Marine Biology 44, 85-96 (1977)

MARINE BIOLOGY

An Annual Carbon Budget for the Kelp *Laminaria longicruris*

B.G. Hatcher, A.R.O. Chapman and K.H. Mann

Department of Biology, Dalhousie University; Halifax, Nova Scotia, Canada

Abstract

Oxygen evolution and uptake by whole thalli of the large marine alga *Laminaria longicruris* de la Pylaie were measured for 24 h, once every 2 weeks for a year, using large chambers to incubate the plants on the sea bed. Diel rates of photosynthesis and respiration were calculated from these measurements and continuous light measurements were used to extrapolate the data between observation dates. The resulting estimates were combined with measurements of growth and carbon content to give an annual carbon budget for a typical mature plant. Annual net assimilation was 6.8 mgC per cm^2 of frond surface (71 cal cm^{-2}). Approximately 45% of this appeared in the production of new frond tissue, and a further 12% was accounted for by storage of carbon in mature frond tissue. About 8% was needed for stipe growth, and the remaining 35% was assumed to be lost as dissolved organic carbon. Diel net photosynthetic rates reached a maximum in June and July and were negative only in November, indicating an ability to produce a photosynthetic surplus throughout winter. In early winter the plants drew on stored reserves to supplement photosynthesis in providing carbon for growth, but from January onwards photosynthesis provided more than enough carbon for growth.

Introduction

Large marine algae in temperate waters often exhibit periods of rapid growth in winter and early spring, when both light and temperature are at low levels. Paradoxically, they grow less rapidly in summer. The phenomenon has been documented in *Desmarestia aculeata* (Chapman and Burrows, 1971), sublittoral fucoids (Suto, 1951) as well as in the laminarians studied by Black (1950), Lüning (1971), Mann (1972), and Lüning *et al.* (1973). Lüning and his co-workers showed for *Laminaria hyperborea* that carbon was stored in summer and was translocated to the meristematic region to provide materials and energy for late winter growth. There was little or no photosynthetic surplus in winter.

Laminaria longicruris in Nova Scotia shows uninterrupted growth throughout the winter, and tissue present in summer is pushed to the tip of the blade and eroded during the winter. Hence, the opportunities for storage and translocation seem more limited.

This study was designed to find out whether *Laminaria longicruris* has a photosynthetic surplus in winter, and to relate annual patterns of photosynthesis and growth to environmental conditions.

Materials and Methods

Field Measurements on Plants

For reasons given in Hatcher (1977), the principal measurements of photosynthesis and respiration were made on whole plants, using specially designed large incubation chambers on the sea floor. The apparatus (Hatcher, 1977) consisted of a transparent and an opaque chamber, each 30 cm diameter x 110 cm high, and fitted with mechanisms for (i) passing the water through 0.45 µm filters to remove phytoplankton and most bacteria, (ii) removing bubbles, (iii) stirring to break down diffusion gradients at the plant surface, (iv) reducing the oxygen tension prior to incubation, to prevent supersaturation and (v) removing water samples during incubation.

Measurements of diel net photosynthesis and respiration were made once every 2 weeks for a year, starting May 1, 1975. On each day, 3 to 5 consecutive incubations totalling 24 h were carried out in both the light and the dark chamber. In order to minimize the effects of nutrient limitation or possible bacterial activity, no incubation exceeded 6 h during the day and 12 h during the night. Initial and final water samples from each incubation were brought to the surface by divers and fixed for later analysis of dissolved oxygen by the Winkler method (Strickland and Parsons, 1972). The diel net photosynthetic rates thus measured were extrapolated to 1 week before and 1 week after that date by reference to continuously measured, *in situ* light levels. In this way, diel net photosynthesis was estimated for every day of the study year.

The site of the experiments was a moderately exposed kelp bed at Fox Point, on the western shore of St. Margaret's Bay, Nova Scotia, Canada, situated about 100 m from shore and 10 m deep. Specimens of *Laminaria longicruris* de la Pylaie used for the experiments were tagged where they grew, within a radius of 10 m of the incubation site. As needed, two plants were freed from the substrate and placed in the incubation chambers. When not in use they were anchored to lead weights by means of surgical tubing. In the course of the year, a total of 8 plants was used. At no time were experimental plants brought to the surface or removed from the water.

On each day of field measurements the apparent frond area of each incubated plant was measured under water by placing it between two flat sheets of Plexiglas and determining its length, and the width at 5 cm intervals along the longitudinal axis, using a measuring grid painted on the plastic. The apparent area was calculated by multiplying the mean blade width by the length. It was then corrected to "true" area as follows: when no longer needed, each of the experimental plants was measured in the field as described, and was then taken to the laboratory and cut into small regular pieces which could be pressed flat and measured without any folds or creases. When summed, the resulting value for surface area was considerably greater than the apparent area measured in the field. The ratio between the two was used as a conversion factor in all subsequent calculations involving that plant. This technique is considered valid because no single plant was used for a period of sufficient length that its morphology could change significantly between the first and last measurements. The ratio of thin peripheral tissue to central blade tissue was also obtained from measurements at this stage.

The elongation of the tagged plants was monitored every 2 weeks as in Parke (1948) by measuring the advancement of 1 cm diameter holes punched in the blades 10 cm above the junction of stipe to blade. The increase in length was multiplied by the mean blade width and the appropriate surface area correction factor to yield the total increase in surface area during a given period of time. In order to compare growth between different plants, the increase in area was expressed as a percentage of the mean total frond area between measuring dates: this is referred to as the normalized growth rate. Note that only one side of a frond was used in the comparisons, even though both sides are photosynthetically active. Table 1 is a sample of the growth measurements and calculated growth rates obtained for a representative plant. Values for other plants used in the study were calculated in the same way.

Measurement of Light and Temperature

The *in situ* quantum irradiance between 400 and 700 nm was monitored continuously during the study year by a recording quanta meter installed on the sea bed (Chapman *et al.*, 1976). Reliable data were obtained for 245 of the 366 days, with interruptions never exceeding 15 days. Light levels at or below the plant's photosynthetic saturation value were integrated to yield daily quantum irradiance in $\mu E\ m^{-2}$. A Ryan model 12 recording thermograph was used to monitor *in situ* temperature continuously during the study period.

Extrapolation of Field Measurements of Photosynthesis

The photosynthetic production of kelp in the sea was estimated by extrapolation, using the recorded *in situ* light data in the following formula:

$$P_{Ni} = \left(P_{Gf} \frac{Q_i}{Q_f}\right) - R_f,$$

where: P_{Ni} is the diel net photosynthetic rate on Day i, P_{Gf} is the calculated diel gross photosynthetic rate determined on the day of field measurements, Q_i is the measured *in situ* quantum irradiance up to the saturation value determined on Day i, Q_f is the *in situ* quantum irradiance up to saturation value determined on the

Table 1. *Laminaria longicruris*. Growth of experimental plant no. 1. Asterisk indicates that a new hole was punched

Measurement date (1975)	Mean frond area (cm^2)	Position of hole (cm)	Distance hole moved (cm)	Mean frond width (cm)	Surface area correction factor	Net production of new tissue: Total for period (cm^2)	Net production of new tissue: Daily rate (cm^2 day^{-1})	Normalized daily rate (% increase)
May 1		10*		27.0	1.55			
May 14	4550	18	8	28.0	1.55	347	25	0.55
May 28	5100	31	13	29.0	1.55	584	42	0.82
June 11	4950	44	13	26.0	1.55	523	37	0.76
June 25	4550	54	10	24.0	1.55	372	27	0.58
July 9	4320	65	11	24.0	1.55	409	29	0.68
July 23	4000	71	6	24.0	1.55	223	16	0.40
Aug. 6	3760	77 10*	6	24.0	1.55	223	16	0.42
Aug. 20	3710	14	4	24.5	1.55	151	11	0.29
Sept. 4	3470	20	6	24.0	1.55	223	15	0.43
Sept. 18	3160	24	4	23.0	1.55	142	10	0.32
Oct. 2	2880	26	2	23.5	1.55	72	5	0.18

day of field measurements, and R_f is the diel respiration rate measured on the day of field measurements. The extrapolation is based on the observation that gross photosynthesis is proportional to light intensity below saturation for the plant. Gross photosynthesis was estimated by summing the diel net photosynthesis and respiration for each day of field measurements. Saturating light values were determined in the laboratory. In the field, allowance was made for 18% light attenuation across the incubation chamber wall.

For days on which the light meter was non-functional (33% of the experimental year), *in situ* light levels were estimated by calculating for each month of the year the linear regression of daily light recorded *in situ* on daily hours of bright sunshine recorded at a nearby (3 km) weather station.

Carbon Analyses

Once a month, 5 representative plants were taken from the study site for analysis of organic carbon content. Five grams (fresh weight) of tissue was cut from the central blade tissue and 5 g from the thin peripheral tissue just above the meristematic region of each plant. These tissue fragments were boiled three times in 80% ethanol and a subsample of the ethanol-soluble fraction was then analysed spectrophotometrically for mannitol (the primary storage product) using the periodate method of Lambert and Neish (1950). The remainder of the ethanol-soluble fraction was evaporated and the weight of the residue was used in conjunction with the alcohol-extracted dry weight to obtain the dry weight of each sample. The ethanol-insoluble fraction was dried by means of two extractions in 100% ethanol, two extractions in ether and then placed *in vacuo* over P_2O_5. This dried tissue was then ground and triplicate subsamples were analysed in a Hewlett Packard model 185-b CHN analyzer to determine the percentage of carbon present. The carbon measured at this stage is assumed to be predominantly laminaran (a storage product), alginate, and cellulose (structural carbon). A detailed analysis of the seasonal variation of these substances throughout the whole plant is presented elsewhere (Chapman and Craigie, 1977). On each day of field measurements two representative plants were collected near the station and 13.65 cm^2 strips of tissue were cut from the same areas of the plant as used for the carbon analysis. These were taken to the laboratory and dried at 105°C for 24 h to determine the dry weight per unit surface area for each tissue type throughout the experimental year.

The mean diel net production of frond tissue in terms of carbon is calculated for two representative field measurement days in Table 2. The carbon content per unit dry weight of the newly produced peripheral and central tissue was obtained by summing the two carbon measurements done on the monthly tissue samples. Applying the surface area to dry weight ratio derived from the 13.65 cm^{-2} tissue samples collected on each field measurement day yielded the total carbon content per unit surface area for each tissue type. The weighted

Table 2. *Laminaria longicruris*. Sample calculation of carbon content of new frond tissue produced. Measurements in Columns 4 to 9 made on 2 plants on each occasion

Extrapolation period	Mean carbon content: Peripheral tissue (P) (μgC cm^{-2})	Mean carbon content: Central tissue (C) (μgC cm^{-2})	Ratio P:C	Weighed carbon content (μgC cm^{-2})	Surface area increment ($cm^{-2}day^{-1}$)	Carbon increment during period (mg)	Average frond area during period (cm^2)	Diel increment in carbon content per cm^2 total frond area (μgC $cm^{-2}day^{-1}$)	Net production of tissue-carbon: average of 2 plants in period (μgC $cm^{-2}day^{-1}$)
May 1-7[a]	869	578	2.32	781	25	19	4400	4.4	
			2.13	776	20	16	4300	3.7	4.3
Oct.10-23[b]	3201	1153	3.00	2689	14	37	1890	19.6	
			2.52	2619	12	32	2210	14.4	17.0

[a]First week of measurements. Extrapolated to 1 week after field measurements, but not week before.
[b]Extrapolated to 1 week before and 1 week after day of field measurements.

average of these was then calculated using the ratio of peripheral to central tissue applicable to the particular experimental plant. The resulting value represents the average carbon content per cm^2 of new tissue produced during each 2 week period. When multiplied by the appropriate daily surface area increment, the 24 h increment in carbon between sampling dates was obtained for each plant. The value was then divided by the average surface area of the plant during that 2 week period. The average of the 2 values obtained on each sample date was multiplied by the number of days in the extrapolation period and the products summed to yield the annual net production of tissue-carbon.

Photorespiration-Type Phenomena

It was important to make a preliminary assessment of photorespiration-type phenomena, as the annual productivity calculations are based in part on estimates of gross photosynthesis. It is now agreed (Tolbert, 1974), that photorespiration is associated with a decrease in net photosynthesis in the presence of high ambient O_2 levels. To check for the occurrence of the phenomenon, experiments were conducted in collaboration with Mr. J. Robbins. The apparatus he developed was described elsewhere (Robbins, 1976). Briefly, it consists of a 3 l transparent, closed chamber situated in a controlled temperature bath on a large magnetic stirrer; the whole surrounded by 4 banks of two 20 W cool white fluorescent lamps. A Radiometer model TT2 pH probe (± 0.25% full scale) and a YSI model 54 oxygen probe (± 1.0% full scale) protrude into the chamber and the oxygen probe is connected through its meter to a Heathkit model IR-18M chart recorder (± 2.0% full scale). A moveable piston allows a 60 ml sample to be withdrawn for micro-Winkler analysis of dissolved oxygen (as in Carritt and Carpenter, 1972), and analysis of total inorganic carbon by the method of Cooke (1972) using a Beckman Infrared Analyser and an Infotronics Model CRS-230 Integrating Digital Voltmeter.

A series of six 2 h incubations were run at increasing levels of ambient oxygen concentration using small whole plants (ca. 250 cm^2) at 5°C in saturating light levels (180 μE m^{-2} sec^{-1}). Net photosynthesis was measured in terms of the flux of dissolved oxygen and inorganic carbon.

Relation between Photosynthesis and Light Intensity

Extrapolation of the photosynthesis data to 1 week before and 1 week after each day of field measurement required laboratory investigations of the relationship between photosynthesis and light intensity. These were made once a month, at two temperatures spanning the range of variation measured in the field during that month. Pieces of mature peripheral tissue measuring 50 cm^2 were cut from representative plants at the study site and acclimated in the dark for at least 12 h. The segments were placed in transparent 300 ml bottles with filtered (0.45 μm) seawater and a Teflon-coated stirring bar. The bottles were placed on magnetic stirrers in a controlled temperature room with a 500 W incandescent light source attenuated with neutral density filters. Duplicate 2 h incubations were run consecutively at increasing light levels (as measured on a Lambda Instruments Li-185 light meter) until no increase in net photosynthesis (as determined by dissolved oxygen evolution) occurred. Concurrent incubations were done in dark bottles to measure respiration and added to net photosynthesis values

to give gross photosynthetic rates. The resulting *P* versus *I* curve was based on at least 10 data points and from it the saturating light value was determined.

Results

Photorespiration-Type Phenomena

Table 3 shows the result of measuring photosynthesis in *Laminaria longicruris* by both O_2 and CO_2 methods, over a wide range of ambient oxygen concentrations. Between 2 and 108% oxygen saturation, the change in photosynthetic rate is less than 10%. This is taken to indicate that photorespiration-type phenomena are of a much lower magnitude than those reported in other algae (Warburg and Krippahl, 1960; Orth *et al.*, 1966; Brown and Tregunna, 1967; Hess *et al.*, 1967) and are thus of little significance in our calculations.

Rate of Assimilation on the Day of a Field Experiment

Changes in oxygen concentration in the opaque and transparent chambers during each experimental incubation were used to calculate the hourly rates of respiration and net photosynthesis in units of $\mu g\ O_2\ cm^{-2}$ plant surface per hour. The appropriate hourly rates were extrapolated to each segment of the day represented by one experimental incubation and summed to give the 24 h rates (Table 4).

Note that the night respiration values obtained from the transparent chamber were expressed as negative net photosynthesis. Thus, the sum of the net photosynthesis during all periods (or the difference between daily net photosynthesis and night respiration in the transparent chamber) was taken to be the diel net photosynthetic rate, i.e., the

Table 3. *Laminaria longicruris*. Measurement of net photosynthesis in laboratory under a wide range of ambient oxygen conditions. On 3 occasions results obtained by the oxygen method were checked by monitoring CO_2 changes. nd: no data

Ambient dissolved O_2		Net photosynthesis ± standard deviation		Photosynthetic quotient
ml/l	% Saturation	mol O_2 $\mu cm^{-2}h^{-1}$	mol CO_2 $\mu cm^{-2}h^{-1}$	
0.15	2.1	0.94±0.07	nd	nd
1.24	17.2	0.94±0.05	0.78±0.07	1.21
5.82	80.8	0.88±0.06	0.75±0.05	1.17
7.68	108.5	0.85±0.03	nd	nd
11.03	153.1	0.80±0.04	0.67±0.06	1.19
16.35	231.2	0.77±0.03	nd	nd

Table 4. *Laminaria longicruris*. Sample calculation of diel rates of respiration and net photosynthesis from *in situ* measurements made on May 14-15, 1975. Excess of respiration over photosynthesis in a light chamber is recorded as negative photosynthesis. Respiration rates in transparent chambers at night were used to calculate diel respiration, since plants in light chambers had a more natural photohistory. Note that Column 2 does not total 24 h on account of time needed to change water between incubations. Calculated diel gross photosynthesis, 62.2 + 63.8 = 126.0 $\mu gO_2 cm^{-2} day^{-1}$

Incubation no.	Hours of incubation	Time for which calculations made (hrs)	Chamber	Respiration		Net photosynthesis	
				Hourly rate ($\mu gO_2 cm^{-2}h^{-1}$)	Period total ($\mu gO_2 cm^{-2}$)	Hourly rate ($\mu gO_2 cm^{-2}h^{-1}$)	Period total ($\mu gO_2 cm^{-2}$)
1	4.0	16.30 - 21.00	Opaque	2.4	10.8	-	-
			Transparent	-	-	-0.3	-1.4
2	9.5	21.00 - 06.30	Opaque	1.0	-	-	-
			Transparent	0.9	8.6	-0.9	-8.6
3	4.0	06.30 - 11.00	Opaque	3.5	15.8	-	-
			Transparent	-	-	2.7	12.2
4	5.0	11.00 - 16.30	Opaque	4.9	27.0	-	-
			Transparent	-	-	11.2	61.6
Total	22.5	16.30 - 16.30		-	62.2		63.8

Table 5. *Laminaria longicruris*. Summary of temperature and light data, diel net photosynthesis, diel respiration, and diel gross photosynthesis calculations for days on which incubations were carried out in field. For method of calculating saturating light level, see text. nd: no data

Measurement date (1975-1976)	Temperature (°C)	Diel quantum irradiance below saturation (millions $\mu E\ m^{-2}day^{-1}$)	Diel net photosynthetic rate		Diel respiration ($\mu gO_2 cm^{-2}$)	Diel gross photosynthesis ($\mu gO_2 cm^{-2}$)
			In situ ($\mu gO_2 cm^{-2}$)	Laboratory ($\mu gO_2 cm^{-2}$)		
May 1-2	3.0	0.81	102	98	46	148
May 14-15	4.0	0.56	64	nd	62	126
May 28-29	8.7	0.65	137	nd	46	183
June 11-12	9.2	1.39	113	249	41	154
June 25-26	9.0	1.57	208	277	56	264
July 9-10	12.5	0.90	134	173	72	207
July 23-24	11.2	1.33	123	nd	52	175
Aug. 6-7	9.0	0.85	35	157	38	73
Aug. 20-21	11.0	1.23	150	225	44	193
Sept. 4-5	15.5	1.01	107	185	53	160
Sept. 18-19	16.0	0.92	172	172	152	324
Oct. 2-3	16.0	0.64	32	109	74	105
Oct. 16-17	13.0	0.63	41	107	71	112
Oct. 30-31	13.0	0.32	-9	26	52	43
Nov. 17-18	10.0	0.41	0	55	68	68
Nov. 27-28	9.5	0.10	-15	15	36	20
Dec. 19-20	6.5	0.37	108	32	115	224
Jan. 7-8	4.0	0.28	-8	23	40	32
Jan. 22-23	2.5	0.33	66	28	52	118
Feb. 5-6	2.0	0.24	45	19	39	84
Feb. 19-20	2.0	0.41	61	36	36	98
Mar. 4-5	2.0	0.39	15	40	26	41
Mar. 19-20	1.2	0.66	100	31	31	130
Apr. 1-2	3.0	0.34	8	42	30	38
Apr. 15-16	2.5	0.46	67	55	45	112

net surplus or deficit of energy for that 24 h period. This method of calculation does not correct for heterotrophic respiration by bacteria on the plant, which could cause an error of underestimation. Table 5 summarizes data obtained on the 25 days of field measurements.

Extrapolation from Field Measurements: The Annual Total

Daily light energy throughout the experimental year is shown in Fig. 1. These values were used to extrapolate from the rates of photosynthesis measured in the field to estimated values for 1 week before and 1 week after. The mean diel rates for each 2-week period are shown in Fig. 2. Note that the method of extrapolation involved the assumption that gross photosynthesis changes in proportion to daily light energy below saturation. Gross photosynthesis for this purpose was taken as the sum of diel net photosynthesis and respiration for each day of field measurements. It is recognized that true gross photosynthesis is almost impossible to measure, and no use is made of the values obtained, except as a step in the extrapolation of net photosynthetic values. Table 6 shows the mean diel rate for each 2-week period, and the conversion to equivalent carbon fixation. When summed for the year, net photosynthesis amounted to 19.4 mg O_2 cm^{-2} $year^{-1}$ or 6.8 mg C cm^{-2} $year^{-1}$. Using the conversion factor of 10.481 kcal = 1 gC (Mann, 1971), this is equivalent to 71 cal cm^{-2} $year^{-1}$.

Results Based on Laboratory Measurements of Photosynthesis

The experiments that were used to determine the relationship between light and gross photosynthesis (*P* versus *I*) were also used to make an independent estimate of the diel net photosynthetic rate for each day of the year. Each light recording point from the quantum irradiance meter was converted to a gross photosynthesis value from the *P* versus *I* curve for that month. Integration of these values for each day gave an estimate of daily gross photosynthesis. Subtraction of the laboratory respiration rate extrapolated to 24 h gives the diel net photosynthetic gain or loss (Fig. 2). These laboratory estimates rarely agreed with those based on field measurements using whole plants; they were usually lower. This finding supports work described in Hatcher (1977). The differences are due to (i) the use of pieces of tissue, which are usually not representative of

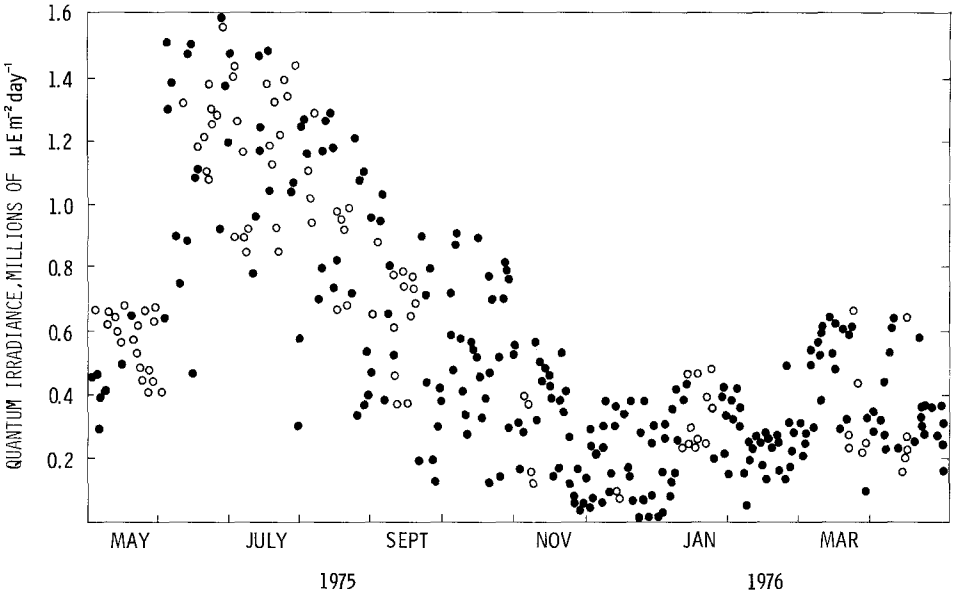

Fig. 1. Quantum irradiance below saturation level of *Laminaria longicruris*. Filled circles represent values measured at depth of 10 m at Fox Point, St. Margaret's Bay, Nova Scotia; open circles are values extrapolated from data collected at a nearby weather station

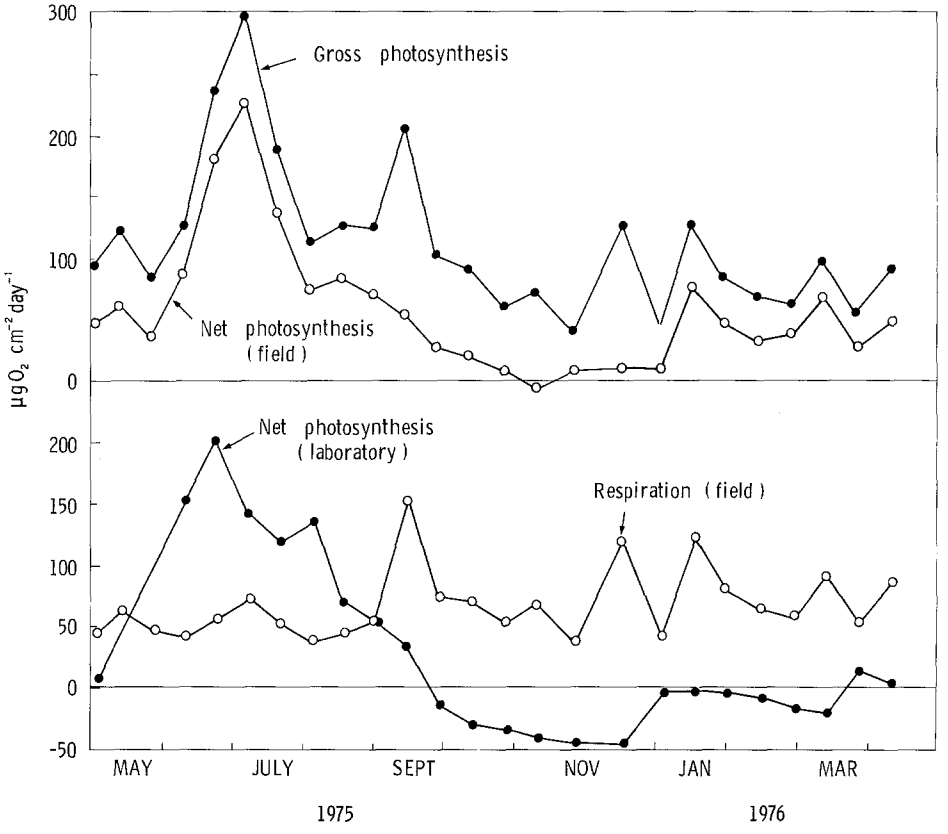

Fig. 2. *Laminaria longicruris*. Open circles: net photosynthesis and respiration measured once every 2 weeks, extrapolated to 1 week before and 1 week after, and expressed as 2-weekly averages. Filled circles: (upper) gross photosynthesis calculated as sum of net photosynthesis and respiration; (lower) 2-weekly average values of net photosynthesis based on laboratory measurements

Table 6. *Laminaria longicruris*. Data on net oxygen production extrapolated from day of measurement to 1 week before and 1 week after, and conversion to equivalent carbon assimilation. Yearly total O_2 = 19.4 mg O_2 cm^{-2}; yearly total carbon = 6.8 mgC cm^{-2}; net tissue-carbon = 3.1 mgC cm^{-2}

Period	Extrapolated net O_2 production (μgO_2 cm^{-2})	Mean diel net O_2 production (μgO_2 cm^{-2})	Photosynthetic quotient[a]	Equivalent diel net carbon assimilation (μgC cm^{-2})	Net production of tissue-carbon: average of 2 plants in period (μgC $cm^{-2}day^{-1}$)
1975					
May 1 - May 7	311	42	1.03	17	4.3
May 8 - May 21	845	60	1.33	17	6.4
May 22 - June 4	491	35	1.33	10	5.2
June 5 - June 18	1191	85	1.03	31	5.6
June 19 - July 2	2506	179	1.03	65	6.2
July 3 - July 16	3155	225	0.86	93	9.5
July 17 - July 30	1892	135	1.29	39	7.5
July 31 - Aug. 13	1000	71	1.50	17	7.5
Aug. 14 - Aug. 27	1132	81	1.11	25	11.4
Aug. 28 - Sept. 11	957	68	1.14	23	10.2
Sept. 12 - Sept. 25	717	51	1.17	17	8.3
Sept. 26 - Oct. 9	344	25	1.11	8	5.9
Oct. 10 - Oct. 23	250	18	1.04	6	17.0
Oct. 24 - Nov. 7	62	4	0.98	2	15.6
Nov. 8 - Nov. 21	-122	-9	0.91	-3	13.5
Nov. 22 - Dec. 7	55	3	1.23	1	6.8
Dec. 8 - Dec. 28	92	4	1.57	1	9.4
Dec. 29 - Jan. 14	62	4	1.05	1	6.9
1976					
Jan. 15 - Jan. 28	987	70	1.05	25	9.0
Jan. 29 - Feb. 11	568	41	0.77	18	8.8
Feb. 12 - Feb. 25	370	26	1.06	9	9.2
Feb. 26 - Mar. 11	457	30	1.04	11	8.1
Mar. 12 - Mar. 25	853	61	1.01	23	6.3
Mar. 26 - Apr. 8	266	19	0.84	8	7.0
Apr. 9 - Apr. 30	889	40	0.67	19	4.2

[a]Unpublished data supplied by Dr. A.R.O. Chapman.

the whole plant, (ii) the long period of adaptation in the dark, which may affect natural metabolic rhythms, (iii) the degree of stirring, which may differ from that in the *in situ* experiments and (iv) the extrapolation of a short-term laboratory respiration measurement to 14 days.

Growth and Carbon Content

The normalized growth rates of the experimental plants used throughout the year and the bi-monthly averages are plotted in Fig. 3. The annual pattern of growth is similar to that observed for this species by Mann (1972) and Chapman and Craigie (1977). Growth rate decreases through the summer and early fall, and increases rapidly through the winter and early spring. The annual net production of tissue-carbon based on growth and carbon content analysis was found to be 3.1 mg C cm^{-2} $year^{-1}$ (32 calories cm^{-2} $year^{-1}$) or 8 µg C cm^{-2} day^{-1} (0.09 calories cm^{-2} day^{-1}) (see Table 6, Column 6).

Annual Carbon Budget

On an annual basis, the average kelp plant showed a net assimilation of slightly more than twice as much carbon as was present in newly produced frond tissue. Much of the fixation took place in the summer months, when it far exceeded the carbon content of new growth (Fig. 4). For 3 months during the fall and winter (October-December), the carbon produced in the form of new frond tissue exceeded that which was fixed. Assimilation was negative for 1 month during the winter (November) and only slightly positive in December.

Based on this budget, the annual net production of a mature *Laminaria longicruris* of 0.42 m^2 frond area (average size of the 8 experimental plants) in 10 m of water at Fox Point is 28.5 g C $year^{-1}$ or 300 kcal $year^{-1}$. If for the purpose of comparison with other studies it is assumed that a kelp bed has 5 to 15 such plants per m^2, the annual production would be 143 to 428 g C m^{-2} $year^{-1}$ or 1,495 to 4,485 kcal m^{-2} $year^{-1}$. This is a minimum estimate as it does not ac-

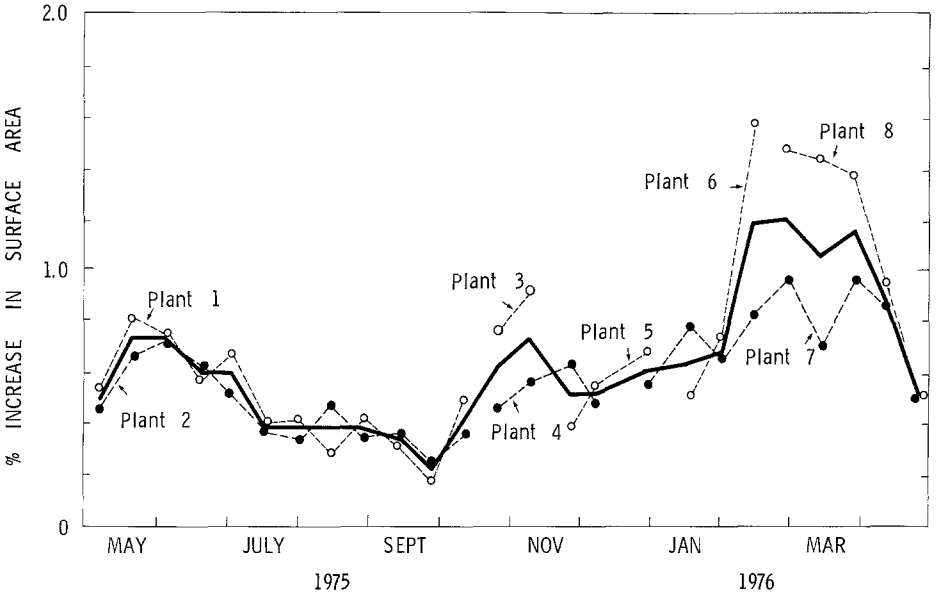

Fig. 3. *Laminaria longicruris*. Daily growth rates, averaged over 2-week periods, for 8 different plants at Fox Point, St. Margaret's Bay. Heavy line indicates the mean value

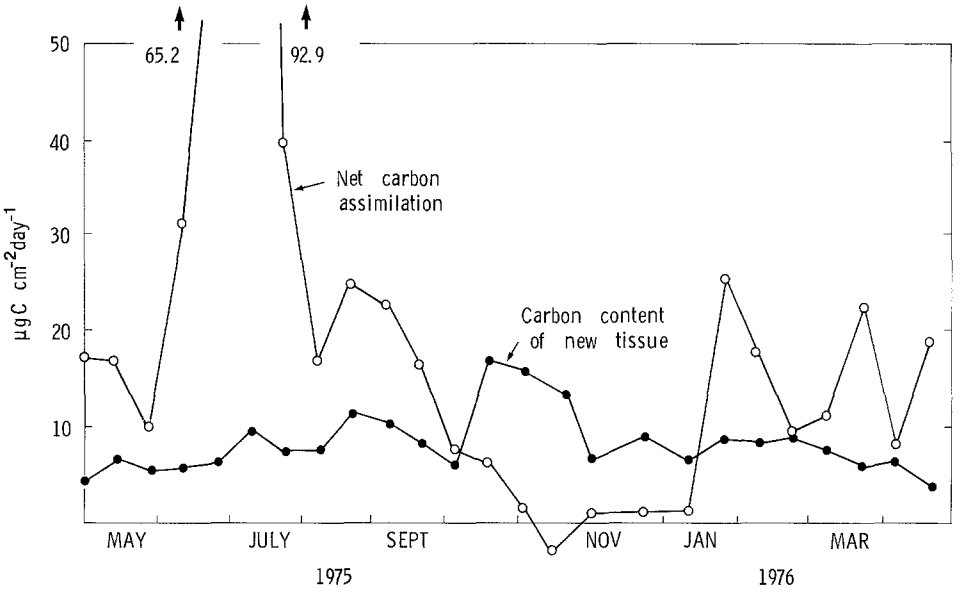

Fig. 4. *Laminaria longicruris*. Mean diel net assimilation by whole plant, and carbon content of new tissue, calculated for 2-week intervals

count for the contribution of younger, more rapidly growing plants.

Discussion

Carbon Budget

It appears that most of the carbon and energy required by *Laminaria longicruris* for winter growth is obtained by photosynthesis during that period, rather than by drawing on stored reserves. Fig. 4 shows the carbon content of new tissue to be in excess of diel net assimilation from October to early January. Note that the measurement of carbon in new tissue will include both structural carbon required for new growth and any stored carbon which is in the process of being translocated through the tissue. It is possible that, during October, photosynthesis supplies the needs for new structural carbon. From January onwards,

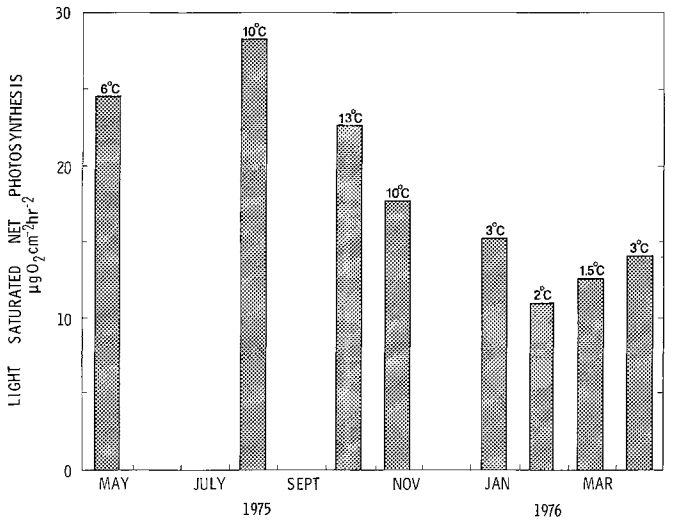

Fig. 5. *Laminaria longicruris*. Net photosynthesis determined in laboratory at saturating light levels and monthly average water temperatures in St. Margaret's Bay

Table 7. *Laminaria longicruris*. Summary of multiple-regression analysis of effect of irradiance and temperature on metabolic rates. nd: no data

Variable	% Variance accounted for by:		
	Irradiance	Temperature	Both
Diel net photosynthesis in field	61**	6 ns	63**
Diel net photosynthesis in laboratory	94**	30**	95**
Light-saturated photosynthesis	nd	56*	nd
Diel respiration	2 ns	27**	28*

** = significant, $P < 0.01$; * = significant, $P < 0.05$; ns = not significant.

photosynthesis clearly supplies the carbon needed for new tissue.

Of the 300 kcal fixed annually by an average plant of the type studied, only 135 kcal (45%) appeared in the new tissue that was routinely sampled. Chapman and Craigie (1977) analysed seasonal variation in the carbon content of other parts of the frond and showed that on average these contained 25% more carbon (primarily laminaran) than the meristematic region. This would account for another 35 kcal in a year. The remaining 130 kcal are not accounted for. Allowing 25 kcal for stipe growth (Mann, 1972; Chapman and Craigie, 1977) there is 105 kcal (35%) which we suggest may have been excreted as dissolved organic matter. In the period between May and August, assimilation far exceeds growth and storage, and we have no better suggestion to offer than the idea (Sieburth, 1969, discussed further in Moebus and Johnson, 1974) that at this time there would be copious production of dissolved organic matter. This is the time of year when light is abundant but nitrate is in very low concentrations. It seems probable that photosynthetic fixation proceeds rapidly but that lack of nutrients prevents cell division and growth.

Strategy of Growth

Chapman and Craigie (1977) have shown that *Laminaria longicruris* at our study site suffers nitrogen limitation during summer months, and that during winter months, when ambient nitrate is at high levels, it builds up internal reserves of nitrogen. At the spring bloom of phytoplankton, nitrate in sea water is reduced to low levels, and *L. longicruris* grows at a decelerating rate while using its internal reserves. During summer, it builds up carbon reserves.

It is now possible to relate the carbon budget to the nitrogen budget and reveal a seasonal strategy of growth. Rapid winter growth is an adaptation to the availability of nitrate in the sea. Growth accelerates between November and January, and reaches its peak in late winter and early spring. In the November to January period growth exceeds assimilation, the carbon reserves are drawn upon, and in fact are reduced to low levels by February (Chapman and Craigie, 1977). From February onwards, growth is sustained entirely by an assimilatory surplus.

Laminaria longicruris differs from *L. hyperborea* in that growth rates in the latter species start to increase in January, reach a maximum in April-May and are very low for the remainder of the year (Lüning, 1971; Larkum, 1972). In *L. longicruris* growth is more nearly continuous. The thallus shows no distinct annual segments and the plant exhibits a longer term of rapid growth beginning as early as October, peaking in January-February, and extending into June. These differences are related to the source of energy used for winter growth. *L. hyperborea* relies primarily on stored reserves. Even at 2.5 m depth off Helgoland, light levels are consistently below the com-

pensation point of tissue segments from October to March inclusive (Lüning, 1971). Hence growth in *L. hyperborea* is probably energy-limited at least until April. However, as can be inferred from the diel net photosynthesis curve (Fig. 2), light levels at 10 m depth in St. Margaret's Bay are below the compensation point of whole *L. longicruris* plants only in November. Hence, the alga is able to show a net assimilation throughout much of the winter and relies less on stored reserves which are not as plentiful as in *L. hyperborea*. Rather than being energy-limited, growth in *L. longicruris* would seem to be primarily nitrogen-limited.

Influence of Environmental Factors

Table 7 shows the result of a multiple-regression analysis (University of Manitoba Statistical Package Program ST 32) of diel respiration and net photosynthesis (as in Table 5) on *in situ* irradiance and temperature. The first point to note is that while light and temperature together account for 95% of the variation in diel net photosynthesis of strips incubated in the laboratory, they account for only 63% of the variation in photosynthesis in the field. As Fig. 5 shows, light-saturated net photosynthesis has markedly different values at different seasons, even when the monthly mean temperature is the same. Temperature accounts for only 56% of the variation in light-saturated photosynthesis (Table 7). A comparison of net photosynthesis measurements obtained in the field with those obtained in the laboratory (Table 5) shows that the field values are usually higher in winter and spring, but lower in summer and fall. Differing levels of nutrient availability could be a contributory factor, but it looks as if there are endogenous rhythms in photosynthetic rate, similar to those reported by Lampe (1935), Montfort (1935), Black (1950), Talling (1957) and Lüning (1971).

Diel respiration varied from 26 µg O_2 cm^{-2} at 2°C to 74 µg O_2 cm^{-2} at 16°C (Table 5). (There were two anomalous high values.) Table 7 shows that temperature accounts for only one-quarter of the variation; another important variable, not quantified, is the previous light history of the plant. In general, it appears that respiration is low in winter, high in summer, and that the low temperatures help to produce the net assimilatory surplus in the winter and spring months. These findings agree with those of Kanwisher (1966), and with Lüning's (1971) measurements calculated on the basis of frond area.

Acknowledgements. The work reported here was made possible by a team effort in support of the 24-h field studies. The authors wish to thank G. Wharton, S. Watts, B. Merdsoy, P. Wainwright, D. McRae and B. Branton for diving assistance, often under difficult conditions; J. Lindley, P. Evans, B. Hawks, A. Martin and L. Therriault for assistance on board ship, J. Robbins, S. Mayo, A. Manders and B. Emmett for use of laboratory equipment, and P. Brien for computer assistance. The work was supported by Negotiated Development Grant D-50 from the National Research Council of Canada, and an operating grant from NRC to K.H. Mann. B. Hatcher was supported by a Dalhousie Postgraduate Award. Dr. J. Craigie kindly assisted in revising the manuscript.

Literature Cited

Black, W.A.P.: Seasonal variation in weight and chemical composition of the common British Laminariaceae. J. mar. biol. Ass. U.K. *29*, 45-72 (1950)

Brown, D.L. and E.B. Tregunna: Inhibition of respiration during photosynthesis by some algae. Can. J. Bot. *45*, 1135-1143 (1967)

Carritt, D.E. and J.H. Carpenter: Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in seawater; a NASCO report. J. mar. Res. *24*, 286-312 (1972)

Chapman, A.R.O. and E.M. Burrows: Field and culture studies of *Desmarestia aculeata* (L.) Lamour. Phycologia *10*, 63-76 (1971)

- and J.S. Craigie: Seasonal growth in *Laminaria longicruris*: relations with dissolved inorganic nutrients and internal reserves of nitrogen. Mar. Biol. *40*, 197-205 (1977)

-, B. Hoyt and B.E. Paton: A self-contained instrument for logarithmic recording of submarine quantum irradiance. Mar. Biol. *38*, 91-94 (1976)

Cooke, R.: Phase phenomena in the calcite-seawater system. Brookhaven Symp. Biol. *24*, 191-203 (1972)

Hatcher, B.G.: An apparatus for measuring photosynthesis and respiration of intact large marine algae and comparison of results with those from experiments with tissue segments. Mar. Biol. *43*, 381-385 (1977)

Hess, J.L., N.E. Tolbert and L.M. Pike: Glycolate biosynthesis by *Scenedesmus* and *Chlorella* in the presence or absence of $NaHCO_3$. Planta *74*, 278-285 (1967)

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

Lambert, M. and A.C. Neish: Rapid method for glycerol in fermentation solutions. Can. J. Res. *28B*, 83-89 (1950)

Lampe, H.: Die Temperatureinstellung des Stoffgewinns bei Meeresalgen als plasmatische Anpassung. Protoplasma *23*, 534-578 (1935)

Larkum, A.W.D.: Frond structure and growth in *Laminaria hyperborea*. J. mar. biol. Ass. U.K. *52*, 405-418 (1972)

Lüning, K.: Seasonal growth of *Laminaria hyperborea* under recorded underwater light conditions near Helgoland. *In*: Proceedings of the Fourth European Marine Biology Symposium, pp 347-361. Ed. by D.S. Crisp. Cambridge: University Press 1971

-, K. Schmitz and J. Willenbrink: CO_2 fixation and translocation in benthic marine algae. III. Rates and ecological significance of translocation in *Laminaria hyperborea* and *L. saccharina*. Mar. Biol. *23*, 275-281 (1973)

Mann, K.H.: Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar. Biol. *14*, 199-209 (1972)

Moebus, K. and K.M. Johnson: Exudation of dissolved organic carbon by brown algae. Mar. Biol. *26*, 117-125 (1974)

Montford, C.: Zeitphasen der Temperatur-Einstellung und jahreszeitliche Umstellungen bei Meeresalgen. Ber. dt. bot. Ges. *53*, 651-674 (1935)

Orth, G.M., N.E. Tolbert and E. Simenez: Rate of glycolate formation during photosynthesis at high pH. Pl. Physiol., Lancaster *44*, 55-59 (1966)

Parke, M.: Studies on the British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. J. mar. biol. Ass. U.K. *27*, 651-709 (1948)

Robbins, J.V.: The photosynthetic and respiratory physiology of *Palmaria palmata* (L.) Stackhouse, as affected by temperature, irradiance, total carbon dioxide, salinity and pH, 87 pp. M.Sc. Thesis, Dalhousie University 1976

Sieburth, J. McN.: Studies on algal substances in the sea, III. The production of extracellular organic matter by littoral marine algae. J. exp. mar. Biol. Ecol. *3*, 290-309 (1969)

Strickland, J.D.H. and T. Parsons: A practical handbook of seawater analysis, rev. ed. Bull. Fish. Res. Bd Can. *167*, 1-311 (1972)

Suto, S.: On the growth of "buds" in *Hijikia fusiforme*. Bull. Jap. Soc. scient. Fish. *17*, 13-14 (1951)

Talling, J.F.: Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater illumination. New Phytol. *56*, 29-50 (1957)

Tolbert, N.E.: Photorespiration. Bot. Monogr. *10*, 474-505 (1974)

Warburg, O. und G. Krippahl: Glycolsäurebildung in *Chlorella*. Z. Naturf. *156*, 197-200 (1960)

Mr. Bruce G. Hatcher
Department of Biology
Dalhousie University
Halifax, Nova Scotia B3H 4J1
Canada

Date of final manuscript acceptance: June 10, 1977. Communicated by T.R. Parsons, Vancouver