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Photosynthesis and Respiration of Exposed Salt-Marsh Fucoids*

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Abstract

Photosynthesis and respiration of the salt-marsh fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* were investigated using an infrared CO_2 gas analyzer under a variety of light intensities, temperatures, and levels of desiccation while the algae were exposed to the atmosphere. Results indicated that net photosynthesis (0.5 to 2.0 mg C/g dry weight/h) saturated rapidly at light intensities (0.1 to 0.2 g cal/cm^2/min) which were approximately 10 to 50% of the daily summer maximum intensities for algae found under phanerogam (*Spartina alterniflora*) canopies. Desiccation exhibited the most pronounced effect on photosynthesis, which increases slightly between 0 and 25% water loss, levels off, and decreases sharply at water losses greater than 50%. Dark respiration (0.1 to 0.3 mg C/g dry weight/h) is also inhibited by desiccation. Both species of algae appear to be broadly adapted to all three parameters investigated.

Introduction

Baker and Bohling (1916) were the first to suggest that the morphological growth patterns of marsh fucoids were, at least partially, related to exposure of the plants to the atmosphere. In the absence of knowledge concerning the extent to which an alga can carry out photosynthesis while exposed to the atmosphere at low tide, however, they found it difficult to assess the influence of exposure upon ecad adaptation. Some 20 years later, Stocker and Holdheide (1938), in studying the relationship between photosynthesis and exposure, found that the photosynthetic rates of rocky shore marine algae under exposed conditions were higher than those under submerged conditions. More recent investigations by Brown and Johnson (1964), Chapman (1965), Imada *et al.* (1970), however, reported that photosynthesis of intertidal algae exposed to the atmosphere was either lower or approximately equal to that under submerged conditions. Johnson *et al.* (1974), on the other hand, found photosynthesis in air, at constant light and temperature, to be considerably greater than that in water for species from the middle or upper intertidal region, while lower littoral species showed reduced photosynthesis in air.

In making productivity measurements based upon photosynthesis of intertidal marine algae, one must account not only for photosynthesis in water but also the amount of photosynthesis that occurs in air under exposed conditions, particularly since photosynthetic responses of algae to light intensity and temperature in water might be quite different from those under similar conditions in air. None of the above-mentioned studies reported on the photosynthetic responses of exposed salt-marsh algae to a variety of light intensities and temperatures.

The current investigation, therefore, is concerned with the determination of photosynthesis in the salt-marsh fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* under different conditions of light intensity, temperature, and desiccation. These particular algae are very common along the shores and upon the banks of the temperate marshes of Long Island, N.Y. (USA), and form a substantial biomass which is exposed for peri-

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ods of 1 to 8 h, depending upon local tide-cycles (Brinkhuis, 1976; Brinkhuis and Jones, 1976).

Materials and Methods

An open-system photosynthesis chamber (Fig. 1A), used to determine the CO_2 exchange of exposed algae, was constructed of a clear, hollow, Plexiglass top (50 x 50 cm), Plexiglass sides (50 x 10 cm) painted black on the interior walls, and a hollow black aluminum base (50 x 50 cm). The total interior volume of the chamber was 25 l. Cooled water was pumped from a refrigerated water bath on the right of the chamber (Fig. 1B) through the hollow base and top of the chamber to aid in temperature control. Natural air (containing 0.03 to 0.05% CO_2) was supplied from a tank (Fig. 1C), circulated through 15 m of small-diameter copper tubing immersed in the cooling bath, and injected into one side of the chamber at 3 l/min through a T-shaped manifold containing numerous small holes. The air to which the algae were exposed was sampled from the opposite side of the chamber through a similar manifold at 1.5 l/min. Excess air was vented through an open-cell foam port on the sampling side of the chamber.

The sampled air was passed through a Mine Safety (Model 200) LIRA Infrared Analyzer (Fig. 2) to determine the CO_2 concentration. The instrument was calibrated at the beginning of each day using absolute-standard calibrating gases in a nitrogen background with a known accuracy of 0.5 parts per million (ppm). Temperature inside the chamber was measured near the plant material using a Copper-Constantan thermocouple accurate to 0.1C°. A dome-type solarimeter (Agromet Data Systems, Science Assoc., Princeton, N.J.) with an input of about 28 mV/g cal/cm^2/min was also placed inside the chamber. The three data inputs (CO_2, temperature, and light intensity) were sampled every 140 sec throughout the experiment. The system used to collect these raw data is a portable unit developed several years ago by the Ecology Group at Brookhaven National Laboratory, Upton, N.Y., USA (Fig. 2). The data logger (A) on the left panel has the ability to measure 5 inputs from each of the 20 stations coming into the center panel (B). The input was digitized and punched onto paper tape for subsequent analysis by computer.

Intertidal specimens of *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* were collected from the northern edge of a salt marsh embankment at Flax Pond, Long Island, New York (USA). Whole plants (10 to 20 cm tall) were obtained from 1.0 m above mean low water (MLW) during the summer-fall months of 1973 and the summer of 1974. The plants were brought to the laboratory and cleansed of mud and macroscopic epiphytes, followed by shaking to remove excess water. A whole plant (15 to 30 g wet weight) was then weighed to determine the initial wet weight, and placed on an insulated board approximately 3 cm above the bottom of the chamber. Incubation periods extended for up to 3 h, during which time light intensities were altered in random sequences by placing varying numbers of 1-mm mesh fiberglass screens over the chamber. Temperature was controlled by regulating water flow through the hollow top and bottom of the chamber. Respiration was assessed at various times by wrapping the chamber with thick black plastic. The chamber was allowed to equilibrate for 15 to 20 min after each alteration of light intensity and/or temperature. Only data from the equilibrated phases were used in the final analyses. At the end of each run, plants were removed from the chamber and weighed to determine water loss due to desiccation. Dry weights were subsequently obtained for each plant by drying them at 110°C for 24 h.

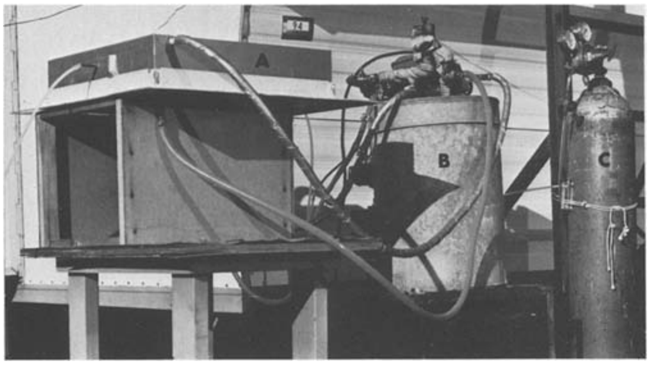

Fig. 1. Plexiglass chamber (A) with hollow top and hollow aluminum base cooled by recirculating water from refrigerated tank (B). Natural air was supplied from tank (C), and passed through 15-m copper tubing coil immersed in cooling bath (B)

The plants in the chamber dehydrated over time at varying rates that were dependent upon temperature and previous water loss. Since the water loss of plants in the chamber was not linear, separate experiments were conducted for both species to determine weight loss over time at 5 temperatures (13° to 40°C). Weights for 4 plants at each temperature

Fig. 2. System for CO_2 gas-exchange measurements developed by Ecology Group at Brookhaven National Laboratory. Data logger (A) digitized up to 5 inputs from 1 to 20 stations (B). In the present study, 3 inputs — light intensity, temperature, and CO_2 [from the infrared analyzer (C)] — were digitized and punched on to paper tape (D). Absolute standard gasses (E) with known CO_2 concentrations in a nitrogen background were used to calibrate the infrared analyzer. The cold trap (F) served to remove moisture from sampled inputs

were recorded every 10 min for 3 h. A table of these data was fed into a computer program to perform a two-dimensional bi-cubic spline interpolation of weight loss versus temperature and time, enabling the calculation of cumulative weight loss at each sampling interval (140 sec) collected in the chamber data above. As a control, the cumulative water loss calculated for the last sample cycle of each plant was compared to the previously determined value for water loss obtained by weighing the plant before and after incubation. Cumulative water-loss data and the paper tape containing CO_2, temperature, and light-intensity data were transferred to data cards and run through the computer to calculate and plot photosynthesis and respiration as functions of light intensity, temperature, and desiccation. The data were empirically fitted to the function

$$\text{mg Carbon/g dry weight/h} = a + be^{-kx} + cxe^{-kx}$$

by a least-squares fit technique. The values for the coefficients a, b, and c are determined by the least-squares fit to that value of the exponential constant k which resulted in a satisfactory error in fit to the projected curve, and the value for x is the independent variable measured.

Results

Water Loss over Time at Various Temperatures

The cumulative % water loss over time at various temperatures, by specimens of *Ascophyllum nodosum* ecad *scorpioides* placed in the experimental chamber, is shown in Fig. 3a. Only 3 of the 5 experimental temperatures are shown because the water-loss curve for 31.2°C was not significantly different from that of 38.9°C and the curve for 19.7°C was similar to that for 13.1°C. The cumulative water loss at 31.2° to 38.9°C rose sharply with time, and leveled-off after about 80 min of exposure in the chamber. Beyond this point no more of the ± 20% residual water content was driven off, and at this stage the plants were stiff but not brittle. Water loss at 26.7°C rose less rapidly and took more than twice as long to reach total values similar to those at 31.2° to 38.9°C. Water loss of *A. nodosum* ecad *scorpioides* at temperatures between 13.1° and 19.7°C occurred even more slowly, not amounting to more than 40% of the initial water content after 150 min. In all cases, the 4 different plants used at each temperature exhibited little plant-to-plant variability. The starting fresh weights of the plants used ranged from 15 to 35 g wet weight.

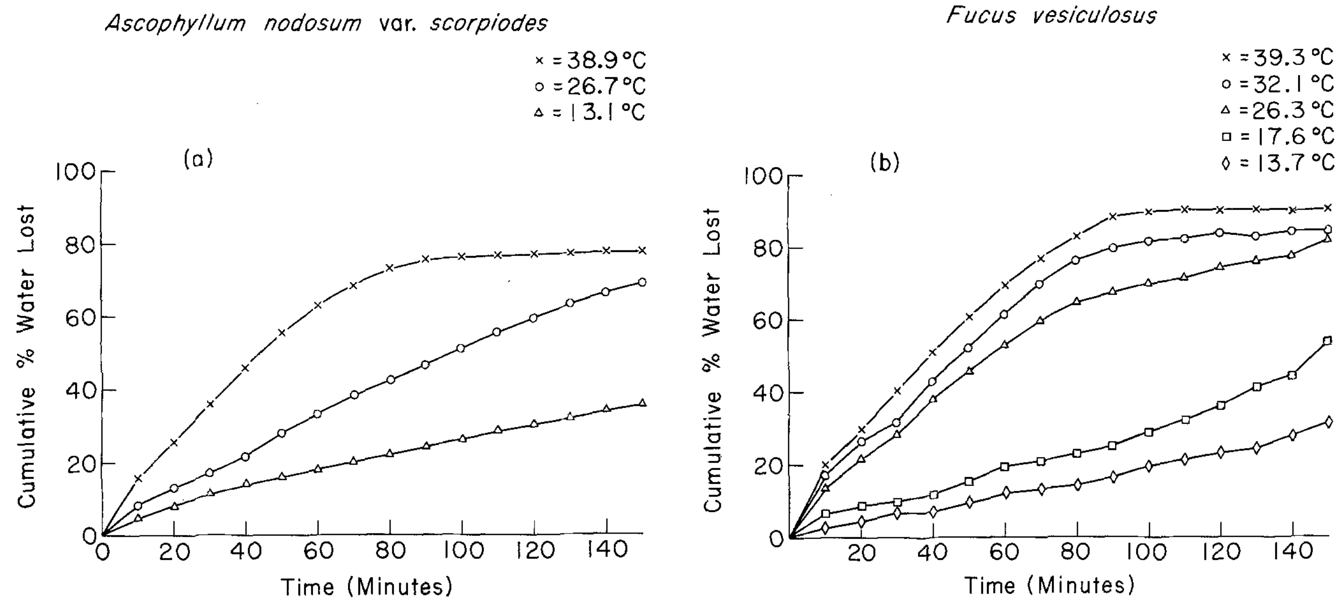

Fig. 3. *Ascophyllum nodosum* ecad *scorpioides* (a), and *Fucus vesiculosus* (b). Cumulative % water loss over time at various temperatures in photosynthesis chamber

The pattern of water loss over time at various temperatures for *Fucus vesiculosus* (Fig. 3b) was somewhat different from that of *Ascophyllum nodosum* ecad *scorpioides*. The cumulative water loss at 39.3°C rose sharply and leveled-off after 90 to 100 min. The plants had lost approximately 90% of the water initially present, and were dry and fragile. Plants exposed to air at 32.1°C had lost only 80% of the initial water content after the same time interval but were not brittle, a condition similar to that encountered in *A. nodosum* ecad *scorpioides* at 38.9°C. Cumulative water loss in *F. vesiculosus* at 26.3°C amounted to about 70% after 90 to 100 min exposure. The rate of water loss at this temperature then decreased slowly until the total water lost at 140 min was about the same as at 32.1° and 39.3°C. Desiccation at 17.6°C occurred less rapidly, amounting to only 50% after 150 min. The cumulative water loss after 150 min at 13.7°C amounted to 30%, compared to 40% for *A. nodosum* ecad *scorpioides* at 13.1°C (see Fig. 3a). Cumulative water loss in *F. vesiculosus* at high temperatures (25° to 40°C) was greater than that for *A. nodosum* ecad *scorpioides*, probably due to the fact that the thin, flat and broad fronds of *F. vesiculosus* provide a greater surface area per unit weight than the thicker, round fronds of *A. nodosum* ecad *scorpioides*. The water losses for *F. vesiculosus* at lower temperatures were lower than those of *A. nodosum* ecad *scorpioides* because the fronds of *F. vesiculosus* tended to collapse after a period of approximately 1 h in the chamber, thereby retaining water between the blades.

Photosynthesis of Fucoids in Air

Photosynthesis of *Ascophyllum nodosum* ecad *scorpioides* in air at different temperatures is characterized by Fig. 4a. Fig.4 presents data from two plants at temperatures between 13° and 27°C, within which the plants fixed between 0.9 and 1.4 mg C/g dry weight/h. It would appear that photosynthesis increases between 13° and 23°C, after which a decline may occur. This apparent inhibition of photosynthesis at higher temperatures is not necessarily caused by temperature alone. The numbered point-clusters indicate the sequence of data points collected during a typical 1 to 3 h experiment. Thus, Data Cluster 4 occurred near the end of the experiment and when the plant had dried out the most. This may be further illustrated by examining Fig. 5, where the data of the plants from Fig. 4 are plotted against cumulative percent water-loss. The data clusters in Fig. 5 naturally occur in a sequence from 1 to 4. Photosynthesis was highest at water losses of less than 25%. A decrease in photosynthesis occurred with an increase in water loss thereafter. This pattern was also noted in data obtained for 12 other *A. nodosum* ecad *scorpioides* plants used in similar experiments. It is evident that desiccation accounts for the deviation of Point Cluster 4 in Fig. 4b and the sharp negative response to temperature

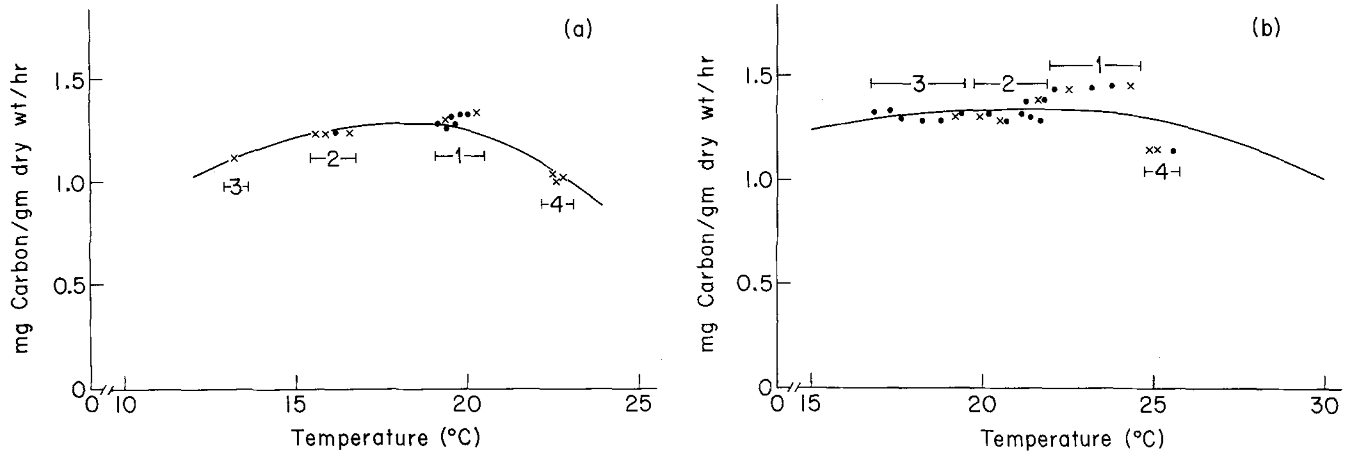

Fig. 4. *Ascophyllum nodosum* ecad *scorpioides*. Photosynthesis of 2 plants in air at various temperatures. Regression lines on these and subsequent figures represent least-squares fits to the function explained in text. In this and subsequent figures, single data-points are expressed as dots, whereas multiple points (two or more) within a small area are expressed by a cross. Note sequence of data clusters with the numbers referring to a time slot in the experimental incubation period. Data in (a) indicates distinctly different temperature conditions while (b) indicates gradual changing of temperature conditions

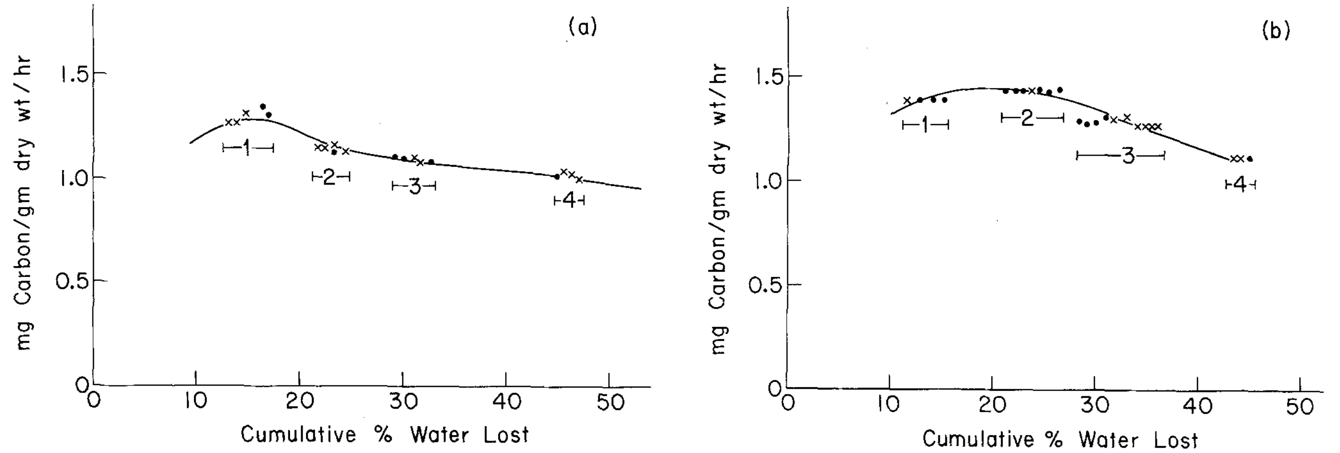

Fig. 5. *Ascophyllum nodosum* ecad *scorpioides*. Photosynthesis of plants from Fig. 4 in air at various cumulative % water losses. Note apparent differences in shape of the least-squares curves of (a) and (b) and sequence of data clusters corresponding to time slots in the experiments. Cluster 1 occurred at beginning of experiment when plants had lost little water, and Cluster 4 at end of experiment when plants had lost approximately 45% of their original water content

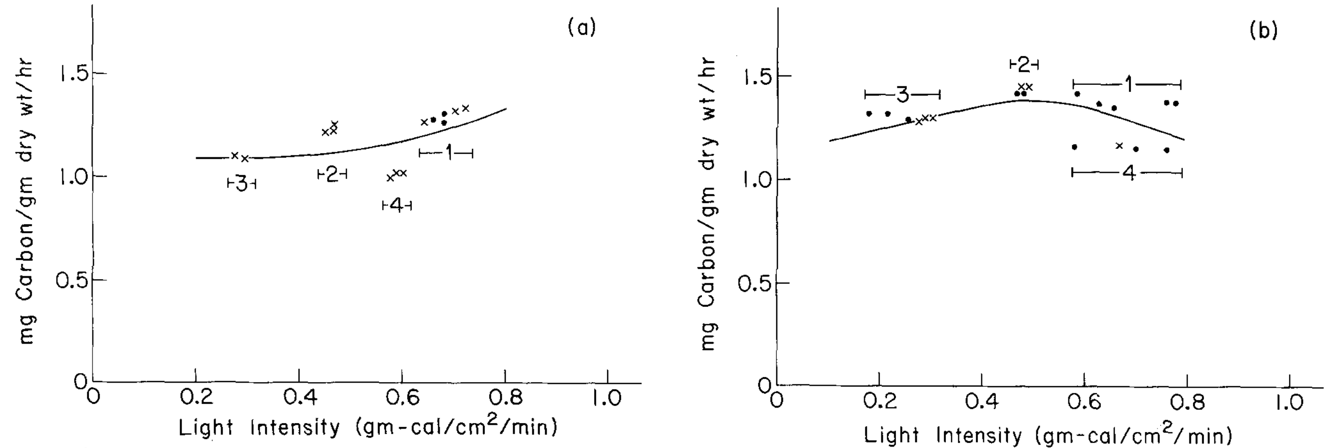

Fig. 6. *Ascophyllum nodosum* ecad *scorpioides*. Photosynthesis of plants from Figs. 4 and 5 in air at various light intensities. Note differences in shape of least-squares fit lines and relative positions of Data Cluster 4 in same range of light intensities as Cluster 1 (a) and at slightly lower light intensities (b)

of Cluster 4 in Fig. 4a. The same data points plotted against light intensity data (Fig. 6) indicate that the same data cluster (4) occurring at high light-intensities has lower values than Cluster 1, which occurred at similar light intensities but at different times in the experiment. Data points in the two Number 1 clusters were obtained when plants had lost only about 15% of their water content upon exposure to air. A multiple linear regression performed on the data of these two plants resulted in the correlation half-matrix in Table 1. It may be noted that cumulative percent water-loss had the largest correlation with carbon fixation. The fact that this is a negative value supports the earlier observation that water loss inhibited photosynthesis. The ratio of the variance accounted for by the multiple linear regression versus the residual variance was highly significant ($P < 0.001$).

Table 1. *Ascophyllum nodosum* ecad *scorpioides* correlation coefficients for photosynthesis in air at different temperatures, light intensities, and levels of water loss. Coefficients were calculated from a multiple linear regression performed on data presented in Figs. 4 - 6

	CO_2	Temperature	Light intensity	Water loss
CO_2	1.000			
Temperature	0.211	1.000		
Light intensity	-0.008	0.529	1.000	
Water loss	-0.680	0.234	-0.251	1.000

The range of cumulative percent water-loss dealt with in the previous two *Ascophyllum nodosum* ecad specimens was only 0 to 48%. A decrease in photosynthesis was noted after a 25% water loss, but the algae did not exhibit strong photosynthetic inhibition resulting from desiccation. Fig. 7 depicts data for *A. nodosum* ecad plants which had undergone water losses up to 65%. The relative photosynthesis values for the specimen represented here were higher than in the previous examples. Photosynthesis in relation to temperature (Fig. 7a) indicated a response pattern similar to that observed in the data of Fig. 4; however, the data gathered near the end of the experiment (Cluster 4) in Fig. 7a was obtained at lower temperatures, and therefore appears to the left of the other data clusters. Some of the data points obtained in Cluster 2 were obtained at similar temperatures as those in Cluster 4; however, Cluster 4 values are considerably lower than Cluster 2 values. Apart from the desiccation effects noted in this and the previous data, photosynthetic responses to temperature are rather flat over the range studied (13° to 29°C). Desiccation affects photosynthesis at both ends of the temperature range investigated.

Photosynthesis of *Ascophyllum nodosum* ecads appeared to increase sharply between 0.16 and 0.23 g cal/cm^2/min light intensities (Fig. 7b). In the specimen represented in Fig. 7, the plant was exposed to low light intensities near the end of the experiment (Cluster 4), as opposed to high light-intensities at the end of the experiment. Data Clusters 2 and 4 (Fig. 7b) were obtained at nearly similar light intensities, but photosynthetic rates exhibited in Cluster 4 data, obtained when the plant had lost 59 to 61% of its initial water content, were considerably lower than the rates in Cluster 2 data points. The data in Cluster 2 were obtained when the plant had only lost 33 to 47% of its initial water content. Photosynthesis plotted against desiccation (Fig. 7c) indicates that a sharp drop in photosynthesis occurs at cumulative water losses of 55% or greater. A tapering-off of photosynthesis as water loss approaches this latter value may actually be observed in the data of Cluster 3, followed by a sharper drop in photosynthesis with greater water loss (Cluster 4). Such explicit inhibition of photosynthesis at water losses between 55 and 65% was observed in several plants which were monitored until they had lost up to 80% of the water initially present. At such high desiccation values, virtually no photosynthesis could be detected. Exclusion of the effects of desiccation on photosynthesis indicates that photosynthetic responses to light intensity were also quite flat.

Photosynthetic responses of *Fucus vesiculosus* to temperature, light intensity and desiccation (Fig. 8) indicated that rates of photosynthesis were quantitatively similar to those of *Ascophyllum nodosum* ecads, however, patterns of response were somewhat different. Photosynthesis of *F. vesiculosus* in air at various temperatures (Fig. 8a) indicates that patterns of net carbon fixation were similar over a range of 13° to 24°C, however, Data Cluster 1 values were lower than those in the other clusters. The points in Cluster 1 overlap the temperature range of points in Cluster 3. Furthermore, when the same data is plotted against light intensity (Fig. 8b), Clus-

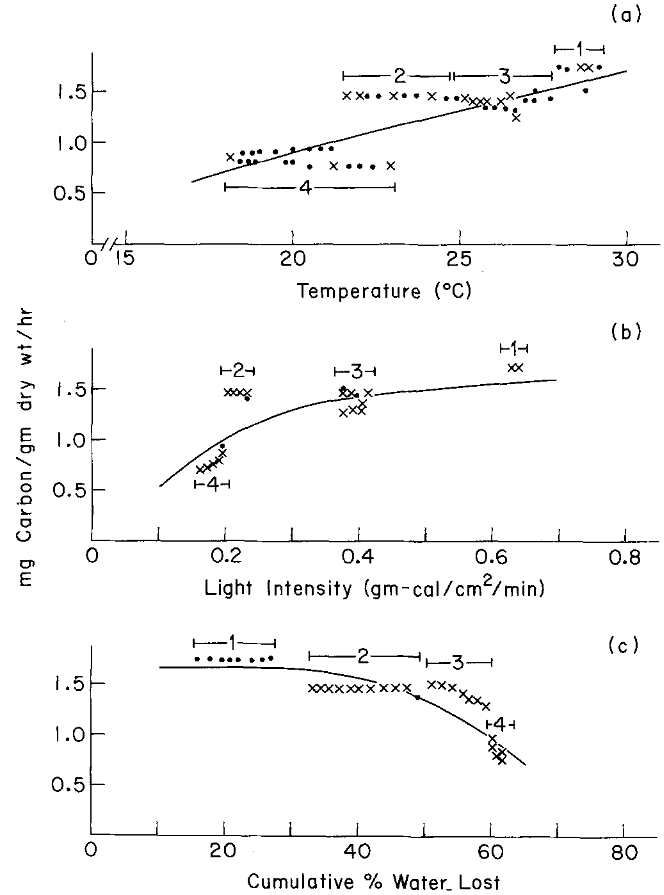

Fig. 7. *Ascophyllum nodosum* ecad *scorpioides*. Photosynthesis of plant in air at various temperatures (a), light intensities (b), and cumulative % water losses (c). Note that this plant was subjected to low temperatures and light intensities at end of experiment (Data Cluster 4) as opposed to the 2 plants in Figs. 4 - 6, which were exposed to high temperatures and light intensities at end of experiment. Note also tapering-off of photosynthesis in Cluster 3 as water losses approached 60% (c), and sharp drop in Cluster 4

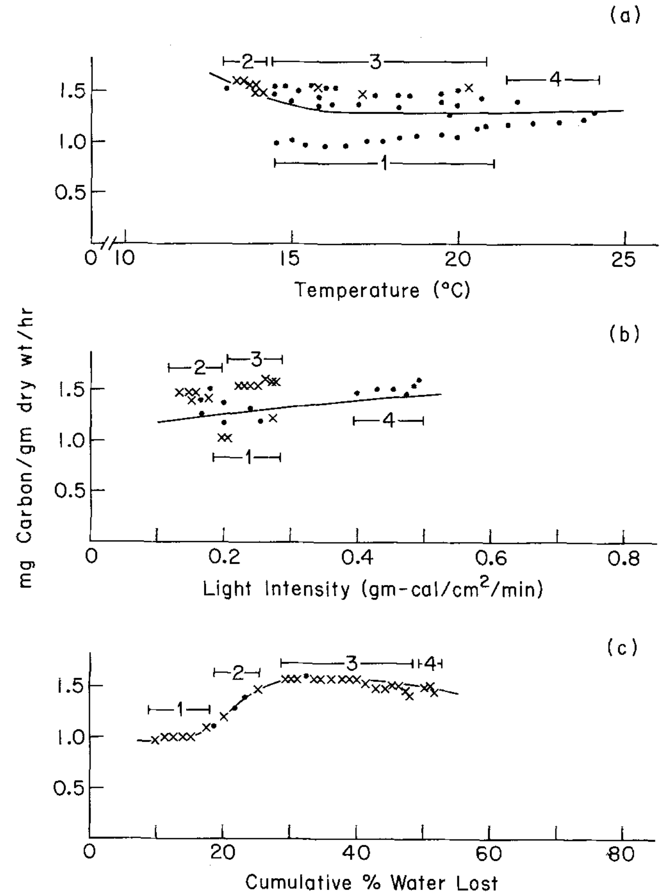

Fig. 8. *Fucus vesiculosus*. Photosynthesis of 3 specimens in air at various temperatures (a), light intensities (b), and cumulative % water losses (c). Note apparent increase in photosynthesis at low cumulative % water losses (c), and differences between Cluster 1 and Clusters 2 and 3 (a and b)

ter 1 data overlap the light intensity range encountered in the data of Clusters 2 and 3. The above data plotted against water loss (Fig. 8c) indicated that photosynthesis significantly increased with increasing desiccation up to a cumulative water loss of 25%. Above water losses of 25%, photosynthesis showed little effect of increasing desiccation up to at least 55% dehydration. The sharp increase in photosynthesis during low water loss was greater for *F. vesiculosus* than for *A. nodosum* ecads. As was the case for *A. nodosum* ecads, photosynthetic responses of *F. vesiculosus* to light intensity and temperature were flat and exhibited a wide range of adaptation. Water losses in excess of 60% resulted in decreased net CO_2-uptake.

Respiration of Fucoids in Air

Respiration experiments conducted in air and darkness at various temperatures and degrees of desiccation indicated that respiration of *Ascophyllum nodosum* ecads was somewhat influenced by temperature (Fig. 9a) in the range of 13° to 35°C. Maximum respiration rates for the 5 specimens depicted in this graph occurred in the data clusters of two of these plants (1 and 3), however, the values for the points in Cluster 1 were greater than those in Cluster 3. Cluster 1 data originated from a plant placed in the dark chamber when it still contained 90% of its normal wet weight water content. Since Clusters 1 and 3 were obtained from different plants, the difference be-

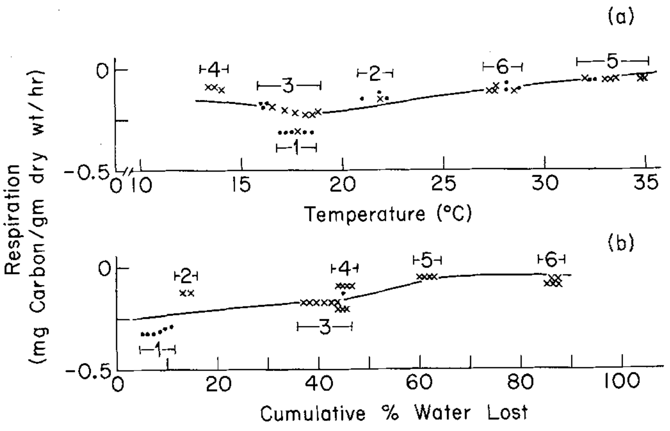

Fig. 9. *Ascophyllum nodosum* ecad *scorpioides*. Respiration of 5 specimens in air at various temperatures (a) and cumulative % water losses (b). In this instance, Clusters 1 and 6 originated from same plant, whereas Clusters 2 - 5 were from different plants. Note apparently minor influence of temperature on respiration, and the plant-to-plant variability between Clusters 1 and 2 at nearly identical water losses

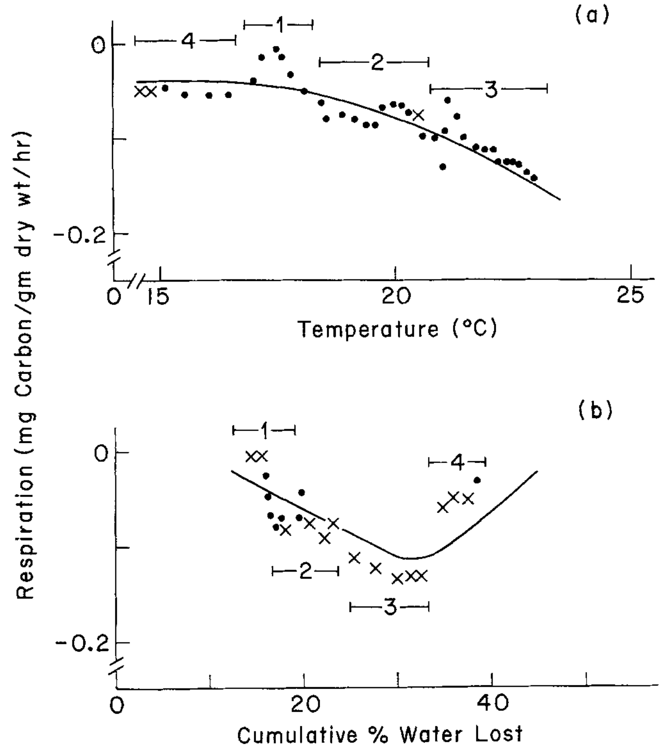

Fig. 10. *Fucus vesiculosus*. Respiration of specimen in air at various temperatures (a) and cumulative % water losses (b). Note reduction in respiration at 35 to 40% water losses

tween these two clusters may just be plant to plant variability. If Cluster 1 data is ignored, respiration responses to temperature (Fig. 9a) were very similar to responses to desiccation (Fig. 9b). Respiration increased from 0.12 to 0.20 mg Carbon/g dry weight/h until a water loss of 35 to 45% was reached. Respiration decreased at greater water losses. The values for respiration in these algae were approximately 5 to 15% of net photosynthesis.

The highest observed respiration rates of *Fucus vesiculosus* occurred at temperatures between 20° and 25°C (Fig. 10a). Furthermore, respiration increased with water loss (Fig. 10b) up to about 30%, beyond which it decreased. The highest observed respiration rates in *F. vesiculosus* (0.13 mg Carbon/g dry weight/h) were approximately 7 to 13% of net photosynthesis under similar temperature and water-loss conditions.

Discussion

Photosynthesis of the marsh fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus* in air remained at almost constant levels over a wide range of temperatures from 10° to 30°C, indicating a broad adaptation of the fucoids to these typical spring and winter *in situ* temperatures. Similarly, photosynthesis of these algae in air appeared to saturate rapidly and remain at constant levels over a wide range of light intensities from 0.2 to 0.8 g cal/cm^2/min. Populations of *A. nodosum* ecads and *F. vesiculosus* may be found in the salt marsh at Flax Pond in open areas along marsh banks and, in the case of *F. vesiculosus*, on top of bare mid-intertidal marsh flats (Brinkhuis, 1976; Brinkhuis and Jones, 1976). Light intensities in these habitats may reach summer maxima of 1.1 to 1.4 g cal/cm^2/min at low tide for a period of ± 3 h about the solar zenith. The greatest bulk of marsh fucoid biomass is encountered on the intertidal marsh flats dominated by the phanerogam *Spartina alterniflora* during May through November (Brinkhuis, 1976). *F. vesiculosus* may be found attached to shells of the ribbed mussel *Modiolus demissus*, which protrude from the mud and peat substrate, whereas

A. nodosum ecads may be found unattached but intertwined among the stalk bases of *S. alterniflora*. Light intensities impinging on these algae under the protective canopy of *S. alterniflora* are, therefore, dependent on the seasonal growth pattern and density of the latter. Light intensities at the base of *S. alterniflora* stalks during periods of maximum phanerogam density (July through October) reach values of 0.1 to 0.5 g cal/cm^2/min at low tide in the middle of the day. This range of light intensity is similar to the experimental range of intensities utilized in this study, and represents 15 to 45% of the surface irradiation encountered just above the *S. alterniflora* canopy. The rather flat, or similar, response of photosynthesis over a wide range of light intensities with water losses of less than 50% indicates that both species of fucoids studied here are broadly adapted to light intensity while exposed to the atmosphere.

Desiccation appeared to exhibit the most pronounced effect on photosynthesis when the fucoids lost more than 50% of their original wet-weight water content. A slight increase in photosynthesis was apparent up to a point when specimens had lost approximately 20% of their water content. This increasing trend of photosynthesis with increasing water loss may be related to the water loss from the surface of the fronds in the initial phases of desiccation, thereby enhancing exchange or detection of CO_2. Subsequent water loss due to desiccation of more interior tissues would tend not to interfere with gas exchange, i.e., photosynthesis, which probably primarily occurs at the surface of fronds. Furthermore, desiccation appeared to have a greater effect on respiration than on photosynthesis. The apparent sharp increase in respiration of *Fucus vesiculosus* at low levels of desiccation was as pronounced as similar increases in photosynthesis at low levels of desiccation. Respiration appeared to be inhibited at somewhat lower cumulative water losses (35 to 45%) as opposed to 55 to 65% water losses that were found to inhibit photosynthesis. The rates of evapo-transpiration determined for the plants incubated at various temperatures in the experimental chamber were somewhat higher than those normally encountered by the algal populations in the field during a 4 to 8 h exposure at low tide. The experimental chamber required air flow velocities of 2.5 to 3.0 l/min to reduce the lag in system response-time to CO_2 changes and, therefore, maintain close correlation with the instantaneous light intensity and temperature inputs. Weight losses due to a 4 to 8 h exposure to air normally does not exceed 50 to 60% for the bulk of the algae found under the protective canopy of *Spartina alterniflora* during June through October. Pringsheim (1923) indicated that desiccation rates of plant material are independent of the tissue water-content as long as there is no equilibrium between the water remaining in the tissue and atmospheric vapor pressure. Relative humidities near the mud surface under phanerogam canopies are higher than those in surrounding exposed environments and, therefore, tend to reduce desiccation of algal material under phanerogam stands (Zaneveld, 1937). Only the algal populations in open areas along marsh banks and on unprotected marsh flats may undergo water losses greater than 50%. Since the distribution patterns of *Ascophyllum nodosum* ecads are such that no plants are found on unprotected marsh flats in the mid-intertidal zone (Brinkhuis, 1976), it may be that desiccation plays a partial role in limiting distribution of *A. nodosum* ecads to protected environments and low intertidal regions where the duration of tidal exposure is short. *F. vesiculosus* is apparently able to inhabit exposed marsh flats to some extent, and this capacity may be partially related to the flattened morphological form of the alga which results in the bulk of the algal material being in contact with the substrate. Immediate contact with the substrate may result in water absorption from the moist mud surface. The three-dimensional growth form of *A. nodosum* ecads would appear to prevent access to water absorption from muddy substrates. It may also be noted that *F. vesiculosus* fronds collapsed to a greater degree at lower temperatures (13° to 17°C) than did fronds of *A. nodosum* ecads. As indicated earlier, exposed populations of salt-marsh fucoids constitute a minor portion of the total biomass in Flax Pond.

Conditions affecting evapo-transpiration from the substrate and algal material are altered during periods when *Spartina alterniflora* stands are absent (December through April). Algae inhabiting the marsh flats near the mid-intertidal regions are unprotected and are subjected to greater air-flow rates. Relative humidities near the substrate are lower than during summer periods when *S. alterniflora* is present. These two factors would tend to increase water-loss rates; however, the data presented here indicates that evapo-transpiration decreases with the lower temperatures that would certainly occur during the winter months. Naturally, unusually high temperatures during the winter and spring months would result in water losses equal to or greater than those experienced by the protected fucoids in the summer months. Insufficient data is available to evaluate the photosynthetic responses of fucoids to desiccation at normal winter temperatures (<10°C).

Earlier investigations by Stocker and Holdheide (1938) indicated that optimum photosynthesis in air of fully wet *Fucus vesiculosus* pieces was in the range of 6 to 7 mg $CO_2/dm^2/h$ (approximately = 2.5 mg CO_2/g dry weight/h) at 20,000 lux and 21° to 24°C. Photosynthesis of *F. vesiculosus* fronds exposed to air for some time, so that specimens had lost 20 to 30% of their water content, amounted to 7 to 8 mg $CO_2/dm^2/h$ under similar light intensity and temperature conditions. Since Stocker and Holdheide used fully wet fronds as an approximation of submerged conditions, exposed specimens had slightly higher photosynthetic rates than submerged fronds. When their optimum photosynthesis in air value is converted to mg Carbon/g dry weight/h, a value of approximately 0.7 is obtained. This latter value is near the range of values found for *F. vesiculosus* in the current investigation (0.9 to 1.7 mg C/g dry weight/h). Brown and Johnson (1964) and Imada *et al.* (1970) also found that photosynthesis in air was approximately equal to that occurring in water for various species of algae. Stocker and Holdheide (1938) reported that respiration in exposed *F. vesiculosus* fronds was approximately 3.00 mg $CO_2/dm^2/h$ at 21° to 22°C, with low degrees of water loss. Converted to mg CO_2/g dry weight/h (using the authors supplied dry-weight to surface-area ratios), this results in a value of 0.53, or 0.15 mg Carbon/g dry weight/h. The latter value is very similar to that found for *F. vesiculosus* in the current study (0.13). Stocker and Holdheide also indicated that both photosynthesis and respiration were more affected by desiccation than light intensity or temperature, and that *F. vesiculosus* collected from rocky shores was, therefore, broadly adapted to light intensity and temperature. Similarly, Newell and Pye (1968) found that respiration of a *Fucus* sp. under submersed conditions was relatively unaffected by temperature within the normal environmental range. No comparative data is available from the literature for *Ascophyllum nodosum* ecads.

Recently, Johnson *et al.* (1974) reported that the maximum photosynthetic rate of *Fucus distichus,* measured in air with a CO_2 analyzer at 43,000 lux and 15°C, was about 1.58 mg C/g dry weight/h. This photosynthesis value is similar to those found for *F. vesiculosus* in the current study; however, the former authors noted that photosynthesis in air was approximately 6 times greater than that occurring under submerged conditions (0.25 mg C/g dry weight/h) at similar light intensities and temperatures. The values obtained for submerged conditions by Johnson *et al.* appear to be an order of magnitude lower than those reported by Ehrke (1931) for *F. serratus* at 3200 lux and 10°C, and are even lower than those reported by Kanwisher (1966) for *F. vesiculosus* (ca. 17 mg C/g dry weight/h) at 4000 ft-candles and 20°C.

In conclusion, the results of the current investigation indicate that for the marsh fucoids *Ascophyllum nodosum* ecad *scorpioides* and *Fucus vesiculosus,* photosynthesis in air is not significantly affected by light intensity, temperature, or desiccation over a wide range of these parameters. Desiccation had the most pronounced effect on photosynthesis and respiration when plants had lost more than 50% of the wet-weight water content. These fucoids, which inhabit the middle intertidal regions of salt marshes, appear to be quite capable of carrying on net photosynthesis and, therefore, growth under exposed conditions. The suggestion by Baker and Bohling (1916) that tidal exposure may limit, or influence, growth in marsh fucoids appears doubtful. In this regard, we support the earlier conclusions by Johnson *et al.* (1974) that exposure cannot be regarded strictly as periods of extreme physical stress which are simply tolerated.

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