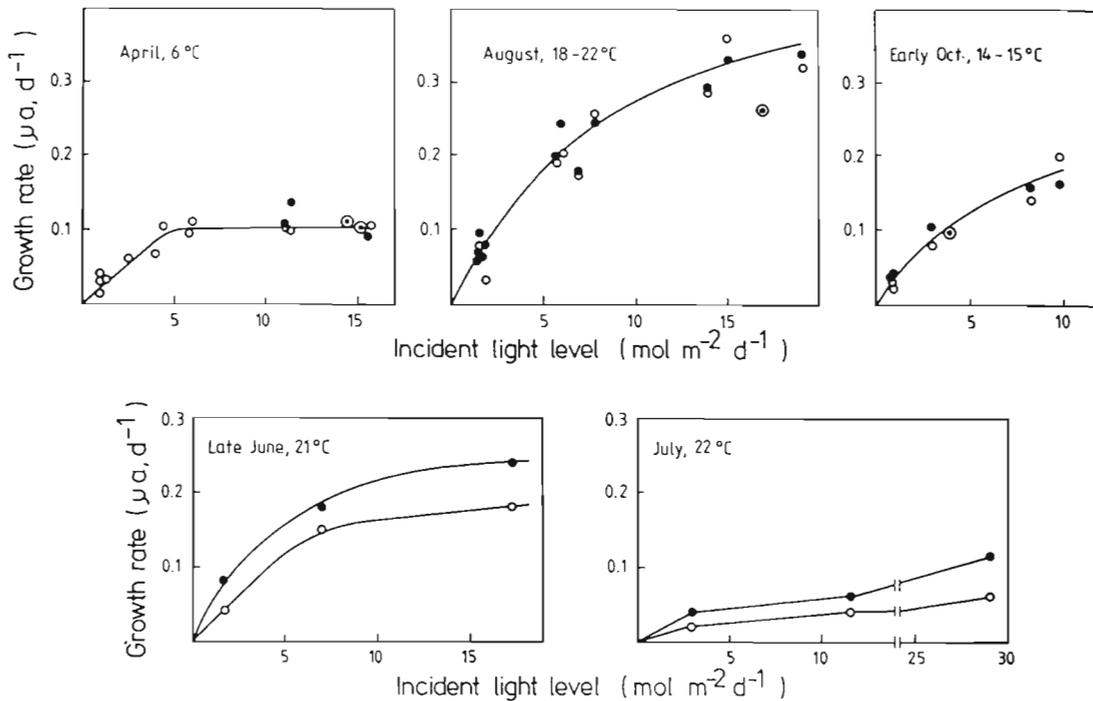


Fig. 2. *Ulva lactuca*. Growth rates (μ_a) as a function of incident photon flux density (●) with or (○) without addition of inorganic N. Upper panel represents 3 periods with no zoospore formation and no effects of N addition. Lower panel represents 2 periods with strong N-limitation and reduced growth due to sporulation (lower right only). Each point is a mean of 7 to 12 measurements

and 100 % of ambient light *U. lactuca* is photosaturated for a longer period of the day, and light is consequently not utilized with the maximum efficiency.

Growth per absorbed photon, ϕ_g , ranged from 6 mmol C (mol absorbed photon)⁻¹ at light saturation in April to a maximum of 61 mmol C (mol absorbed photon)⁻¹ at 10 % of ambient light in August (Fig. 3). The ϕ_g showed the same overall pattern as α_g except that ϕ increased less with reduced light availability because the increased absorbance of shade acclimated *Ulva lactuca* is corrected for in the calculation of ϕ_g . The ϕ_g is still markedly higher in incubations at 10 % of ambient light [e.g. 40 to 61 mmol C (mol absorbed photon)⁻¹ in August–September], since growth here is never photosaturated, though we cannot exclude partial saturation during periods of high surface light.

Natural photon yields of *Ulva lactuca* growth were in the same range as values for *U. lactuca* in laboratory cultures and for terrestrial plant communities under optimum growth conditions. The α_g of well-adapted *U. lactuca* cultures kept at 7 °C was 12 mmol C (mol incident photon)⁻¹ at 2.14 mol photon m⁻² d⁻¹ of continuous and constant light and 16 mmol C (mol incident photon)⁻¹ at 0.76 mol photon m⁻² d⁻¹ (Table 1 in Sand-

Jensen 1988b). Natural α_g values at comparable light levels of 10 % of the ambient ranged from 4.5 to 21.7 mmol C (mol incident photon)⁻¹ with an overall mean value of 12.3 mmol C (mol incident photon)⁻¹. The maximum α_g values at high temperatures in August–September, between 16.5 and 21.7 mmol C (mol incident photon)⁻¹, exceeded the laboratory values for continuous light at 7 °C, even though the natural daily variations in illumination as well as the night period would probably induce higher respiratory costs and make shade adaptation less perfect in the field. These results also suggest a high temperature preference (i.e. ca 20 °C) for growth of *U. lactuca* in the north-temperate Danish waters which is in accordance with previous laboratory measurements (Ho 1975) and the occurrence of *U. lactuca* also within south-temperate and subtropical regions. The preference for high temperatures may reflect the need for higher enzyme concentrations and thus greater maintenance and running costs when *Ulva* is growing in cold water. A simpler explanation could be that growth rates are limited by rate of enzyme reactions imposed by low temperatures and lack of space to pack more enzymes in. Temperature effects on light saturated growth are well known, but are here expressed under light limitation as well. Unfortunately, it is often forgotten that even though the rate limiting step of photosynthesis under light limitation is a temperature insensitive photochemical process, the subsequent carbon fixation, the production of light harvesting apparatus and the growth process all involve numerous temperature sensitive enzyme reactions.

The α_g and ϕ_g values for net growth in the field are not directly comparable to the frequently measured photon yields of light-limited gross photosynthesis, based on incident and absorbed photons, mainly because respiratory costs are included in the former and growth may not have been exclusively light-limited. The maximum photon yield, ϕ_m , is 125 mmol O₂ produced (mol absorbed photon)⁻¹ based on the Z-scheme for photosynthesis (Myers 1980). Assuming a photosynthetic quotient of 1.25 mol O₂ produced (mol C fixed)⁻¹ we predict a theoretical maximum for gross C fixation of 100 mmol C (mol absorbed photon)⁻¹. Photon yields of photosynthesis close to the theoretical maximum have been observed in unicellular algae (Geider et al. 1985), but most values for unicells and terrestrial leaves range from 40 to 80 mmol C (mol absorbed photon)⁻¹ (Ehleringer & Björkman 1977, Bannister & Weidemann 1984). For conversion of early photosynthates into net growth we have to consider a loss due to costs of synthesis of the different growth products (Penning de Vries et al. 1974) and costs of respiratory maintenance. These costs are variable but probably not less than 40 % (Penning de Vries et al. 1974, Geider & Osborne 1986). If we include these costs we would

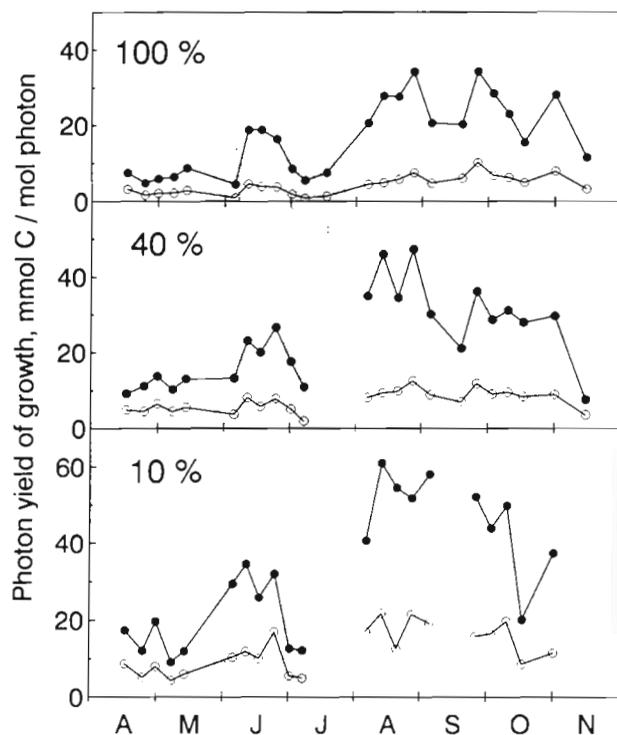


Fig. 3. *Ulva lactuca*. Seasonal variations of photon yield of growth expressed as (○) growth per incident photon, α_g ; and (●) growth per absorbed photon, ϕ_g . Upper panel: 100 % of ambient light; middle panel: 40 % light; lower panel: 10 % light. Shading indicates periods with strong N-limitation and/or sporulation

therefore predict a theoretical maximum photon yield of net growth (ϕ_g) of about 60 mmol C (mol absorbed photon)⁻¹, i.e. 100 mmol C (mol absorbed photon)⁻¹ minus 40 % because of respiratory losses. The ϕ_g values for net growth of *Ulva lactuca* in field experiments averaged 33 ± 17 mmol C (mol absorbed photon)⁻¹ (\pm SD, $n = 21$) at 10 % of ambient light, which comes as close as possible to light-limited conditions in our experiments. During optimum growth conditions in August–September, ϕ_g averaged 53 ± 7 mmol C (mol absorbed photon)⁻¹ (\pm SD, $n = 6$). We therefore conclude that growth of *U. lactuca* at low light in the field proceeds at efficiencies approaching the maximum possible for conversion of absorbed light energy into new biomass, when temperature and nutrient supply are suitable. This had not been shown previously for aquatic plant populations, but is perhaps of widespread occurrence among fast-growing, opportunistic species resembling *Ulva*. Obviously, the highest photon yields were attained in *U. lactuca* growing in the most shaded cages, receiving 5 to 7 % of the surface light, and low light is a necessary prerequisite for reaching the highest yields, also in other macroalgae. Nevertheless, relatively high photon yields [mostly 10 to 50 mmol C (mol absorbed photon)⁻¹] were even attained by *U. lactuca* in cages receiving about 25 and 60 % of surface light during August–October.

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