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Effect of Boundary Layer Transport on the Fixation of Carbon by the Giant Kelp *Macrocystis pyrifera*

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Abstract

The uptake of inorganic carbon into the thallus of *Macrocystis pyrifera* (L.) C. Ag. requires first that the inorganic carbon pass through the water medium to the plant surface. This transfer of inorganic carbon to the thallus must take place through a boundary layer. Experiments in water tunnels indicate that the boundary layer adjacent to the *M. pyrifera* blade may be turbulent in water speeds as low as 1 cm sec^{-1}. Photosynthetic output of the blade can be increased by a factor of 300% by increasing water speeds over the blade surface from 0 to 4 cm sec^{-1}. This is consistent with a decrease in the thickness of the boundary layer. Above 4 cm sec^{-1}, the assimilation of carbon was limiting. The assimilation of carbon is generally known to follow Michaelis-Menten-like kinetics. Combining the two uptake steps into an overall model of carbon uptake agrees well with photosynthetic data obtained from *M. pyrifera* under varying conditions of water speed and bicarbonate concentrations in the laboratory. The ecological and morphological consequences of these findings are discussed.

Introduction

The overall rate of photosynthesis depends on the rates of light absorption, electron transfer and the fixation of carbon. The latter is in turn governed by a complex series of interactions between biological and environmental variables. The fixation of carbon in the dark depends upon the molecular transport of CO_2 through the external fluid, cell wall, membrane and cytoplasm to the sites of carbon fixation. Molecular transport to these sites is governed by the physical properties of the fluid and the plant.

The greatest transport distance is through the boundary layer, which is a thin layer of fluid through which momentum, heat and mass are transported from the fluid stream to the plant surface. The metabolic functions of algae may, then, be enhanced by decreasing this transport distance. This can be accomplished by adding substrate to the culture vessel (Emerson and Green, 1934; Tseng and Sweeney, 1946; Falco *et al.,* 1975), which increases the concentration gradient, or by increasing the water motion around the plant, thereby decreasing the boundary layer thickness (Munk and Riley, 1952; Ambühl, 1959; Schumacher and Whitford, 1965; Westlake, 1967; Conover, 1968; Schwenke, 1971; Pasciak and Gavis, 1974; Dromgoole, 1978; Lehman, 1978).

The purpose of this study was to determine the effect of the boundary layer resistance on the apparent photosynthetic rate of blades of the giant kelp *Macrocystis pyrifera* (L.) C. Ag., and to try by direct measurement to model the effects of the boundary layer resistance on the photosynthetic rate. New methods were developed in the laboratory to measure the effect of water flow rates on the photosynthetic oxygen production. These, along with measurements of water flow rates in the sea, made it possible to estimate the effect of water motion on the photosynthetic productivity of the giant kelp in its natural habitat.

Materials and Methods

A system of storage jars was used for the productivity measurements. Water motion in this jar system was provided by Teflon stirring bars which were rotated from beneath by a magnet. 6 magnets (1 for each jar) were all connected to a single motor through a pulley system. The speed of rotation was varied by changing the size of the drive pulley (see Wheeler, 1980b). Water speeds in the jars were measured using a hot wire anemometer (Thermosystems Inc. Model 1053 Bl with a 1269 NaCl probe). Using a very fine thread attached to the probe housing, the 3-dimensional pattern of the water movement around the plant discs (8 cm diameter) in the jars was mapped. The probe was then positioned in the jars

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Table 1. *Macrocystis* sp. Constants and variables used in determining potential effect of water motion on kelp photosynthetic productivity

Symbol	*Definition*	*Units*	*Value*	*Source*
C	Inorganic carbon concentration in free stream	$mol\ l^{-1}$	$2\ mmol\ l^{-1}$	Sverdrup *et al* (1942)
C_f	Local skin-friction drag coefficient		Variable	Levich (*k*), (1962)
C_o	Inorganic carbon concentration at thallus surface	$mol\ l^{-1}$	Variable	
D	Diffusion constant	$cm^2\ sec^{-1}$	$2.4 \times 10^{-5}\ HCO_3^-$ $1.7 \times 10^{-5}\ O_2$	Leyton (1975)
J	Photosynetic flux	$mol\ cm^{-2}\ h^{-1}$	Variable	
K_s	Half-saturation constant	$mol\ l^{-1}$	Variable	
K_s'	Half-saturation constant, whole process	$mol\ l^{-1}$	Variable	
P	Diffusion parameter	$mol\ l^{-1}$	Variable	
R	Boundary-layer resistance	$sec\ cm^{-1}$	Variable	
Re_x	Reynolds number		Variable	Leyton (1975)
Sc	Schmidt number		522	Leyton (1975)
T	Diffusion boundary-layer thickness	cm	Variable	
T_l	Laminar diffusion boundary-layer thickness	cm	Variable	
T_t	Turbulent diffusion boundary-layer thickness	cm	Variable	
U	Water speed (velocity)	$cm\ sec^{-1}$	Variable	
U_P	Critical water speed (velocity)	$cm\ sec^{-1}$	Variable	
V_m	Maximum uptake rate constant	$mol\ O_2\ cm^{-2}\ h^{-1}$	Variable	
X	Half mean length of kelp blade	cm	25 cm	
Y	General boundary-layer thickness	cm	Variable	

so that the movement of the water around the kelp blade discs could be measured in the direction of the flow vector. The x and y vectors were monitored with the probe inserted from the top of the jar. The z directional vectors were more difficult to measure. For these, a wax replica of the jar was made which was then used to mold a jar of the same dimensions from casing resin. Holes could then be easily drilled from the side to position the probe. The mean velocity at 18 equally spaced positions within the jar over the blade surface was then estimated. The average speed of the water was then calculated from the mean value of the 18 vectors. The water speeds over the blades in the jars varied as follows: still water ($0\ cm\ sec^{-1}$), 1.6 ± 0.5, 3.2 ± 0.5, 4.9 ± 0.8, and 7.0 ± 1.0 $cm\ sec^{-1}$. The flow pattern over the blade in the jar is different, of course, from that in the water tunnels.

The water tunnel used for the data presented below was a modification of the system described by Wheeler (1980a). The working section of the tunnel was set up so that dye could be injected into the main stream of the water flow ahead of either flat plates or sections of *Macrocystis pyrifera* (L.) C. Ag. blades. Water velocity through the working section of the tunnel was varied by means of a rheostat on the driving pump.

Whole fronds of *Macrocystis pyrifera* were collected from November to April in the vicinity of the University of California at Santa Barbara (U.C.S.B.), and within 30 min were returned to the laboratory where they were maintained in a flowing seawater tank for not more than 48 h. Blades were selected, cleaned of visible epiphytes, and discs of about 8 cm diameter were cut from the basal portion. The discs were then preconditioned to experimental regimes for about 10 min. Apparent photosynthetic rates were determined by the Winkler technique (Strickland and Parsons, 1972).

Measurements were made of photosynthesis under varying water speeds and total dissolved inorganic carbon (DIC) concentrations. The DIC concentration of the seawater was modified by first removing the DIC by acidification to pH2 or below with HCl, and then bubbling nitrogen through the water overnight to remove the gaseous CO_2. The pH was then elevated to 8.1 with the addition of NaOH under nitrogen. Inorganic

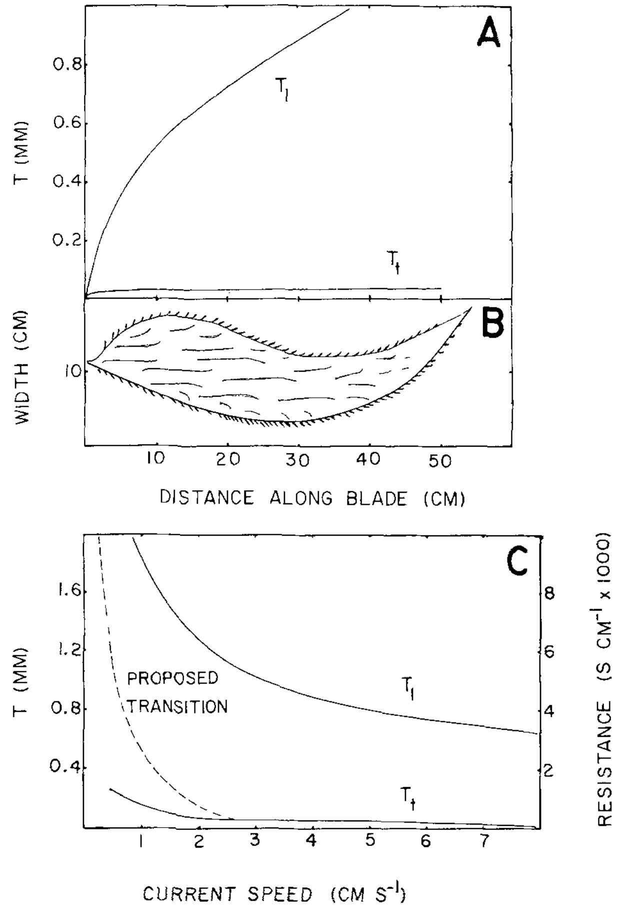

Fig. 1. *Macrocystis* sp. Theoretical curves based on Eqs. (3)–(6) for boundary layer thicknesses (T) and diffusion resistances. (A) Diffusion boundary-layer thickness over a kelp blade with a water flow rate of 5 cm sec^{-1}; the laminar boundary layer thickness (T_l) and the turbulent boundary layer thickness (T_t) are computed from Eqs. (3)-(6). (B) Drawing of kelp blade. (C) Laminar (T_l) and turbulent (T_t) diffusion boundary-layer thicknesses at a point 25 cm along the blade, plotted for different water velocities; boundary layer resistance to the diffusion of bicarbonate is calculated on the right; dashed line is estimated transition from laminar to turbulent boundary layer

carbon was added back to the jars in the form of $NaHCO_3$, and the resultant inorganic carbon concentration and pH were measured by the methods of Strickland and Parsons (1972). The calculated concentrations were found to agree well (± 10%) with the amounts measured. Salinity varied by less than 2 ‰.

Results

The boundary layer enhances the transport of molecules to a plant surface by adding convective to conductive transport. However, biologists prefer to view the boundary layer as a "resistance" to the transport of molecules to biological surfaces (Nobel, 1974).

The concept of resistance is taken from electrical terminology. The resistance of a circuit is the voltage divided by the current (Ohm's Law). In biological terms, this means that the resistance (R) of the boundary layer to the passage of a particular molecule is the concentration gradient developed between the fluid stream and the plant surface divided by the rate at which these molecules move through the boundary layer. Thus,

$$R = (C - C_0)J^{-1}; \tag{1}$$

(see Table 1 for explanation of variables and constants). The flux, J, of a molecule through the boundary layer can be estimated from Fick's First Law assuming an ideal, laminar fluid:

$$J = D\,dC\,dY^{-1}. \tag{2}$$

The diffusion constant, D, depends upon the volume of the diffusing molecule and the viscosity of the fluid in which it is diffusing (Stokes Law; Leyton, 1975). In air, oxygen and carbon dioxide have diffusion constants on the order of 10^{-1} cm^2 sec^{-1}, while in water, these same molecules have the constants of 1.7 and 2.4 x 10^{-5} cm^2 sec^{-1}, respectively. Solutions of the diffusion equation (Nobel, 1974) show that this difference in the diffusion constant results in much higher boundary-layer resistances for plants living in water than for those living in air (Raven, 1970).

Model

Assuming that a *Macrocystis pyrifera* blade is 2-dimensional, with a zero pressure gradient, and further assuming that the water movement in the ocean and that created in the laboratory contain low levels of turbulence, the following equation gives a rough approximation of the laminar diffusion boundary-layer thickness on such a blade (Levich, 1962),

$$T_l = 3\,Sc^{-1/3}\,Re_x^{-1/2}\,x. \tag{3}$$

If, on the other hand, the water motion contains high levels of turbulence, or the surface is not a 2-dimensional flat, smooth surface, the boundary layer may be turbulent. In such a case the diffusion thickness can be approximated by the relation (Levich, 1962):

$$T_t = 1.41\,a\,C_f^{-1}\,Sc^{-1/4}\,Re_x^{-1}\,X, \tag{4}$$

where a is an experimental constant determined to be close to unity (Levich, 1962). The local skin-friction drag coefficient, C_f, is estimated (under conditions of a 2-dimensional, flat, smooth surface with a zero pressure gradient) to be,

$$C_f = 0.32\,Re_x^{-1/4}. \tag{5}$$

Thus, the turbulent diffusion boundary-layer thickness becomes:

$$T_t = 2.49\,Sc^{-1/4}\,Re_x^{-7/8}\,X. \tag{6}$$

This thickness is shown to vary with both the distance (Fig. 1) along a theoretical *Macrocystis* sp. blade (shown in Fig. 1B) and with water speed (Fig. 1C).

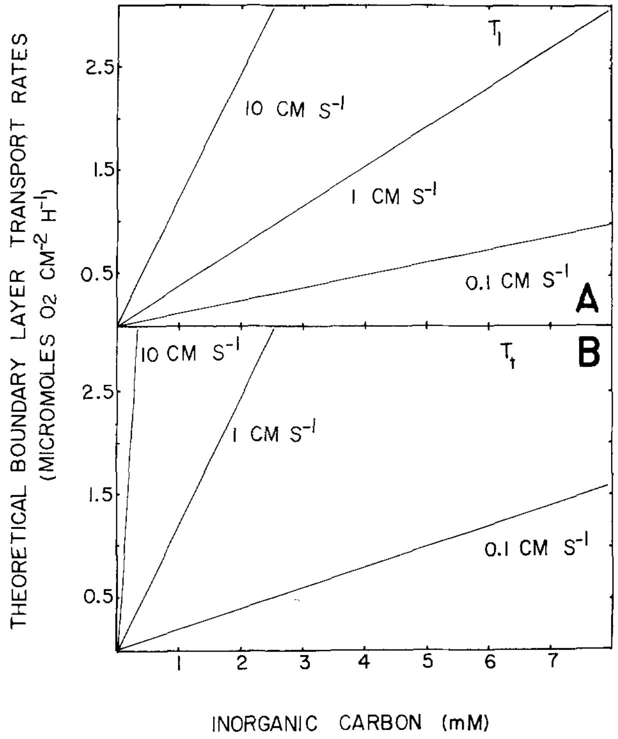

Fig. 2. *Macrocystis* sp. Calculated rates (Eq. 8) of boundary layer transport through laminar (A) and turbulent (B) boundary layers, expressed as oxygen evolved through photosynthesis

The resistance equation (1) can be rewritten as

$$R = TD^{-1}, \tag{7}$$

and T_t or T_l substituted for T. Further,

$$J = D(C - C_0)T^{-1} = (C - C_0)R^{-1}, \tag{8}$$

from Fick's First Law, assuming an ideal, laminar fluid. T and R can be either laminar or turbulent or in a state of transition. The resultant flux, J, or calculated boundary-layer transport rate is shown in Fig. 2 using both the laminar (Fig. 2A) and the turbulent (Fig. 2B) boundary-layer equations. It can be seen that the uptake of inorganic carbon by *M. pyrifera* should increase as water speed is increased, and further increase if the boundary layer is turbulent.

However, it is not realistic to assume that the uptake rate remains linear. At a certain speed, the enzymatic uptake systems of the plant will become saturated and show no further response to water speed. The chemical process of carbon fixation has been described in the form of the Michaelis-Menten equation, which is used here only in the operational sense and does not imply any particular knowledge of the actual mechanism;

$$J = (V_m C_o)(C_o K_s)^{-1}. \tag{9}$$

The relationship between boundary-layer flux and enzymatic flux has been described in detail elsewhere for land plants (Lommen *et al.*, 1971), for phytoplankton (Gavis, 1976) and for larger algae (Dromgoole, 1978), with the result that:

$$J = [(C + K_s + RV_m) - ([C + K_s + RV_m]^2 - 4RCV_m)^{1/2}]\,2R^{-1}. \tag{10}$$

The uptake of inorganic carbon by an aquatic plant such as *Macrocystis pyrifera* should then be determinable for a given DIC concentration, C, by knowing R, V_m and K_s. R, resistance, is dependent upon the condition of the boundary layer and the water speed.

Boundary Layer Structure

Dye-stream photographs (Fig. 3) taken in a water tunnel help to visualize the character of the boundary layer under low velocity flows. Streamlines over a smooth, flat plate (Fig. 3A) are smooth and linear, while these same lines over a segment of *Macrocystis pyrifera* blade (Fig. 3B) indicate a possible turbulent vorticity with a

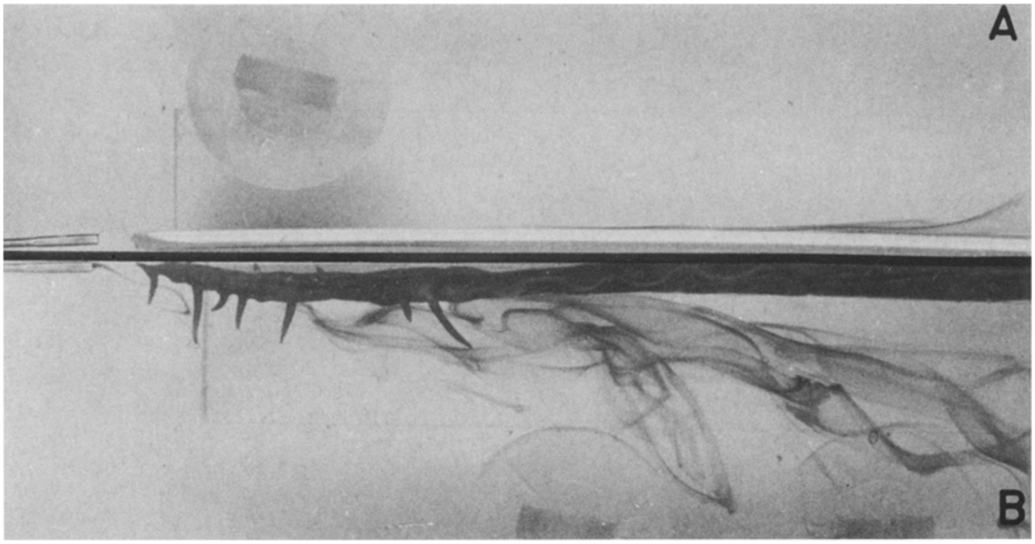

Fig. 3. Dye streams injected upstream of a flat plate (A) and a *Macrocystis pyrifera* blade (B) reveal laminar and turbulent boundary layers. Water flow is from left to right at a velocity of 2 cm $\sec^{-1}$

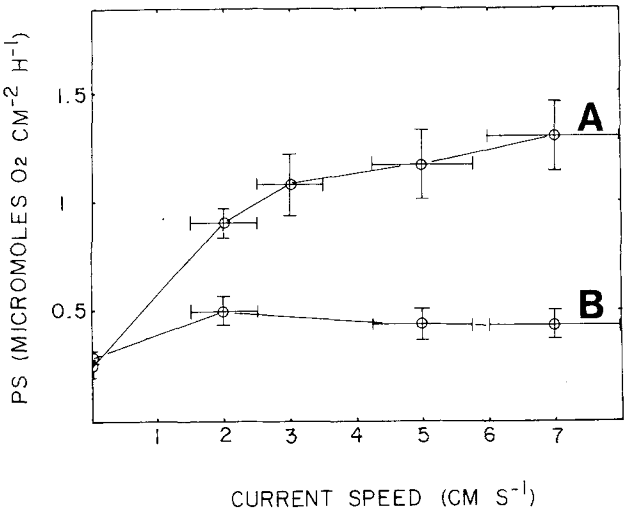

Fig. 4. *Macrocystis pyrifera.* Photosynthetic oxygen production (*PS*) as a function of water speed. Upper curve (A) shows production under saturating quantum irradiance of 125 μmol m^{-2} sec^{-1}, while lower curve (B) shows production rates under a low quantum irradiance of 25 μmol m^{-2} sec^{-1}. Means ± standard deviation for 5 plant discs are shown.

flow separation probably caused by leading edge spines and corrugations on the blade surface. Further experiments using a water tunnel system developed by Fletcher (1974) have established that the rough surface of the *M. pyrifera* blade produces a turbulent boundary layer with water speeds as low as 1 cm sec^{-1}.

Photosynthetic Rate Measurements

The apparent photosynthetic rate of blades of *Macrocystis pyrifera* varies with the speed of the water moving past them (Fig. 4). In an experiment from November, oxygen production increased from 0.3 μmol O_2 cm^{-2} h^{-1} when water was not stirred to 1.3 μmol O_2 cm^{-2} h^{-1} when the water speed was 7 cm sec^{-1}, with most of the change taking place within the range 0 to 3 cm sec^{-1}. When the quantum irradiance was dropped below saturation (Fig. 4, Curve B), no such response was found; rather, water speed had little or no effect, the photosynthetic rate varying from 0.3 to 0.4 μmol O_2 cm^{-2} h^{-1} over the range 0 to 7 cm sec^{-1}.

Fig. 5A shows the apparent photosynthetic rate when both DIC and water speeds were below saturation. Both an increase in water speed (from unstirred to 3 cm sec^{-1}) and DIC (from 0 to 5 mmol l^{-1}) enhanced the photosynthetic rate, with the highest rate being found with the highest speed and the highest DIC concentration and the lowest with the lowest of these parameters.

To find the V_m and K_s, the relationship between DIC and apparent photosynthesis must be measured under saturating water speeds. Fig. 5B shows this relationship; when linearized as a C versus C/J plot (not shown), the extrapolation of the x intercept gives the $-K_s$ value and the slope gives the $V_m{}^{-1}$. Thus, in January, the V_m for an isolated blade was estimated to be 1.51 μmol O_2 cm^{-2} h^{-1}, with a K_s of 1.4 mmol l^{-1}. However, the value of V_m was variable and dependent not only on the age of the tissue (Wheeler, 1980b) but also on the season (own unpublished data). Thus, values of V_m measured during April were much higher, (2.34 μmol O_2 cm^{-2} h^{-1}), with a correspondingly higher K_s (3.4 mmol l^{-1}).

The model (Eq. 10), when used with the turbulent boundary-layer equations (Eqs. 6 and 7) and supplied with the kinetic constants here derived from the January data and graphed over the same range as the data in Fig. 5, produced the curves shown in Fig. 6. These results should be directly comparable to the data in Fig. 5, and indeed show a close correlation. The use of the laminar boundary-layer equations (Eqs. 3 and 7) produces a similar curve, but the correlation with the data is not as good. This points out the almost overwhelming influence of the enzyme kinetics on the overall reaction, although the lower the water speed, the greater the influence of water speed on boundary layer structure.

Discussion

The hyperbolic relationship between water motion and photosynthesis for *Macrocystis pyrifera* expressed in Fig. 4 is the result of an interaction between the boundary layer resistance and the enzyme uptake properties of the plant. Such a relationship can be modeled using a modified Michaelis-Menten type equation. In such a case, the K_s' (the half saturation constant for the entire process diffusion and uptake) is shown to be influenced by water motion, and the V_m, by the plant's ability to take up inorganic carbon. This is reasonable, since the V_m might be interpreted in a biochemical sense as being solely dependent on the number of uptake sites and the turnover rate of the system. The K_s' might in turn be interpreted as being dependent on the availability of the diffusing molecule, which is partially controlled by the boundary layer. The result is that care should be taken in utilizing these constants in an ecological context as has been done for some phytoplankton populations (Eppley *et al.*, 1969) and some larger algae (D'Elia and DeBoer, 1978).

Since the value of K_s' is responsive to the boundary layer resistance, the uptake rate will approach 0 as the resistance approaches infinity; and as the resistance approaches 0, the uptake rate will approach that defined by the enzyme kinetics. There must be some arbitrary point at which the transport of DIC through the boundary layer no longer plays a significant role in the overall uptake process and is limiting to *Macrocystis pyrifera*. Here, this arbitrary value will be set at the value of R, for which $C_o = 0.95\ C$ or $(C - C_o) = 0.1$ for a C of 2 mmol l^{-1}. The diffusion resistance, however, also depends upon the magnitude of J. Thus, the value of R if it is to be applicable to any J must be incorporated into a parameter that is independent of J. This is accomplished by defining a "diffusion parameter",

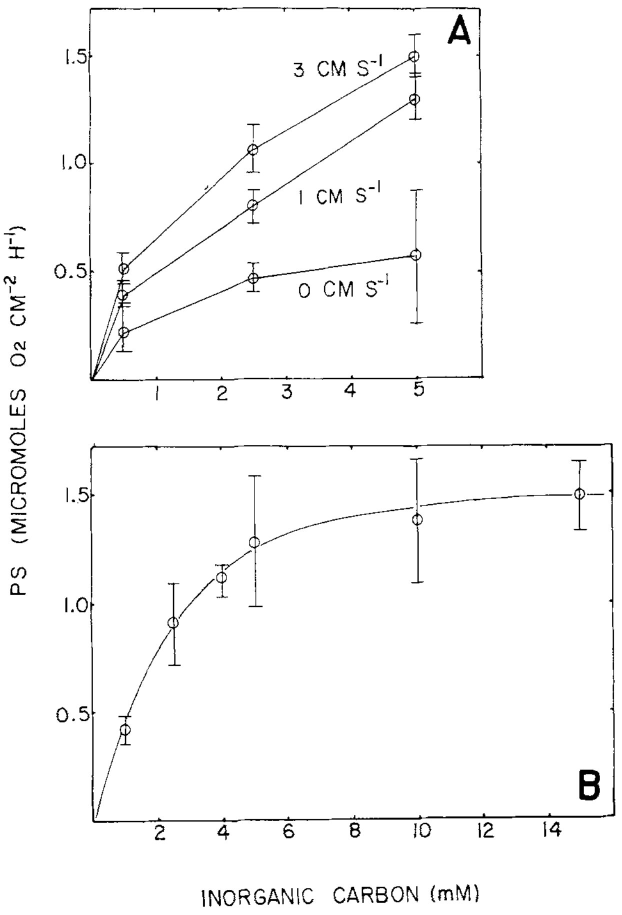

Fig. 5. *Macrocystis pyrifera.* Photosynthetic oxygen production (*PS*) as a function of inorganic carbon concentration (mmol l^{-1}). Upper curves (A) show effect of non-saturating water speed on plant discs under non-saturating concentrations of dissolved inorganic carbon; lower curve (B) shows effect of concentration under saturating water motion (7 cm sec^{-1}). Means ± standard deviation for 15 plant discs are shown

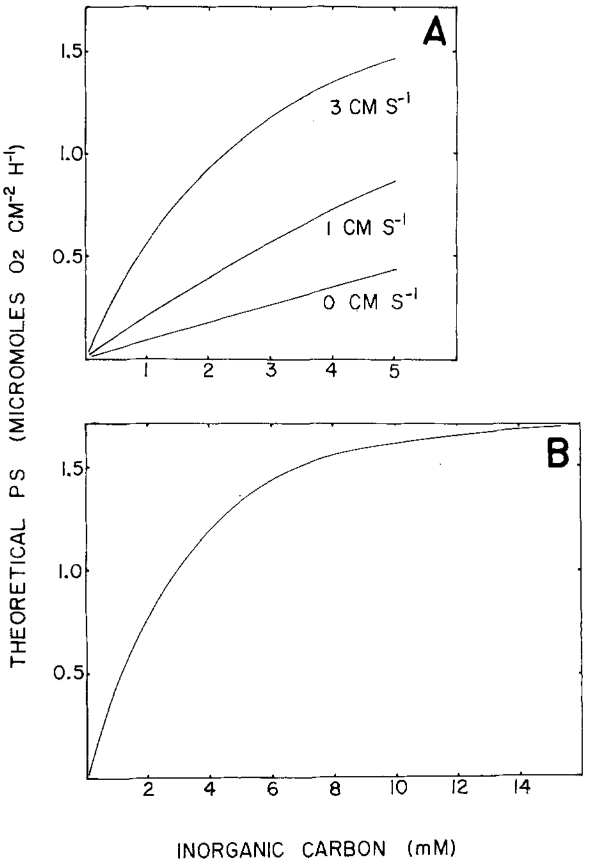

Fig. 6. *Macrocystis* sp. Theoretical photosynthetic rate (*PS*) expressed as O_2 production as a function of dissolved inorganic carbon; curves were calculated from Eq. (10). Upper curves (A) show effect of non-saturating current velocities, while lower curve (B) is calculated for saturating water velocity, over same range as in Fig. 5

$$P = V_m R, \tag{11}$$

similar to those developed by Pasciak and Gavis (1974) and Thornley (1976). This value of P for which the boundary layer transport becomes significant can be determined if the value of J is replaced by its maximum value, V_m. Thus:

$$R = (C - C_0)J^{-1} = 0.1\ J^{-1} \text{ and}$$

$$P = RV_m = 0.1\ V_m\ V_m{}^{-1} = 0.1.$$

The critical value of P is therefore 0.1. A J of less V_m would tend to increase R. Increased R would tend to increase P, so that a P greater than 0.1 would indicate a diffusion-limited (mass-transport limited) process.

Using Eqs. (4) and (7), R can be solved in terms of U to determine the maximum velocity for which the boundary layer transport is significant ($C - C_0 = 0.1$), by assuming that J has its maximum value, V_m (given in Fig. 5B) and using a "representative distance" along the blade, X, of 25 cm to calculate an average boundary-layer thickness. This saturation point velocity, U_p, varies as the V_m varies, between a low of 3.6 cm sec^{-1} and a high of 6 cm sec^{-1} as V_m varies from 1.5 to 2.3 μmol O_2 cm^{-2} h^{-1}. Direct measurement of the photosynthetic oxygen output as a function of water speed (Fig. 4), indicates that actual values of U_p lie within the predicted region. The uptake of molecules other than inorganic carbon also show U_p values within the predicted ranges (Wheeler, in preparation).

The influence of the V_m on the U_p further reinforces the importance of the cellular uptake kinetics. However, the lower the water motion surrounding the plant, the greater the influence of the boundary layer becomes. Within this region of influence, turbulence can have a stimulating effect on the uptake process, and for this reason, a discussion of it is in order.

Experiments (Schlichting, 1968) have shown that the transition on a flat, smooth semi-infinite plate in flows having a low inherent level of turbulence and a zero pressure gradient takes place at Reynolds numbers on the order of 10^5. However, transitions have been observed to take place several orders of magnitude lower if the laminar boundary layer is disrupted by effects such as surface roughness, leading edge irregularities, or high levels of inherent flow turbulence (Schlichting, 1968). These effects as well as 3-dimensional effects such as the proximity of turbulent boundary layers in the center to the flow along the edge of the *Macrocystis pyrifera* blade probably account for the observed turbulent boundary layers at Reynolds numbers of 10^4 or lower (Charters, 1940). *Macrocystis* spp. live in many locations in relatively quiet waters that have low water motion, as will be discussed later. Its morphology would probably become less useful under more turbulent water motion conditions.

Pace (1972) has compared the morphology of the blades of *Macrocystis integrifolia* Bory from high- and low-turbulence habitats. He found the morphology to be variable. Under more turbulent conditions, the blades were thicker (due to a thicker cortex), and more rugose, with marginal spines assuming an acute angle to the blade edge. In contrast, blades under calm conditions, i.e., diffusion stress, were more likely to be thinner as diffusion distances to cortical and meristodermatic chloroplasts were decreased. Rugosity both increases rigidity and increases surface roughness (roughness is already so great that this probably adds little), while spines lying closer to the turbulent-condition blade margin would reduce the spoiler effect and reduce drag. It would appear from Pace's observations and the present study that the morphological changes which occur in kelp blades under differing water-motion regimes can at least in part be explained as hydrodynamic adaptations.

Near the mainland coast the currents in and near the kelp beds are low. The Marine Review Committee (Connell *et al.*, 1977) working at San Onofre (California, USA), had continuous current measurements made for a 2 month period in late summer near a typical coastal kelp bed. The currents generally followed a tidal rhythm, and were quite low: 52% of the time the currents near the surface were less than 10 cm $\sec^{-1}$, 32% of the time less than 6 cm $\sec^{-1}$, and 20% of the time less than 4 cm $\sec^{-1}$. In another study, Bray (1978) followed the currents on Naples Reef about 8 km north of U.C.S.B. From 39 observations on the reef, the mean current speed entering the reef was 10.8 cm $\sec^{-1}$. Currents on the downside of the reef were significantly lower due to the resistance of the kelp. McFarland and Prescott (1959). Jackson (1976) and Wheeler (1980a) have recorded current speeds generally less than 5 cm $\sec^{-1}$ and frequently less than 1 cm $\sec^{-1}$ in Southern California coastal kelp beds. This picture of extremely calm forests is reinforced by diving observations, during which sediment frequently falls like dust when blades are disturbed.

In view of what is known about water velocities in kelp forests it can be assumed that diffusion resistance commonly influences the photosynthetic uptake rate and that the overall productivity of these forests is limited when water motion through them is less than 4 cm $\sec^{-1}$, which seems to occur quite frequently. Thus, it would seem logical to develop harvesting and planting strategies that would enhance the water flow through coastal kelp beds, so that their productivity is increased.

The morphological variations of the blades of *Macrocystis* spp. that have so confused systematists (Skottsberg, 1907) may well be important indicators to the ecologist of the prevailing environmental conditions in a given kelp habitat. These morphological variations are likely to represent adaptations to enhance the uptake of inorganic carbon and other macronutrients in slow-water-motion environments.

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Literature Cited

Ambühl, H.: Die Bedeutung der Strömung als ökologischer Faktor. Schweiz. Z. Hydrol. *21*, 133–264 (1959)

Bray, R. N.: Daily foraging migrations of the blacksmith, *Chromus punctipinnis*, Ph.D. thesis, University of California, Santa Barbara 1978

Charters, A. C.: Transition between laminar and turbulent flow by transverse contamination. Tech. Notes natn. advis. Comm. Aeronaut., Wash. *891*, (1940)

Connell, J. H., B. J. Mechalas and J. A. Mihursky (Eds): Analysis of the physical/chemical environment near San Onofre Nuclear Generating Station in September, October, 1976. Docums mar. Rev. Comm., mar. Sci. Inst., Univ. Calif., S Barbara *2* (77–06 3), 4–2, 4–99 (1977)

Conover, J. T.: The importance of natural diffusion gradients and transport of substances related to benthic marine plant metabolism. Botanica mar. *11*, 1–9 (1968)

D'Elia, C. F. and J. A. DeBoer: Nutritional studies of two red algae. II. Kinetics of ammonium and nitrate uptake. J. Phycol. *14*, 266–272 (1978)

Dromgoole, F. I.: The effects of oxygen on dark respiration and apparent photosynthesis of marine macroalgae. Aquat. Bot. *4*, 281–297 (1978)

Emerson, R. and L. Green: Manometric measurement of photosynthesis in the marine alga *Gigartina*. J. gen. Physiol. *17*, 817–842 (1934)

Eppley, R. W., J. N. Rogers and J. J. McCarthy: Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnol. Oceanogr. *14*, 912–920 (1969)

Falco, J. W., P. C. Kerr, M. B. Barron and D. L. Brockway: The effect of mass transport on biostimulation of algal growth. Ecol. Modelling *1*, 117–131 (1975)

Fletcher, J. S.: Visualization of flows around swimming fish using the hydrogen bubble and shadowgraph methods, 79 pp. M.S. thesis, University of California, Santa Barbara 1974

Gavis, J.: Munk and Riley revisited: nutrient diffusion transport and rates of phytoplankton growth. J. mar. Res. *34*, 161-179 (1976)

Jackson, G. A.: Nutrients and productivity of the giant kelp, *Macrocystis pyrifera*, in the near shore, 134 pp. PhD thesis, California Institute of Technology, Pasedena 1976

Lehman, J. T.: Enhanced transport of inorganic carbon into algal cells and its implications for the biological fixation of carbon. J. Phycol. *14*, 33-42 (1978)

Lommen, P. W., C. R. Schwintzer, C. S. Yocum and D. M. Gates: A model describing photosynthesis in terms of gas diffusion and enzyme kinetics. Planta *98*, 195-220 (1971)

Levich, V. G.: Physiochemical hydrodynamics, 700 pp. Englewood Cliffs: Prentice-Hall 1962

Leyton, L.: Fluid behaviour in biological systems, 234 pp. Oxford: Clarendon Press 1975

McFarland, W. N. and J. Prescott: Standing crop, chlorophyll content, and *in situ* metabolism of a giant kelp community in Southern California. Contr. mar. Sci. Univ. Tex. *6*, 109-132 (1959)

Munk, W. H. and G. A. Riley: Absorption of nutrients by aquatic plants. J. mar. Res. *11*, 215-240 (1952)

Nobel, P. S.: Biophysical plant physiology, 488 pp. San Francisco: W. H. Freeman 1974

Pace, D. R.: Polymorphism in *Macrocystis integrifolia* Bory in relation to water motion, Part I. 75 pp. M.S. thesis, University of British Columbia, Vancouver 1972

Pasciak, W. J. and J. Gavis: Transport limitation of nutrient uptake in phytoplankton. Limnol. Oceanogr. *19*, 881-888 (1974)

Raven, J. A.: Exogenous inorganic carbon sources in plant photosynthesis. Biol. Rev. *45*, 167-221 (1970)

Schlichting, J.: Boundary layer theory, 648 pp. New York: McGraw-Hill 1968

Schumacher, G. J. and L. A. Whitford: Respiration and ^{32}P uptake in various species of freshwater algae as affected by current. J. Phycol. *1*, 78-80 (1965)

Schwenke, H.: Water movement: plants. *In*: Marine ecology, Vol I. Environmental factors, Pt 2, pp 1091-1121. Ed. by O. Kinne. New York: Wiley-Interscience 1971

Skottsberg, C.: Zur Kenntnis der Subantarktischen und Antarktischen Meeresalgen. Phaeophyceen. Wiss. Ergebn. schwed. Südpolarexped. *4*, 1-172 (1907)

Strickland, J. D. H. and T. R. Parsons: A practical handbook of seawater analysis, rev. ed. Bull. Fish. Res. Bd Can. *167*, 1-310 (1972)

Sverdrup, H. V., M. W. Johnson and R. H. Fleming: The oceans, 1087 pp. Englewood Cliffs: Prentice-Hall 1942

Thornley, J. H. M.: Mathematical models in plant physiology, 318 pp. New York: Academic Press 1976

Tseng, C. K. and B. M. Sweeney: Physiological studies of *Gelidium cartilagineum*. I. Photosynthesis with special reference to the carbon dioxide factor. Am. J. Bot. *33*, 706-715 (1946)

Westlake, D. F.: Some effects of low-velocity currents on the metabolism of aquatic macrophytes. J. exp. Bot. *18*, 187-205 (1967)

Wheeler, W. N.: Laboratory and field studies of photosynthesis in the marine crop plant *Macrocystis*. Proc. int. Seaweed Symp. *8*, (in press). (1980a)

Wheeler, W. N.: Pigment content and photosynthetic rate of the fronds of *Macrocystis pyrifera*. Mar. Biol. *56*, 97-101 (1980b)

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