

In situ Water Motion and Nutrient Uptake by the Giant Kelp *Macrocystis pyrifera*

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Abstract

Rates of NO_3^- uptake by individual blades of *Macrocystis pyrifera* (L.) C. Agardh were measured at different flow rates in the laboratory. Dissolution rates of hemispherical, plaster buttons attached to the blade surface provided a relative measure of flow rates over blades used in uptake experiments and also over intact blades of adult kelp plants *in situ* (Laguna Beach, California, USA; 1981). Laboratory results indicated that uptake was saturated at a flow rate equivalent to 2.5 cm s^{-1} current velocity. Flow rates over intact blades *in situ* always exceeded this uptake saturation level. Wave surge and movement of plant surfaces relative to the surrounding water provided sufficient flow to saturate uptake, even in a dense kelp canopy during low-current and calm sea-state conditions.

Introduction

Nutrient uptake by aquatic macrophytes is influenced by water motion. An increase in flow rate up to some saturation level enhances uptake rate by accelerating nutrient transport through the diffusion boundary layer adjacent to the plant surface (Whitford and Schumacher, 1961, 1964; Schumacher and Whitford, 1965; Westlake, 1967; Wheeler, 1978, 1980). Transport is faster through turbulent than through laminar boundary layers, and thallus morphology influences the flow rate at which this transition occurs (Wheeler, 1980; Anderson and Charters, in press).

Water motion influences growth and production of marine macrophytes, especially when nutrient availability is low (Conover, 1968; Steever *et al.*, 1976; Gerard and Mann, 1979). Uptake rates of nitrogen, various micronutrients, and CO_2 have been examined as potentially limiting to growth and production of *Macrocystis pyrifera* (L.) C. Agardh. Ambient NO_3^- and NH_4^+ concentrations

are generally low along the southern California coast, and uptake rates predicted for adult sporophytes are just sufficient to support typical growth rates (Gerard, in press). Manganese uptake rates predicted for adult *M. pyrifera* are also only marginally sufficient (Manley, in press). These uptake predictions are based on the assumption that *in situ* water motion is always saturating. That assumption may be erroneous, according to results of previous studies. NO_3^- and NH_4^+ uptake by *M. pyrifera* in the laboratory are saturated at current velocities of 3 to 4 cm s^{-1} (Wheeler, 1978). Current velocities in coastal kelp forests are often lower (Wheeler, 1980; Jackson and Winant, in preparation). Wheeler (1980) described a similar situation for carbon assimilation and predicted that productivity of *M. pyrifera* forests would be significantly enhanced by increased water flow.

If current velocities determined within coastal forests accurately represent flow rates over kelp surfaces, low nutrient uptake rates due to slow boundary-layer transport probably are important in limiting kelp growth and production. Current measurements, however, do not record local water motion caused by wave surge or by movement of plant surfaces relative to the surrounding water. The purpose of this study was to provide a relative measure of *in situ* flow rates over intact blades on adult sporophytes of *Macrocystis pyrifera* under various sea-state conditions. These results were compared to similar flow-rate measurements made in the laboratory in conjunction with determinations of nutrient uptake by detached kelp blades.

Materials and Methods

I measured rates of NO_3^- uptake by individual, mature blades of *Macrocystis pyrifera* (L.) C. Agardh at various flow rates in a laboratory aquarium. Blades were collected at 2 to 3 m depth from canopy fronds of adult kelp plants located at 7 to 12 m bottom depths (Laguna Beach,

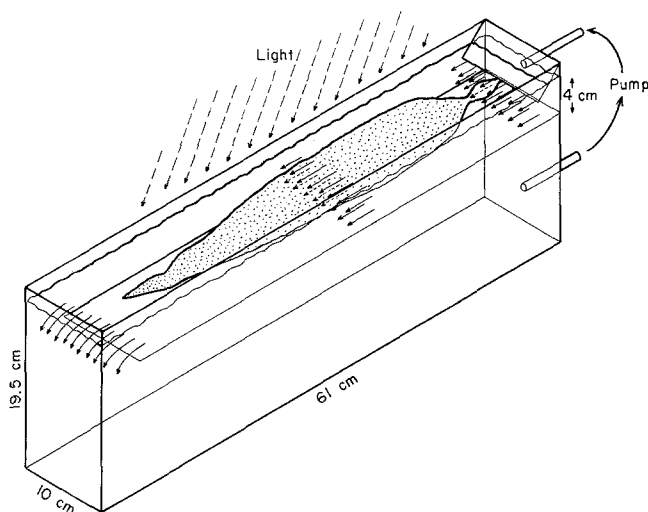


Fig. 1. *Macrocyctis pyrifera*. Detached blade positioned in experimental aquarium during NO_3^- uptake experiment. Direction of water flow is indicated by arrows

California; 1981) and were exposed to air for less than 5 s during transfer to the experimental aquarium. During each uptake experiment, a blade was positioned above a shelf extending almost the length of the aquarium (Fig. 1). Water pumped over this shelf provided unidirectional flow rates averaging 0.4 to 6.3 cm s^{-1} . The lowest flow rate provided adequate turnover of water to maintain similar NO_3^- concentrations above and below the shelf during uptake experiments. Prior to each experiment, NaNO_3 was added to 11.5 liters of offshore surface water to give initial NO_3^- concentrations of approximately 5 or $25 \mu\text{M}$. Actual NO_3^- concentrations before and after each experiment were determined according to the method of Strickland and Parsons (1972). Incubations ran 1 h, a period shown to give accurate results during similar measurements made *in situ* (Gerard, in press). Temperature was maintained between 14° and 17°C . Light ($190 \mu\text{E m}^{-2} \text{ s}^{-1}$) was well above saturation levels for photosynthesis (S. Manley, personal communication) and NO_3^- uptake (Wheeler, 1978). At the end of the incubation period, the experimental blade was blotted and weighed. Lamina surface area was measured with a LI-COR area meter. For uptake rate computations, microbial uptake and diffusion into tissue-free space were assumed negligible (Gerard, in press).

I used the dissolution rates of plaster buttons attached to the surface of kelp blades to provide a relative measure of water motion by a method similar to that of Doty (1971). The buttons consisted of 7 mm radius, plaster of Paris hemispheres, molded onto brass paper fasteners. Buttons reached a constant dry weight of 1.7 to 2.0 g after 24 h at 60°C . Preweighed buttons were fastened to kelp blades in aquaria or *in situ* for 24 h, then rinsed in fresh water, dried, and reweighed. In order to determine the diffusion factor as defined by Doty (1971), I divided mean dry weight loss of experimental buttons by weight loss of buttons in still water at an appropriate temperature. Mean weight losses of 6 buttons submerged in still seawater for

24 h showed a linear relationship to temperature between 7° and 18°C .

To determine diffusion factor as a function of flow rate, I fastened 8 buttons to a kelp blade and held them in the experimental aquarium for 24 h. Four buttons were placed on each surface of the blade: 3 cm from the pneumatocyst, in the center of the lamina, 3 to 5 cm from the distal tip, and at the margin halfway along the lamina. One to four measurements were made at each flow rate used in the NO_3^- uptake experiments.

To determine diffusion factors *in situ*, I fastened buttons to intact blades on canopy fronds of adult kelp plants. The plants formed a dense stand at the 8 to 10 m depth contour within a larger kelp forest at Laguna Beach. Ambient temperature during exposure periods varied from 14° to 19°C . To test replicability, I placed 18 pairs of buttons side by side on subcanopy blades (2 to 3 m depth). Deviation between paired buttons averaged 2% of mean weight loss. Diffusion factors were compared for proximal, central, and distal locations on subcanopy blades. For all other determinations, 12 to 20 replicate buttons were used, each fastened to the center of a different blade. Abrasion of buttons by adjacent blades had no measurable effect on weight loss: diffusion factors were similar for plants with all blades intact ($\bar{x}=3.8$, $\text{SE}=0.1$) and for plants from which all blades without buttons were removed ($\bar{x}=3.85$, $\text{SE}=0.1$). Diffusion factors were measured in the canopy, at subcanopy depths, and on basal blades, 1 to 2 m above the holdfast. Diffusion factors were determined under different sea-state conditions. Maximum wave height, wave period, and current velocity were estimated at the beginning and end of each 24 h exposure period. I disregarded determinations made during changing sea state conditions or when current velocity exceeded 5 cm s^{-1} .

Results

NO_3^- uptake by detached *Macrocyctis pyrifera* blades was saturated at a flow rate of 2.5 cm s^{-1} in the experimental aquarium (Table 1). Flow increases from 0.4 to 0.7 cm s^{-1} and from 1.2 to 2.5 cm s^{-1} caused significant uptake enhancement at both low and high initial concentrations (Student's *t*-test, $p < 0.05$). A further increase up to

Table 1. *Macrocyctis pyrifera*. NO_3^- uptake rates ($\text{ng-at cm}^{-2} \text{ h}^{-1}$) by detached blades at various flow rates in experimental aquarium ($\bar{x} \pm \text{SE}; n = 3 - 4$)

Flow rate (cm s^{-1})	Initial NO_3^- concentration:	
	4–6 μM	22–27 μM
0.4	10 ± 1	23 ± 4
0.7	22 ± 1	38 ± 3
1.2	21 ± 3	37 ± 1
2.5	34 ± 2	49 ± 4
6.3	35 ± 7	46 ± 4

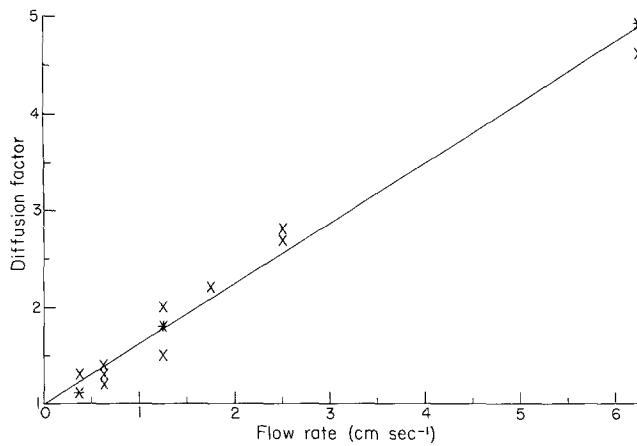


Fig. 2. *Macrocyctis pyrifera*. Relationship between flow rates in experimental aquarium and diffusion factors determined using plaster buttons ($r=0.99$, $p<0.01$). * and * indicate 2 and 3 coinciding points, respectively

6.3 cm s^{-1} had no measurable effect on uptake rate. The apparent lack of influence on uptake rate between flow rates of 0.7 and 1.2 cm s^{-1} may have been due to coincidental effects of varying nutritional history. Occasional, brief upwelling events occurred during those experiments, and tissue preconditioning at high nutrient levels has been shown to affect uptake rates (Haines and Wheeler, 1978).

Diffusion factors showed a significant linear relationship with flow rates in the experimental aquarium (Fig. 2). The uptake saturating flow rate of 2.5 cm s^{-1} corresponded to a diffusion factor of 2.7.

Diffusion factors measured *in situ* ranged from 3.6 to 4.8 (Fig. 3), equivalent to flow rates of 4 to 6 cm s^{-1} which exceed the minimum flow rate saturating NO_3^- uptake. Diffusion factors measured at different locations on kelp

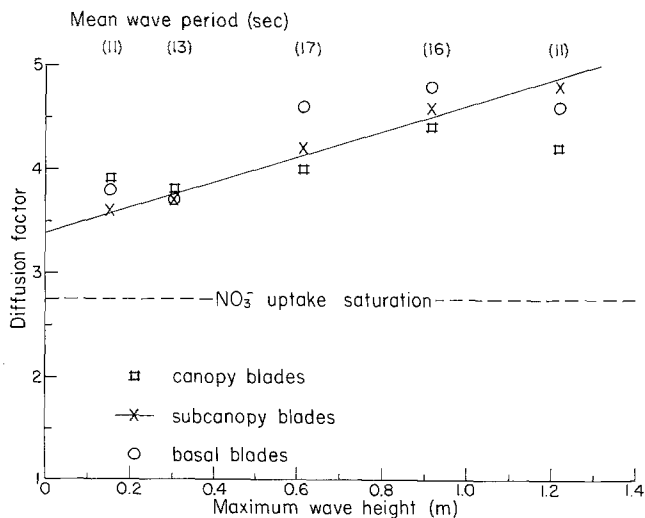


Fig. 3. *Macrocyctis pyrifera*. Diffusion factors measured *in situ* for intact blades on canopy fronds of adult sporophytes. Sea-state conditions are indicated as maximum wave heights and mean wave periods. For each point, $n=12$, $\text{SE}=0.1$. Line represents data for subcanopy blades only ($r=0.99$, $p<0.01$)

blades did not differ significantly. Buttons fastened 3 to 5 cm from the pneumatocyst or from the distal tip of the lamina gave results similar to buttons fastened in the center of the same subcanopy blades ($\bar{x}=4.2$, 4.0, and 4.1, respectively; $\text{SE}=0.1$ for all means).

Water motion over kelp blades *in situ* was influenced by sea-state conditions. Diffusion factors measured for subcanopy blades were significantly correlated with maximum wave heights (Fig. 3). Ranges of diffusion factors measured for subcanopy and basal blades were similar, but basal diffusion factors were disproportionately high when wave periods were long. Long-period waves produce greater horizontal water motion at near-bottom depths than short-period waves (Bascom, 1964). Diffusion factors measured for canopy blades had a smaller range than that for basal or subcanopy blades. Canopy blades had the highest diffusion factors of the three blade types during calm sea states and the lowest diffusion factors during rough conditions. Sea-state conditions during the *in situ* experiments were typical for this area of the Southern California Bight, a relatively protected section of the California coast. Daily sea-state observations 10 km north of the study site showed that maximum wave heights less than 0.2 m occurred on only 1% and heights exceeding 1.2 m on 10% of the days in 1981 (data from the Newport Beach Marine Department).

Discussion

Overall, boundary-layer transport limits macronutrient uptake by *Macrocyctis pyrifera* when flow rates over blade surfaces are less than 3 or 4 cm s^{-1} . Results presented in this study (Table 1) and by Wheeler (1978) showed saturation of NO_3^- uptake at 2.5 and 3 cm s^{-1} , respectively. Saturating flow rates have been determined as 3 cm s^{-1} for NH_4^+ uptake, 4 cm s^{-1} for PO_4^{3-} uptake, and 3 to 4 cm s^{-1} for CO_2 uptake by *M. pyrifera* blade tissues (Wheeler, 1978, 1980). When water motion exceeds these saturating levels, uptake rates are limited by enzymatic assimilation.

Boundary-layer transport is probably not an important limiting factor to growth and production of *Macrocyctis pyrifera* in southern California. Under all commonly encountered sea-state conditions, diffusion factors measured for kelp blades *in situ* were equivalent to flow rates of 4 cm s^{-1} or more. These data do not necessarily indicate that *in situ* current velocities always exceeded 4 cm s^{-1} . On the contrary, current was usually imperceptible within the dense kelp stand, probably often as low as 1 cm s^{-1} . Such low current velocities occur frequently in coastal kelp forests of southern California (McFarland and Prescott, 1959; Wheeler, 1980; Jackson and Winant, in preparation). Current, however, probably contributes less to *in situ* flow rates over kelp blades than wave surge. Wave-surge velocities measured within the kelp forest at Point Loma, California, were approximately five times greater than current velocities measured simul-

taneously (G. A. Jackson, unpublished data). Furthermore, movement of kelp surfaces relative to the surrounding water enhances flow rates, particularly during calm sea-state conditions. This movement is a function of frond morphology. The length of a canopy frond section held vertically in the water column by buoyant pneumatocysts changes with passing wave troughs and crests, resulting in horizontal movement of the surface section of the frond through the water. Blades located along vertical frond sections are also affected by very slight swells. Each blade is attached by one end to a point fixed in relation to the substratum (the stipe, buoyed by pneumatocysts) and shows a flaglike movement with passing waves. Current, wave surge, and blade movement together provide sufficient flow over all blade surfaces to saturate nutrient uptake, even in a dense kelp stand during calm sea-state conditions.

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