

Composition and dynamics of epilithic algae in a forest stream at Shillong (India)

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Abstract

The seasonal dynamics of epilithic algae in a third order pristine forest stream were analyzed over a period of 2 years. Stream water was slightly acidic and nutrient poor. Encrusting, filamentous flocs, and filaments were found. Algal standing crop was high (mean concentration of Chl *a* 16–43 mg m⁻²) in spring. Filamentous algae contributed most to standing crop. Diatoms made up over 85% by number of the epilithon. Blue-greens were abundant upstream, and chlorophytes downstream. This shift was ascribed to greater light availability downstream. The community was more diverse during spring. Water current was the most important variable regulating epilithon structure. Total phosphorus (TP), orthophosphate (O-PO₄³⁻), silica (Si⁴⁺), nitrate (NO₃⁻) and conductance correlated negatively with flow rate. Green algae showed a positive correlation to phosphorus during low and stable flow. During rapid runoff, diatoms were the most resistant forms. Seasonal change in the epilithic community was mainly regulated by fluctuations in flow rate.

Introduction

Many lower order forest streams are influenced by the riparian vegetation which reduces autotrophic production by shading, and contributes large amounts of allochthonous detritus (Vannote *et al.*, 1980). The primary producers in such systems are largely epilithic algae. Often, their productivity appears to be light limited (Hill & Knight, 1988; Stevenson *et al.*, 1991). With increased availability of light, increase in algal biomass and changes in community structure have been reported (Rounick & Gregory, 1981; Lowe *et al.*, 1986). The study of structure and dynamics of the algal community in forest streams is rather complicated, because of the multitude of factors that co-vary in the system. Thus, the application of multivariate statistical methods becomes necessary for this type of study. Few studies assess the community of algal species in streams, using such methods (Wehr, 1981; Duncan & Blinn, 1989).

Despite the large amount of literature on spatial and temporal variation in epilithic primary production in temperate streams, few studies have quantitatively examined physical and chemical variates concurrently (Horner & Welch, 1981; Duncan & Blinn, 1989; Sabater, 1990). Studies on the Indian subcontinent are limited to phytoplankton of large rivers (Singh, 1988; Venkateswarlu, 1983; Venkateswarlu *et al.*, 1987) and some thermal springs (Saha & Dutta, 1983; Jha, 1985; Singh, 1991).

The aim of the present study was to describe the community structure and dynamics of the epilithic algal community in an Indian third-order forest stream and correlate it with physical and chemical variates by using Canonical Correspondence Analysis (CCA).

Study area

Wah Dienglieng is a third-order perennial stream draining a forested catchment in the East Khasi Hills district of Shillong, Meghalaya (25°33' N latitude and 91°53' E longitude) (Fig. 1). Two stations, one upstream (altitude 1605 m) and one downstream (altitude 1520 m), approximately 1 km apart, were selected for regular sampling. The stream is unpolluted, as its drainage area is protected by the forest department. The catchment area does not have any human settlement. The region has a tropical monsoon climate. Total annual rainfall was 3838 mm in 1988 and 2781 mm in 1989. The substrate in the streambed is primarily granitic and quartzitic cobbles. The soil of the drainage area is made up of laterite and loamy silt, and acidic in nature (pH 4.6–5.0). *Quercus dealbata*, *Daphneplum himalayana*, *Machlus kinghaili*, *Schima khasiana*, *Schima wallichii*, *Rhododendron arbocarium* and *Pinus kesiya* form a dense canopy along the stream bank at the upstream site, but the canopy is minimal at the downstream site. This results in 30–40% exposure to the streambed upstream, and 80–90% exposure downstream. The width and depth of the stream varied from 1 to 5 m and 3 to 45 cm, respectively during the study period. Discharge varied from 0.1 to 1 m³·sec⁻¹.

Materials and methods

Stream water and epilithic algae were sampled every month (January 1988 to December 1989). Water samples were collected in triplicate in 500 ml polyethylene bottles; standard methods were followed for sampling and chemical analysis (Wetzel & Likens, 1979; Suess, 1982; APHA, 1985). Light intensity (PAR) was measured by an infrared gas analyser (ADC London). Various physiognomic forms were studied by point intercept method considering two hundred points at 5 cm intervals over two stretches along the stream length (Rout & Gaur, 1990). Chlorophyll *a* was calculated after Strickland & Parsons (1968). For algal identification Hustedt (1930), Smith (1950), Prescott (1951), Randhawa (1959), Desikachary (1959), Sarode & Kamat (1984) keys were used. Enumeration of algae was done in a Spencer's brightline haemocytometer, a Utermohl chamber and an inverted microscope, (Will Wetzlar Ph). Cell volumes were determined from camera lucida drawings of about 20 specimens of each species, and mean cell volumes calculated on the basis of their geometrical shapes (Clarke *et al.*, 1987). In the

case of algae other than diatoms, average cell volume was estimated from direct measurements of length, breadth and depth (Moore, 1977). The data for Chlorophyll *a* and biovolume were converted to unit area.

Statistical analysis

The species diversity was calculated using the expression of Shannon (1948).

$$H' = \sum_{i=1}^K Pi \ln Pi,$$

where *K* is the number of categories and *Pi* is the proportion of the observations found in category *i*.

The data on physical and chemical characteristics and epilithic algal biovolume of different species was subjected to Canonical Correspondence Analysis (CCA) using computer programme CANOCO (ter Braak, 1986).

Results

Physical and chemical characteristics of the stream

Maximum and minimum water temperatures were recorded in July–August (17–20 °C) and January–February (10.5–13 °C) respectively. Downstream temperatures were higher than upstream. The downstream site received direct sunlight (1600–1800 E m² s⁻¹), while upstream received only diffuse light (460–810 E m⁻² s⁻¹). The water was slightly acidic (pH 5.5–6.5) and rather stable. The flow is at minimum in spring (6.8–13.1 cm s⁻¹), with typical wet summer freshets (56–64 cm s⁻¹) (Fig. 2). Conductivity was inversely related to flow. Dissolved O₂ was below saturation throughout, without seasonal trend. Dissolved silica was relatively high (5.3–11.4 mg l⁻¹) (Fig. 2). Orthophosphate (O–PO₄³⁻) and total phosphorus (TP) were highest in spring (Fig. 2). NH₄⁺ did not show a seasonal trend (Fig. 2). NO₃⁻ fluctuated, with higher values in autumn (Fig. 2). Ca²⁺ and Mg²⁺ decreased from winter and spring to summer and autumn. Low trace element concentrations rendered their analysis redundant.

The algal flora

One hundred and thirty two algal species belonging to 36 genera were identified. Bacillariophyta was the predominant group, represented by *Achnanthes* (9 species), *Eunotia* (18 species), *Gomphonema* (13 species), *Navicula* (29 species), *Nitzschia* (10 species),

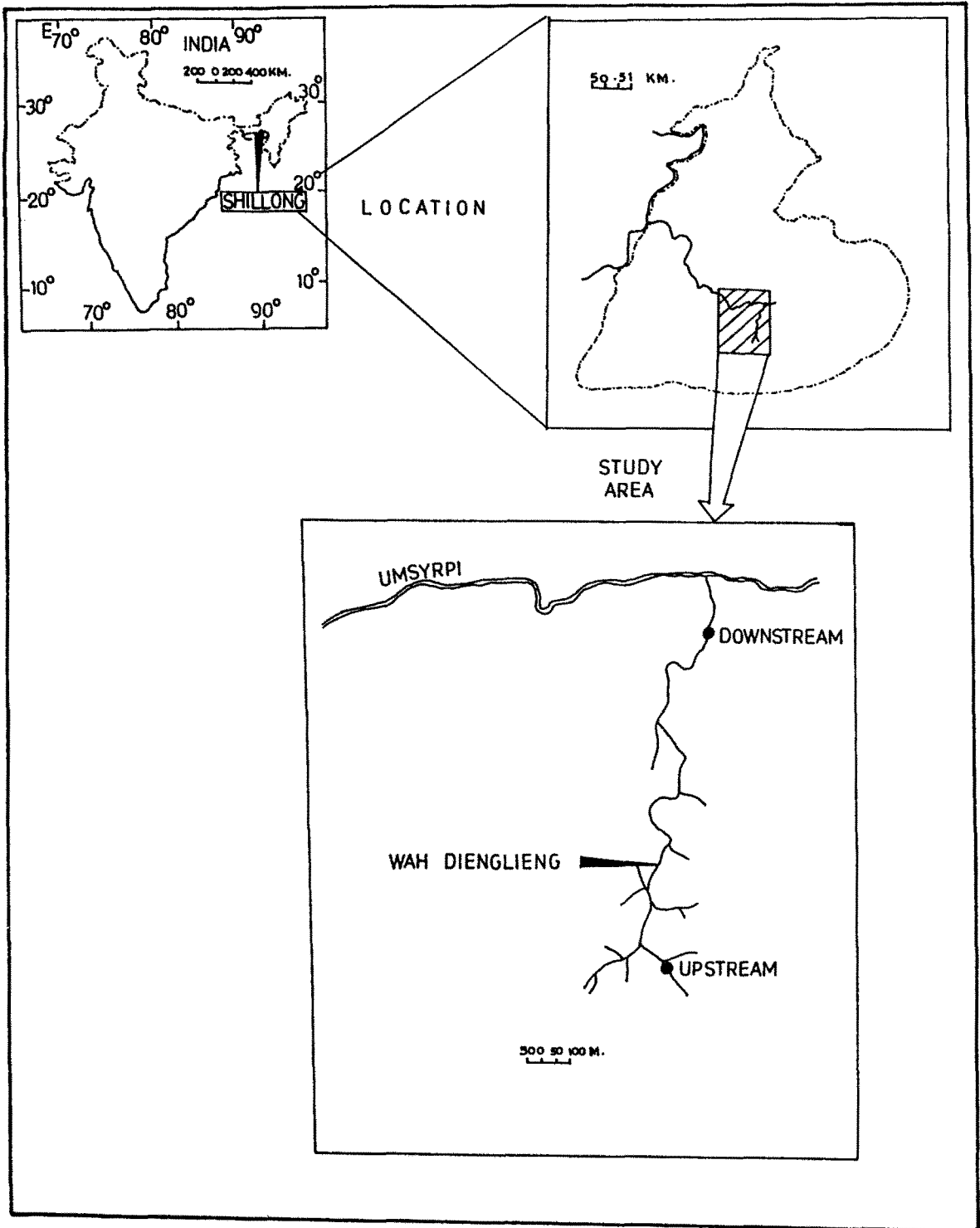


Fig. 1. Map of the Shillong region showing two sampling sites in Wah Dienglieng stream.

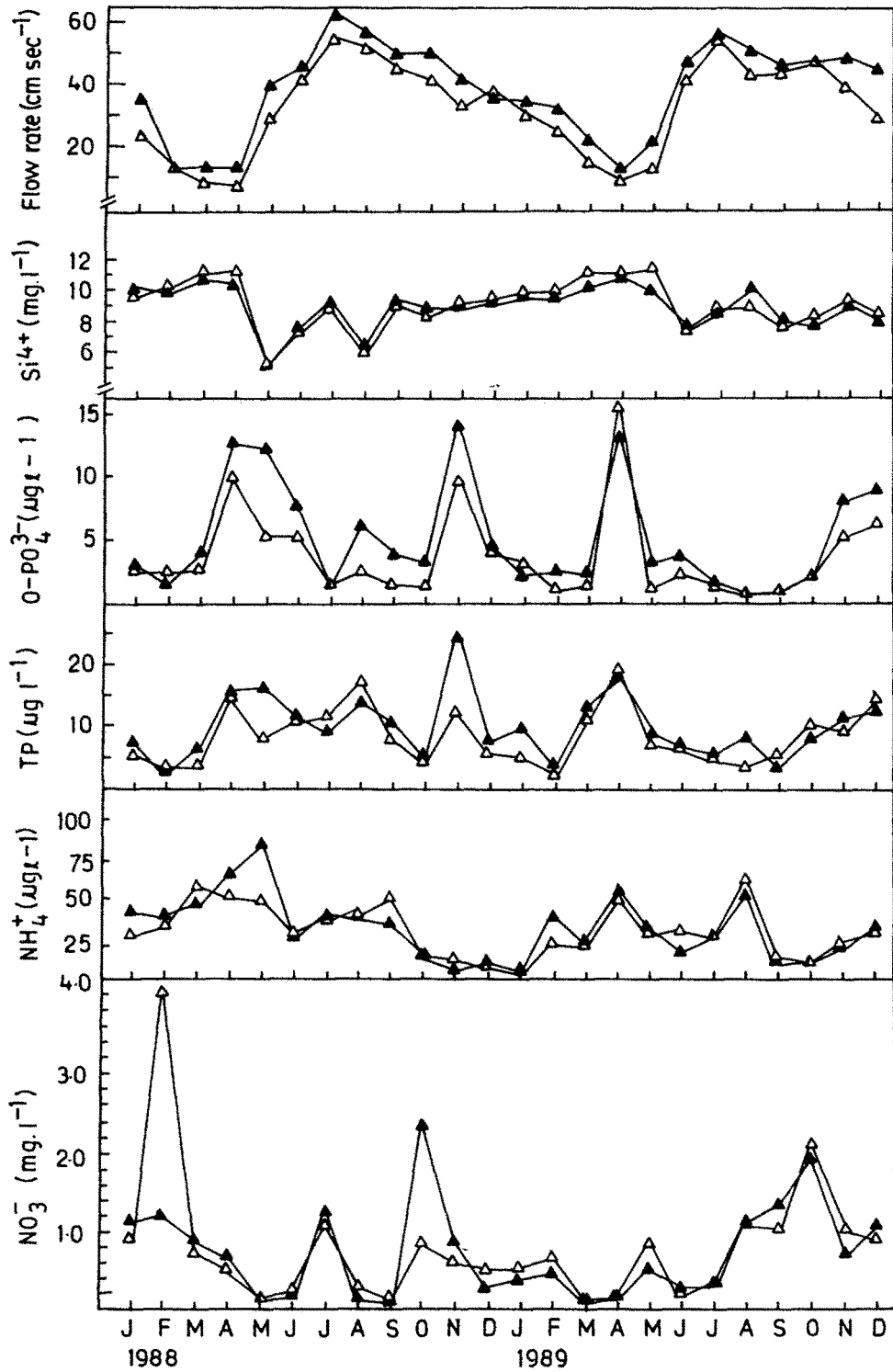


Fig. 2. Monthly variations in flow rate, Si^{4+} , O-PO_4^{3-} , TP, NH_4^+ and NO_3^- at the selected stations: upstream (Δ), downstream (\blacktriangle).

Synedra (5 species). Among blue-green algae, *Oscillatoria willei* and among green algae, *Spirogyra communis* dominated the community.

The downstream station showed higher species richness than the upstream one in all seasons (Fig. 3). Highest value was recorded in spring, lowest in summer. A similar trend was observed for total numbers. Shannon-Weaver species diversity indices generally correlated with species richness. The lower diversity was often associated with summer (1.6–2.1). Diversity was particularly high in spring (3.1–4.1). Biomass in terms of chlorophyll *a* (5–46 mg m⁻²) varied in time and space (Fig. 4). Biomass was lowest during summer, mainly July, and peaked in spring. Values were substantially greater downstream than in upstream. The trends in pigment data were similar to the biovolume data. The contribution of Chlorophyta, Cyanophyta, Bacillariophyta and Rhodophyta to biovolume varied among stations. Cyanophyta dominated upstream, whereas Chlorophyta were dominant downstream. Rhodophyta were represented by *Audouinella violacea* and formed a small component of the attached community. *Oscillatoria willei* the predominant member of the Cyanophyta, contributed maximally to total biovolume upstream (Fig. 5). *O. chlorina*, another blue-green was also important. *Spirogyra communis* and *Hyalotheca dissiliens* (Chlorophyta) were responsible for much of the late winter–spring increase in biovolume downstreams (Fig. 6). The former contributed 70–90% of the total epilithic biovolume. Another Chlorophyte, *Cylindrocapsa conferta* was typically important during summer. Diatoms were consistently present in the assemblage throughout the study period. Despite the occurrence of so many species, their contribution to epilithic biovolume was meagre. *Synedra ulna* was the most common diatom at both stations. It grew well even during high flow. *S. acus*, *Gomphonema lanceolatum*, *G. gracile*, some species of *Eunotia* and *Navicula* were also seen frequently, but their contribution was relatively small. Other genera of diatoms were of minor importance.

Synthesis of biological and physical-chemical results
Canonical Correspondence Analysis (CCA) of physical-chemical data and biovolume of different species for each station, and the ordination diagrams are presented in Figs 7 & 8. Since species (as coded in Table 1) are assumed to have unimodal response surfaces with respect to linear combinations of environmental variables, the species are represented by points

corresponding to their approximate optima in the two-dimensional environmental subspace. The environmental variables were denoted by arrows indicating their direction and rate of change through the subspace. The points jointly reflect species distributions along each of the environmental variables. Various environmental factors were significantly related with species composition over time. Flow, O-PO₄³⁻, TP and NO₃⁻ with longer arrows were strongly correlated with the coordination axes, and closely related to the pattern of community variations shown in the ordination diagrams.

Correlation coefficients or intraset coefficients of environmental factors with the first two axes of CCA are given in Table 2. The first axis at the upstream station is defined by high conductivity and high NO₃⁻, and the second axis by high NH₄⁺ and high Si⁴⁺. At the downstream station areas with low flow on the first axis had relatively higher pH and Ca²⁺, whereas the second axis showed nutrient deficiency. The eigenvalues (Table 3) show that the extracted gradients are quite short. The scores (optima) of most species therefore lie outside the centre region. CCA ordination diagrams show that summer samples are highly influenced by flow, temperature, and TP. Similar factors also influenced the autumn samples. NO₃⁻, NH₄⁺, Si⁴⁺ were of secondary importance. During winter, temperature and phosphorus were extremely important for the algal community. Spring samples were mainly influenced by nutrients.

The dominant species are present near the centroid of the ordination diagrams which is suggestive of an importance in the species composition of the epilithon. *Oscillatoria chlorina* was near to PO₄³⁻, suggesting that it needs much phosphorus. *O. willei*, *Audouinella violacea*, *Cylindrocapsa conferta* and *Mougeotia genulflexa* were influenced by high flow, temperature and phosphorus. At low flow, DO and phosphorus favoured *Tolypothrix distorta* and *Hyalotheca dissiliens*. *Spirogyra communis* preferred moderate flow. *Synedra ulna*, *S. pulchella*, *S. acus* and *Neidium iridis* were resistant to flow. While *Gomphonema olivaceum* showed a preference to low flow. *G. gracile* preferred high temperature. *Eunotia pectinalis*, *Pinnularia gibba*, *P. interrupta*, *Closterium acerosum* and *Cosmarium bioculatum* preferred high nutrient levels. A preference for high pH was seen in two species of *Frustulia* (*F. vulgaris*, *F. jogensis*) and *Scytonema coactile*. While *Gomphonema hebridica* preferred a low pH. *Navicula cari* preferred high NH₄⁺ whereas, *N. cryptocephala*, *N. mutica* and *N. gracilis* showed

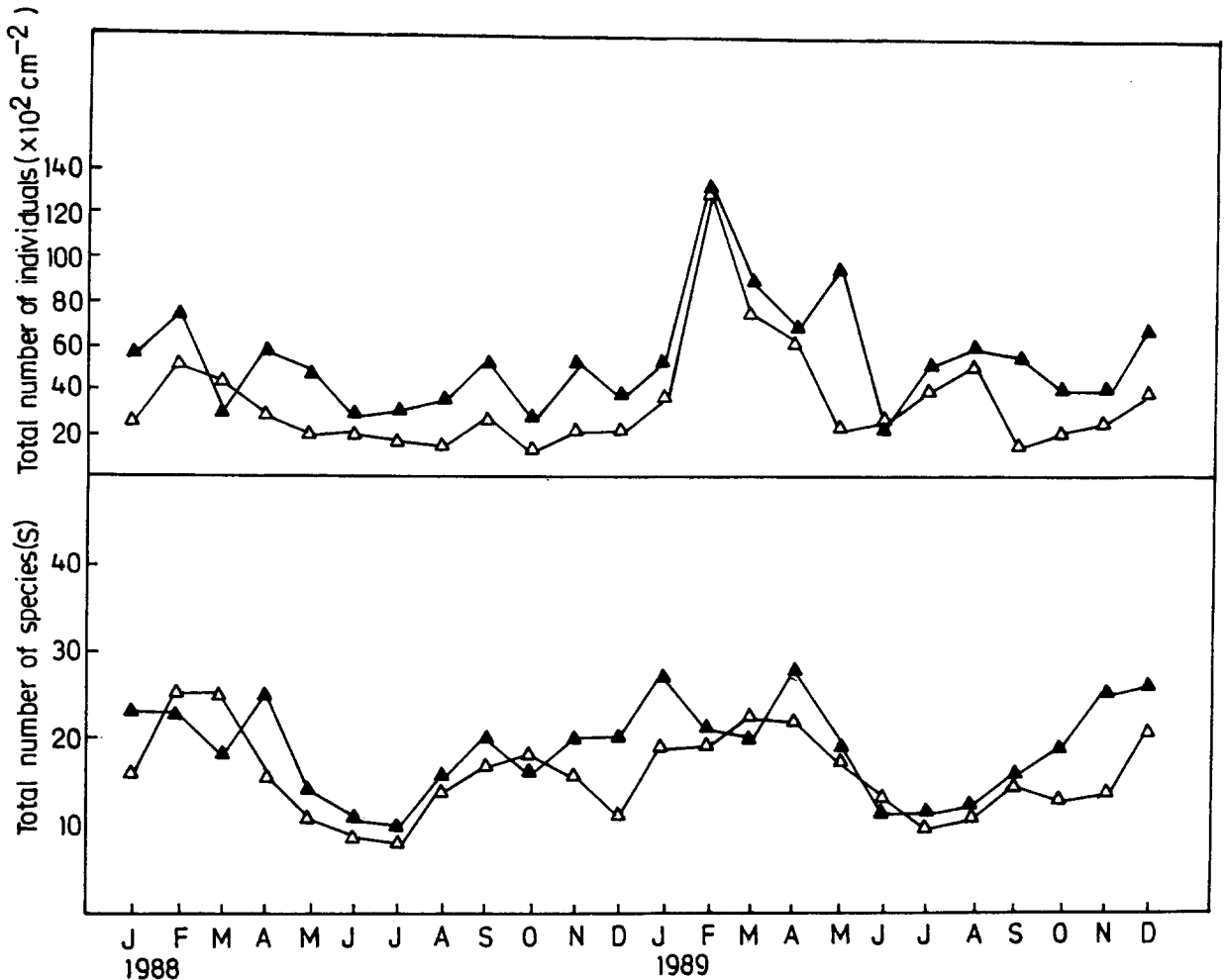


Fig. 3. Seasonal changes in total number of individuals and species number in the epilithon at the selected stations: upstream (Δ), downstream (\blacktriangle).

preference for high phosphorus. *Caloneis silicola* and *Nitzschia pseudofonticola* were influenced by a subtle interaction among TP, temperature and flow.

Discussion

The levels of calcium and magnesium in Wah Dienglieng matches those of softwater streams elsewhere (Marker, 1976), although they were considerably lower than in some reports (Moore, 1977; Holmes & Whitton, 1981). Silica was markedly higher ($5.3\text{--}11.4\text{ mg l}^{-1}$) than in streams elsewhere, (Moore, 1977; Holmes & Whitton, 1981), presumably owing to the presence of silica-rich rocks in the stream bottom. Nutrients were low and this could inter-alia be

ascibed to the presence of nutrient impoverished soil in the drainage area (Singh, 1990), and the absence of eutrophication.

The epilithic algal community of the stream showed broad compositional similarity with streams of North America and Europe (Moore, 1977; Hamilton & Duthie, 1987; Steinman & Lamberti, 1988; Duncan & Blinn, 1989). Biomass and species richness were always higher downstream, mainly due to greater light availability. Late-winter and spring favoured growth of most epilithic algae, due to a longer photoperiod and increased light intensity. Filamentous chlorophytes, abundant downstream, may require high light intensity due to a lack of pigment diversity. The abundance of blue-green algae upstreams agrees with Regan (1988) who suggested they grow well at low light intensity.

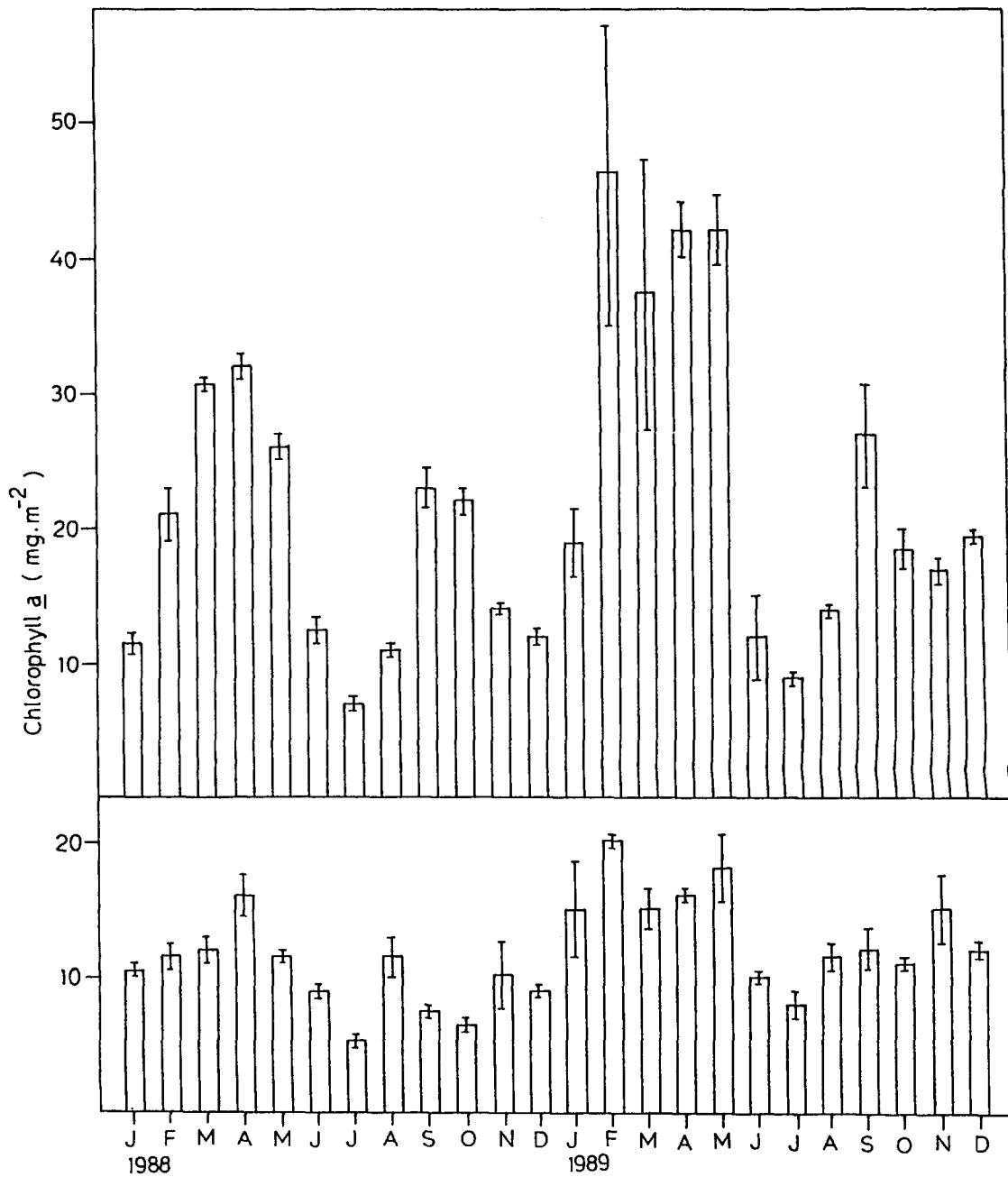


Fig. 4. Chlorophyll *a* of algal epilithon at two sampling stations (lower figure: upstream, upper figure: downstream). Vertical bars denote \pm SD of the mean.

In the present study, light was not inhibitory to epilithic algae, although Duncan & Blinn (1989) ascribed reduced periphytic biomass in a canyon stream to a photoinhibitory effect. Beside light, flow rate was important. The epilithic biomass, species richness and

diversity showed minima in summer due to extremely high flow rates ($54\text{--}63\text{ cm s}^{-1}$). Although many algae require a continuous flow to facilitate their immigration, emigration, growth and metabolism (Stevenson,

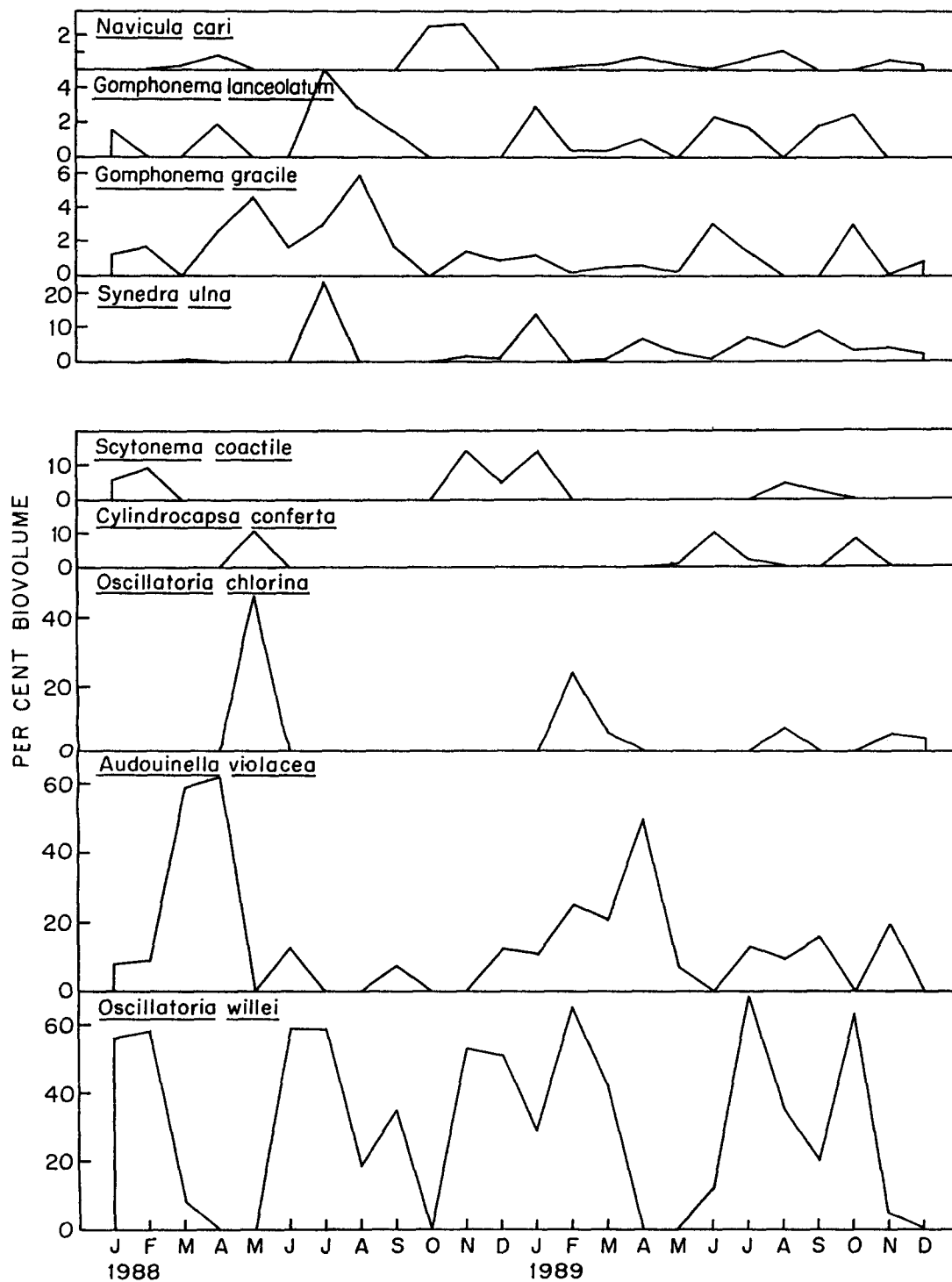


Fig. 5. Seasonal changes in the biovolume of dominant algal species upstream.

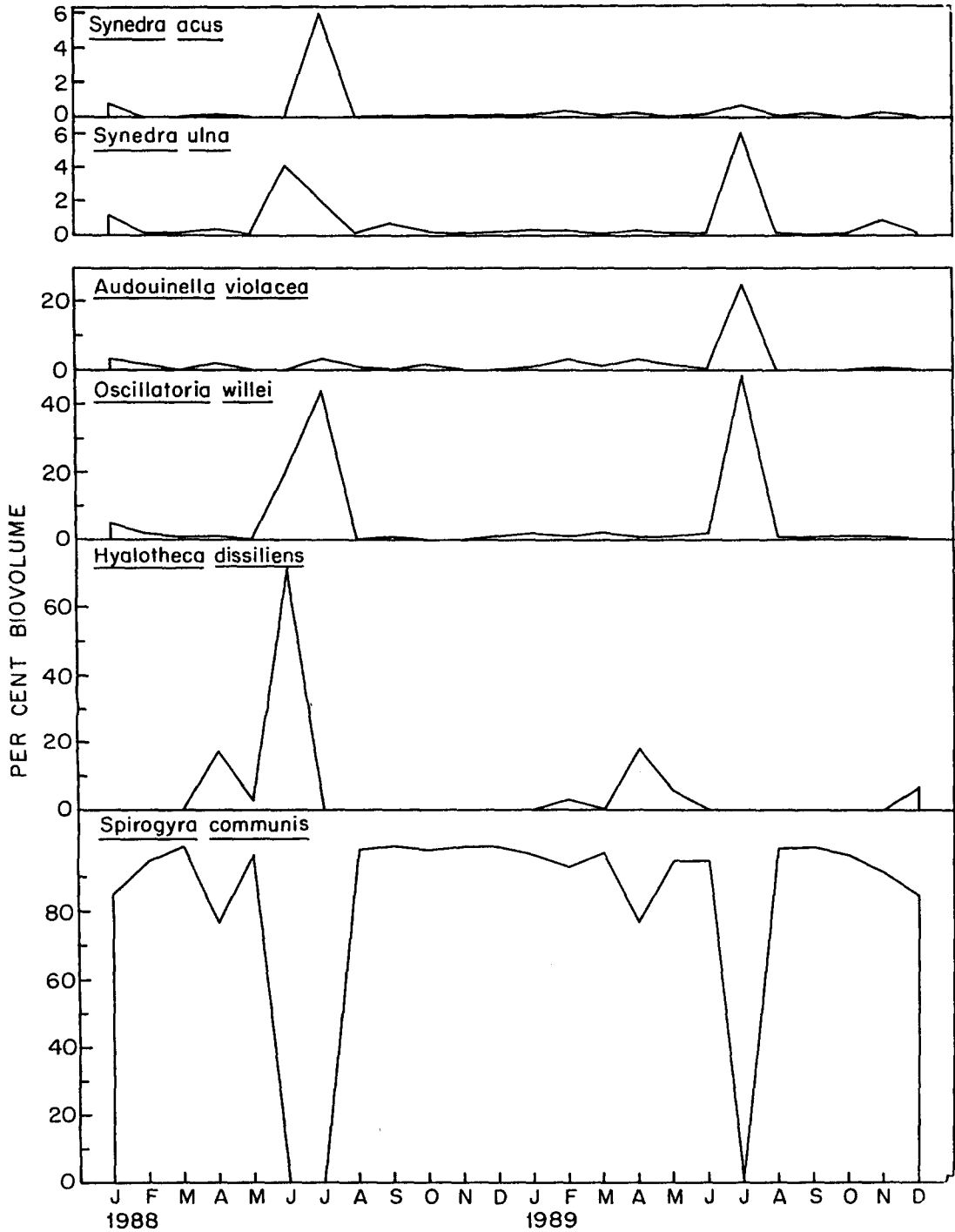


Fig. 6. Monthly variations in biovolume of dominant epilithic algal taxa downstream.

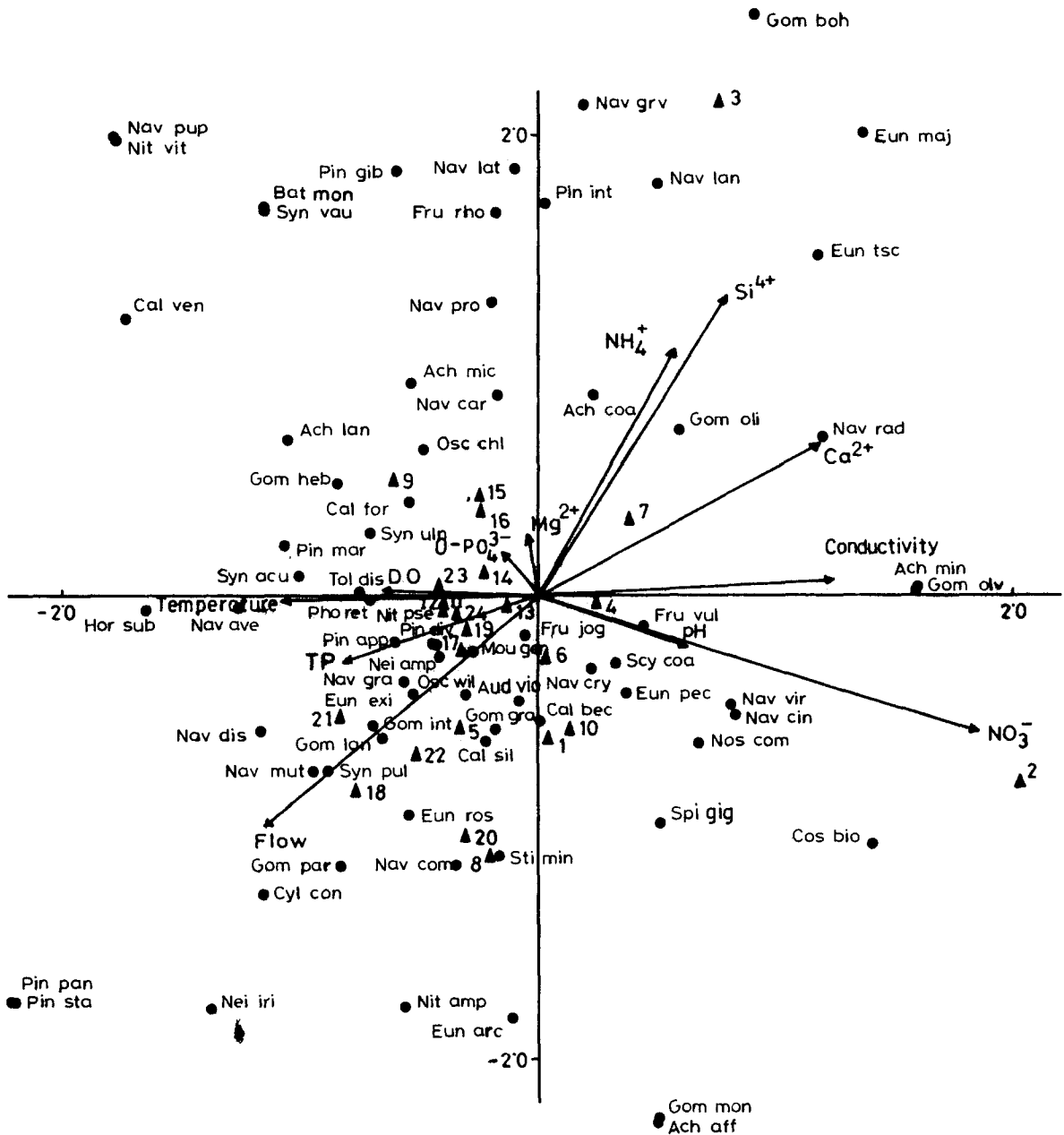


Fig. 7. Canonical Correspondence Analyses (CCA) ordination diagram showing monthly distribution of algal species (●) in relation to environmental variables (arrows) in the epilithon upstream. First axis is horizontal, second axis vertical. See Table 1 for species codes. Numbers (▲) representing the sampling months are: 1-Jan'88, 2-Feb'88, 3-Mar'88, 4-Apr'88, 5-May'88, 6-Jun'88, 7-Jul'88, 8-Aug'88, 9-Sep'88, 10-Oct'88, 11-Nov'88, 12-Dec'88, 13-Jan'89, 14-Feb'89, 15-Mar'89, 16-Apr'89, 17-May'89, 18-Jun'89, 19-Jul'89, 20-Aug'89, 21-Sep'89, 22-Oct'89, 23-Nov'89, 24-Dec'89.

1984), extreme flow rate cause abrasion of algae from rock surfaces.

CCA defines specific flow requirements for some species: high to moderate flow (*Audouinella violacea*,

Cylindrocapsa conferta, *Synedra* species), low flow (*Hyalotheca dissiliens*, *Gomphonema olivaceum*). The persistence of *Spirogyra communis* during high discharge is due to colonisation of sheltered microhabi-

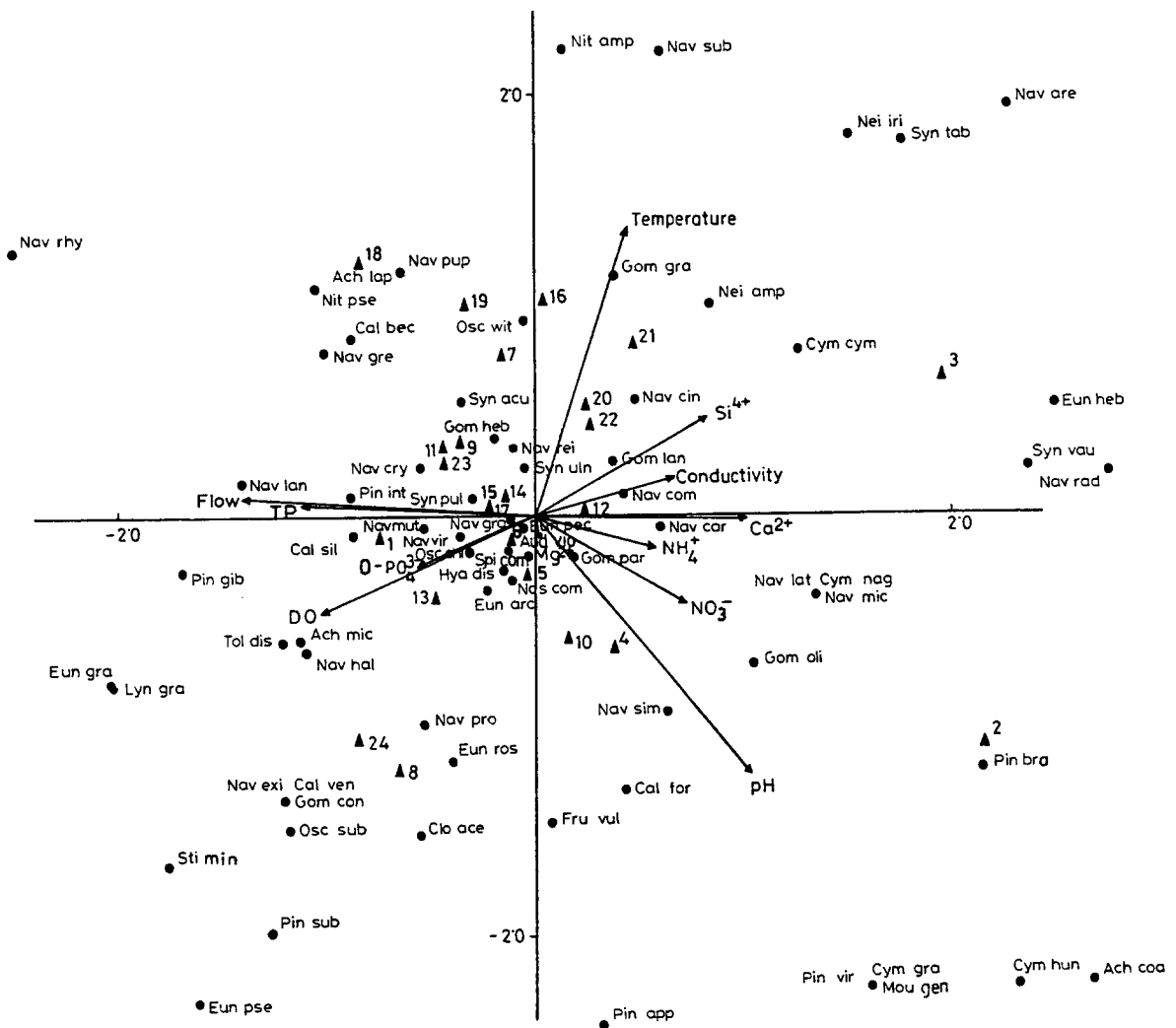


Fig. 8. CCA ordination diagram with epilithic algae (●), sampling period (▲) and environmental variables (arrows) downstream. Numbers representing the sampling months are as in Fig. 7. Table 1 contains codes for various species.

tats. Many diatoms encountered in the present work were either indifferent to pH or alkaliphilous (Lowe, 1974). *Audouinella violacea*, abundant upstream, was indifferent to pH, a characteristic of red algae (Sheath & Burkholder, 1980).

CCA showed that most green algae were stimulated by increased phosphorus. In this context it is pertinent to highlight that filamentous algae have relatively high phosphorus requirements. The nitrogen (excluding organic fraction) to phosphorus ratio (redfield ratio) was >16 , suggesting phosphorus limitation (Redfield *et al.*, 1963). Low phosphorus concentration therefore seems responsible for the low epilithic biomass (5.3–

46.1 mg m⁻²). Low levels of chlorophyll *a* as well as PO₄³⁻ suggest that the epilithic biomass has not yet reached the nuisance level [100–150 mg chlorophyll *a* m⁻²] (Horner *et al.*, 1983).

The pattern of epilithic seasonality broadly resembles the pattern obtained for the temperate streams (Moore, 1977; Holmes & Whitton, 1981; Duncan & Blinn, 1989; Sabater, 1990). The study shows that epilithic algae could also grow well during winter, due to a high temperature in the stream relative to that in temperate regions. A majority of dominant species existed throughout the year in epilithic community, although their population size showed temporal

Table 1. List of algal species with their species code indicated in ordination diagrams.

Algal species	Species code
<i>Achnanthes affinis</i> Grun.	ACH AFF
<i>A. coarctata</i> Bréb	ACH COA
<i>A. lanceolata</i> (Bréb) Grun.	ACH LAN
<i>A. lapponica</i> (Hust.) Hust.	ACH LAP
<i>A. microcephala</i> (Kütz.) Grun.	ACH MIC
<i>A. minutissima</i> (Kütz.) Grun.	ACH MIN
<i>Audouinella violacea</i> (Kütz.) Hamel	ACH VIO
<i>Batrachospermum moniliforme</i> Roth	BAT MON
<i>Caloneis beccariana</i> Grun.	CAL BEC
<i>C. formosa</i> (Greg.) Cl.	CAL FOR
<i>C. silicula</i> (Ehr.)	CAL SIL
<i>Closterium acerosum</i> (Schrank) Ehr.	CLO ACE
<i>Cosmarium bioculatum</i> Bréb	COS BIO
<i>Cylindrocapsa conferta</i> W. West	CYL CON
<i>Cymbella ventricosa</i> (Ehr.) Meist	CAL VEN
<i>C. cymbiliformis</i> (Ag.) Kütz.	CYM CYM
<i>C. gracilis</i> (Rabh.)	CYM GRA
<i>C. hungarica</i> (Grun.) Pant	CYM HUN
<i>C. nagpurensis</i> Sarode & Kamat	CYM NAG
<i>Eunotia arcus</i> Ehr.	EUN ARC
<i>E. exigua</i> (De Bréb) Rabh.	EUN EXI
<i>E. gracilis</i> (Ehr.) Rabh.	EUN GRA
<i>E. hebridica</i> A°. Berg.	EUN HEB
<i>E. major</i> (W. Sm.) Rabh.	EUN MAJ
<i>E. pectinalis</i> (Kütz.) Rabh.	EUN PEC
<i>E. pseudoparallela</i> A° Berg.	EUN PSE
<i>E. rostellata</i> Hust.	EUN ROS
<i>E. tschirchiana</i> O. Mull.	EUN TSC
<i>Frustuia jogensis</i> Gandhi	FRU JOG
<i>F. rhomboides</i> (Ehr.) De Toni	FRU RHO
<i>F. vulgaris</i> Thwaites	FRU VUL

Table 1 cont..

<i>Gomphonema constrictum</i> Ehr.	GOM CON
<i>G. gracile</i> Ehr.	GOM GRA
<i>G. hebridense</i> (Greg.) Her	GOM HEB
<i>G. intricatum</i> (Kütz.)	GOM INT
<i>G. lanceolatum</i> Ehr.	GOM LAN
<i>G. montanum</i> Schum.	GOM MON
<i>G. olivaceoides</i> Hust.	GOM OLI
<i>G. olivaceum</i> (Lyng.) Kütz.	GOM OLV
<i>G. parvulum</i> (Kütz.) Grun.	GOM PAR
<i>Hyalotheca dissiliens</i> (J.E. Sm.)	HYA DIS
<i>Lyngbya gracilis</i> (Menegh.) Rabh.	LYN GRA
<i>Mougeotia genuflexa</i> (Dillw.) Ag.	MOU GEN
<i>Navicula arenaria</i> Donk.	NAV ARE
<i>N. avenacea</i> Bréb	NAV AVE
<i>N. cari</i> Ehr.	NAV CAR
<i>N. cincta</i> (Ehr.) Kütz.	NAV CIN
<i>N. complanatula</i> Hust.	NAV COM
<i>N. cryptocephala</i> Kütz.	NAV CRY
<i>N. disjuncta</i> Hust.	NAV DIS
<i>N. exigua</i> (Greg.) O. Mull	NAV EXI
<i>N. gracilis</i> Ehr.	NAV GRA
<i>N. gregarica</i> Donk.	NAV GRE
<i>N. grevillei</i> Ag.	NAV GRV
<i>N. halophila</i> (Grun.)	NAV HAL
<i>N. lanceolata</i> (Kütz.)	NAV LAN
<i>N. laterostrata</i> Hust.	NAV LAT
<i>N. microcephala</i> Grun.	NAV MIC
<i>N. mutica</i> Kütz.	NAV MUT
<i>N. protracta</i> Grun.	NAV PRO
<i>N. pupula</i> Kütz.	NAV PUP
<i>N. radiosa</i> Kütz.	NAV RAD
<i>N. reinhardtii</i> Grun.	NAV REI
<i>N. rhychocephala</i> Kütz.	NAV RHY

changes. The disappearance of commoner species from one community is very rare. This particular tendency is unlike phytoplankton where species build up and disappear during succession (Round, 1971). Vannote *et al.* (1980) believe that the term 'biological succession' with its sequence of discrete successional stages may be obsolete for lotic system and the abundance of species merely shift along a temporal or spatial axis. Our result thus supports the hypothesis of Vannote *et al.* (1980).

The tools used here for measuring the different complexities for the understanding of the structural properties of algal epilithon were effective. The present investigation is expected to offer some basic informations regarding the algal epilithon in an Indian forest stream.

Acknowledgements

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Table 1 cont..

<i>N. similis</i> Krauske	NAV SIM
<i>N. subdopaliformis</i> Gandhi	NAV SUB
<i>N. viridula</i> Kütz.	NAV VIR
<i>Neidium amphigomphous</i> (Ehr.) Cl.	NEI AMP
<i>N. iridis</i> (Ehr.) Cl.	NEI IRI
<i>Nitzschia amphibia</i> Grun.	NIT AMP
<i>N. pseudofonticola</i> Hust.	NIT PSE
<i>N. vitrea</i> Norman	NIT VIT
<i>Nostoc comminutum</i> Kütz.	NOS COM
<i>Oscillatoria chlorina</i> Kütz.	OSC CHL
<i>O. subuliformis</i> Kütz.	OSC SUB
<i>O. willei</i> Gardn.	OSC WIL
<i>Phormidium retzii</i> (Ag.) Gom.	PHO RET
<i>Pinnularia appendiculata</i> (Ag.) Cl.	PIN APP
<i>P. braunii</i> (Grun.)	PIN BRA
<i>P. divergens</i> W. Sm.	PIN DIV
<i>P. gibba</i> Ehr.	PIN GIB
<i>P. interrupta</i> W. Sm.	PIN INT
<i>P. marathwadensis</i> Sarode & Kamat	PIN MAR
<i>P. panhalgarhensis</i> Gandhi	PIN PAN
<i>P. stauroptera</i> (Rabh.) Cl.	PIN STA
<i>P. subcapitata</i> Greg.	PIN SUB
<i>P. viridis</i> (Nitz.) Ehr.	PIN VIR
<i>Scytonema coactile</i> Mont.	SCY COA
<i>Spirulina gigantea</i> Schmidle	SPI GIG
<i>Stigonema minutum</i> (Ag.) Hoss.	STI MIN
<i>Synedra acus</i> Kütz.	SYN ACU
<i>S. pulchella</i> (Ralfs.) Kütz.	SYN PUL
<i>S. tabulata</i> (Ag.) Kütz.	SYN TAB
<i>S. ulna</i> (Nitz.) Ehr.	SYN ULN
<i>S. vaucheriae</i> Kütz.	SYN VAU
<i>Tolypothrix distorta</i> Kütz. ex. Born. et Flah	TOL DIS

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Table 2. Correlation coefficients or intraset coefficients of environmental variables with the first two axes of canonical correspondence analysis (CCA)

Axis variable	Intraset coefficients			
	Upstream		Downstream	
	Axis 1	Axis 2	Axis 1	Axis 2
Temperature	-0.42	-0.01	0.18	0.57
pH	0.24	-0.09	0.41	-0.52
Conductivity	0.48	0.02	0.27	0.08
Flow	-0.46	-0.41	-0.57	0.04
DO	-0.25	0.01	-0.41	-0.19
O-PO ₄ ³⁻	-0.06	-0.08	-0.22	-0.10
TP	-0.32	-0.12	-0.46	0.03
NH ₄ ⁺	0.22	0.43	0.23	-0.06
NO ₃ ⁻	0.72	-0.24	0.28	-0.18
Si ⁴⁺	0.31	0.52	0.33	0.19
Ca ²⁺	0.46	0.26	0.41	-0.01
Mg ²⁺	-0.01	0.11	0.01	-0.05

Table 3. Eigenvalues of the four axes as obtained from CCA

	Axis			
	1	2	3	4
Upstream	0.41	0.33	0.31	0.27
Downstream	0.34	0.30	0.26	0.25

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