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Seasonal Variations in Salt-Marsh Macroalgae Photosynthesis. I. *Ascophyllum nodosum* ecad *scorpioides**

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Abstract

Photosynthesis in whole plants of the intertidal alga *Ascophyllum nodosum* ecad *scorpiodes* was evaluated by measuring ^{14}C-uptake under a variety of light intensities and approximately monthly intervals during a 15 month study. Photosynthetic rates were determined in terms of dry weight, pigment content and uptake into ethanol-soluble and insoluble fractions. The specimens, naturally acclimated to *in situ* light intensities and temperatures, exhibited photosynthetic responses to light intensity which differed with time of year. Maximum photosynthetic potential occurred during the spring months and minimum potential occurred during late summer and winter months. Variations in photosynthetic potential were closely related to seasonal changes in field biomass. Both photosynthetic potential and biomass were inversely related to growth patterns of the salt-marsh phanerogam *Spartina alterniflora*.

Introduction

Photosynthetic responses of intertidal marine algae to light intensity and temperature in the laboratory have been reported for many of the species inhabiting salt marshes. However, most of these investigations have been directly concerned with populations from other communities, such as rocky shores. Furthermore, few studies have attempted to elucidate patterns of photosynthesis in macroalgae on a temporal basis or to relate photosynthesis to the seasonal character of *in situ* light intensity and temperature. All too often, investigations have attempted to demonstrate temperature and light intensity relationships to photosynthesis based on studies of these variables in material collected at only select times of year, usually summer (e.g. Blinks, 1955; Ogata and Matsui, 1965; Kanwisher, 1966; Mathieson and Burns, 1971). Studies by Zavodnik (1973) and Mathieson and Norall (1973) are among the recent few which have attempted to analyze photosynthesis in macroalgae in relation to seasonal environmental characters. Yokohama (1972) and Brinkhuis and Jones (1974) have indicated that results quite different from those obtained with single-batch collections may be recorded if periodic samples are collected and these then tested for photosynthetic potential at a variety of light intensities.

No previous reports have dealt with photosynthesis in salt-marsh varieties of fucoids under submerged conditions. The present paper relates photosynthesis of *Ascophyllum nodosum* ecad *scorpioides* to temporal variations in light intensity and temperature. Investigations were conducted over a 15 month period in 1973 and 1974 to determine patterns of photosynthesis in material that was naturally acclimated to *in situ* conditions. Furthermore, as recommended by Brinkhuis and Jones (1974), extensive investigations in various frond segments were conducted to determine profiles of carbon fixation in whole plants. Uptake of carbon-14 into ethanol-soluble and insoluble fractions was also investigated. Photosynthetic carbon-14 uptake was expressed in terms of dry weight and total chlorophyll *a* concentrations.

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Materials and Methods

Intertidal specimens of *Ascophyllum nodosum* ecad *scorpioides* were collected from the northern edge of a salt-marsh embankment at Flax Pond, Long Island, New York (USA) (see Brinkhuis, 1976) at elevations of 1.0 m above mean low water (MLW). Whole plants were collected at 4 to 6 week intervals between March, 1973 and August, 1974 and usually 2 to 3 days prior to photosynthesis determinations. Specimens were returned to the nearby laboratory and maintained in 50 l glass aquaria supplied with running seawater from the marsh at *in situ* temperatures. Light was supplied by a bank of 8 "warm white", 90 W fluorescent tubes, supplemented by a single 150 W photoflood light for spectral balance (not shown on Fig. 1a). The light:dark cycle was adjusted periodically to maintain natural daylength periods. Four light intensities were used for photosynthesis determinations - 4.73, 6.37, 8.48 and 9.82 g cal cm^{-2} h^{-1}. These different intensities were obtained by turning off varying numbers of fluorescent tubes and by raising or lowering the supporting rack. The algae were maintained for at least 3 to 4 h at the light intensity to be tested, prior to the start of an experiment run. Generally, a different light intensity was used on each of 4 consecutive days and in sequence from low to high or high to low intensities. On a given experiment day, two sets of incubations were carried out at the same light intensity.

For photosynthesis experiments, three 4 l chambers (Fig. 1b) were filled with filtered seawater (nylon bag, 10 µm mesh). A single plant (10 to 20 cm tall) was placed in a retaining support in each chamber after epiphytic material had been removed as much as possible by gently rubbing the fronds between pieces of paper towelling. Approximately 20 µCi of $NaH^{14}CO_3$ (specific activity = 40 to 50 mC mM^{-1}) were added to each photosynthesis chamber while the contents were stirred with magnetic mixers (Fig. 1). After a 3 min mixing period, triplicate 1 ml aliquots of seawater were sampled from each chamber and pipetted into scintillation vials containing 10 ml "Aquasol" (New England Nuclear Corp.) to determine the total radioactivity added to each chamber. A 150 ml sample of incubation seawater was analyzed for pH with a Beckman-G pH meter before and after acidification to determine free-CO_2 and alkalinity (Strickland and Parsons, 1968). The chambers were sealed and immediately placed onto water-driven magnetic mixers in a large glass aquarium supplied with seawater at *in situ* temperatures. Chambers were covered with approximately 15 cm of seawater when immersed in the aquarium. Generally, one incubation was conducted between 10.00 and 12.00 hrs while the replicate was conducted between 13.00 and 15.00 hrs. After incubation for approximately 2 h (actual time recorded), the chambers were removed from the aquarium and opened. Plants were removed from their retaining supports and excess water was carefully shaken off. Plants were immediately placed in individual dark containers in a -40°C freezer until analysis. Approximately 400 whole-plant speci-

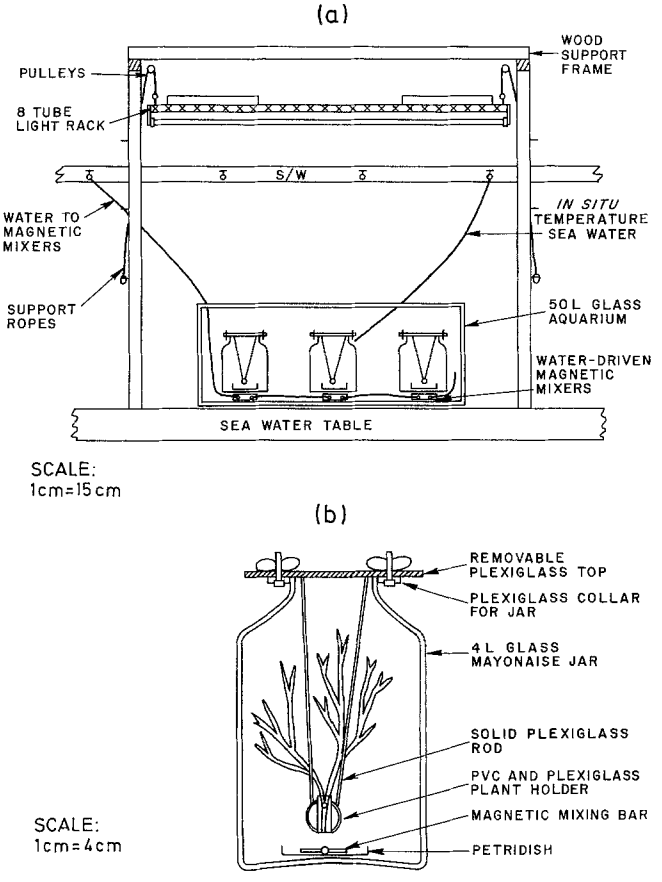

Fig. 1. Details of laboratory set-up and incubation chambers. Experimental photosynthesis chambers were placed in a 50 l glass aquarium (a) continuously filled with running seawater (s/w) pumped from Flax Pond. Aquarium was situated under bank of 8 fluorescent tubes which was moved vertically by a set of pulleys. Running seawater was also used to drive magnetic mixes to stir contents of chambers. Experimental chambers (b) were constructed from glass 4 l jars fitted with Plexiglass collars and a top bolted to the collar. Dichotomously branched plants may be supported in the plant holder which is retained by a piece of coated wire

mens were incubated during the 15 month study.

The algae were analyzed for total ^{14}C-uptake by methods similar to those reported by Towle and Pearse (1973) and Brinkhuis and Jones (1974). Frozen algae were lyophilized and ground into a semi-fine homogeneous powder in a mortar and pestle. One out of each set of three specimens of algae used in each replicate incubation was treated differently. Instead of grinding up these whole plants as a homogenized sample, 2 cm long apical sections were removed from each of these plants and ground into a separate fraction. Since it was difficult and tedious to remove all of the growing apices from *Ascophyllum nodosum* ecad *scorpioides* plants, limited numbers (10 to 15) were removed and a separate powder fraction was made from basal frond segments. The remaining material was designated as the middle fraction. These divisions permitted comparisons of photosynthetic profiles in whole plants.

Triplicate 20 mg dry powder samples from each whole and partitioned plant were prepared for liquid scintillation counting to determine total ^{14}C-uptake. A 0.5 ml aliquot of acid-alcohol (1:10 v/v 1N HCl:95% ethanol) was added to each vial containing powder samples to remove residual bi-carbonate (^{14}C), and evaporated in a fumehood for 24 h at room temperature (ca. 23°C). The material in each vial was then solubilized by the addition of 1 drop of 1N NaOH and 1 ml of "Soluene" (Packard Inst. Co.). Solubilization was conducted at 40° to 50°C for 24 h, after which 10 ml toluene containing 0.8% 2,5-diphenyloxazole (PPO) and 0.02% 1,4-bis-(4-methyl-5-phenyl-oxaxole-2-1)benzene (POPOP) were added. All samples were counted thrice in a Beckman LS-250 Liquid Scintillation Spectrometer. The count data were then converted to mg C/g dry weight (gdw) h^{-1} by the formula of Brinkhuis and Jones (1974). As recommended by Morris *et al.* (1971), no subtraction for dark-uptake was included.

The amount of carbon-14 taken up into ethanol-soluble and insoluble fractions in each of the partitioned plants was investigated in an attempt to further elucidate the patterns of photosynthesis in relation to light intensity and tissue types over the 15 month study. For these analyses, another set of three 20 mg dry powder fractions were prepared for the determination of ^{14}C-uptake into ethanol-soluble and ethanol-insoluble fractions by the method reported by Brinkhuis and Jones (1974).

Total chlorophyll *a* (chl *a*) concentrations in each whole-plant or partitioned-plant sample were also determined. A single 50 mg powder fraction from each sample was extracted in the dark by the addition of 1 ml of distilled water to soften the lyophilized tissue, followed by 9 ml of 100% acetone. Samples were sonicated for 15 to 30 min in a dark refrigerator at 4°C and maintained in the same refrigerator for 24 h to complete extraction. Samples were then inspected for completion of extraction. Those in which powdered material was not clearly white were further extracted with 90% acetone in a glass-teflon homogenizer. Extracts from the same sample were then combined and all samples were centrifuged at 1500 rpm. Total volume of each supernatant was recorded and chl *a* concentrations were determined by scanning wavelengths of 630, 645, and 663 nm on a Beckman DU Spectrophotometer. Parsons and Strickland equations (Strickland and Parsons, 1968) were used to calculate chl *a*. Carbon uptake:chl *a* ratios (photosynthetic efficiency) were then calculated for each whole-plant or partitioned-plant fraction. A sum of squares-simultaneous test procedure (SS-STP) (Sokal and Rohlf, 1969) was performed on photosynthesis and pigment data to determine significance of observed differences. All references to significance are based on these analyses.

Results

Total Photosynthetic ^{14}C-Uptake

Total carbon-14 taken up by *Ascophyllum nodosum* ecad *scorpioides* (based on triplicate analyses of ^{14}C-labelled tissues in 3 plants in duplicate experiments at each light intensity, i.e., 18 data points per light intensity, is shown in Fig. 2. The data indicate the photosynthetic potential of this alga at different light intensities over a 15 month period. Although the natural light intensities over this period often exceeded experimental ones, attenuation of light by the tidally varying water column depth and the seasonal presence of *Spartina alterniflora* usually reduced maximum surface irradiation (about 85 g cal cm^{-2} h^{-1} at noon on a bright sunny day in June) to within the range of light intensities studied in the laboratory (4.73 to 9.82 g cal cm^{-2} h^{-1}). Natural light intensities often exceeded experimental ones during low tides near midday in the spring when *S. alterniflora* was absent.

Individual studies indicated that photosynthesis in April, 1973 (Fig. 2a) remained at a constant level slightly below 0.50 mg C gdw^{-1} h^{-1} at light in-

tensities between 4.73 and 8.48 g cal cm^{-2} h^{-1}. Water temperatures, as shown in Fig. 3, indicated that incubation temperatures at that time of year averaged 8.0°C. Photosynthesis in May and June, 1973, on the other hand, increased significantly from approximately 0.30 to 1.58 mg C gdw^{-1} h^{-1} over the same range of light intensities. During these two months, temperatures had risen to 12.5° and 19.0°C, respectively. Photosynthesis in July and August, 1973 was significantly less, ranging from 0.15 to no more than 0.65 mg C gdw^{-1} h^{-1} over the same range of light intensities. Water temperatures in July, 1973 averaged 23.0°C, whereas those in August of that year averaged 22.3°C. In October, when water temperatures had decreased to 18.0°C, photosynthesis increased significantly from 0.35 mg C gdw^{-1} h^{-1} at a light intensity of 4.73 g cal cm^{-2} h^{-1} to a value of 1.43 mg C gdw^{-1} h^{-1} at a light intensity of 9.82 g cal cm^{-2} h^{-1}. This photosynthetic response pattern was similar to that observed in June of that year at the same water temperature. Photosynthetic rates in December (12.5°C) averaged 0.26 mg C gdw^{-1} h^{-1} at a light intensity of 4.73 g cal cm^{-2} h^{-1} and appeared to saturate at the higher light intensities tested. Photosynthesis in February, 1974 (3.0°C) increased significantly from 0.35 to 0.89 g C gdw^{-1} h^{-1} over the range of light intensities studied. Photosynthetic rates in June, 1974 (17.0°C) remained below 0.35 mg C gdw^{-1} h^{-1} over the whole range of experimental light intensities, while rates in July, 1974 (22.0°C) increased from 0.17 to 1.34 mg C gdw^{-1} h^{-1} over the same range. The data, including standard deviations (in parentheses), are summarized in Table 1.

Total chl *a* concentrations in homogenized whole-plant samples (Fig. 4) exhibited fluctuations which did not appear to have any distinct relation to the time of year, except that somewhat higher, but not always significant, values were found during the winter months. Total chl *a* concentrations varied between 1.0 and 1.7 mg chl *a* gdw^{-1}. For the most part, the amount of photosynthetic carbon-14 fixed per unit chl *a* (Fig. 2b) in these whole plants exhibited response patterns to light intensity which were similar to those expressed on a dry weight basis. It may be noted, however, that this index of photosynthetic efficiency appeared to increase significantly in October, 1973 at all light intensities tested and at a time when chl *a* concentrations appeared to decrease. On the other hand, photosynthetic efficiency appeared to be low during the late fall,

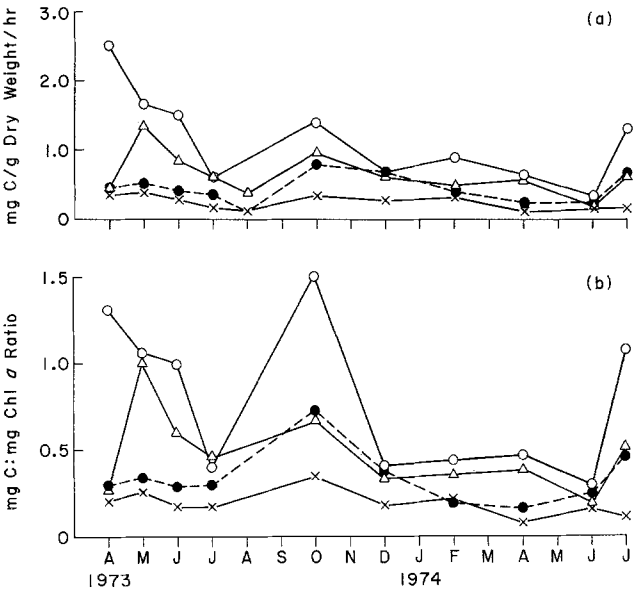

Fig. 2. *Ascophyllum nodosum* ecad *scorpioides*. Total ^{14}C assimilated at 4 light intensities: 4.73 (crosses), 6.37 (filled circles), 8.48 (triangles) and 9.82 (open circles) g cal cm^{-2} h^{-1} in terms of dry weight (a) and total chlorophyll *a* (chl *a*) (b) between April, 1973 and July, 1974. Each data point is based on triplicate analyses of 3 plants incubated at each light intensity in duplicate experiments

winter, and early spring months — periods during which chl *a* concentrations were at high levels. The photosynthesis per unit chl *a* data are also summarized in Table 1.

Profiles of ^{14}C-Uptake in Plant Segments

When particular segments of *Ascophyllum nodosum* ecad *scorpioides* plants were analyzed for carbon-14 uptake, it was noted that the frond apices (tips) generally exhibited the highest photosynthetic rates (in terms of dry weight) (Fig. 5a). Photosynthetic rates of these apical fractions remained at nearly constant levels at a light intensity of 4.73 g cal cm^{-2} h^{-1} throughout the period of investigation, but fixed carbon at somewhat higher rates than those observed in whole-plant samples (see Fig. 2a). Furthermore, this pattern of elevated photosynthetic rates in the tip fractions also occurred at higher light intensities and appeared to follow the seasonal trends observed in whole plants. Photosynthetic rates of the middle segments, which included main fronds, air bladders and, when present, small lateral branches (Fig. 5b), were very similar to

Table 1. *Ascophyllum nodosum* ecad *scorpioides*. Summary of photosynthesis data for homogenized whole plants in terms of dry weight and chlorophyll *a* (chl *a*) content. Values in parentheses are standard deviations for means of up to 18 data points per light intensity. Light intensities are in g cal cm^{-2} h^{-1}. Dashes indicate missing data points

Month	mg C g dry weight^{-1} h^{-1} at light intensities of:				mg C mg chlorophyll a^{-1} at light intensities of:			
	4.73	6.37	8.48	9.82	4.73	6.37	8.48	9.82
1973								
Apr.	0.379(.094)	0.476(.136)	0.485(.280)	2.542(.295)	0.206(.048)	0.289(.059)	0.273(.139)	1.321(.134)
May	0.388(.083)	0.524(.297)	1.378(.310)	1.658(.385)	0.260(.058)	0.332(.181)	1.028(.234)	1.056(.321)
June	0.274(.123)	0.419(.175)	0.842(.420)	1.530(.289)	0.186(.100)	0.297(.191)	0.621(.385)	0.997(.192)
July	0.154(.044)	0.365(.239)	0.628(.215)	0.526(.116)	0.165(.137)	0.291(.153)	0.455(.200)	0.400(.069)
Aug.	0.220(.063)	0.229(.080)	0.414(.112)	-	-	-	-	-
Oct.	0.348(.098)	0.810(.218)	0.964(.631)	1.432(.378)	0.348(.098)	0.730(.162)	0.687(.519)	1.506(.464)
Dec.	0.262(.056)	0.650(.085)	0.613(.099)	0.666(.205)	0.189(.076)	0.384(.064)	0.349(.058)	0.407(.159)
1974								
Feb.	0.346(.258)	0.418(.103)	0.534(.157)	0.893(.177)	0.234(.216)	0.205(.044)	0.349(.058)	0.437(.080)
Apr.	0.131(.023)	0.249(.047)	0.588(.331)	0.623(.072)	0.078(.025)	0.157(.036)	0.392(.230)	0.452(.073)
June	0.160(.058)	0.211(.127)	0.183(.054)	0.350(.121)	0.139(.057)	0.239(.206)	0.173(.046)	0.297(.088)
July	0.168(.059)	0.672(.078)	0.657(.338)	1.336(.299)	0.115(.043)	0.458(.078)	0.522(.289)	1.082(.351)

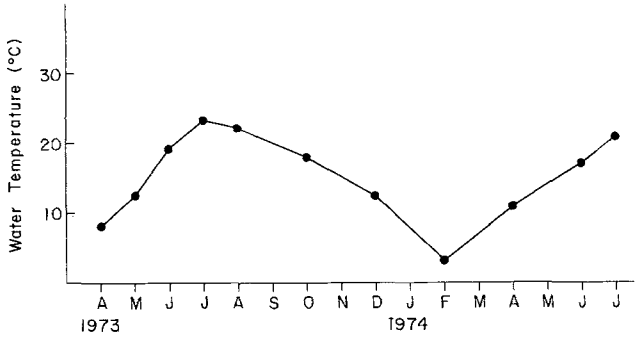

Fig. 3. Seasonal variation in water temperature based on average temperatures recorded during experiments between April, 1973 and July, 1974

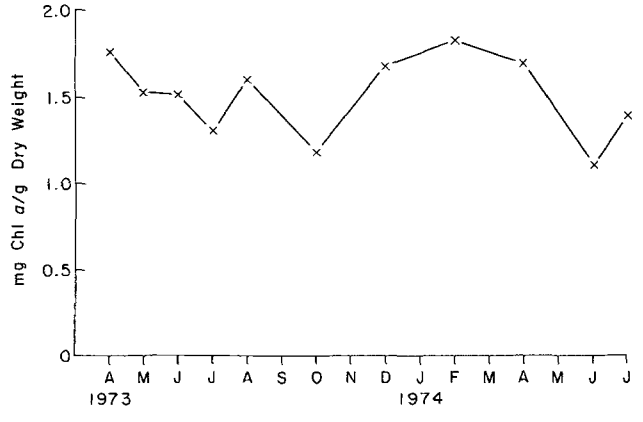

Fig. 4. *Ascophyllum nodosum* ecad *scorpioides*. Total chlorophyll *a* (chl *a*) concentrations in homogenized whole-plant tissues between April, 1973 and July, 1974. Each data point is based on single analysis of 6 plants

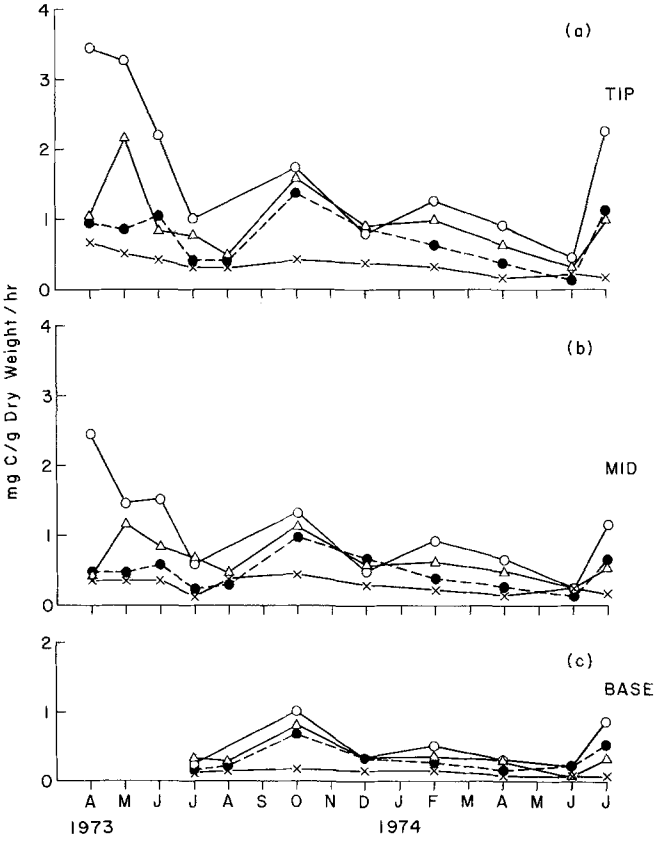

Fig. 5. *Ascophyllum nodosum* ecad *scorpioides*. Total ^{14}C assimilated per unit chl *a* by 1 to 2 cm long apical (a) middle (b) and basal (c) segments of plants at 4 light intensities between April, 1973 and July, 1974. Note that basal segments were not isolated until July, 1973. Each data point is based on triplicate analyses of 1 plant incubated at each light intensity in duplicate experiments. For explanation of symbols see legend to Fig. 2

those observed in whole-plant samples and followed the same seasonal trends. This similarily is not surprising since the bulk of the whole-plant sample consisted of material characterized in the middle fractions. Photosynthetic rates of basal segments, which consisted of the lower, older main fronds from which all lateral branches were removed, exhibited relatively low photosynthetic rates at a light intensity of 4.73 g cal cm^{-2} h^{-1} and indicated little seasonal variation (Fig. 5c). Photosynthesis at higher light intensities was significantly greater throughout the year, indicating that these older plant tissues fixed carbon at substantial rates, albeit at rates lower than in younger segments.

Total chl *a* concentrations in isolated fractions from the partitioned plants (Fig. 6) exhibited somewhat clearer seasonal relationships than the data from whole-plant tissues (see Fig. 4); this may partly be attributed to sampling variability. Chl *a* concentrations in all three tissue types were significantly higher during the winter months and lower during the late spring and summer months. It is interesting to note that pigment concentrations in the middle fractions were greater than those found in tip and basal fractions. Total chl *a* concentrations in middle segments varied between 1.25 and 2.05 mg Chl *a* gdw^{-1}, and those in tip fractions ranged from 0.6 to 1.80 mg chl *a* gdw^{-1}. On the other hand, pigment concentrations in basal segments varied less and ranged from 0.42 to 1.20 mg chl *a* gdw^{-1}. It should be pointed out that the drop in chl *a* concentrations from the whole plants in October, 1973 (see Fig. 4) was not apparent in the data from the partitioned plants.

Photosynthetic efficiency in the partitioned plants (Fig. 7) often exhibited higher values than those obtained in the homogenized whole-plant samples (see Fig. 2b). Again, this may be partly due to sampling differences. Tip fractions (Fig. 7a) exposed to the higher light intensities exhibited efficiencies that were approximately two times greater than efficiencies observed in middle fractions (Fig. 7b) and basal fractions (Fig. 7c). Photosynthetic efficiencies of middle portions were similar to those observed in whole-plant tissues throughout the year. Carbon uptake per unit chl *a*, especially in tip fractions, increased with higher light intensities in the spring of 1973 and subsequently decreased during the summer months. A similar increase in the spring of 1974 was expected but not observed, even though chl *a* concentrations in the tip fractions were not greatly different in

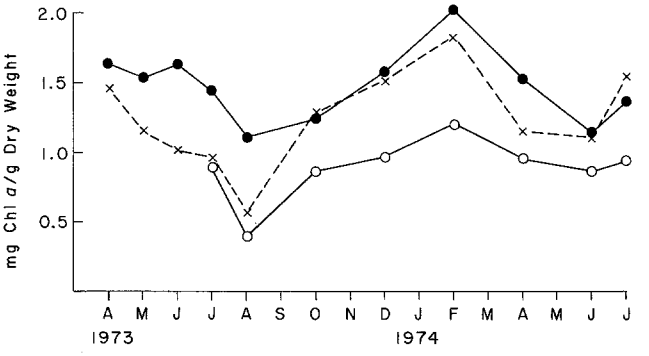

Fig. 6. *Ascophyllum nodosum* ecad *scorpioides*. Total chl *a* concentrations in (a) apical (crosses), (b) middle (filled circles) and (c) basal segments (open circles) between April, 1973 and July, 1974. Note that basal segments were not isolated until July, 1973. Each data point is based on single analysis of 2 plants

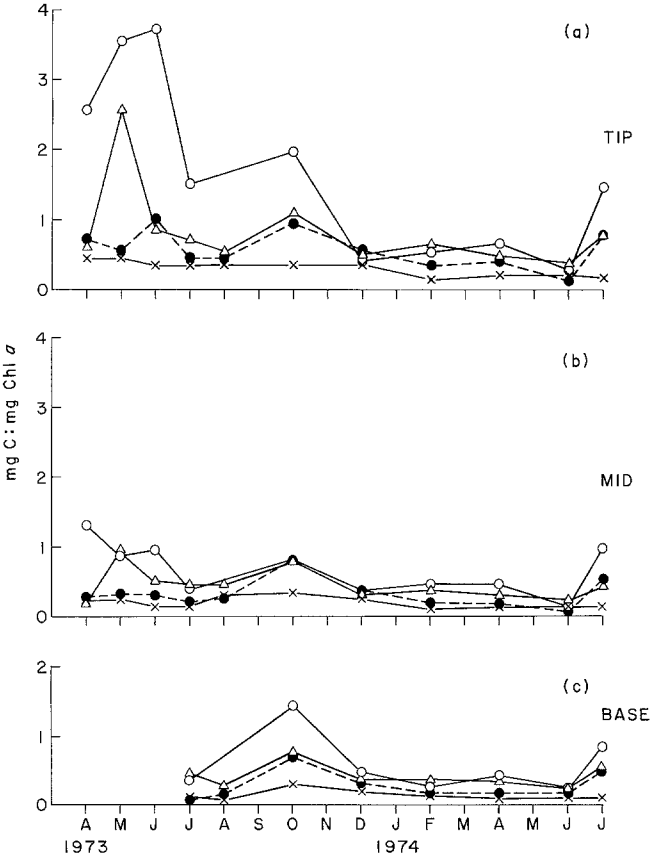

Fig. 7. *Ascophyllum nodosum* ecad *scorpioides*. Total ^{14}C assimilated per unit chl *a* by 1 to 2 cm long apical (a) middle (b) and basal (c) segments of plants at 4 light intensities between April, 1973 and July, 1974. Note that basal segments were not isolated until July, 1973. Each data point is based on triplicate analyses of 2 plants incubated in duplicate experiments. For explanation of symbols see legend to Fig. 2

spring of both years. However, this difference between the two springs may not be attributable to sampling variability and will be discussed further in the discussion.

Carbon-14 Uptake into Ethanol-Soluble and Insoluble Fractions

Changes in the proportion of labelled carbon incorporated into ethanol-soluble fractions (mainly low molecular weight compounds) and into ethanol-insoluble fractions (mainly proteins and polysaccharides) revealed a pattern of photosynthesis more clearly illustrating responses to light and, possibly, temperature. Individual studies indicated that the rate of ^{14}C-uptake into the protein and polysaccharide (ethanol-insoluble) fractions during April, 1973 (Fig. 8a) remained unchanged with increasing light intensity. The relative proportion of carbon-14 assimilated into this fraction, however, decreased with increasing light intensity. Similar patterns of carbon-14 incorporation were observed in both middle and apical fractions, but incorporation into the ethanol-soluble fraction of frond apices was much greater than in the older middle segments and reflects the relatively greater photosynthetic potential of apical segments mentioned earlier. Carbon-14 assimilation in May, 1973 (Fig. 8b) indicated a similar pattern of photosynthesis. The large increase in the insoluble fraction activity noted at a light intensity of 9.82 g cal cm^{-2} h^{-1} appears to indicate that protein and polysaccharide synthesis increased greatly at this intensity. In fact, activity in the insoluble fraction was approximately equal to that found in the ethanol-soluble fraction. The reliability of this data point, however, may be questioned since the analysis was based on only one plant instead of the usual two plants. In June, 1973 (Fig. 8c) carbon-14 uptake into the ethanol-insoluble fractions of the middle and tip segments resembled patterns of photosynthesis found in May of the same year. Activity in the insoluble fractions in July, 1973 (Fig. 8d) exhibited significantly increased levels in all three tissue types. The relative proportions of activity in the insoluble fractions were considerably greater than in previous months, and indicated increased protein and polysaccharide synthesis. Activity levels in the ethanol-soluble fractions increased with increasing light intensity, whereas activity in the insoluble fractions did not increase with increasing light intensity. This would indicate that photosynthesis activity of the alga occurred mainly in the production of low molecular compounds during the short-term measurements of 2 h. Carbon-14 uptake into ethanol-insoluble fractions remained at relatively high levels in August, 1973 (Fig. 8e), but was quite variable. This variability may also be due to the fact that the data originated from a single plant instead of two. Duplicate experiments were not conducted at each light intensity during this month. Incorporation of ^{14}C into the soluble fraction of the basal segments of the plant incubated at a light intensity of 4.73 g cal cm^{-2} h^{-1} was unusually high. Protein and polysaccharide synthesis in October, 1973 (Fig. 8f) remained at fairly high levels, and appeared to increase significantly in all three tissue segments at a light intensity of 9.82 g cal cm^{-2} h^{-1}. Activity in the insoluble fractions was greater than that found in the ethanol-soluble fractions. In December, 1973 (Fig. 8g), uptake levels in the different plant segments were lower at all four light intensities tested. Carbon-14 uptake into the insoluble fractions remained at fairly low and constant levels, whereas incorporation into the soluble fractions increased slightly with increasing light intensity. Photosynthesis patterns in February, 1974 (Fig. 8h) indicated that protein and polysaccharide synthesis proceeded at low rates, as did the proportion of low molecular weight compound production. Carbon-14 uptake into the soluble fractions appeared to increase at light intensities between 4.73 and 6.37 g cal cm^{-2} h^{-1} and level-off at higher light intensities. In April, 1974 (Fig. 8i), protein and polysaccharide synthesis remained at low levels. On the other hand, synthesis of low molecular weight molecules increased with increasing light intensity. A similar pattern of carbon-14 uptake into ethanol-soluble and insoluble fractions was noted in June, 1974 (Fig. 8j), although the amounts of ^{14}C taken up into each fraction were somewhat lower than in April. In July, 1974 (Fig. 8k), the relative proportion of ^{14}C taken up into ethanol-insoluble fractions was high, mainly because of decreased uptake into ethanol-soluble fractions.

These data on incorporation of carbon-14 into low molecular weight compounds and that going into protein and polysaccharide synthesis appear to indicate that levels of protein and polysaccharide synthesis increased during the late summer and fall months, but generally did not increase with increasing light intensity. Synthesis of low molecular

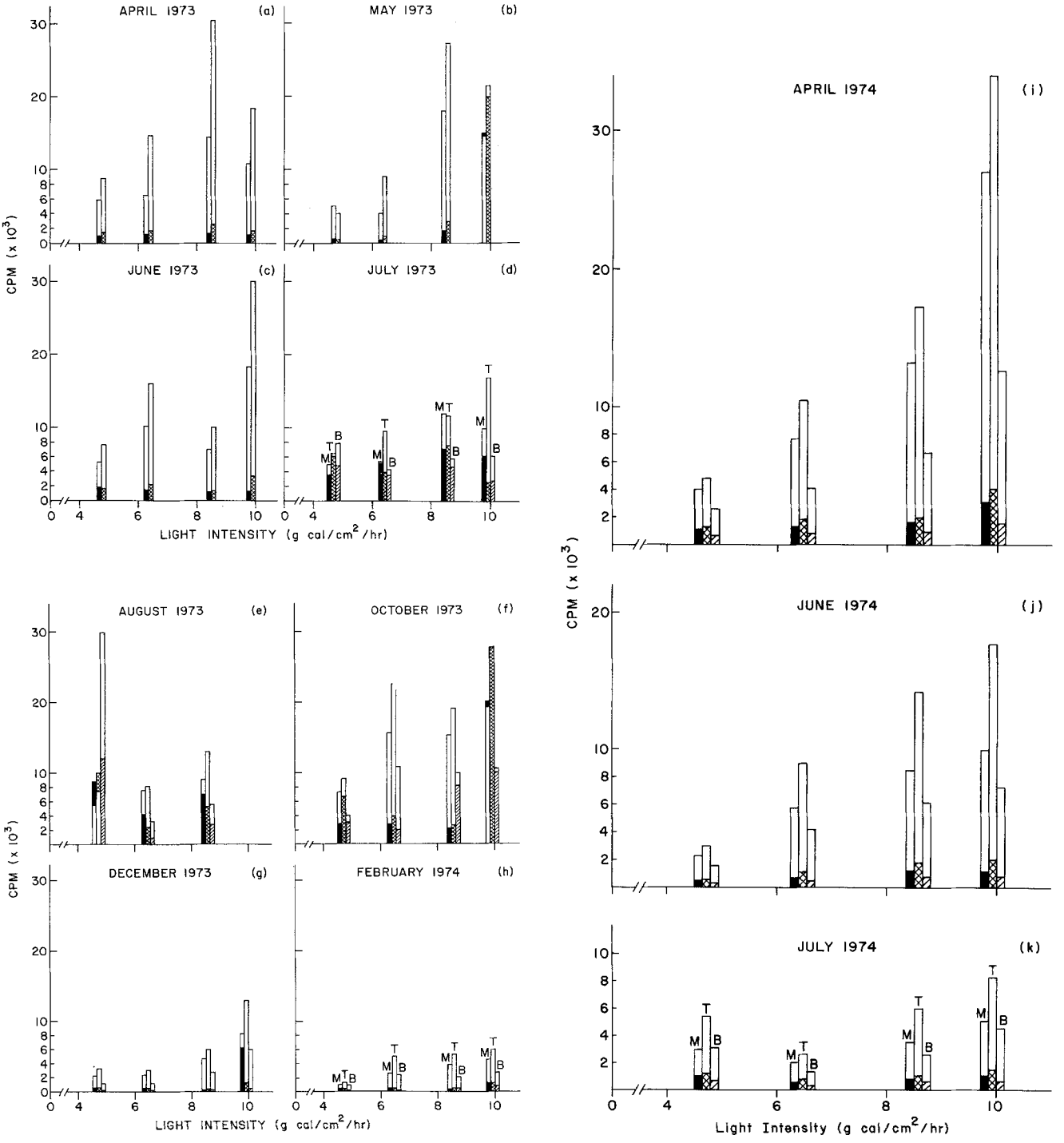

Fig. 8. *Ascophyllum nodosum* ecad *scorpioides*. ^{14}C-uptake into ethanol-soluble fractions (open and hatched bars) and ethanol-insoluble fractions (black and cross-hatched bars) by middle (M), apical (T) and basal (B) segments (see July, 1973 for identification) between April, 1973 (a) and July, 1974 (k). Where no third segment data is shown (a-c), only (M) and (T) (in that order) segment data are given. In some instances, ^{14}C-incorporation into insoluble fractions was greater than into soluble fractions. Consequently, black or cross-hatched portions extend above open or hatched bars. Each bar is based on triplicate analyses of 2 plants in duplicate experiments. Light intensities are same as those in Fig. 2

weight compounds appeared to respond to increased light intensities the most; however, the levels of synthesis decreased during the late summer, thereby increasing the relative proportion of protein and polysaccharide synthesis at that time. During the late summer and fall months, the increased levels of protein and polysaccharide synthesis further affected the ratio of ^{14}C taken up into soluble and insoluble fractions.

Discussion

Photosynthetic responses of the intertidal salt-marsh alga *Ascophyllum nodosum* ecad *scorpioides* to different light intensities (light intensities which are comparable to those found frequently in its habitat) vary over time. The alga exhibits a large degree of plasticity in its relationship between photosynthesis and light intensity. Furthermore, synergistic effects of seasonally varying water temperatures on the rate of photosynthesis at different times of the year are likely, although no distinct effect of temperature alone could be isolated in this study. For example, photosynthetic rates of *A. nodosum* ecad *scorpioides* in February, at a temperature of 3.0°C, were equal to or greater than those occurring during the summer months when temperatures exceeded 20°C. Results of this nature are quite different from those obtained in studies of photosynthesis of marine algae versus different light intensities or temperatures measured at only one time of year (e.g. Kanwisher, 1966; Mathieson and Burns, 1971). In the latter types of studies, photosynthesis was usually found to increase with increasing light intensity, and decreased temperatures were observed to lower the relative rate of photosynthesis. On the other hand, Brinkhuis and Jones (1974) found that photosynthesis of *Chondrus crispus* at different temperatures and at different times of the year did not exhibit "classic" responses. Mathieson and Norall (1975), in more detailed studies of photosynthesis of *C. crispus*, subsequently found that this alga exhibited lower light optima during the fall and winter months compared to spring and summer months. Results from the current study cannot adequately illustrate shifts in light optima for photosynthesis during any time of year. On the other hand, photosynthetic rates at low light intensities were quite similar throughout the study and a reduction in photosynthesis that one might expect at colder temperatures, i.e., winter, was not observed at low light intensities. Therefore, these results do indicate possible adaptation or plasticity in the photosynthetic apparatus.

Results in the current study indicated that similar patterns of photosynthesis occurred in apical and middle segments of *Ascophyllum nodosum* ecad *scorpioides*, although photosynthetic activity in apices was generally greater on both a dry weight and pigment content basis. The older basal segments also showed significant rates of photosynthesis and exhibited temporal patterns similar to other tissue types. When carbon assimilation was expressed in terms of chl *a* content, patterns of photosynthesis were obtained which were very similar to those expressed on a dry weight basis and differences did not always appear to account for variations in photosynthesis per unit weight patterns. Pigment concentrations in *A. nodosum* ecad *scorpioides* appeared to be greatest during winter months and lowest during summer months. This seasonality was more apparent in the data based on plants partitioned into various tissue types. Similar seasonality in pigment concentrations in macroalgae have been reported for *Fucus virsoides* by Zavodnik (1973) and other species by Seoane-Camba (1964). Furthermore, results indicated that chl *a* concentrations in frond apices of *A. nodosum* ecad *scorpioides* were lower than in main frond (middle) tissues which are shaded from direct exposure to higher light intensities.

Photosynthetic carbon uptake into ethanol-soluble and insoluble compounds or into low molecular weight compounds and proteins and polysaccharides indicated that protein and polysaccharide synthesis in *Ascophyllum nodosum* ecad *scorpioides* underwent seasonal changes in their capacity to respond to light intensity. During the spring and early summer months, which corresponded to periods of maximum photosynthetic potential, protein and polysaccharide synthesis in *A. nodosum* ecad *scorpioides* generally did not increase with increasing light intensities. The amount of carbon-14 taken up into low molecular weight compounds, on the other hand, did increase with increasing light intensity at that time of year. Therefore, the relative proportion of protein and polysaccharide synthesis decreased with increasing light intensity. During the late summer and early autumn months, however, protein and polysaccharide synthesis appeared to increase with increasing light intensity and proceeded at higher ^{14}C-incorporation rates than during previous months. This increased relative rate was sometimes accompanied by a decrease in the propor-

tion of carbon-14 incorporated into the ethanol-soluble fractions. Morris *et al.* (1974) also found that the proportional protein synthesis in relation to ethanol-soluble compounds in some species of phytoplankton was highest at low light intensities. These authors concluded that this ability to synthesize protein under conditions of low light intensity (and other environmental stresses) indicates that protein synthesis is conserved more than that of other compounds. Low light intensities and temperatures during winter month periods, during which the algae grow slowly or become senescent, may similarly be imposing environmental stresses on intertidal salt-marsh algae. Although the analysis of carbon incorporation in the current study did not distinguish between protein and polysaccharide synthesis, a general conclusion may be reached that ^{14}C-incorporation into ethanol-insoluble fractions appears to be conserved more than incorporation into ethanol-soluble fractions during the fall and winter months.

The relative rates of photosynthesis in *Ascophyllum nodosum* ecad *scorpioides* obtained by the incubation of whole-plant specimens, which were naturally acclimated to *in situ* light intensity and temperature and analyzed by methods described in this paper, yielded a range of values (up to approximately 2 mg C gdw^{-1} h^{-1}) which were similar to those reported for other species of macroalgae (Kanwisher, 1966; Mathieson and Burns, 1971; Zavodnik, 1973; Brinkhuis and Jones, 1974; Mathieson and Norall, 1975). Furthermore, photosynthesis of *A. nodosum* ecad *scorpioides* under submerged conditions was found to be similar to photosynthetic rates observed under exposed (emerged) conditions by Brinkhuis *et al.* (1976). This comparableness is in agreement with that reported by Brown and Johnson (1964), Chapman (1965) and Imada *et al.* (1970) for other species of algae. On the other hand, results obtained for intertidal specimens of macroalgae by Stocker and Holdheide (1938) and Johnson *et al.* (1974) yielded photosynthesis-in-air values greated than those measured in water. Kremer and Schmitz (1973) found that the ratio of photosynthesis in air:photosynthesis in water increased with vertical distribution (i.e., degree of potential desiccation) of various species of intertidal algae. The broad adaptability of *A. nodosum* ecad *scorpioides* photosynthesis to environmental parameters while exposed to the atmosphere (Brinkhuis *et al.*, 1976) seems also to be apparent in photosynthesis under submerged conditions.

Comparison of photosynthesis results obtained here with observed seasonal patterns of biomass distribution reported by Brinkhuis (1976) yields some insight into the relationship of *Ascophyllum nodosum* ecad *scorpioides* to environmental conditions. The lack of replication in photosynthesis rates and patterns in the two spring periods (1973 and 1974) does not necessarily indicate effects caused by experimental variability. It is most interesting to note that high photosynthetic potentials of *A. nodosum* ecad *scorpioides* (at higher light intensities) in April, 1973 may be correlated with higher standing-crops in the field (see Fig. 4 of Brinkhuis, 1976), and that lower photosynthetic potential in April, 1974 paralleled lower observed standing-crops. Furthermore, after a decline in photosynthetic potential and biomass during the summer months of 1973, the subsequent increase in photosynthetic potential in October, 1973 was followed by concurrent increases in field biomass. It appears as though a complex interaction between natural light intensities and, possibly, temperatures and some other environmental parameter may be effecting the observed patterns in photosynthetic potential. The observed fluctuations in photosynthetic potential are further substantiated by the tests for significance. Furthermore, an analysis of variance reported by Brinkhuis and Jones (1974) for photosynthesis data on *Chondrus crispus*, using very similar experimental procedures and analysis as described here, is probably applicable to photosynthesis data for *A. nodosum* ecad *scorpioides*. In that study, the authors found that plant-to-plant variability accounted for 34% of the variance, while within-the-plant variability (primarily ascribed to weight differences in the 20 mg subsamples) accounted for 15% of the variance.

Relating temporal variations in photosynthesis of mid-intertidal populations of *Ascophyllum nodosum* ecad *scorpioides* to seasonal light intensity patterns alone is difficult. Daily irradiation curves (g cal cm^{-2} min^{-1}) over the year usually indicate that maximum light quantities falling on the surface of the earth occur during the summer months. In salt marshes such as Flax Pond, however, the seasonal growth pattern of the phanerogam *Spartina alterniflora* reduces light intensities at the substrate level during the summer months (Brinkhuis, 1976). The growth pattern of *A. alterniflora* shifts the surface irradiation profile such that maximum irradiation in the algal habitat actually occurs during the spring when *S. alterniflora* is absent. A model which simulates *in situ* light intensities

at various tidal elevations in the salt marsh (light intensities which change seasonally with changes in daylength and maximum daily irradiation and with light attenuation by the tidal water mass and growth of *S. alterniflora*) may elucidate patterns in insolation related to observed photosynthetic potential in the laboratory. This model, including calculations of seasonal productivity and comparisons of productivity based on photosynthesis measurements, *in situ* growth determinations, and field biomass changes, will be the subject of a future paper.

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