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## Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration

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**SUMMARY.** 1. Research was performed in laboratory streams to evaluate periphytic biomass accrual, export, and community composition over a range of limiting nutrient (phosphorus) concentrations with variable velocity, and suspended sediment addition, in comparison to constant velocity and no suspended sediment. In fixed-velocity treatments, velocity increase to  $60 \text{ cm s}^{-1}$  significantly enhanced biomass accrual, but further increase resulted in substantial biomass reduction. Average biomass loss rates did not change significantly over a velocity range of  $10\text{--}80 \text{ cm s}^{-1}$ . Diatoms were favoured at relatively high velocities and low phosphorus concentrations, whereas the blue-green *Phormidium* tended to dominate at higher SRP concentrations and the green *Mougeotia* seemed to prefer lower velocities.

2. Sudden increases in velocity raised instantaneous loss rates by an order of magnitude or more, but these high rates persisted only briefly. As a result, marked biomass reductions were not apparent a day after the velocity change. Dominance change from filamentous green or blue-green to diatoms immediately after the increase was reversed within 2 days. Loss rate increases due to solids addition were much smaller than those accompanying velocity increase, but simultaneous velocity elevation and solids addition produced instantaneous loss rates approximately double those with velocity increase alone.

3. The experiments demonstrated that an elevation in velocity, above that to which algae were accustomed, led to increased loss rates and temporarily reduced biomass. However, recolonization and growth after biomass reduction were apparently rapid. Substantial export of periphyton following solids addition required erosion of the protective boundary layer accompanied by a velocity increase. These results are applicable to understanding the response of lotic periphytic algae to elevated, turbid storm discharges and similar runoff or high-flow events.

4. Areal uptake rates of P by algae growing in the laboratory streams increased with soluble reactive phosphorus (SRP) concentration, up to approximately  $15 \mu\text{g l}^{-1}$  in overlying water. They also increased above

35 cm s<sup>-1</sup>. Overall, uptake rate seemed to vary inversely with biomass. The ratio of areal uptake rate/biomass was significantly less where mean biomass was 411±6 mg chl *a* m<sup>-2</sup> compared to 223±17 mg chl *a* m<sup>-2</sup>.

5. The results suggested that although nutrient uptake is primarily a surface phenomenon, diffusion to interior cells can also determine the responses of attached communities. Both diffusion and uptake rate were stimulated by increasing nutrient concentration and velocity up to certain levels, but became limited by biofilm thickness and scouring.

## Introduction

Stream periphyton is of interest because of its productive potential but also because of undesirable effects in streams of excessive filamentous algal growths. Many factors affect the development of periphytic algae in streams, including macro- and micro-nutrients, light, temperature, substrata, grazing, current velocity, and particles transported by the flow. Some of these have received more attention than others, and investigations of interactions among factors have been rare.

In the velocity range from 0 to 50 cm s<sup>-1</sup>, larger biomass accumulation (and/or productivity) has been reported in natural or laboratory stream reaches at higher velocities than at lower velocities (Whitford & Schumacher, 1964; McIntire, 1966, 1968b; Rodgers & Harvey, 1976; Horner, Welch & Veenstra, 1983; Welch *et al.*, 1988). Even though colonization of a bare surface was sometimes slower at higher velocity, ultimate biomass exceeded that at the lower velocity (Horner & Welch, 1981; Korte & Blinn, 1983; Stevenson, 1983). However, lower biomass has often been reported at velocities above 50 cm s<sup>-1</sup> (Horner & Welch, 1981; Horner *et al.*, 1983).

To explain these observations, Horner & Welch (1981) hypothesized offsetting mechanisms that are both functions of velocity. Velocity increase apparently enhances algal growth by reducing the thickness of the relatively stagnant and nutrient-depleted laminar boundary layer adjacent to the growing surfaces (Geankoplis, 1972; Grady & Lin, 1980; Stevenson, 1983; Sand-Jensen, 1983). As a consequence, the diffusion gradient and, hence, the rate of molecular diffusion across the boundary layer increases (Whitford, 1960). Thus, both Whitford & Schumacher (1964) and Lock (1979) found that when periphytic algae were exposed to a current, <sup>32</sup>P uptake rates were higher than

under quiescent conditions, and Horner & Welch (1981) and Horner *et al.* (1983) showed that an increase in velocity stimulated biomass accumulation, presumably as a result of an increased rate of nutrient utilization. Whitford & Schumacher (1964) suggested that a velocity greater than 15 cm s<sup>-1</sup> is necessary to have a significant effect on the diffusion gradient. In contrast, any velocity increase adds to the frictional shear force of the passing flow, impeding colonization and removing a progressively greater portion of biomass attached to the surface.

Increased enrichment of running water that has low nutrient content can result in increased growth and biomass of periphytic algae (Stockner & Shortreed, 1978; Grimm & Fisher, 1986; Horner *et al.*, 1983; Perrin, Bothwell & Slaney, 1987). However, the question is unresolved as to whether saturation of nutrient uptake and growth at very low concentrations (Bothwell, 1985) occurs only with thin films of diatoms, or whether biomass accumulation and uptake by thick mats of large filamentous species can also occur at low nutrient concentrations (Freeman, 1985). Diffusion of nutrients and penetration of light into the algal mat may be limited by its thickness. Within the mat, limited supplies of nutrients, light, or both, may result in respiration-dominated metabolic activities, senescence, and sloughing from the attachment surface. Some results suggest that this may be the case with diatom and filamentous green algae alike (Horner *et al.*, 1983; Bothwell, 1988; Wong & Clark, 1976; Biggs & Close, 1989). The species-specific effect of nutrients and the role of mat thickness in producing nuisance biomass levels of periphytic algae is important when managing stream quality.

Losses of biomass have frequently been observed following increases in stream flow, resulting either from storms or reservoir releases (Ball, Kevern & Linton, 1969; Rounick &

Gregory, 1981; Lowe, 1979; Horner & Welch, 1981; Sloane-Richey, Perkins & Malueg, 1981; Hauer & Stanford, 1982; Fairchild & Lowe, 1984; Nielsen *et al.*, 1984). Ball *et al.* (1969) and Horner & Welch (1981) documented greater erosion of periphyton during elevated storm flows than would be expected from consideration of velocity magnitude alone, probably as a result of abrasion by suspended sediments. On the other hand, Horner & Welch (1981) found that biomass that had developed at higher velocities exhibited less reduction as a result of a storm event than if it had developed in slower current.

McIntire (1966, 1968a) reported that export in laboratory channels was significantly greater at  $35 \text{ cm s}^{-1}$  than at  $14 \text{ cm s}^{-1}$ . McIntire & Phinney (1965) noted that loss rates at constant velocity were significantly greater during periods of high turbidity in the feed water than at other times. Horner *et al.* (1983) measured biomass export rates, in terms of both chlorophyll *a* and particulate organic carbon, in laboratory streams supplied with water consistently low in suspended sediment. They observed no significant differences in loss rates among constant velocities ranging from  $5$  to  $75 \text{ cm s}^{-1}$ . This result was unexpected, because, despite the lack of particle abrasion, shear stress has been shown to increase approximately with the square of velocity (Leopold, Wolman & Miller, 1964).

Current velocity also influences the species composition of algal assemblages. Patrick (1948) noted that algae that thrive in swift streams are those that attach firmly to substrate by means of gelatinous masses or stalks. Traaen & Lindstrom (1983) documented adaptations of certain species to high velocities ( $>80 \text{ cm s}^{-1}$ ), resulting in relatively large accumulations in patchy distributions. McIntire (1966, 1968a, b) found that diatoms were more abundant in laboratory streams with current velocities of  $38 \text{ cm s}^{-1}$ , whereas filamentous green algae dominated at  $9 \text{ cm s}^{-1}$ . Horner *et al.* (1983) seeded laboratory channels with rocks from a natural stream containing filamentous forms. The filamentous green alga *Mougeotia* dominated in thirty of thirty-six treatments, but in those treatments with combinations of the highest phosphorus concentrations and the highest velocities, a filamentous blue-green (*Phormidium*) was most abundant.

These various results suggest that, while

turbulent diffusion and velocity shear exert general control over periphyton development, there are species-specific individual adaptations to different velocities. Both abrasion by particles and increased shear stress due to velocity increase can cause biomass losses accompanying storm events, but the relative importance of the two effects has not been determined previously. Observations by Horner & Welch (1981) in the field and by Horner *et al.* (1983) in the laboratory further suggest that biomass removal was more a function of velocity change from the norm to which the algae have adapted, through the strength of their attachment, than of the magnitude of the ultimate velocity.

The present paper describes the results of research performed in laboratory streams to clarify certain aspects of the relationships among current velocity, limiting nutrient, suspended sediments, and periphytic algal biomass export. Specifically, biomass accrual and export and algal taxonomic composition were determined over a range of limiting nutrient (phosphorus) concentrations and constant velocities. The same determinations were then made on periphyton communities grown at relatively low velocities and subsequently subjected to substantially higher velocities, abrasion by suspended sediments, or both. Another objective of the experiments was to investigate the relationships among phosphorus uptake rate, P concentration, velocity, and periphyton biomass.

## Materials and Methods

*Apparatus.* Laboratory streams were constructed to permit the growth of periphyton under conditions of controlled nutrient, velocity, temperature, light and suspended sediment. The laboratory stream system consisted of nine Plexiglas channels, a water supply reservoir, a chemical diluter and distribution tubing, compressed air manifolds with valving and tubing, lighting, a suspended sediment delivery system, and drainage pipes.

Each channel, illustrated in plan view in Fig. 1, was  $20 \text{ cm}$  in width by  $1 \text{ m}$  in length and had a partial centre wall to allow for recirculation of water. Placement of the drain pipe  $8 \text{ cm}$  above the channel bottom maintained water depth. For quantitative sampling of periphyton, small Plexiglas plates were installed between guides

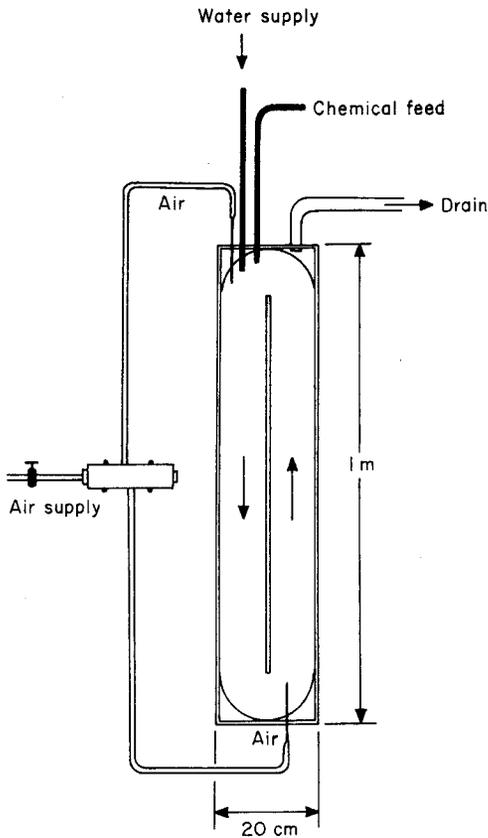


FIG. 1. Experimental design, showing positions of water and nutrient inputs and outputs and air inputs to control current velocity in the recirculating channels.

along the vertical outside wall and centre wall in one race of each channel.

Water supply was piped to the laboratory from a concrete-lined campus pond under gravity flow. The pond water was consistently low ( $\leq 2 \mu\text{g l}^{-1}$ ) in soluble reactive phosphorus (SRP). Pond water was discharged into a plastic coated metal reservoir, equipped with a thermostatically controlled immersion heater, before being conveyed to a flow-through diluter in which nutrient solution was added. The diluter system, diagrammed in Fig. 2, is a modification of the Mount & Brungs (1967) proportional diluter and was developed by the Battelle Pacific Northwest Laboratory (Anderson & Lusty, 1980; Bean, Gibson & Anderson, 1981). A polyvinyl chloride manifold distributed supply

water to each of nine dilution cells at a rate of  $1 \text{ l min}^{-1}$ . In the dilution cells, supply water was mixed with concentrated nutrient stock solutions drawn from 50 litre Nalgene carboys and metered at set flow rates by a Cole-Parmer Masterflex model 7568 peristaltic pump equipped with multiple discharge ports. Solutions flowed from the dilution cells through Nalgene tubing into the channels, in which water residence times were 16 min. All components of the diluter system and tubing were covered with either opaque polyethylene sheeting or tape, to exclude light and inhibit growth of algae introduced with the supply water.

$\text{K}_2\text{HPO}_4$  was used as the supplemental P source. Since P was chosen to be the limiting nutrient in these experiments, levels of nitrogen were adjusted, using  $\text{NaNO}_3$  as the supplemental nitrogen source, to attain N:P ratios of at least 15:1 by weight. This ratio is double that generally required for algal growth (Redfield, Ketchum & Richards, 1963).

Currents were produced in the channels using the compressed air system developed and described by Horner *et al.* (1983). Light was provided continuously during experiments by four 91.4 cm long General Electric Deluxe warm white F 40/wwx fluorescent tubes suspended 60 cm over each set of three channels. This source provided approximately  $142 \pm 1.5 \mu\text{E m}^{-2} \text{ s}^{-1}$  at the channel surface.

The suspended sediment delivery system consisted of a slurry tank, a head tank, a distribution tank, and tubing. The slurry tank was a 100 litre Nalgene barrel in which a plastic cone was placed to form a tapered side wall. The slurry, composed of water from the campus supply pond and added solids, was kept in suspension by continuously pumping from the apex of the cone to the top of the barrel using a submersible pump. Fine sediments ('glacial flour') from the White River, near Mount Rainier National Park, Washington, were used as the suspended solids in these experiments. This material was selected because it is easily suspended, somewhat abrasive, and presumably uncontaminated with nutrients and toxic substances. From the slurry tank, the slurry was pumped to a head tank comprised of a 25 litre bucket with a standpipe, which returned overflow to the slurry tank. The head tank outlet was equipped with a valve that controlled flow to a glass aquarium distribution tank. Both the head tank and the

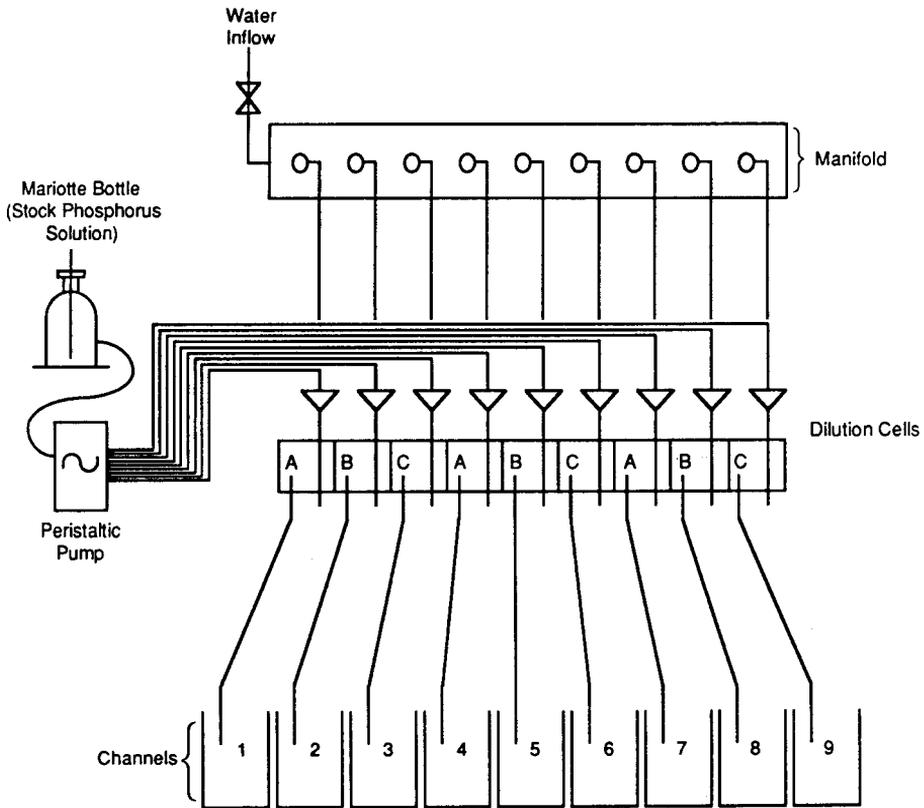


FIG. 2. Design of dilution system to deliver the nutrient-water mixtures to respective channels. A, B, C = nutrient concentrations.

distribution tank were continuously mixed with propellers. In the distribution tank, the slurry was diluted with additional pond supply water before being conveyed by gravity to the channels. Hose clamps were used to set the flow to the channels at the same rate as that from the flow-through delivery system ( $1 \text{ l min}^{-1}$ ).

**Experimental design.** Four series of treatments were performed: fixed velocity (without solids addition), velocity increase (without solids addition), fixed velocity (with solids addition), and velocity increase (with solids addition) (Table 1). The fixed-velocity (without solids) treatment series represented sixteen different combinations of target influent SRP concentration, ranging from 5 to  $50 \mu\text{g l}^{-1}$ , and current velocity as measured near the slide surfaces, ranging from 10 to  $80 \text{ cm s}^{-1}$ .

The first experiment within the velocity-increase (without solids) treatment series

exposed periphyton grown for 16 days at  $20 \text{ cm s}^{-1}$  and influent SRP concentrations of 15, 25 and  $50 \mu\text{g l}^{-1}$  to a velocity increase to  $80 \text{ cm s}^{-1}$ , which was sustained for three more days. In the second experiment in this series (performed simultaneously with the first experiment), slides with periphyton grown for 18 days in these same conditions were transferred to a current of  $80 \text{ cm s}^{-1}$  for 30 min, after which the slides were removed for sampling. The final velocity-increase series experiment exposed periphyton grown for 14 days at  $20 \text{ cm s}^{-1}$  and 5, 15 and  $25 \mu\text{g SRP l}^{-1}$  to a velocity increase to  $60 \text{ cm s}^{-1}$ , which was maintained for three more days.

Experiments in the two treatment series involving solids addition were performed simultaneously with some experiments in the other series in order to allow direct comparisons. In one of these experiments, White River sediment was added to produce a target concentration of

TABLE 1. Experimental design summary.

Treatment series	Target velocity <sup>a</sup> (cm s <sup>-1</sup> )	Target influent SRP ( $\mu\text{g l}^{-1}$ )				
		5	8	15	25	50
I. Fixed velocity (without solids addition)	10		X	X	X	
	20		X	X <sup>b</sup>	X <sup>b</sup>	X
	30		X	X	X	
	60	X		X	X <sup>c</sup>	
	80			X	X	X
II. Velocity increase (without solids addition)	20–80 <sup>d</sup>			X	X	X
	20–80 <sup>e</sup>			X	X	X
	20–60 <sup>f</sup>	X		X	X <sup>c</sup>	
III. Fixed velocity (with solids addition)	60				X <sup>c</sup>	
IV. Velocity increase (with solids addition)	20–60 <sup>f</sup>				X <sup>c</sup>	

<sup>a</sup> Near periphyton slide collectors. <sup>b</sup> Experiment performed twice, at different times.

<sup>c</sup> Experiment performed in duplicate channels, simultaneously. <sup>d</sup> Velocity increase on day 16, followed by three more days of growth. <sup>e</sup> Slides from 20 cm s<sup>-1</sup> channel transferred to 80 cm s<sup>-1</sup> channel on day 18 for 30 min, followed by removal for sampling. <sup>f</sup> Velocity increase on day 14, followed by three more days of growth.

25 mg l<sup>-1</sup> in duplicate channels in which periphyton had been grown for 19 days at 60 cm s<sup>-1</sup> and influent SRP of 25  $\mu\text{g l}^{-1}$ . The other experiment exposed periphyton grown in duplicate channels for 14 days in the same SRP concentration, but at 20 cm s<sup>-1</sup>, to both sediment addition at the same concentration and velocity increase to 60 cm s<sup>-1</sup>. The experiments extended for seven and four more days, respectively, after conditions were modified.

Prior to each experiment, the channels were seeded with algae through natural transport from the supply pond and deliberately with rocks gathered from a local stream. The rocks selected were of similar size and had similar coverings of periphyton, including filamentous green algae. One rock was placed in each channel for approximately 2 weeks, during which time background SRP concentrations (1–2  $\mu\text{g l}^{-1}$ ) and low velocities (5 cm s<sup>-1</sup>) were the same in all channels.

Data from these treatments were used to investigate P uptake per unit biomass throughout the channels. For that purpose, actual in channel average SRP concentrations and average channel velocities were computed (Table 2). The altered condition of raised velocity and suspended solids addition persisted

for relatively short periods and were thus assumed to have minimal effects on the average uptake of P through the entire experiment.

*Sampling and analysis.* Samples for determination of periphytic biomass were collected from the Plexiglas plates and the circulating water (to represent export) at least six times during each experiment. Export samples were collected from the circulating water, prior to removing slides, by dipping beakers into the channels. Slide collections were made by scraping measured plate areas with a microscope slide into a wide-mouth jar. Periphyton collections were transported in the dark of the laboratory, suspended in a known water volume, homogenized, filtered (in duplicate), and frozen for later analysis of chlorophyll *a* (chl *a*). Chl *a* was determined according to the procedure outline by Strickland & Parsons (1972), using a Turner model 110 fluorometer for the first nine treatments of series I (Table 2), and by the spectrophotometric method of Lorenzen (1967), using a Perkin-Elmer Lambda 3 scanning spectrophotometer, during all remaining work. Periphyton accumulation was expressed in terms of mg chl *a* m<sup>-2</sup> of surface, while material suspended in the water was expressed as  $\mu\text{g chl a l}^{-1}$  of water.

Treatment series	Velocity (cm s <sup>-1</sup> )									
	1		2		Channel <sup>a</sup>					
	Slide	Channel	Slide	Channel <sup>a</sup>						
	Influent SRP (μg l <sup>-1</sup> )	Channel SRP (μg l <sup>-1</sup> )	Channel NO <sub>3</sub> + NO <sub>2</sub> -N + NH <sub>3</sub> -N (μg l <sup>-1</sup> )	Channel N:P ratio	Channel TP (μg l <sup>-1</sup> )					
I. Fixed velocity (without solids addition)	7.2 (0.7) 13.4 (0.4) 22.3 (1.9) 6.9 (0.8) 11.8 (1.0) 22.8 (0.9) 6.2 (0.5) 13.0 (0.4) 22.1 (1.2) 13.5 (0.5) 22.8 (0.8) 14.6 (0.1) 22.8 (1.6) 46.6 (1.9) 4.7 (1.0) 24.2 (1.1) 22.8 (1.5) 12.2 (1.3)	4.6 (1.6) 7.8 (1.2) 16.9 (2.5) 4.5 (0.7) 4.9 (0.8) 13.4 (2.2) 4.8 (0.7) 6.8 (1.5) 14.4 (2.9) 9.1 (0.8) 14.2 (1.3) 40.8 (1.1) 8.0 (1.1) 14.9 (0.8) 39.4 (1.6) 1.9 (0.8) 13.8 (2.0) 16.2 (1.1) 5.7 (1.1)	249.2 (34.2) 237.0 (35.5) 242.5 (38.0) 239.8 (23.7) 218.0 (26.8) 232.8 (23.2) 244.0 (16.8) 221.2 (25.0) 207.0 (33.8) 256.0 (23.6) 378.0 (16.3) 927.3 (109.2) 241.3 (15.0) 438.0 (106.9) 749.8 (88.8) 236.0 (28.9) 513.3 (40.9) 509.3 (38.5) 392.7 (26.2)	54.2 30.4 14.3 53.0 44.3 17.4 50.7 32.6 14.4 28.1 26.7 22.7 30.3 29.4 19.0 122.3 37.1 31.3 69.1	40.5 (8.6) 33.0 (9.0) 45.0 (10.7) 22.4 (4.9) 27.8 (4.3) 46.6 (10.5) 15.4 (2.8) 24.6 (5.0) 28.7 (5.0) 25.0 (2.4) 27.0 (0.8) 60.7 (3.4) 21.2 (2.0) 34.5 (3.7) 57.2 (1.3) 19.5 (1.5) 35.2 (10.6) 36.4 (1.2) 25.2 (2.0)	10.2 (1.8) 8.0 (0.5) 11.3 (1.0) 31.7 (11.6) 29.5 (2.2) 33.5 (2.6) 21.5 (2.2) 17.2 (2.8) 23.3 (2.6) 82.0 (4.0) 72.0 (9.0) 79.5 (3.5) 24.0 (1.0) 15.0 (1.0) 18.5 (2.5) 67.5 (5.5) 66.0 (10.0) 63.0 (11.0) 46.0 (11.0)	n.m. <sup>b</sup> n.m. n.m. n.m. n.m. n.m. n.m. n.m. n.m. 35.0 (8.9) 32.5 (8.1) 34.0 (8.5) 14.3 (1.6) 11.1 (1.6) 10.9 (5.9) 27.6 (8.2) 35.7 (8.4) 28.8 (7.2) 31.8 (5.9)	n.m. n.m. n.m. n.m. n.m. n.m. n.m. n.m. n.m. 83.0 (1.0) 71.0 (11.0) 75.5 (3.5) 25.5 (1.5) 14.5 (0.5) 16.5 (1.5) n.m. n.m. n.m. n.m.	Channel <sup>a</sup>	
II. Velocity increase (without solids addition)	13.9 (0.7) 24.3 (0.9) 55.9 (3.6) 27.5 (1.2) 5.2 (2.6) 25.6 (2.4) 14.6 (1.4)	8.6 (0.4) 15.4 (0.2) 46.0 (4.0) 18.4 (1.3) 1.9 (1.0) 16.5 (1.1) 8.1 (2.0)	242.0 (10.3) 374.0 (16.1) 833.0 (102.9) 522.9 (17.9) 195.6 (20.6) 485.6 (20.8) 423.6 (65.7)	28.0 24.2 18.1 28.4 105.2 29.4 52.5	26.7 (2.9) 29.7 (1.5) 61.7 (3.5) 30.5 (3.7) 14.1 (3.1) 30.8 (1.8) 24.4 (2.5)	19.5 (0.5) 22.2 (1.2) 25.2 (1.2) 18.0 (5.0) 19.0 (4.0) 18.5 (2.5) 17.0 (4.0)	12.9 (2.5) 14.7 (2.5) 17.2 (2.3) 20.0 (3.5) 19.4 (3.5) 22.4 (4.8) 21.4 (3.8)	82.5 (1.5) 78.5 (2.5) 76.5 (2.5) 66.0 (12.0) 60.5 (9.5) 65.0 (11.0) 59.5 (4.5)	45.0 (8.6) 42.8 (8.9) 46.0 (8.6) 39.8 (8.0) 40.6 (7.3) 48.0 (7.4) 45.8 (7.4)	n.m.
III. Fixed velocity (with solids addition)	22.8 (1.5) 23.2 (1.2)	13.9 (1.1) 15.7 (1.9)	428.0 (88.0) 546.7 (66.4)	30.8 34.8	46.4 (13.1) 46.8 (17.9)	59.0 (8.0) 62.0 (6.0)	32.8 (5.7) 33.8 (8.4)	n.m. n.m.	n.m. n.m.	
IV. Velocity increase (with solids addition)	27.7 (1.2) 29.1 (3.3)	18.4 (1.0) 20.0 (2.4)	517.6 (30.0) 596.2 (48.6)	28.1 29.3	38.5 (9.2) 46.8 (14.4)	18.0 (3.0) 19.5 (5.5)	16.7 (3.1) 21.1 (3.5)	59.5 (10.5) 68.0 (12.0)	38.9 (7.0) 47.6 (7.4)	

<sup>a</sup> Average channel velocity was determined from ten measurements taken throughout the channel.

<sup>b</sup> n.m. = not measured.

Additional periphyton samples were collected from slides for qualitative analysis of taxonomic composition on the last day for treatment series I experiments and before and after treatment change in others. These collections were preserved with Lugol's solution for later determination of relative abundance of taxa on a scale of 1–10, representing 'present' to 'very abundant'.

The supply pond feedwater and channel water were analysed for SRP, total phosphorus (TP), ammonia-nitrogen ( $\text{NH}_3\text{-N}$ ), nitrate + nitrite-nitrogen ( $\text{NO}_3 + \text{NO}_2\text{-N}$ ), and total suspended solids (TSS) on a regular schedule during each experiment. Diluter effluent to each channel was also monitored regularly for SRP. Dissolved oxygen (DO) and pH were measured in each channel once during each experiment.

SRP was determined by the ascorbic acid method (American Public Health Association (APHA), 1980). TP was analysed by the same technique following persulphate digestion of unfiltered samples.  $\text{NH}_3\text{-N}$  was determined manually according to the automated phenate method, while  $\text{NO}_3 + \text{NO}_2\text{-N}$  analysis was performed using the automated cadmium reduction method (APHA, 1980) on a Technicon Auto Analyzer II).

TSS was analysed by the gravimetric method of APHA (1980). In addition, the inorganic portion of TSS, which is referred to as total inorganic suspended solids (TISS), was determined after combusting the organic material at 600°C. TISS excluded exported periphyton present in the channels and was used as the measure of solids concentration to which the attached community was exposed in treatments with suspended sediment.

Dissolved oxygen was analysed by the azide modification of the Winkler method (APHA, 1980), while pH values were obtained initially with a Corning model 5 and later with an Extech pH meter. These quantities were determined to indicate whether varying rates of compressed air introduction and levels of attached growth affected the quantity of oxygen available for uptake or the inorganic carbon equilibrium.

Velocities were measured approximately 1 cm from the surface of the Plexiglas plates from which algae were sampled using a Pygmy Teledyne-Gurley meter that had been calibrated with a Marsh-McBirney current meter. Light intensity was measured with a Lambda Instru-

ment Company Quantum Radiometer/Photometer model LI-185.

Total periphytic biomass, which had developed in the channels throughout each treatment, was determined by washing down all surfaces of the channel at the end of the period and sampling the resulting algal suspension. In the first nine treatments of series I, three grab samples were collected in wide-mouth amber bottles directly from the channels after channel surfaces were cleaned and the algae were suspended. In the remaining experiments, channel contents were drained and blended prior to collecting the grab samples. Average biomass in the composite samples was calculated as  $\text{mg chl } a \text{ m}^{-2}$  by correcting the volumetric concentrations for the channel area and volume.

Uptake was determined by subtracting the value of SRP (as  $\mu\text{g l}^{-1}$ ) determined in the channel water from that determined in the influent water. Since the rate at which water entered and exited the channels was set at  $1 \text{ l min}^{-1}$ , the difference between these two values is equivalent to uptake rate in  $\mu\text{g SRP min}^{-1}$ , which was converted to  $\text{mg SRP h}^{-1}$ . Average uptake rate was determined from measurements taken over the course of the treatments. Uptake rates were also determined from the last observation at the end of treatment periods. Areal uptake rate, in  $\text{mg SRP m}^{-2} \text{ h}^{-1}$ , was computed by dividing the mass removed from channel water by total channel surface area. Uptake rate  $\text{biomass}^{-1} \text{ h}^{-1}$ , was determined by taking the quotient of uptake rate and total biomass as  $\text{chl } a$  in the channels.

The magnitude of uptake rate was examined with respect to variations in biomass, velocity and SRP concentration. In addition, the ratio of uptake rate  $\text{biomass}^{-1}$  was evaluated in relation to SRP concentration. Since uptake rate was expressed as an average for the whole channel, it was also related to the average channel velocity.

*Experimental conditions.* Influent water temperature was maintained above 15°C (maximum 20°C), except on two days when it dropped to 14 and 14.5°C. Mean temperature for the four experimental series ranged from 16.2 to 19.8°C. Mean light readings, ranged from  $134 \pm 2$  to  $159 \pm 1 \mu\text{E m}^{-2} \text{ s}^{-1}$  (mean  $\pm 1$  SE) just above the water surfaces in the nine channels over the course of the experiments. The pH in the channel water ranged between 6.7 and 7.4 with-

out solids and rose as high as 7.9 with solids addition. Channel DO was very consistent among channels during each experimental period and ranged between 8.8 and 9.8 mg l<sup>-1</sup> over the four experiments.

Deviations from targeted values averaged less than 10% for both velocities near the periphyton slide surfaces and influent SRP concentrations (9.8% and 9.5%, respectively). Mass ratios of dissolved inorganic nitrogen (NH<sub>3</sub>-N and NO<sub>3</sub> + NO<sub>2</sub>-N) to SRP were never lower than 14.3 and were usually considerably higher. Therefore, P was maintained as the potentially most limiting nutrient at all times. In the four channels receiving solids additions, mean TISS concentrations were measured at 21.6 ± 2.1, 19.4 ± 3.1, 25.7 ± 3.5 and 29.8 ± 2.6 mg l<sup>-1</sup> (mean ± 1 SE), compared to the target of 25 mg l<sup>-1</sup>. Otherwise, mean TSS concentrations were always less than 6 mg l<sup>-1</sup> (which was mostly periphyton), except in one channel during one series.

## Results

### Effects of current and SRP at fixed velocity

Fig. 3 presents maximum periphyton biomass (chl *a* ± 1 SE), accrued in several fixed-velocity (without solids) treatments, in relation to SRP concentration. Channel water SRP concentrations were lower than influent concentrations as a result of algal uptake. Because nutrient uptake and growth are dependent upon ambient rather than inflow concentrations, analysis of results was based on channel water concentrations.

Biomass accrual was significantly enhanced by increasing SRP concentration from background levels to 7.5 µg l<sup>-1</sup> at 60 cm s<sup>-1</sup> and at 20 cm s<sup>-1</sup>, but appeared to have no effect at other velocities. Accrual was also enhanced by velocity increase to 60 cm s<sup>-1</sup>. Increase in SRP concentration did not result in higher levels of biomass; however, further increase in velocity resulted in substantial reductions in maximum biomass. The highest maximum biomass observed on the slides was 301 mg chl *a* m<sup>-2</sup>, which occurred at 7.5 µg SRP l<sup>-1</sup> and a velocity of 60 cm s<sup>-1</sup>. This biomass was much less than that observed as a maximum previously (560 mg chl *a* m<sup>-2</sup>; Horner *et al.*, 1983). The lowest maximum biomass was 45 mg chl *a* m<sup>-2</sup>, which

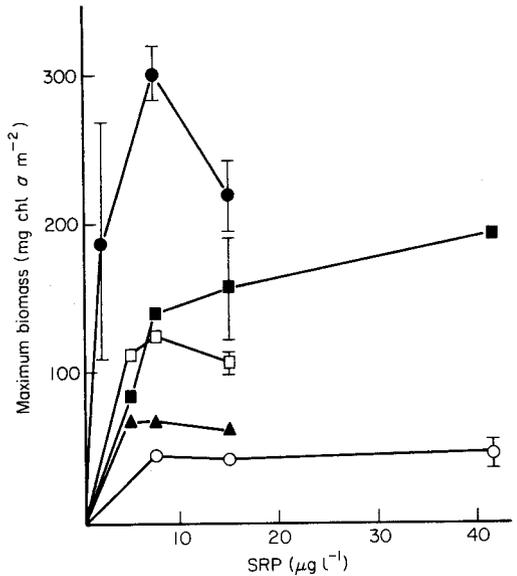


FIG. 3. Maximum periphyton biomass (as mg chl *a* m<sup>-2</sup>) (± SE) versus in-channel SRP concentration for five fixed current velocities: ○, 80 cm s<sup>-1</sup>; ●, 60 cm s<sup>-1</sup>; □, 30 cm s<sup>-1</sup>; ■, 20 cm s<sup>-1</sup>; ▲, 10 cm s<sup>-1</sup>.

occurred at a velocity of 80 cm s<sup>-1</sup> and three SRP concentrations ranging from 7.5 to 42 µg l<sup>-1</sup>. Biomass levels greater than 100 mg chl *a* m<sup>-2</sup>, which was hypothesized to signify the beginning of nuisance conditions in natural streams (Horner *et al.*, 1983; Welch *et al.*, 1988), were observed at all nutrient concentrations when velocities were 30 or 60 cm s<sup>-1</sup>. At a velocity of 20 cm s<sup>-1</sup>, this biomass level was reached when SRP was 7.5 µg l<sup>-1</sup> or higher. Maximum biomass in the channels having the lowest (10 cm s<sup>-1</sup>) and highest (80 cm s<sup>-1</sup>) velocities did not exceed 70 mg chl *a* m<sup>-2</sup>.

There was no relation between velocity and average loss rates of biomass (chl *a*) in fixed-velocity (without solids) treatments regardless of channel SRP concentrations. As had been observed by Horner *et al.* (1983), large variations were evident in loss rates, but rates were low and no significant patterns were apparent. Average loss rates were always less than 1.7 mg chl *a* m<sup>-2</sup> h<sup>-1</sup> and were usually under 1.1 mg chl *a* m<sup>-2</sup> h<sup>-1</sup>.

The pattern of taxonomic composition under the several regimes of velocity and SRP content was varied. In general, *Phormidium* was present

in most treatment combinations. Although not deliberately inoculated, *Phormidium* was apparently seeded from the water supply system. In some instances, *Phormidium* showed greater dominance at high SRP (Fig. 4). Biomass at the  $42 \mu\text{g l}^{-1}$ ,  $60 \text{ cm s}^{-1}$  treatment was almost completely composed of *Phormidium*. In the other fixed ( $60 \text{ cm s}^{-1}$ ) and variable velocity ( $20\text{--}60 \text{ cm s}^{-1}$ ) treatments involving solids addition, *Phormidium* was consistently more dominant at  $15 \mu\text{g l}^{-1}$  than at 2 or  $7.5 \mu\text{g l}^{-1}$ , although it was abundant at all concentrations. On the other hand, there was a tendency for diatoms to be more dominant at lower SRP content and higher velocity (Fig. 4), although that was not always the case. *Mougeotia* showed no pronounced preference for high or low SRP, but seemed to occur more at lower than higher velocities (Fig. 4). It was not prevalent at any velocity-SRP combination in the treatments involving solids addition, in which *Phormidium* was so abundant, as indicated above.

#### Effects of velocity increase

Fig. 5 illustrates biomass loss rates from whole channels (maintained at  $25 \mu\text{g SRP l}^{-1}$ ) before and immediately after sudden velocity increases, as well as from channels where the current was maintained constant. Immediately after velocity changes, instantaneous loss rates increased by an order of magnitude or more from the low average rates ( $<1 \text{ mg chl a m}^{-2} \text{ h}^{-1}$ ) that generally prevailed before velocity increase and in the fixed-velocity treatments. The magnitude of velocity increase affected the loss rates observed. Velocity increase from  $20$  to  $80 \text{ cm s}^{-1}$  resulted in instantaneous loss rates more than double those observed immediately after an increase to  $60 \text{ cm s}^{-1}$ . Within 12 h after the velocity increases, loss rates declined to  $<1 \text{ mg chl a m}^{-2} \text{ h}^{-1}$  again and dropped further in the next 12 h. Velocity was recorded at the slide surface where velocity was highest, but biomass loss occurred from surfaces in the whole channel with mean velocity much lower than these values. Therefore, the reported loss rates are underestimated for the reported velocities.

Fig. 6 shows the response of biomass on slides to velocity increase at one SRP concentration ( $25 \mu\text{g l}^{-1}$ ). Transferring slides that had a relatively large biomass ( $\geq 130 \text{ mg chl a m}^{-2}$ ) from velocities of  $20$  to  $60$  and  $80 \text{ cm s}^{-1}$  resulted

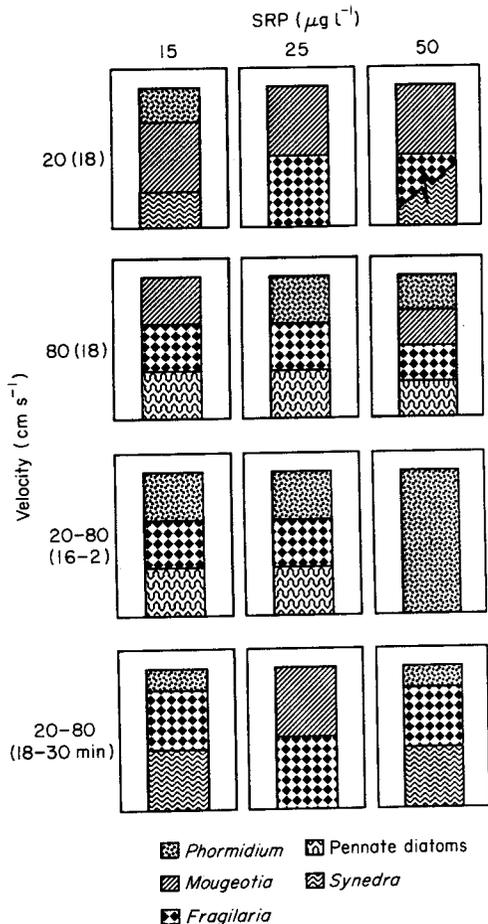


FIG. 4. Relative abundance of dominant genera observed at the end of one series of fixed ( $20$  or  $80 \text{ cm s}^{-1}$ ) and variable ( $20 \text{ cm s}^{-1}$  increased to  $80 \text{ cm s}^{-1}$ ) velocity treatments. Values in parentheses refer to days (and minutes) at respective velocities.

in more than 40% reductions in biomass within 15 min. However, high rates of loss declined rapidly on slides that remained in  $60$  or  $80 \text{ cm s}^{-1}$  current, after elevation from  $20 \text{ cm s}^{-1}$ , and biomass remained stable 1 day or more after the velocity increase. Comparison of results in velocity-increase treatments with those in fixed velocities at  $20$ ,  $60$  or  $80 \text{ cm s}^{-1}$  indicates that further fluctuations in biomass were not greater than in the unmanipulated velocities. The high instantaneous losses observed apparently were of short duration, and losses were at least partially recovered by the day after velocity had been increased.

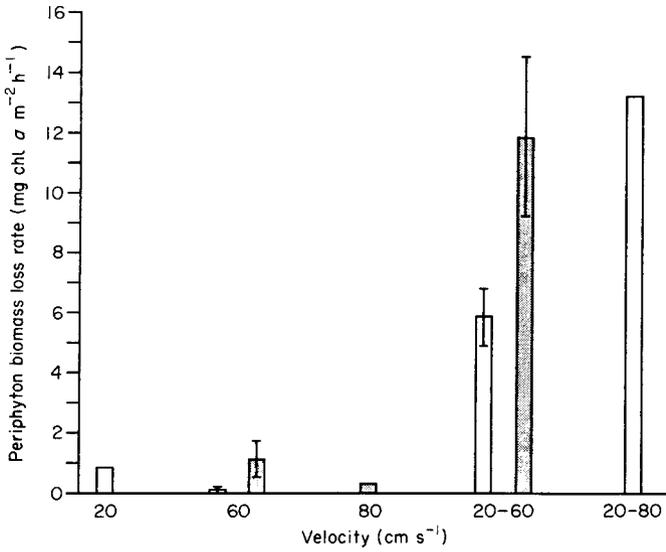


FIG. 5. Periphyton biomass loss rates ( $\pm$  SE) before and immediately (15 min) after velocity increase and solids addition (to  $25 \mu\text{g l}^{-1}$  TISS) in channels that received  $25 \mu\text{g SRP l}^{-1}$ . Velocities of 60 and 20-60 refer to channels with (open columns) and without (hatched columns) solids addition.

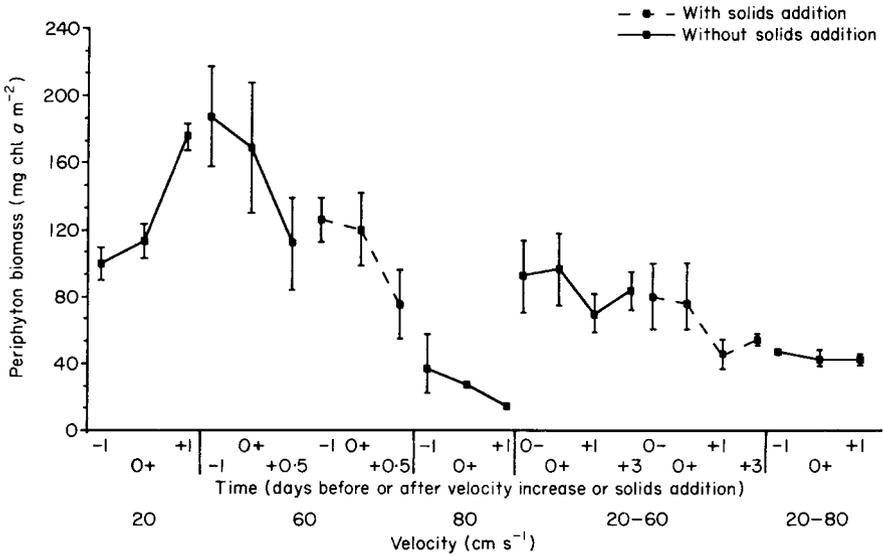


FIG. 6. Periphyton biomass ( $\pm$  SE) before and immediately after velocity increase and solids addition in channels that received  $25 \mu\text{g SRP l}^{-1}$ . The final three sets of data are from slide transfers from  $20 \text{ cm s}^{-1}$  to 60 and  $80 \text{ cm s}^{-1}$ . The first four sets are from untransferred slides.

Velocity elevation generally changed dominance from *Phormidium*, *Mougeotia*, or both at  $20 \text{ cm s}^{-1}$  to *Fragilaria* or *Synechra* immediately

after the increase to  $80 \text{ cm s}^{-1}$ . However, within 2 days, slides remaining in an  $80 \text{ cm s}^{-1}$  current returned to *Phormidium* dominance at  $42 \mu\text{g}$

SRP  $l^{-1}$  or co-dominance by *Phormidium*, *Fragilaria*, and other pennate diatoms at lower SRP concentrations.

#### Effects of solids addition

Velocity elevation from 20 to 60  $cm\ s^{-1}$  had a much greater effect on loss rate (0.1 at constant 60  $cm\ s^{-1}$  to 5.9  $mg\ chl\ a\ m^{-2}\ h^{-1}$ ) than with the addition of solids at a fixed velocity (0.1–1.1  $mg\ chl\ a\ m^{-2}\ h^{-1}$ ; Fig. 5). Simultaneous velocity elevation to 60  $cm\ s^{-1}$  and solids addition resulted in the highest loss rate of 11.8  $mg\ chl\ a\ m^{-2}\ h^{-1}$ . Within 1 day after velocity increase, solids addition, or both, loss rates had declined in all treatments to  $<1\ mg\ chl\ a\ m^{-2}\ h^{-1}$ .

As was noted with velocity increase alone, after the initial reductions, further fluctuations in biomass in treatments receiving solids were not much more evident than in channels where conditions were not altered, and biomass reductions were at least partially recovered in a short time (Fig. 6).

There was no discernible difference in periphyton assemblages following solids addition.

This was the case whether or not the solids addition was accompanied by velocity increase.

#### P uptake

Areal uptake rates of P tended to decrease as biomass increased, although there was considerable scatter in the data (Fig. 7;  $r=0.49$ ). The relationship was nevertheless significant at the  $P<0.05$  level. These data include values over a range of velocity and SRP concentrations which no doubt contributes to some of the variability.

Areal uptake rate of P increased as the concentration of SRP increased (Fig. 8). Uptake rate tended to level off (saturate) at in-channel concentrations greater than about  $15\ \mu g\ l^{-1}$ . The relationship between P uptake rate and SRP concentration appeared to be logarithmic, and was statistically significant ( $P<0.05$ ;  $r=0.68$ ) if the data were so transformed. Uptake was related to in-channel SRP concentration, because the channel system best represented a continuous, stirred tank reactor, in which added nutrient solutions were quickly diluted throughout and algae were exposed to the diluted, in-

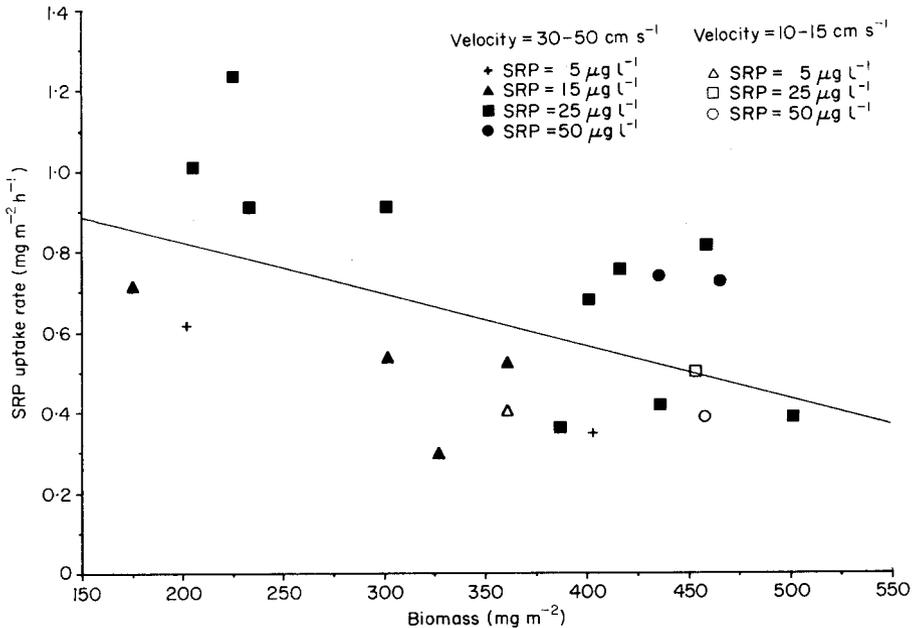


FIG. 7. Areal uptake rate of SRP in relation to biomass, determined at the end of treatment periods using data from all nutrient and flow regimes and in channel SRP concentrations. Legend values represent targets for inflow SRP and velocity.

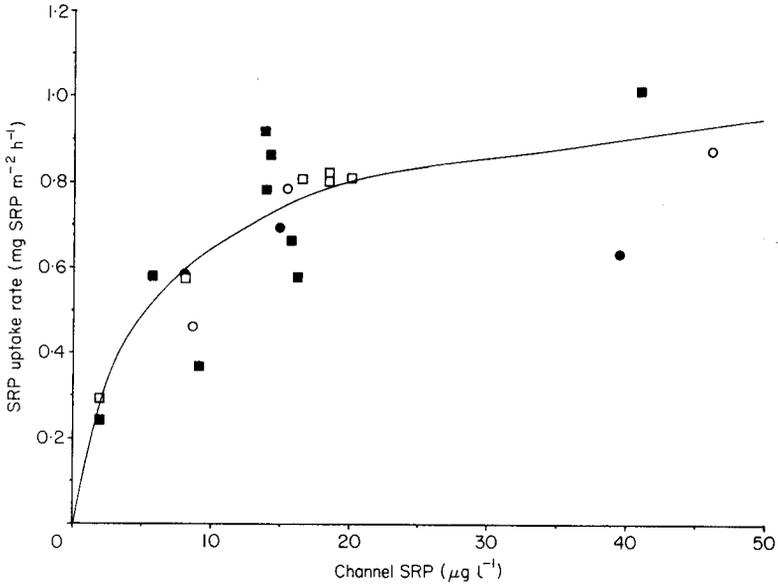


FIG. 8. Uptake rate of SRP in relation to in-channel SRP data from all nutrient and flow regimes. Uptake rates are averages based on measurements made every 4–7 days during the treatment periods. ●, Velocity = 10–15  $\text{cm s}^{-1}$ ; ■, velocity = 30–50  $\text{cm s}^{-1}$ ; ○, velocity increased from 15  $\text{cm s}^{-1}$  to 45  $\text{cm s}^{-1}$ ; □, velocity increased from 20  $\text{cm s}^{-1}$  to 40–50  $\text{cm s}^{-1}$ .

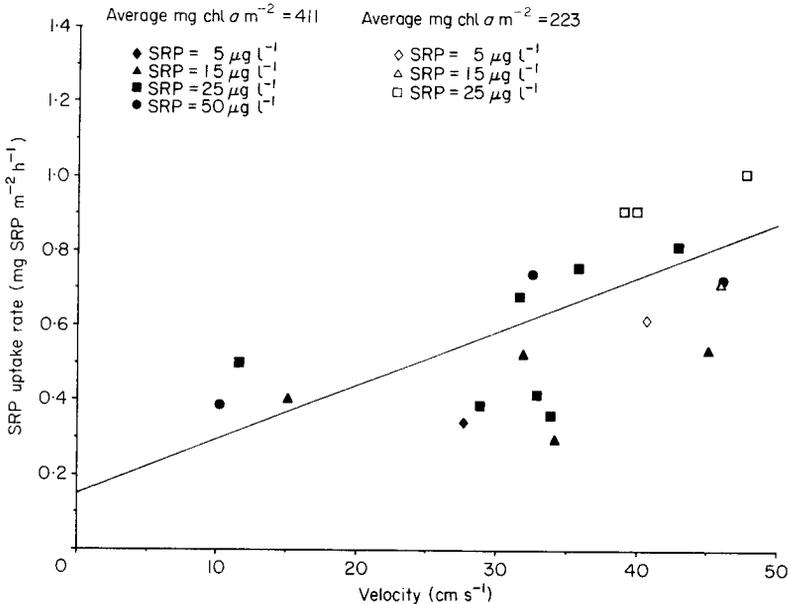


FIG. 9. Areal uptake rate of SRP in relation to velocity, based on data from all nutrient and flow regimes. Uptake was determined at the end of the treatment periods.

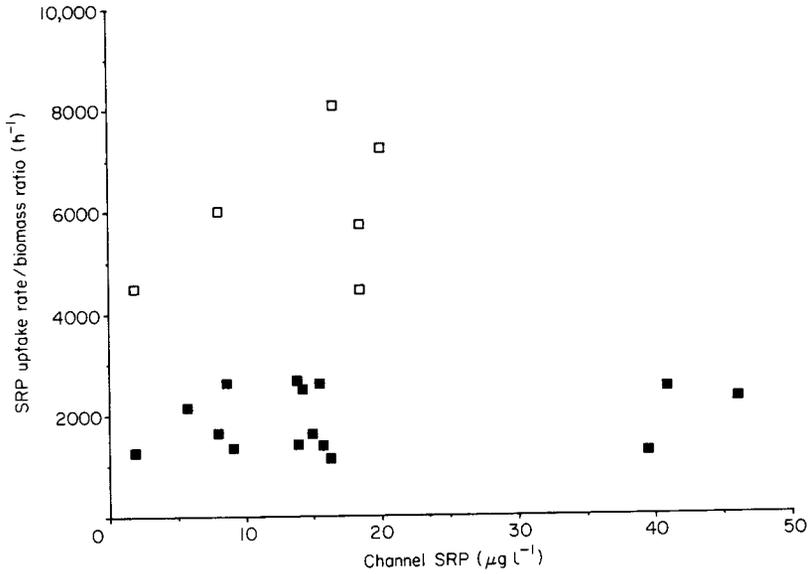


FIG. 10. Uptake rate of soluble reactive phosphorus per unit biomass in relation to in-channel SRP. Uptake was determined at the end of the treatment periods. Average biomass: ■, 411 mg chl *a* m<sup>-2</sup>; □, 223 mg chl *a* m<sup>-2</sup>.

channel concentrations and not the higher inflow concentrations.

Areal uptake rates of P were also positively related to velocity, although there was much scatter in the data (Fig. 9). The highest rate of 1.2  $\mu\text{g m}^{-2} \text{ h}^{-1}$  occurred at the highest average channel velocity, 48  $\text{cm s}^{-1}$ . The relationship between velocity and areal uptake rate was most apparent for velocities between 35 and 50  $\text{cm s}^{-1}$ . Uptake rates at velocities less than 15  $\text{cm s}^{-1}$  were comparable to those observed at velocities of 25–35  $\text{cm s}^{-1}$ . Some of the reason for high uptakes at the high velocities may have been due to lower biomass levels. Nevertheless, the relationship of uptake rate and velocity was significant ( $P < 0.05$ ;  $r = 0.64$ ).

Fig. 10 shows areal uptake rate per unit biomass in relation to in-channel SRP. There is no apparent relationship but the data are separated clearly into two distinct sets, which are differentiated by biomass level. In one set, average biomass was  $411 \pm 6 \text{ mg chl } a \text{ m}^{-2}$ , and values for areal uptake rate/biomass were between 1000 and 3000  $\text{h}^{-1}$ . The ratio was much greater at lower biomass levels in the second set (mean  $223 \pm 17 \text{ mg chl } a \text{ m}^{-2}$ ), with values

ranging between 4000 and 9000  $\text{h}^{-1}$ . Although differences between areal uptake rate/biomass ratios for the two biomass levels were not significant according to the parametric *t*-test, the non-parametric Mann-Whitney-Wilcoxon test (Zar, 1984) did show a significant difference at the  $P < 0.025$  level.

## Discussion

### *Effects of current at fixed velocity*

Both velocity increase to 60  $\text{cm s}^{-1}$  and SRP increase enhanced accrual of periphytic algal biomass, although further velocity increase reduced biomass. The effect of velocity was pronounced throughout this range, while the effect of SRP increase was evident only up to a channel concentration of 7.5  $\mu\text{g l}^{-1}$ . The velocity results are generally consistent with those from several studies cited earlier and with the mechanistic explanation of offsetting positive and negative influences of velocity increase.

The positive effect of velocity was somewhat more evident at low ( $\leq 7.5 \mu\text{g l}^{-1}$ ) than at high SRP concentrations. This result suggests that

higher velocity especially benefits algae in relatively nutrient-poor systems. This benefit could stem both from a reduced boundary layer thickness, allowing cells to encounter higher nutrient concentrations than available through a thicker boundary layer, and from improved diffusion of relatively scarce nutrient molecules to cell surfaces. This effect is also probably related to the relatively low concentration at which growth is saturated (Bothwell, 1985; Welch, Horner & Patmont, 1989).

Loss rates were similarly low under all fixed-velocity treatment conditions. This similarity of loss rates in such experiments has been reported previously (McIntire, 1966; Horner *et al.*, 1983). McIntire noted, however, that these rates began to differ at 9 and 38 cm s<sup>-1</sup> when the communities reached a steady state of alternate partial sloughing and recolonization. The communities in the experiments described here did not attain that state.

Taxonomic observations showed that *Phormidium* was favoured by higher nutrient content compared to *Fragilaria* and other pennate diatoms. *Phormidium*'s dominance at the highest nutrient content was reported earlier (Horner *et al.*, 1983). Diatoms were favoured over blue-green algae at relatively high velocities. *Mougeotia*, a filamentous green alga, was less tolerant of elevated velocity than the diatoms and *Phormidium* and showed no nutrient preference.

#### *Effects of velocity increase and solids addition*

The experiments demonstrated that an elevation in velocity, above that to which algae were adapted, led to increased loss rates and temporarily reduced biomass. These results were more pronounced with velocity elevation of greater magnitude. Therefore, while algal species certainly differ in their attachment ability, it seems to be generally true that the relative strength of the attachment that develops is a function of the current prevailing during colonization and growth. A sudden increase in that current will remove substantial material, although a periphyton community grown in a steady current of the higher velocity will continue with low loss rates. As a mechanistic hypothesis, periphyton communities are probably protected from high shear stresses by the existence of a boundary layer, while velocity increase erodes the bound-

ary layer and exposes the sessile algae to higher frictional forces.

Suspended solids addition of approximately 25 mg TISS l<sup>-1</sup> also eroded periphyton biomass, although not nearly as effectively alone as did the sudden velocity increases. Presumably, higher solids concentrations and particles of different sizes and shapes would differ in their effectiveness as shear stress inducers. Further testing is required to express quantitatively the response of periphytic algae to solids transport. Nevertheless, these results indicate that an interaction does occur between solids and velocity on periphyton scour.

Elevating velocity from 20 to 60 cm s<sup>-1</sup> raised instantaneous algal biomass loss rate from considerably less than 1 to approximately 6 mg chl *a* m<sup>-2</sup> h<sup>-1</sup>. The loss rate resulting from 25 mg TISS l<sup>-1</sup> addition alone was only about 1 mg chl *a* m<sup>-2</sup>. Considering that initial biomass on the slides was in the order of 50 mg chl *a* m<sup>-2</sup>, and with evidence that high instantaneous loss rates prevailed only briefly, it is not surprising that solids addition alone did not cause substantial biomass reduction. However, the combination of solids addition and velocity increase from 20 to 60 cm s<sup>-1</sup> resulted in an instantaneous loss rate that was more than an order of magnitude greater than that with solids added alone. These results suggest that in order for fine particles (<75 µm diameter) to have a significant effect, they must gain entry to the boundary layer protecting the algae, which can be accomplished by a velocity increase that reduces the width of the original boundary layer. Algae reportedly adhere better to natural than to artificial substrates (Nielsen *et al.*, 1984). Therefore, the quantitative values of loss rates measured in these experiments may not be representative of natural systems.

When large losses of attached material occurred, either due to velocity increase or combined solids addition and velocity increase, biomass levels remained low only briefly. Evidently, free-living algal cells are opportunistic, and both recolonization of available bare surface and growth after recolonization are rapid. In a natural system receiving stormwater runoff, the continued availability of suitable substrate for periphyton growth may be more problematic than the ability of the community to recover from periodic stress from increased velocity and solids. Cobble and rocks that best support the

epilithic periphyton are often buried by the fine materials eroded by storm runoff and delivered to receiving streams.

### *P uptake*

Uptake rate and biomass were determined when the internal channel surfaces were densely covered by filamentous-green algae, so that differences in biomass were mainly due to thickness of the algal mat rather than to the amount of surface coverage. Although P uptake rate might be expected to increase with biomass, the opposite tendency was observed. The occurrence of higher uptake rates at lower biomass levels may be attributable to effects of velocity, which are discussed below. The lack of positive association between biomass and uptake rates also suggests that uptake is predominantly a surface phenomenon, and that the inner layers of the algal mat are not as active as the surface layer in taking up nutrients. McIntire (1968a, b) postulated that benthic communities are composed of an outer pigmented layer of young, photosynthetically active cells, and an inner layer of older, decomposing cells. The reduced activity of the older cells would inevitably result in reduced rates of nutrient uptake.

Nutrient uptake by the inner cells may also be controlled by diffusion processes. Stevenson (1983) and Sand-Jensen (1983) have postulated that a significant portion of periphytic algae grow within a laminar boundary layer, where flow is substantially reduced. In order for phosphorus to reach periphytic algae, it must be transferred across this boundary layer. In the boundary layer, mass is transferred by molecular diffusion, which is a relatively slow process (Geankoplis, 1972). Since the algal uptake rate generally exceeds the rate of diffusion, there is a concentration gradient across this boundary, with the highest concentrations at the interface between the boundary layer and the bulk liquid (Grady & Lin, 1980). As the distance from the interface increases, the phosphorus concentration progressively decreases. Consequently, nutrient concentrations would not be as great in the inner layers of the algal mat as they are at the mat surface, resulting in slower uptake.

There are two factors that can affect the diffusion process. The first is the overlying water SRP concentration. As the P concentration increases, the rate of diffusion through the

boundary layer also increases, which could lead to higher uptake rates. The results here indicate that the rate of limiting nutrient uptake by filamentous algae increased most dramatically as SRP concentration increased, up to in-channel concentrations of about  $15 \mu\text{g l}^{-1}$ . Beyond that concentration, the increase in uptake rate with SRP concentration diminished. If uptake rate is compared against inflow SRP concentration, uptake decreased beyond about  $25 \mu\text{g l}^{-1}$ . This corroborates the results of Horner *et al.* (1983), who showed that biomass accumulation of filamentous greens increased most rapidly with SRP up to influent concentrations of  $25 \mu\text{g l}^{-1}$ .

Velocity is another factor that can affect the diffusion process, through its effect on the laminar boundary layer. As velocity increases, the depth of the boundary layer decreases (Stevenson, 1983). Consequently, the diffusion distance will not be as great at higher velocities, enabling the algae to encounter higher nutrient concentrations. Increasing velocity also increases the rate at which nutrients are delivered to the algae by enhancing the diffusion gradient between the algae and overlying water. The effect that velocity has on nutrient delivery should be related to uptake rates, with higher delivery rate resulting in higher uptake rates. The results of these experiments lend support to this hypothesis, in that areal uptake rates of P increased with velocity.

The relationship between biomass and uptake rate should be more evident during early colonization phases, before the surface is covered to maximum capacity. As Sand-Jensen (1983) pointed out, exchanges between the water column and the algal mat are more important during early phases of growth, and correlations between water quality variables and biomass are more readily observed at that time. As the algal mat matures, internal processes, such as nutrient recycling, come into play and overlying water conditions are not as important. Unfortunately, uptake rates were not determined while the channels were colonizing in these experiments.

As demonstrated by Fig. 10, uptake was clearly more efficient at lower than at higher biomass levels. This observation may be related to diffusion limitation and cell activity, as discussed above. At higher biomass levels a greater percentage of the cells would be in the inner

layers of the algal mat, where diffusion limitation could be a significant factor and cell activity may be reduced. The high biomass levels were 1–2 weeks older than the low biomass levels, and age difference could have had some influence on uptake rates. Older cells may have a reduced demand for nutrients compared to younger cells, and light and CO<sub>2</sub> may be limiting metabolic P demands as well.

These results demonstrate that algal uptake is dependent on both P concentration and velocity. They are consistent with previous findings regarding the effects of P concentration and velocity on periphytic biomass and accrual (Horner *et al.*, 1983). Since uptake rates have a bearing on algal growth rates and biomass, elucidation of factors affecting uptake rates can give an indication of how periphyton will respond to different combinations of P and velocity. Uptake rates observed in these experiments appeared to level off at higher P concentrations in a manner similar to what one would expect from Michaelis-Menton uptake kinetics. From Fig. 8, a maximum uptake rate for this filamentous algal community may occur near 1 mg P m<sup>2</sup> h<sup>-1</sup>, which would correspond with a half-saturation constant of around 8 µg l<sup>-1</sup> SRP. Although the uptake units are unit-area-based, rather than calculated on a biomass basis, such a half-saturation constant has been shown to be reasonable in predicting potential biomass levels (Horner *et al.*, 1983; Welch *et al.*, 1989). It may be inappropriate to express uptake per unit total biomass for periphyton because of the mat-thickness phenomenon.

If one accepts the postulate that periphytic algae develop within a laminar boundary layer, then the P concentration governing uptake is the concentration within this layer, rather than the concentration in the overlying water. As discussed above, the P concentration in the laminar boundary layer is lower than that in the open water, and will be affected by both channel P concentration and velocity. Furthermore, as biomass increases, cells within the mat become more limited by diffusion, suggesting that higher P could benefit growth at relatively high biomass levels. This consideration offers a likely resolution of an apparent inconsistency that exists in the literature between, on the one hand, the observation of growth rate saturation of thin algal films at low limiting nutrient concentrations and, on the other, stimulation of bio-

mass accrual by additions of much higher concentrations.

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