Marine Biology 56, 21–28 (1980)

**MARINE BIOLOGY**
© by Springer-Verlag 1980

# Diurnal Photosynthetic Performance of Seaweeds Measured Under Natural Conditions

J. Ramus[1] and G. Rosenberg[2]

[1] Botany Department, Duke University; Durham, North Carolina 27706, USA, and Duke University Marine Laboratory; Beaufort, North Carolina 28516, USA
[2] Department of Biology, Yale University; New Haven, Connecticut 06520, USA

## Abstract

Statements comparing photosynthetic performance characteristics of species rely upon empirical data, usually light-saturation curves (photosynthesis, $P$, versus incident-light flux-density, $I_0$, relationships) derived from instantaneous measurements. The specific comparative parameters are initial slope and maximum photosynthesis, $P_{max}$. For phytoplankton, diurnal variation in specific productivity at maximum incident light, $I_{max}$ is typically asymmetrical, i.e., there is a morning maximum followed by an afternoon depression. Five seaweed species, numerical dominants from the Outer Banks of North Carolina, were examined for patterns of diurnal photosynthetic performance in sunlight of habitat equivalence. These were *Codium decorticatum* (Woodw.) Howe and *Ulva curvata* (Kütz.) De Toni in the Chlorophyceae, *Dictyota dichotoma* (Huds.) Lamour. and *Petalonia fascia* (O.F. Müll.) Küntze in the Phaeophyceae, and *Gracilaria foliifera* Forssk.) Bφrg. in the Rhodophyceae. Diurnal patterns of oxygen exchange were varied, some symmetrical about the midday axis, others asymmetrical, and were specific for (1) species, (2) derived habitat, (3) thallus absorptance ($1\text{-}I/I_0$, where $I$ is the transmitted light), (4) developmental stage, and (5) diurnal photosynthetically active radiation (PAR) history. All species show a depression in oxygen exchange rates at less than 0.1 $I_{max}$, and show varying degrees of recovery when $I_0$ decreases from that value. Diurnal photosynthetic performance of some species at 0.03 $I_0$ (total diurnal maximum) exceeds several times that at 0.70 $I_0$ (total diurnal maximum), an observation not predicted by instantaneous measurements. Specific day-rate integrals of $I_0$ vary, producing transient initial slope and $P_{max}$ values. Thus, initial slope and $P_{max}$ values derived from instantaneous measurements in the laboratory bear little relationship to actual diurnal production. At this time there appears to be no substitute for direct measurement of diurnal photosynthesis.

## Introduction

The design and application of equations for daily photosynthetic production ultimately depend on empirical data. Since most of the variance in primary production is accounted for by variations in light (Platt *et al.*, 1977), such models usually incorporate a mathematical expression for the "$P$ versus $I_0$ curve" which expresses the dependence of photosynthetic rate on the incident-light flux-density. The general features of the $P$-$I_0$ curve are well known. At low light flux-density, the rate of photosynthesis is linearly related to incident light. At sufficiently high flux-density, the rate of photosynthesis becomes independent of light flux-density, i.e., it saturates ($P_{max}$). At light flux-density beyond saturation ($I_k$), photosynthesis may decline, due, presumably, to photoinhibition.

There still appears to be some question about the significance of photoinhibition in natural algal populations (Kremer and Nixon, 1978). Early mathematical expressions for the $P$-$I_0$ curve did not take this phenomenon into account. Blackman (1905), followed by Baly (1935), and Smith (1936), proposed models in which the photosynthetic rate leveled off above the saturating light flux-density.

We owe the first mathematical treatment of photoinhibition to Steele (1962). His equation adequately expressed the main characteristics of the $P$-$I_0$ curve and has been fruitfully applied to a general model of plankton dynamics (Kremer and Nixon, 1978). The closeness of fit to experimental data was improved by Parker (1974) who introduced an additional fitting parameter (Parker's $\alpha$) into Steele's equation. Another approach was that of Vollenweider (1965), who modified the equation of Smith by introducing two free parameters (Vollenweider's $\alpha$ and $n$). His equation is capable of describing a wide variety of $P$-$I_0$ curves, which is not surprising in view of the number of free parameters. The properties of this model, with varying types and degrees of photoinhibition have been elaborated upon by Fee (1969). Jassby and

0025-3162/80/0056/0021/$01.60

Platt (1976) have explicitly compared the adequacy of several mathematical formulations of the $P$-$I_0$ curve, including those of Blackman, Baly, Smith, and Steele, for describing experimental data from natural marine phytoplankton populations up to light saturation.

Modifications of the original models have largely consisted of adding free parameters in order to improve the fit to empirical data. This approach has two major drawbacks: (1) the resulting equations are difficult to integrate over depth and time for estimates of daily production, and (2) some of the introduced parameters, unlike $P_{max}$ for example, have no meaningful biological interpretation. Part of the difficulty of incorporating photoinhibition into productivity models is due to our poor understanding of the fundamental biochemical mechanisms involved.

Another aspect which has received scant attention in productivity models is the fact that $P$-$I_0$ curves and, thus, the parameters used to characterize them, are variable in space and time. They are influenced by light history, nutrient availability, temperature, diurnal rhythms in photosynthetic capacity, and physiological adaptation to short-term fluctuations in the environment (Platt *et al.*, 1977). In view of the variability of $P_{max}$, Bannister (1974) attempted to simplify the earlier productivity models of Steele (1962) and Vollenweider (1965) by replacing this parameter by the initial slope of the $P$-$I_0$ curve, which he thought to be more nearly constant. However, it has recently been shown for phytoplankton that initial slope (as well as $P_{max}$) varies seasonally (Platt and Jassby, 1976) and with time of day (MacCaull and Platt, 1977). Thus, the simplifying assumption of Bannister would not seem justified.

The values for $P_{max}$ and initial slope determined by instantaneous measurement must be viewed as transient. As such, they are unsuitable for use in the integrated forms of equations for daily production. Typically, in laboratory determinations of $P$-$I_0$ curves, samples of phytoplankton which have been previously maintained in the dark or in weak light are exposed to increasing flux-density during the measurement of photosynthetic rates. Phytoplankton maintained at saturating light flux-density are seldom used in such determinations. Yet, it has been shown that the $P$-$I_0$ curve obtained is affected by the flux-density to which the phytoplankton have been acclimated (Platt and Jassby, 1976). It is therefore to be expected that $P$-$I_0$ curves for phytoplankton maintained at different light flux-density will yield different values for $P_{max}$ and initial slope. Since light is more variable in the course of a day than on an annual basis, this fact has important implications for daily production.

Diurnal measurements of photosynthetic performance in phytoplankton have been made using either continuous or semicontinuous monitoring (Harris, 1973; Marra, 1978). The pattern of diurnal photosynthesis in both laboratory and field studies shows an asymmetry which is particularly pronounced at the surface on clear days. Typically, photosynthesis is maximal in the morning and decreases in the afternoon. Light saturation occurs early in the day as the sun begins its course to the zenith. At the surface, this results in about 70% of the total daily photosynthesis being carried out during the first half of the day (Parsons *et al.*, 1977).

In addition to photoinhibition, other causes of the asymmetry may be the intrinsic diel rhythm in photosynthetic capacity first described by Doty and Oguri (1957) and photorespiration. The most frequently observed pattern in phytoplankton (Sournia, 1974) is a maximum in photosynthetic capacity in the late morning and a minimum in the early evening. No attempt has been made to incorporate this circadian rhythm into a model for daily production.

In the laboratory, diurnal photosynthetic performance in phytoplankton has been measured under idealized steady-state light regimes (Marra, 1978; Harris and Lott, 1973) where light is varied as a cosine function of time and equal flux-density doses are administered in successive experiments. Some measurements have been made for light regimes which fluctuated according to a pre-set pattern (Marra, 1978). Under natural conditions, diurnal isolation on successive days is unequal and unpredictable.

Although many instantaneous determinations of $P$-$I_0$ curves have been made for seaweeds (e.g. Kanwisher, 1966), there have been few measurements of diurnal photosynthesis (e.g. Hatcher *et al.*, 1977). On the basis of what is known about phytoplankton, we predicted that net diurnal photosynthesis in seaweeds would vary as a function of (1) the PAR flux-density, (2) the pattern (cosine function or fluctuating) of the flux-density supplied, (3) the light habitat (high to low flux-density) from which the seaweed originated, and (4) the developmental stage (juvenile or mature) of the seaweed.

In order to test these predictions, we carried out a series of measurements of diurnal photosynthesis using 5 species of seaweeds which are numerically dominant in the waters of the Outer Banks of North Carolina. We sought to determine: (1) whether or not there were discrete diurnal patterns in photosynthetic performance, (2) whether such patterns were predictable, (3) the relationship of the derived $P$-$I_0$ curves to diurnal photosynthetic performance, and (4) the utility of instantaneously derived $P_{max}$ and initial slope values for the prediction of daily production.

## Materials and Methods

The 5 species used in the experiments were selected to represent the 3 taxonomic divisions of seaweeds. They were *Codium decorticatum* (Woodw.) Howe and *Ulva curvata* (Kütz.) DeToni in the Clorophyceae, *Dictyota dichotoma* (Huds.) Lamour. and *Petalonia fascia* (O. F. Müll.) Küntze in the Phaeophyceae, and *Gracilaria foliifera* (Forssk.) Bϕrg. in the Rhodophyceae. *C. decorticatum* and *G. foliifera* are optically opaque, *U. curvata* is optically translucent, whereas, *D. dichotoma* and *P. fascia* are intermediate between the two extremes.

The light regime was the natural one on the day that each measurement was carried out. Incident light was monitored continuously with a Licor 193S spherical

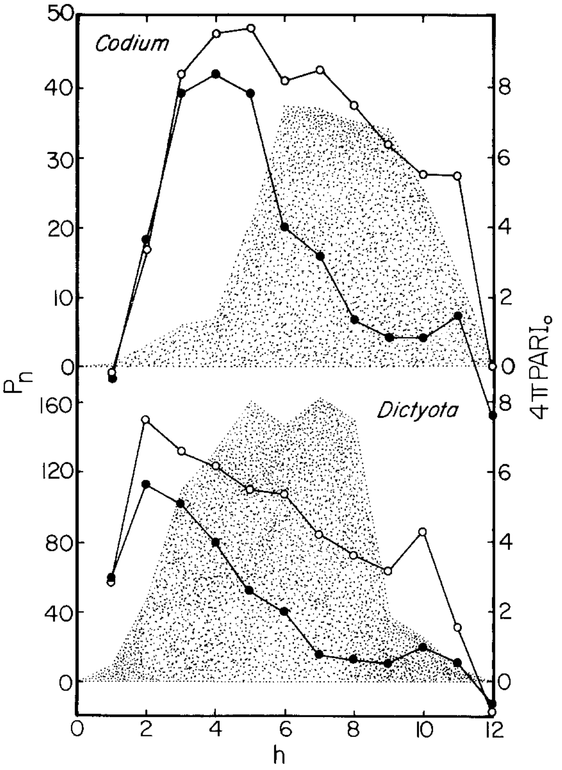

Fig. 1. *Codium decorticatum* and *Dictyota dichotoma*. Diurnal photosynthetic performance ($P_n$, in moles $O_2$ evolved mole$^{-1}$ chlorophyll *a* h$^{-1}$) for plants from two light habitats (open circles: sun plants; filled circles: shade plants) at 0.70 $I_0$. Diurnal $P_n$ for sun plants is 1.83 times greater than for shade plants in *C. decorticatum* and 2.1 times greater in *D. dichotoma*. Stippled area: incident light ($4\pi$ PAR $I_0$), in E m$^{-2}$ h$^{-1}$. Abscissa shows hours after sunrise (h)

(approaching $4\pi$) quantum sensor which provided input to a Licor Model 550 printing integrator. Only photosynthetically active radiation (PAR, 400 to 700 nm) was measured.

The seaweeds were incubated in standard biological oxygen demand bottles. Photosynthetic rates (expressed as moles $O_2$ evolved mole$^{-1}$ chlorophyll *a* h$^{-1}$) were determined by measuring the change in dissolved oxygen at hourly intervals, using a Clark-type polarographic electrode (Yellow Springs Instruments Model 5750) with a YSI Model 57 oxygen meter. During oxygen measurements, stirring was provided by a magnetic bar driven by a Tri-R Ms-7 battery-powered submersible stirrer. After each hourly incubation, the samples were transferred to freshly filtered seawater in order to minimize bottle effects.

The bottles were incubated outdoors in a glass tank provided with circulating seawater at the ambient temperature. The seawater surrounding the bottles had the effect of reducing the measured incident light ($I_0$) to 70% of its initial value. This is equivalent to the amount of light the seaweeds would experience in exposed intertidal habitats. For some measurements, the incident light was attenuated to 0.03 and 0.13 $I_0$ with neutral-density filters constructed of fiberglass screening wrapped around the bottles containing the seaweeds. The contents of the bottles were continuously mixed by bars turned by water-driven magnetic stirrers. Measurements of dissolved oxygen were made at hourly intervals from sunrise to sunset.

Chlorophyll *a* was extracted from fresh tissue by breaking the tissue in 90% acetone in a chilled Ten Broeck hand tissue homogenizer in the presence of trace quantities of $MgCO_3$. The homogenate was then allowed to extract at –5 °C for 30 min. Following centrifugation, the pellet was extracted again in order to release any residual pigment. The chlorophyll *a* concentration was calculated from the equations of Jeffrey and Humphrey (1975).

Thallus absorptance was determined with a calibrated Optronic Laboratories Model 740 scanning spectroradiometer system. The use of this device is described in Ramus (1978). Absorptance ($\alpha$), that fraction of incident light absorbed, was calculated as $1\text{-}I/I_0$ where $I_0$ = incident PAR and $I$ = transmitted PAR.

Growth was measured throughout the fall of 1978 in all species except *Petalonia fascia*. Two methods were employed. In the first, the plants were placed in Plexiglas "aquatubes" and suspended *in situ* from the surface at 1 m intervals. Plastic screening at each end of the tube allowed water to circulate through the tubes. The light attenuation of the water column was measured using a Licor spherical quantum sensor. After 1 week, the plants were removed, blotted, and weighed. Growth was expressed as the relative growth rate, *h*, in g week$^{-1}$ g$^{-1}$ fresh weight. Alternatively, the plants were incubated for 1 week in outdoor running seawater tanks in which light flux-density was varied using neutral-density filters. Sun plants received incident light at greater than 0.35 $I_0$, while shade plants received less than 0.18 $I_0$. Growth measurements for all species were made on at least two, and usually three, occasions.

## Results

### Effect of Light Habitat

Curves of diurnal net photosynthetic performance were produced for *Codium decorticatum* taken from high and low light (sun and shade) habitats. The medullary tissue of sun plants was filled with gas. The role of this adaptation in reflecting incident light has been demonstrated by Ramus (1978). The medulla of shade plants was not gas-filled. Integrated photosynthetic performance curves for net diurnal production (diurnal $P_n$) are shown in Fig. 1. Both sun and shade plants received 0.70 $I_0$ during the measurements. There was a marked asymmetry about the time of the sun's zenith for the curves for *C. decorticatum* from both habitats. Photosynthetic rate was maximal late in the morning and showed a decline in the afternoon, which was more pronounced for shade plants (Fig. 1). The total net diurnal production for the sun plants was almost twice that of the shade plants (Fig. 1).

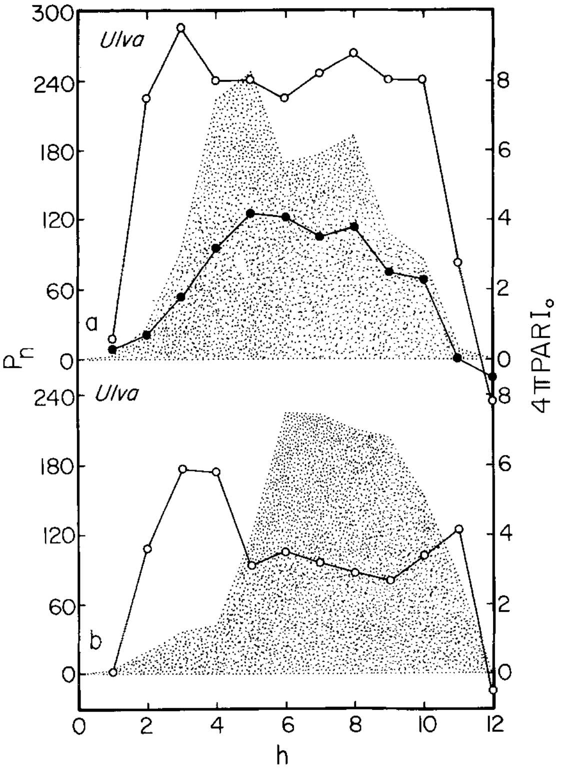

Fig. 2. *Ulva curvata.* Diurnal net photosynthetic performance ($P_n$, in moles $O_2$ evolved mole$^{-1}$ chlorophyll *a* h$^{-1}$) when (a) the maximum incident-light flux-density occurred in the morning, and (b) the maximum occurred in the afternoon. Filled circles: $P_n$ at 0.03 $I_0$; open circles: $P_n$ at 0.70 $I_0$. Stippled area: incident light (4π PAR $I_0$), in E m$^{-2}$ h$^{-1}$. Abscissa shows hours after sunrise (h)

Table 1. *Codium decorticatum* and *Ulva curvata.* Net diurnal photosynthesis ($P_n$), in moles $O_2$ evolved mole$^{-1}$ chlorophyll *a*. Incident diurnal photosynthetically active radiation ($I_0$), in E m$^{-2}$, is also shown

| Species | $I_0$ | $P_n$ at 0.03 $I_0$ | $P_n$ at 0.70 $I_0$ | $P_n$ ratio $\frac{0.03\,I_0}{0.70\,I_0}$ |
|---|---|---|---|---|
| *C. decorticatum* | | | | |
| Sun | 44.6 | 209.7 | 234.7 | 0.89 |
| Shade | 50.0 | 242.0 | 297.8 | 0.81 |
| *U. curvata* | | | | |
| Sun | 44.6 | 780.7 | 2307.6 | 0.34 |
| Shade | 50.0 | 1105.6 | 2582.2 | 0.43 |

Diurnal photosynthetic performance for *Dictyota dichotoma* collected from a marsh and from the intertidal also showed significant differences (Fig. 1). The light flux-density which the seaweeds had experienced in the salt marsh was considerably higher than at the intertidal site, where the plants were shaded by an adjacent sea wall and pier. The plants received 0.70 $I_0$ during the measurements.

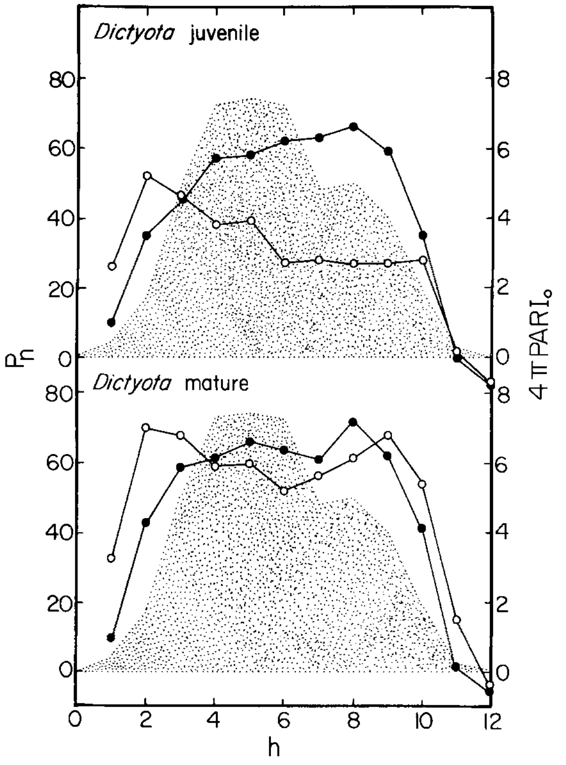

Fig. 3. *Dictyota dichotoma.* Diurnal net photosynthetic performance ($P_n$, in moles $O_2$ evolved mole $^{-1}$ chlorophyll *a* h$^{-1}$) for juvenile and mature plants. Filled circles: $P_n$ at 0.13 $I_0$; open circles: $P_n$ at 0.70 $I_0$. Diurnal $P_n$ for mature plants at 0.70 $I_0$ was 1.8 times greater than for juvenile plants. Stippled area: incident light (4π PAR $I_0$), in E m$^{-2}$ h$^{-1}$. Abscissa shows hours after sunrise (h)

The same pattern of asymmetry was again noted. Comparing *Dictyota dichotoma* from the two habitats, $P_{\max}$ was lower and the midday depression was more pronounced in the shade plants. Total net diurnal production in the shade plants was only about half that of the *D. dichotoma* collected from the salt marsh (Fig. 1).

## Effect of Thallus Architecture

Although *Codium decorticatum* and *Ulva curvata* are both in the Chlorophyta and share in common a suite of antenna pigments, save siphonein and siphonoxanthin in the former, the two species differ radically in their thallus architecture (Ramus, 1978). *C. decorticatum* is a siphonous form with a branched cylindrical axis 3 to 4 mm in diameter and is optically opaque (mean absorptance = 0.98), whereas *U. curvata* consists of a sheet only two cell-layers thick and is optically translucent (mean absorptance = 0.43).

Total net diurnal photosynthesis in *Codium decorticatum* exposed to 0.03 and 0.70 $I_0$ was always considerably less than in *Ulva curvata* under the same conditions (Table 1). However, there was much less difference in the performance of *C. decorticatum* between the low

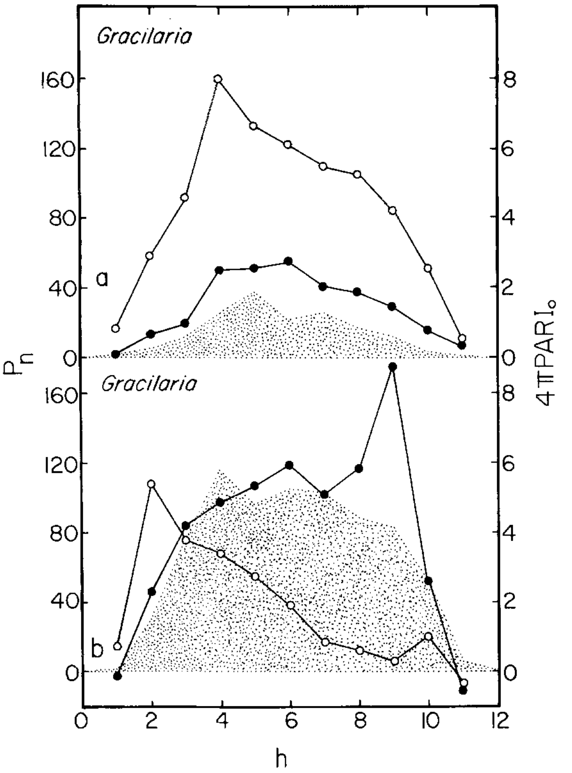

Fig. 4. *Gracilaria foliifera.* Diurnal net photosynthetic performance ($P_n$, in moles $O_2$ evolved mole$^{-1}$ chlorophyll *a* h$^{-1}$) on a day of (a) minimum insolation and (b) moderately high insolation. Filled circles: $P_n$ at 0.03 $I_0$; open circles: $P_n$ at 0.70 $I_0$. In (b), diurnal $P_n$ at 0.03 $I_0$ was 2.1 times that at 0.70 $I_0$. Stippled area: incident light ($4\pi$ PAR $I_0$), in E m$^{-2}$ h$^{-1}$. Abscissa shows hours after sunrise (h)

and high light environments than for *U. curvata*, the difference being only 11 to 19% for the former and 57 to 66% for the latter. *C. decorticatum* photosynthesis light-saturates at a lower value than *U. curvata*; further, the initial slope of *C. decorticatum* is steep whereas that of *U. curvata* is extended. It has been suggested that this is a consequence of the relative quantum capture-capacities of the two genera (Ramus, 1978).

## Effects of Temporal Pattern of Light Flux-Density

Depending on cloudiness and local weather conditions, the maximum in the curve of incident light flux-density may occur in either the morning or the afternoon, rather than at the time of the sun's zenith. This will in turn affect the pattern of diurnal net photosynthetic performance.

During a morning light flux-density maximum (Fig. 2a), a depression in oxygen exchange rate in *Ulva curvata* occurred early in the day. However, with decreased light flux-density in the afternoon, recovery from the depression was almost complete. On the other hand, when the light maximum was in the afternoon (Fig. 2b), the depression occurred much later and recovery from its effects was not as complete. This resulted in a lower total net diurnal production since, on a cloudless day, most of the total daily photosynthesis is carried out during the morning.

## Effect of Developmental Stage

The pattern of diurnal photosynthetic performance may change in the course of ontogeny. Diurnal photosynthesis was measured for both juvenile and mature plants of *Dictyota dichotoma* taken from the same light habitat (Fig. 3) at both 0.13 and 0.70 $I_0$. A midday depression occurred in both developmental stages at 0.70 $I_0$. However, while the mature plants recovered in the afternoon, the juvenile plants did not. This enhanced recovery in the mature plants, together with their somewhat higher $P_{max}$, resulted in a total net diurnal production that was almost twice as high as that of the juvenile plants. Plants maintained at 0.13 $I_0$ showed no indication of depressed oxygen exchange rates, and little difference was evident at this light flux-density between the net diurnal performance of juvenile and mature plants.

## Effect of Total Diurnal Light Flux-Density

The light flux-density to which a seaweed has previously been exposed can affect the subsequent time-course of photosynthetic adaptation. This is shown in the curves of diurnal photosynthetic performance for *Gracilaria foliifera* maintained at 0.03 and 0.70 $I_0$. In the plants exposed to high light flux-density, 0.70 $I_0$ (Fig. 4b), a depression in oxygen exchange rate occurred early in the day and recovery was very poor. On the other hand, at 0.03 $I_0$, light saturation did not occur and the $P_{max}$ was 1.6 times higher than at 0.70 $I_0$ (Fig. 4b).

This suggests that, in *Gracilaria foliifera*, adaptation to low light flux-density can occur on a time scale of half a day. The diurnal pattern that results is very different, since the photosynthetic peak at 0.03 $I_0$ occurs in the mid-afternoon. This marked asymmetry in the photosynthetic curves for *G. foliifera* occurred even though the supply of incident light was symmetrical about midday (Fig. 4b). Surprisingly, total net diurnal production at 0.03 $I_0$ was actually over two times higher than at 0.70 $I_0$! *G. foliifera*, the most light-sensitive of the species studied, experienced an oxygen exchange rate depression even on days of minimal insolation (Fig. 4a).

## Interspecific Comparisons

Values of total net diurnal production measured at 0.03, 0.13, and 0.70 $I_0$ are given for the 5 experimental species in Table 2. Since total daily irradiance varied (from 7.8 to 50 E m$^{-2}$) on the dates of the experiments, it is not possible to establish a simultaneous comparison of the photosynthetic performances of all 5 species. Neverthe-

**Table 2.** Summary data of net diurnal photosynthesis ($P_n$, in moles $O_2$ evolved $\text{mole}^{-1}$ chlorophyll *a*) for all seaweed species examined, arranged in order of increasing thallus absorptance. Incident diurnal photosynthetically active radiation ($I_0$) is in E $m^{-2}$. Each line represents diurnal performance of an individual on a particular day. Dashes indicate no data

| Species and (mean absorptance[a]) | $I_0$ | $P_n$ at $0.03\,I_0$ | $P_n$ at $0.13\,I_0$ | $P_n$ at $0.70\,I_0$ |
|---|---|---|---|---|
| *Ulva curvata* (0.43) | | | | |
| Sun | 44.0 | – | – | 1210.4 |
| Sun | 44.6 | 780.7 | – | 2307.6 |
| Shade | 50.0 | 1105.6 | – | 2582.2 |
| Shade | 37.8 | 524.2 | – | 878.6 |
| *Petalonia fascia* (0.54) | | | | |
| Juvenile | 7.8 | 217.3 | – | 827.9 |
| Mature | 7.9 | 151.8 | – | 691.4 |
| *Dictyota dichotoma* (0.72) | | | | |
| Sun | 49.4 | – | – | 1018.0 |
| Shade | 49.4 | – | – | 518.9 |
| Juvenile | 44.8 | | 491.5 | 331.9 |
| Mature | 44.8 | – | 540.1 | 595.8 |
| *Gracilaria foliifera* (0.84) | | | | |
| Shade | 37.8 | 885.1 | – | 429.9 |
| Sun | 7.8 | 275.2 | – | 894.3 |
| Shade | 7.8 | 321.1 | – | 935.1 |
| *Codium decorticatum* (0.98) | | | | |
| Sun | 44.0 | – | – | 348.4 |
| Shade | 44.0 | – | – | 188.4 |
| Sun | 44.6 | 209.7 | – | 234.7 |
| Shade | 50.0 | 121.0 | – | 148.9 |

[a]Absorptance = that fraction of incident light absorbed, calculated as $1\text{-}I/I_0$, where $I_0$ = incident PAR and $I$ = transmitted PAR

**Table 3.** Summary of growth data for 4 of the species of seaweeds studied. *h* is relative growth rate expressed as g $\text{week}^{-1}$ $g^{-1}$ fresh weight ± σ

| Species | *n* | *h* | | |
|---|---|---|---|---|
| | | Shade | Sun | Shade:Sun |
| *Codium decorticatum* | 12 | 0.331 ± 0.066 | 0.379 ± 0.126 | 0.87 |
| *Dictyota dichotoma* | 12 | 0.164 ± 0.145 | 0.508 ± 0.255 | 0.32 |
| *Ulva curvata* | 23 | 0.151 ± 0.086 | 0.971 ± 0.580 | 0.16 |
| *Gracilaria foliifera* | 23 | 0.065 ± 0.029 | 0.249 ± 0.091 | 0.26 |

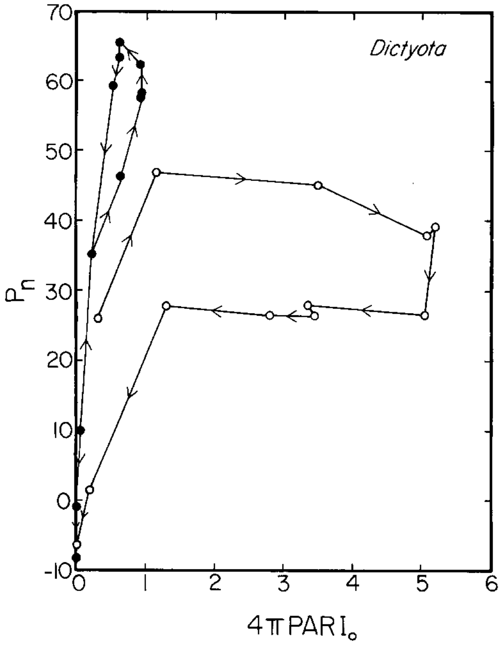

Fig. 5. *Dictyota dichotoma.* $P_n$ versus $I_0$ curve for juveniles, replotted from data of Fig. 3. Filled circles: $P_n$ at 0.13 $I_0$; open circles: $P_n$ at 0.70 $I_0$. Sequence of measurements of photosynthetic rate at succeeding hourly intervals from sunrise to sunset on the day of the experiment is indicated by arrowheads. Net photosynthesis ($P_n$) is in moles $O_2$ evolved $\text{mole}^{-1}$ chlorophyll *a* $h^{-1}$, and incident light (4π PAR $I_0$) is in E $m^{-2}$ $h^{-1}$

less, there are indications that net diurnal photosynthesis is greater in *Ulva curvata, Gracilaria foliifera* and *Petalonia fascia* than it is in *Codium decorticatum* and *Dictyota dichotoma.* Diurnal $P_n$ at 0.70 $I_0$ ranged from 149 moles $O_2$ evolved $\text{mole}^{-1}$ chlorophyll *a* in *C. decorticatum* to 2582 moles $O_2$ evolved $\text{mole}^{-1}$ chlorophyll *a* in *U. curvata* (Table 2). There does not appear to be any correlation between taxonomic division and diurnal photosynthetic performance at different light flux-densities. This is not surprising in view of the ubiquitous occurrence of all three divisions at all depths above the compensation point (Crossett *et al.*, 1965).

If growth were simply equal to net photosynthesis integrated over time, then we would expect the growth data (Table 3) to show the same ordering. This was not the case. At high light flux-density, the growth rates in *Dictyota dichotoma* and *Ulva curvata* exceeded those in the optically more opaque *Codium decorticatum* and *Gracilaria foliifera.* At low light flux-density, on the other hand, the growth rate of *C. decorticatum* was highest (0.87 times the growth rate in sun plants). This is another reflection of *C. decorticatum's* extraordinary light-trapping ability. Growth rates in sun plants ranged from 0.249 g $\text{week}^{-1}$ $g^{-1}$ fresh weight in *G. foliifera* to 0.971 g $\text{week}^{-1}g^{-1}$ in *U. curvata* (Table 3).

## $P_n$-$I_0$ Curves from Diurnal Photosynthesis Data

There is an analogy between the way in which $P_n$-$I_0$ curves are determined in the laboratory and the daily course of changes in light flux-density. The photosynthetic performance curves of Figs. 1–4 can be replotted as curves of $P_n$ versus $I_0$ using the daily light flux-density records. An example of such a plot is shown in Fig. 5, using the data from Fig. 3 (juveniles).

Each curve of photosynthetic performance at 0.03 and 0.70 $I_0$ will yield two $P_n$-$I_0$ curves: one for the increasing light flux-density preceding local noon and one for the decrease which follows. It should be borne in mind that these plots are not classic $P_n$-$I_o$ curves of the type customarily generated in the laboratory. Nevertheless, we expect that if the assumption of constant $P_{max}$ and initial slope (for a particular day) is justified, then these two curves should be more or less congruent at either low (0.03 $I_o$) or high (0.70 $I_o$) light flux-density. That this is usually far from being the case indicates that, during the day, the values of these two parameters are subject to change.

The ranges for $P_{max}$ and initial slope in the 5 species of seaweeds used in our experiments are subject to similar degrees of variance. In $P_n$-$I_o$ curves, such as Fig. 5, the depression in the oxygen exchange rate is reflected in the downward deflection of the upper curve before the light flux-density reaches a maximum. Recovery is shown by the upward deflection which just precedes the general decrease in light flux-density approaching sunset. The position of the morning $P_n$-$I_o$ curve with respect to the afternoon curve reflects the asymmetry of the original curve of diurnal photosynthetic performance.

## Discussion

In general, the observed pattern of diurnal photosynthetic performance on moderately bright days is asymmetrical for *Codium decorticatum, Dictyota dichotoma, Ulva curvata, Gracilaria foliifera* and *Petalonia fascia.* There is a morning maximum, followed by an afternoon depression, with a late afternoon recovery. This is the same pattern which is found in phytoplankton populations (Vollenweider and Nauwerck, 1961; Harris and Lott, 1973; Jassby, 1978; Marra, 1978).

We have observed what is commonly interpreted as photoinhibition of seaweed photosynthesis both in instantaneous laboratory and *in situ* measurements (Ramus *et al.*, 1976). The afternoon depression in oxygen exchange rates may be due to a number of factors, including photoinhibition, photorespiration, a circadian periodicity in photosynthetic capacity and an increase in "dark" respiration. The consensus of plant physiologists who participated in the Great Barrier Reef Photorespiration Expedition was that "photorespiratory metabolism via the glycollate pathway is a significant component of photosynthetic carbon flux in marine plants of tropical waters under natural conditions" (Tolbert and Osmond, 1976). Circadian rhythms of chloroplast orientation and photosynthetic capacity have been documented for seaweeds (Vanden Driessche, 1966; Britz and Briggs, 1976). Finally, Jassby (1978) has suggested that the afternoon depression in oxygen exchange rates may be due to a build-up of photosynthates, thus stimulating "dark" respiration. The late-afternoon recovery which we observed in our experiments indicates that the depression is transient and reversible, whatever its biochemical or physiological basis.

On cloudy days, when light saturation does not occur, the curve of diurnal photosynthetic performance approaches symmetry about the time of the sun's zenith. Surprisingly, as has been shown in the case of *Gracilaria foliifera,* such seemingly adverse conditions ($I = 0.03\, I_o$) may yield a total net diurnal production even higher than that measured on sunny days.

It is interesting to note that the incident-light flux-density at which saturation occurs is less than 1 E $m^{-2}$ $h^{-1}$ for all 5 species used in our experiments. Yet, all of these seaweeds commonly occur where $I_o$ typically reaches 8 E $m^{-2}$ $h^{-1}$. Therefore, in most intertidal habitats, the afternoon depression in net photosynthesis must occur, since $I_k$ is estimated to be less than 0.1 $I_o$ for all of the species examined.

The asymmetry in the pattern of diurnal photosynthesis leads to the conclusion that is not possible to predict daily production by selecting a particular time period in the day over which to measure productivity, as Vollenweider (1965) has suggested. For the mathematical formulations of this problem, it would be more appropriate to use averaged $P$-$I_o$ curves rather than the instantaneous curves determined in the laboratory. Even so, it would still be necessary to account for seasonal variations in the photosynthetic parameters $P_{max}$ and the initial slope.

Our results generally support the conclusions of Platt and Jassby (1976) and MacCaull and Platt (1977), who have called attention to seasonal and circadian variations in $P_{max}$ and the initial slope. Variation in $P_{max}$ has long been associated with the dark reactions of photosynthesis (Yentsch and Lee, 1966). The initial slope was originally thought to be less variable (Bannister, 1974), since it reflected the quantum yield (moles C fixed per mole of quanta absorbed) of the light reactions. We did not measure quantum yield *in situ,* i.e., we did not continuously monitor absorptance in the field–it is seldom done due to the technical difficulties involved. However, our measurements show that the absorptance of an individual seaweed does not change significantly in the course of a solar day. Therefore, photosynthesis at light flux-density less than $I_k$ is proportional to the initial slope (quantum yield). We conclude that initial slope is variable in the seaweeds tested, primarily as a function of the duration of light flux-density at or above $I_k$ (see for example Fig. 5). Moreover, as Platt *et al.* (1977) have pointed out, even if the initial slope did depend solely on quantum yield, the variable metabolic demands made on photosynthetically-produced adenosine triphosphate could still result in a variable quantum yield under natural conditions.

There are many difficulties in designing an empirically accurate equation for the prediction of gross daily photosynthesis. The mathematical descriptions of photoinhibition, circadian periodicity in photosynthetic capacity, and physiological adaptation all present special problems of their own. In the absence of complete understanding at the biochemical level, empirically-derived fitting parameters devoid of biological meaning have served to plug the gaps in the equations. Jassby (1978) has crystallized the current malaise. "It is impossible," he concludes, "to derive the diel pattern of photosynthesis from an (instantaneous) light saturation curve . . . There is no substitute for direct measurement (of this pattern)".

This is particularly distressing to the physiologist, but it need not be so for the production ecologist. For example, Platt *et al.* (1977) have proposed fitting different simple mathematical functions to the different regions of the $P$-$I_0$ curve, with the principal criterion being closeness of fit to experimental data rather than physiological fidelity. This type of approach has been successfully applied to calculating the daily production of the brown seaweeds *Ascophyllum nodosum* and *Fucus vesiculosus* (Brinkhuis, 1977). In general, seaweeds lend themselves nicely to the testing of production models since, unlike phytoplankton, they grow attached to the substratum and usually occur in a discrete light habitat.

Total net diurnal production, as reported herein, is a much more satisfactory measure of photosynthetic performance than net production measured in an interval of several hours around midday (e.g. Littler and Murray, 1974). Based solely on this data, however, it is not possible to establish a hierarchy of competitive dominance. This depends on the ability of the competing seaweeds to occupy limited primary space (Ramus, 1978) which is, in turn, a function of their growth rates and strategies (i.e., timing of growth). The relationship between daily net production and growth, which can both be measured directly on the same time scale, is thus a matter deserving of the attention of seaweed ecologists.

*Acknowledgements.* This research was supported by National Science Foundation Grants OCE 18698 (to J.R.) and OCE 77-27130 (to G.R.) from the Biological Oceanography Program.

## Literature Cited

Baly, E. C. C.: The kinetics of photosynthesis. Proc. R. Soc. (Ser. B) *117*, 218-239 (1935)

Bannister, T. T.: Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnol. Oceanogr. *19*, 1-12 (1974)

Blackman, F. F.: Optima and limiting factors. Ann. Bot. Lond. *19*, 281-295 (1905)

Brinkhuis, B. H.: Comparisons of salt-marsh fucoid production estimated from three different indices. J. Phycol. *13*, 328-335 (1977)

Britz, S. J. and W. R. Briggs: Circadian rhythms of chloroplast orientation and photosynthetic capacity in *Ulva*. Pl. Physiol., Baltimore *58*, 22-27 (1976)

Crossett, R. N., E. A. Drew and A. W. D. Larkum: Chromatic adaptation in benthic marine algae. Nature, Lond. *207*, 547-548 (1965)

Doty, M. S. and M. Oguri: Evidence for a photosynthetic daily periodicity. Limnol. Oceanogr. *2*, 37–40 (1957)

Fee, E. J.: A numerical model for the estimation of photosynthetic production, integrated over time and depth, in natural waters. Limnol. Oceanogr. *14*, 906-911 (1969)

Harris, G. P.: Diel and annual cycles of net plankton photosynthesis in Lake Ontario. J. Fish. Res. Bd Can. *30*, 1779-1787 (1973)

Harris, G. P.: and J. N. A. Lott: Light intensity and photosynthetic rates in phytoplankton. J. Fish. Res. Bd Can. *30*, 1771-1778 (1973)

Hatcher, B. G., A. R. O. Chapman, and K. H. Mann: An annual carbon budget for the kelp *Laminaria longicruris*. Mar. Biol. *44*, 85-96 (1977)

Jassby, A. D.: Polarographic measurements of photosynthesis and respiration. *In*: Handbook of phycological methods: physiological and biochemical methods, pp 285-296. Ed. by J. A. Hellebust and J. S. Craigie. London: Cambridge University Press 1978

Jassby, A. D. and T. Platt. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. *21*, 540-547 (1976)

Jeffrey, S. W. and G. F. Humphrey: New spectrophotometric equations for determining chlorophylls *a*, *b*, $c_1$, and $c_2$, in higher plants, algae, and natural phytoplankton. Biochem. Physiol. Pfl. *167*, 191-194 (1975)

Kanwisher, J. W.: Photosynthesis and respiration in some seaweeds. *In*: Some contemporary studies in marine science, pp 407–420. Ed. by H. Barnes. London: Allen & Unwin 1966

Kremer, J. N. and S. W. Nixon: A coastal marine ecosystem. simulation and analysis, 217 pp. Berlin: Springer-Verlag 1978

Littler, M. M. and S. N. Murray: The primary productivity of marine macrophytes from a rocky intertidal community. Mar. Biol. *27*, 131-135 (1974)

MacCaull, W. A. and T. Platt: Diel variations in the photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. *22*, 723-731 (1977)

Marra, J.: Effect of short-term variations in light intensity on photosynthesis of a marine phytoplankter: a laboratory simulation study. Mar. Biol. *46*, 191-202 (1978)

Parker, R. A.: Empirical functions relating metabolic processes in aquatic systems to environmental variables. J. Fish. Res. Bd Can. *31*, 1550-1552 (1974)

Parsons, T. R., M. Takahashi and B. Hargrave: Biological oceanographic processes, 2nd ed. 332 pp. Oxford: Pergamon Press 1977

Platt, T., K. L. Denman and A. D. Jassby: Modeling the productivity of phytoplankton. *In*: The sea, Vol. 6. pp 807-856. Ed. by E. D. Goldberg. New York: John Wiley & Sons 1977

Platt, T. and A. D. Jassby: The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. *12*, 421–430 (1976)

Ramus, J.. Seaweed anatomy and photosynthetic performance: the ecological significance of light guides, heterogeneous absorption, and multiple scatter. J. Phycol. *14*, 352-362 (1978)

Ramus, J., S. I. Beale and D. Mauzerall: Correlation of changes in pigment content with photosynthetic capacity of seaweeds as a function of water depth. Mar. Biol. *37*, 231-238 (1976)

Smith, E. L.: Photosynthesis in relation to light and carbon dioxide. Proc. natn. Acad. Sci. U.S.A. *22*, 504-511 (1936)

Sournia, A.: Circadian periodicities in natural populations of marine phytoplankton. Adv. mar. Biol. *12*, 325-389 (1974)

Steele, J. H.: Environmental control of photosynthesis in the sea. Limnol. Oceanogr. *7*, 137-150 (1962)

Tolbert, N. E. and C. B. Osmond: The Great Barrier Reef Photorespiration Expedition: introduction. Aust. J. Pl. Physiol. *3*, 1-8 (1976)

Vanden Driessche, T.: Circadian rhythms in *Acetabularia:* photosynthetic capacity and chloroplast shape. Expl Cell Res. *42*, 18-36 (1966)

Vollenweider, R. A.: Calculation models of photosynthesis-depth curves and some implications regarding day rate estimates in primary production measurements. *In*: Primary productivity in aquatic environments, pp 425–457. Ed. by C. R. Goldman. Berkeley: University of California Press 1965

Vollenweider, R. A. and A. Nauwerck: Some observations on the $^{14}C$ method for measuring primary production. Verh. int. Verein. theor. angew. Limnol. *14*, 134-139 (1961)

Yentsch, C. S. and R. W. Lee: A study of photosynthetic light reactions and a new interpretation of sun and shade phytoplankton. J. mar. Res. *24*, 319-337 (1966)

Date of final manuscript acceptance: January 18, 1980.
Communicated by I. Morris, West Boothbay Harbor