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Chlorophyll, primary productivity, and respiration in a lowland Costa Rican stream

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Abstract: *In situ* nutrient enrichment bioassays were conducted in open and closed canopy sites of a third order stream draining primary rain forest and abandoned pasture land in northern Costa Rica. Artificial sand+agar substrata spiked with nitrogen, phosphorus, N+P, molybdenum, N+Mo, and a mix of manganese, zinc, and molybdenum were incubated for 15 and 21 days. The colonizing periphyton in the forested streamsites (4 mg chlorophyll *a* m^{-2}) showed extreme light limitation when compared with the open, pasture areas (14-45 mg chlorophyll *a* m^{-2}) after 15 days of colonization. Chlorophyll *a* concentrations, oxygen production and consumption, and assimilation ratios did not show a significant nutrient addition effect indicating that ambient nutrient concentrations are at saturation levels for periphyton growth. Ten-to-fifteen day old periphyton was autotrophic (P/R>1) on all treatments. Compared with other tropical streams, similar chlorophyll but lower rates of primary productivity (<300 mg O_2 m^{-2} h^{-1}) and respiration (70 mg O_2 m^{-2} h^{-1}) occurred in this stream.

Key words: Tropical streams, periphyton, nutrient limitation, stream primary productivity.

Tropical forest ecosystems are characterized by having poor soils and much of the nutrients tied up in the living or decaying biomass (Jordan 1985). The floors of the tropical forest exhibit high rates of litter decomposition and soil nitrogen mineralization (Vitousek & Denslow 1986). With a high precipitation, these processes may result in an efficient and rapid nutrient turnover (Jordan 1985). For these systems, nutrients lost into the headwater streams may be very low. Thus, primary producers in tropical streams are expected to most commonly experience nutrient impoverished waters. Because the primary producers in streams are strongly dependent on light for carbon fixation and nutrients for growth, the presence of benthic algae may further determine the loss rate of nutrients from the lotic system. *i.e.* "nutrient spiraling", by incorporating them into organic compounds (Newbold *et al.* 1981).

In a variety of temperate zone streams, periphyton biomass and primary productivity have been studied under natural conditions (Jasper & Bothwell 1986) or in controlled situations to assess the effects of light (McIntire & Phinney 1965), riparian vegetation (Shortreed & Stochner 1983), current (Horner & Welch 1981), substrate type (Lamberti & Resh 1985), nutrient availability (Pringle 1985; Grimm & Fisher 1986), grazing (Lamberti & Resh 1983), and physical disturbance (Robinson & Rushford 1987).

In contrast to the studies in the temperate zone, the tropical zone has been characterized by the lack of a functional approach to investigations of headwater stream periphyton (Pringle *et al.* 1986). Hence, this study has focused on the algal colonization of unenriched and nutrient enriched artificial substrata incubated in a low order tropical stream that flows through forested and logged areas. Chlorophyll *a* concentrations, oxygen production and consumption rates were used to evaluate the relative importance of light and nutrient enrichment on the colonization and growth of periphyton.

MATERIAL AND METHODS

Study site: This study was conducted at La Selva Biological Station (Organization for Tropical Studies) in Puerto Viejo de Sarapiquí, Province of Heredia, Costa Rica (Fig. 1). The property (*ca.* 1500 ha) ranges from 35 to 150 m above sea level in the Atlantic foothills of Volcán Barba (10° 26'N, 86° 00'W), has a yearly mean temperature of 24 °C, and receives *ca.* 4000 mm annual rainfall. The stream selected for the study was the Surá of *ca.* 11 Km in length. It drains various disturbed and undisturbed catchments with a mixture of vegetational types. Table 1 summarizes the Surá's physical-chemical characteristics. Sanford *et al.* (in press) describe in detail the aquatic system of the La Selva Biological Station.

In January 1986, periphyton accumulation bioassays were run in two main stream reaches, E2 and E3. In each of these areas, an abandoned pasture and a forest site 50-100 m apart were selected (Fig. 1). In April, the enrichment bioassays were compared between two pasture sites, B2 and E2, which strongly differed in phosphorus concentrations (Table 1). Mid-stream flow ranged between 0.18-0.22 $m \cdot s^{-1}$ at all sites.

Methods: Nutrient limitation of *in situ* periphyton colonization and growth was determined using artificial substrata made of petri-dishes filled with sand and agar (Pringle & Bowers 1984). These plates were either unenriched (controls) or enriched with various nutrient compounds (treatments). In January, the nutrients were nitrogen (N), phosphorus (P), and molybdenum+zinc+manganese (Mo+Zn+Mn). In April, the bioassay included additions of nitrogen, phosphorus, N+P, molybdenum, and N+Mo. The concentrations used in each treatment are listed in Table 2.

The sand-agar plates were arranged at random (Completely Randomized Design, Little & Hills 1978) on wooden boards (1.60 m) with perforated styrofoam to hold the plates down by pressure. This approach was preferred over glueing them directly onto the board as turbulence on the colonizing surface was then minimized. The boards were fastened 30 cm off the stream bed and *ca.* 20 cm from the surface.

The field design, incubation times and analyses performed are summarized in Table 3. Each specific site was sampled every week at which time an entire SET of replicated substrata was retrieved and taken to the laboratory.

Primary productivity and respiration rates: The primary productivity (PPR) and respiration rates (R) were measured on substrata set in the abandoned pasture sites (Table 3). The *in situ* PPR determination was done using "styren utility boxes" as still-water incubation chambers. Two holes drilled in the box allowed water samples to be collected without creating turbulence. Two light and one dark chamber were used per treatment to determine gross, net PPR and community R (Wetzel & Likens 1979). The dark chamber (for R determination) was covered with black electrical tape, as well as aluminum foil and white tape to eliminate light and prevent solar heating. The lid joints of both light and dark chambers were sealed with silicon grease to prevent O_2 diffusion. Before the periphyton colonized plates were taken to the laboratory, all treatments were incubated simultaneously for at least 2 hours. Carbon fixation was measured by the rate of O_2 production. Samples of incubated water were fixed immediately in the field in 125 ml O_2-bottles with manganous sulfate and alkali-iodine-azide solutions. Dissolved oxygen analyses were always done within a three-hour period with the microWinkler method (APHA 1985) and 0.14 N thiosulfate for titration.

Chlorophyll *a* determination: After the PPR incubation, the plates were covered with a petri-dish lid, put into plastic bags, kept wet with stream water, and transported to the laboratory in a black box for final processing. Periphyton separation from sand particles was done following Pringle & Bowers' (1984) procedure. A 20 ml subsample was filtered through a 0.45 um millipore filter which was submersed in alkaline acetone for chlorophyll extraction (Strickland & Parsons 1972). The samples were left for 12-14 hours in the dark, at 21 C before measuring absorbancy with a spectrophotometer at 665 and 750 nm before and after acidification to correct for phaeopigments (Wetzel & Likens 1979).

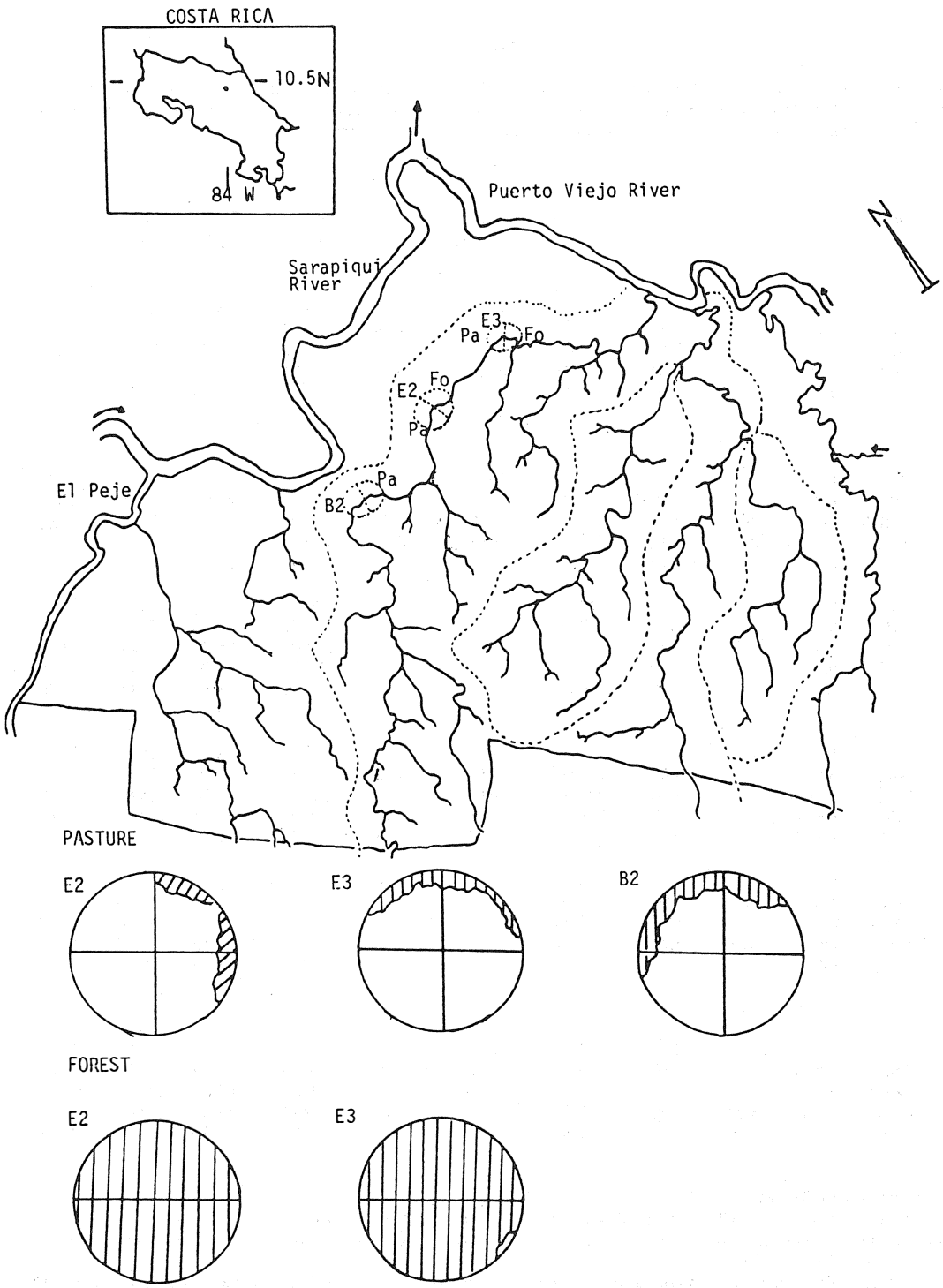

Fig. 1. Streams of La Selva Biological Station. Location of sites E2, E3 and B2. Canopy cover of each of the study stations used in the bioassays is illustrated in the circles. La Selva, Costa Rica. Pa= pasture, Fo= forest, striped areas represent proportion of canopy cover.

TABLE 1

Summary of physical and chemical characteristics of chosen bioassay stream reaches. El Surá stream. La Selva Biological Station. Costa Rica. Temp: temperature. Alkal: alkalinity. TIC: total inorganic carbon, Conduc: conductivity, SRP: soluble reactive phosphorus. TP: total phosphorus, n: number of measurements. s.d.: standard deviation

Site	Season		Temp °C	pH	Cond uS/cm	Alkal mgCaCO3/l	TIC mg/l	SRP+ ug/l	TP+ ug/l	NO3-N ug/l	N:P
		n		14	14	14	14	28	28	28	28 **
	Jan	min		6.40	116.00	39.00	17.94	118.00	149.00	124.00	1.80
	(dry)	max		7.40	200.00	70.00	28.56	160.00	182.00	178.00	3.30
	1986	mean		6.62	175.86	61.50	23.22	141.64	159.07	152.00	2.40
		s.d.		0.24	24.41	7.20	2.75	11.79	8.84	13.87	0.36
E2											
		n	14	11	12	10	10	30	30	30	30 **
	April	min	23.5	6.30	150.00	50.00	19.84	99.00	86.00	78.00	1.20
	(begin.	max	24.0	6.90	255.00	76.00	38.76	155.00	195.00	162.00	3.20
	rainy)	mean .	23.93	6.45	213.75	64.80	28.19	140.07	151.73	117.00	1.90
	1986	s.d.	0.17	0.16	32.48	7.05	4.79	14.87	26.42	21.29	0.55
		n	11	13	13			24	24	24	24 *
	Oct.	min	24.00	6.60	140.00			80.00	64.00	77.00	2.50
	(rainy)	max	24.50	7.20	170.00			108.00	96.00	144 .00	4.80
	1985	mean	24.14	6.90	156.00			94.00	73.00	110.83	3.40
		s.d.	0.23	0.15	9.06			7.91	8.63	19.06	0.70
E3											
		n		14	14	14	14	28	28	28	28 **
	Jan.	min		6.60	120.00	42.00	15.75	117.00	138 .00	123.00	1.80
	(dry)	max		7.00	200 00	66.00	23.87	152 .00	175.00	215.00	3.90
	1986	mean		6.79	173.29	60.29	20.19	136.07	162.14	169.71	2.80
		s.d.		0.12	23.25	6.13	1.95	11.79	11.20	25.04	0.55
		n	6	8	8				16	16	16 *
	Oct.	min.	23.50	5.90	18.00				34 .00	160.00	8.50
	(rainy)	max	24.00	6.20	19 00				44 .00	188.00	11.50
	1985	mean	23.58	5.99	18.44				39.50	176.88	10.01
		s.d.	0.20	0.25	0.56				3.66	9.64	1.24
B2											
		n	13	12	12	12	12	28	28	28	28 **
	April	min	22.50	3.80	20 00	0.00	3.88	1.00	3 00	129.00	14.00
	(begin	max	24.00	5.80	23.00	6.00	14.52	30.00	45.00	222.00	395.00
	rainy)	mean	23.23	5.32	21.50	3.00	7.14	6.50	17.00	168.00	135.86
	1986	s.d	0.46	0.50	0.76	1.53	3.19	7.32	10.38	27.14	126.11

* N:P = NO_3-N uM/TP uM

** N: P ratio calculated with SRP (when turbidity was not interfering with the analyses)

+ Note: Some problems exist when SRP is determined during the rainy season Turbidity is not always eliminated with filtering (color, colloids)
Apparently some of the compounds responsible for the coloring are absorbed in the same wavelength as the P. This problem does not exist in TP analyses because the acid digestion takes care of the coloring compounds also. This is the reason why some SRP reading are higher than the respective TP readings.

SRP: Molybdenum-blue method (APHA 1985)
(NO_2+NO_3)-N: Hydrazine reduction method (Kamphabe *et al.* 1967).
Alcalinity: acid titration method (Wetzel and Libens 1979).

TABLE 2

Concentration of nutrients used in the fertilization bioassay in January and April 1986. Surá stream, La Selva

Season	Treatment	Concentration
January	Control	0.0
	Nitrogen (N)	0.040 M $NaNO_3$
	Phosphorus (P)	0.057 M $KHPO_4$
	Trace elements (Mn+Zn+Mo)	0.126 x 10^{-6} M MnCl $4H_2O$ + 0.048 x 10^{-6} M $ZnCl_2$ + 0.026 x 10^{-6} M Na_2MoO_4 $2H_2O$
April	Control	0.0
	Nitrogen	1.0 M $NaNo_3$
	Phosphorus	0.5 M $KHPO_4$
	N + P	1.5 M $NaNO_3$ + 0.093 M $KHPO_4$
	Molybdenum	306 x 10^{-6} M Na_2MoO_4 $2H_2O$
	N + Mo	1.5 M $NaNO_3$ + 306 x 10^{-6} M Na_2MoO_4 $2H_2O$

TABLE 3

Field design of the nutrient enrichment bioassays conducted in the Surá stream. Nitrogen:N, phosphorus:P, trace mix: manganese (Mn)+zinc(Zn)+molybdenum(Mo). La Selva Biological Station

Season	Sites	Riparian vegetation	Treatment	n *	Total incubation (weeks)	Analyses
January	E2	pasture	control	5	3	chl. *a*,oxygen prod,respiration
			N, P,	3	3	"
			trace mix	3	3	"
		forest	control	3	5	Chl. *a*
	E3	pasture	control	5	3	Chl. *a*,oxygen prod,respiration
			N, P,	3	3	"
			trace mix	3	3	"
		forest	control	3	5	Chl. *a*
April	B2	pasture	control	3	2	Chl. *a*,oxygen prod,respiration
			N, P, N+P	3	2	"
			Mo, N+Mo	3	2	"
	E2	pasture	control	3	2	Chl. *a*,oxygen prod,respiration
			N, P, N+P	3	2	"
			Mo, N+Mo	3	2	"

* n replicates retrieved per week = SET
respiration: n=1

Data analysis: Nutrient enrichment response was determined by comparing unenriched against nutrient enriched treatments using planned F-tests (parametric two-way analysis of variance (AOV), Least Significant Difference) within sites. Variability within stream "biotopes" (*i.e.* pasture, forest) was assessed by comparing chlorophyll *a* and PPR data of each treatment between sites using *t*-tests and two-way ANOVA's. The effect of canopy cover was assessed by contrasting unenriched substrata of pasture against forest sites. Because of a logarithmic distribution in chlorophyll *a* accumulation and because of non-independence between means and variance, chlorophyll *a* and PPR data were $\log_{10}(X+1)$ transformed before any statistical analysis was performed. Covariance tests, with chlorophyll *a* as the covariate, were used to test for nutrient additions and incubation time on periphyton respiration rates. In addition, the relation between chlorophyll a and oxygen production was examined using a Spearman Rank association index.

RESULTS

Chlorophyll a, productivity and assimilation ratios: Substrata incubated at forest sites (E2,E3) (Fig. 2) showed significantly less chlorophyll *a* than in pasture sites ($P<0.001$) (Fig. 3). Even after 5 weeks of incubation, the forest unenriched plates did not acquire pasture accumulation levels. In addition, the chlorophyll *a* accrual was not significantly ($P>0.05$) different between the closed canopy sites.

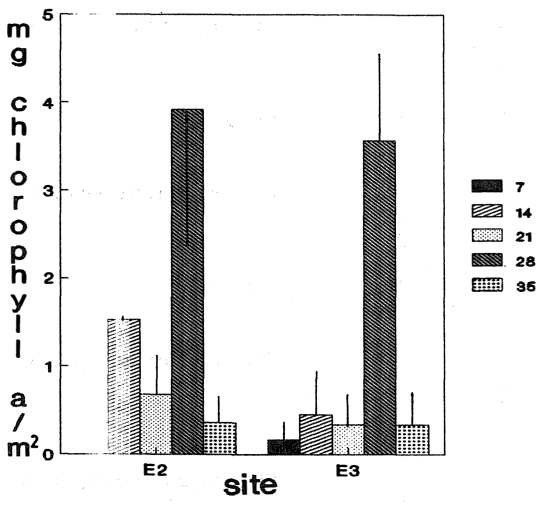

Fig. 2. Chlorophyll *a* (mg m^{-2}) accumulation after 7, 14, 21, 28 and 35 days on unenriched sand-agar substrata incubated in forested stream sites. Error bars= standard error. January 1986. Surá stream, La Selva.

After one week of incubation in the non-light limiting pasture sites, the artificial substrata accumulated almost undetectable chlorophyll *a* concentrations (Fig. 3). The heterotrophic activity is dominating the overall periphyton production on all treatments in the early stages of colonization. This dominance is evidenced when comparing productivity (net primary) vs. consumption (respiration). The proportion of net primary productivity vs. respiration is illustrated in Figure 4 (see the double-line group of treatments) where autotrophy dominates after 10-14 days of incubation. All substrata, after 10-14 days, sustained attached algae in concentrations significantly ($P<0.05$) greater than found in the previous 5-7 day retrieval. Therefore, it appears that the growth and reproduction of the periphytic component over-rates the passive-cell immigration process as well as the community respiration (Fig. 4).

To assess for nutrient limitation in the pasture sites (non-light limiting situation) we compared the unenriched and nutrient enriched algal communities. Non-significant differences ($P>0.05$) were found in chlorophyll *a* accumulation (Fig. 3) and areal net primary productivity (Fig. 5). Because the chlorophyll concentrations varied among the within-treatment-PPR-incubated plates we calculated a biomass-specific net primary productivity (also known as the assimilation rate) (Table 4) to control for the variance. An ANOVA test resulted in insignificant differences ($P>0.05$) in periphyton assimilation rates between unenriched and nutrient enriched treatments (i.e. unenriched and nutrient enriched communities were equally efficient per unit chlorophyll).

In January and April, several of the plates incubated to determine respiration had no measurable chlorophyll accumulation. Respiration for these treatments were then assumed to be the result of heterotrophic

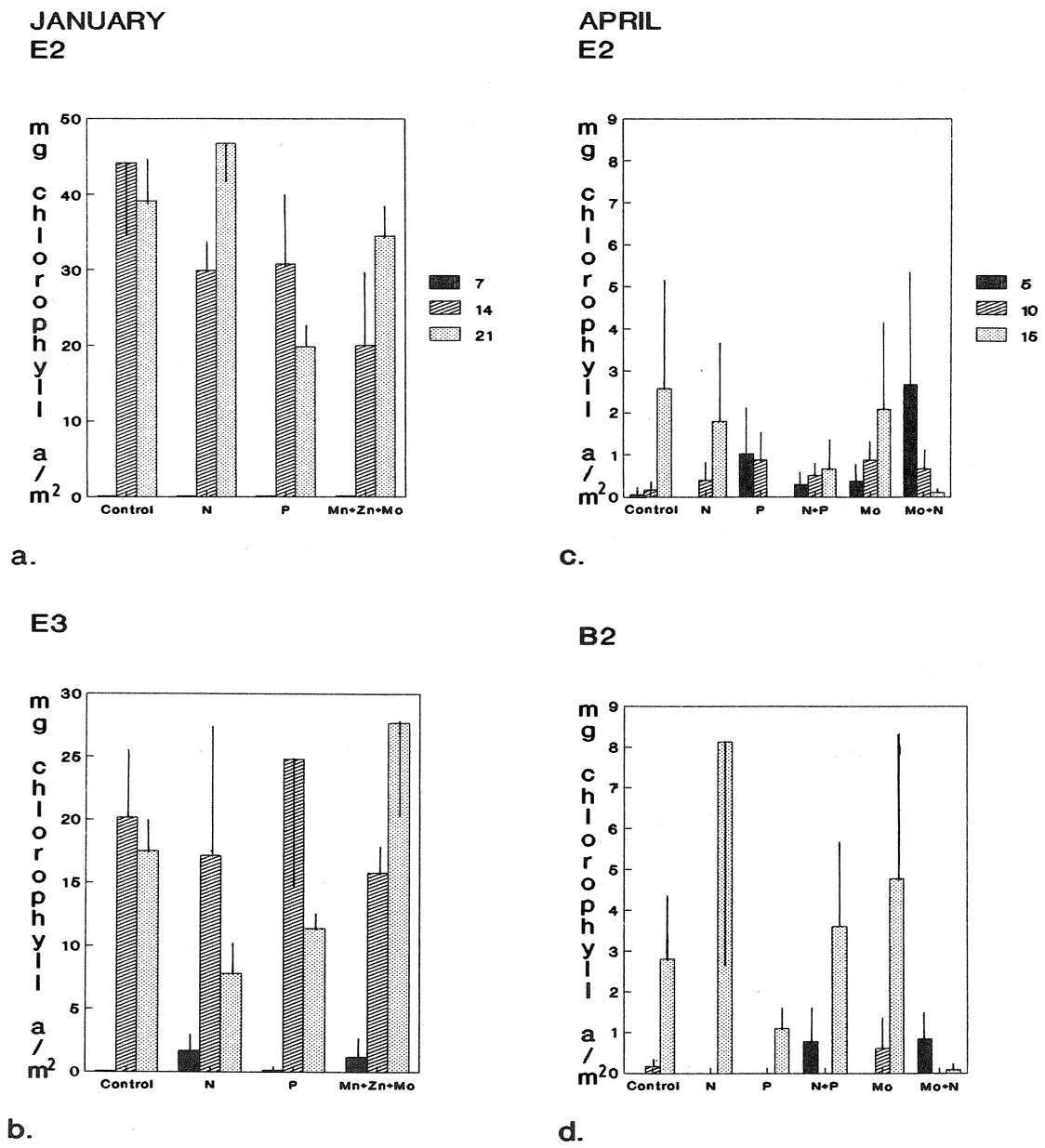

Fig. 3. Chlorophyll *a* (mg m^{-2}) accumulation on unenriched (control) and nutrient (nitrogen:N, phosphorus:P, and manganese+zinc+molybdenum:Mn+Zn+Mo) enriched sand-agar substrata in pasture stream sites. a. January incubation in site E2 for 7,14 and 21 days. b. January incubation in site E3 for 7,14 and 21 days. c. April incubation in site E2 for 5,10 and 15 days. d. April incubation in site B2 for 5,10 and 15 days. Error bars= standard error. Surá stream, La Selva. Note the difference in scales between seasons.

TABLE 4

Chlorophyll-specific net primary productivity and respiration rates (mg O_2 mg chlorophyll a^{-1} h^{-1}) in the Surá stream pasture sites. Trace mix: manganese (Mn) + zinc (Zn) + molybdenum (Mo). January and April 1986. La Selva Biological Station

January

Incubation days		7		14		21	
Site	Treatment	Net PPR	Resp	NetPPR	Resp	Net PPR	Resp
E2	Control	-	-	4.22	0.87	4.29	0.43
			-	5.04	-	8.90	-
	Nitrogen (N)	-	-	4.84	2.10	6.09	1.35
		-	-	5.75	-	5.97	-
	Phosphorus (P)	-	-	10.62	2.31	7.96	4.26
		-	-	4.52	-	31.94	-
	Trace mix	-	-	8.14	10.54	5.37	2.16
		-	-	5.20	-	6.86	-
E3	Control	-	32.20	-	-	115.95	1.92
		-	-	-	-	80.44	-
	Nitrogen	-45.20	5.07	-	-	17.12	10.50
			-	-	-	6.10	-
	Phosphorus	-	12.80	-	-	8.98	5.10
		-	-	-	-	11.67	-
	Trace mix	-	-	-	-	2.68	2.38
		-4.57	-	-	-	27.18	-

April

Incubation days		5		10		15	
E2	Control	-	-	-	2.94	-	3.84
	Nitrogen	-83.75	-	-	-	-	-
	Phosphorus	-	3.65	27.72	2.55	-	-
		-	-	-	-	-	-
	N + P	-	-	46.57	2.97	-	16.34
		13.08	-	-	-	-	-
	Molybdenum	-	12.16	20.35	7.45	-	16.62
		-	-	52.50	-	-	-
	N + Mo	-	1.56	34.90	-1.29	-	-
		-	-	-	-	-	-
B2*	Control	-	-	26.88	-	-	-
	N + P	-	-	-	-	-	-
		-4.03	-	-	-	-	-
	Mo	-	-	-44.40	-	-	-
		-	-	-6.27	-	-	-
	N + Mo	-20.33	-	-	-	-	-
		-8.64	-	-	-	-	-

\- non-measurable chlorophyll *a*.
* nitrogen and phsophorus had non-measurable chlorophyll *a*.

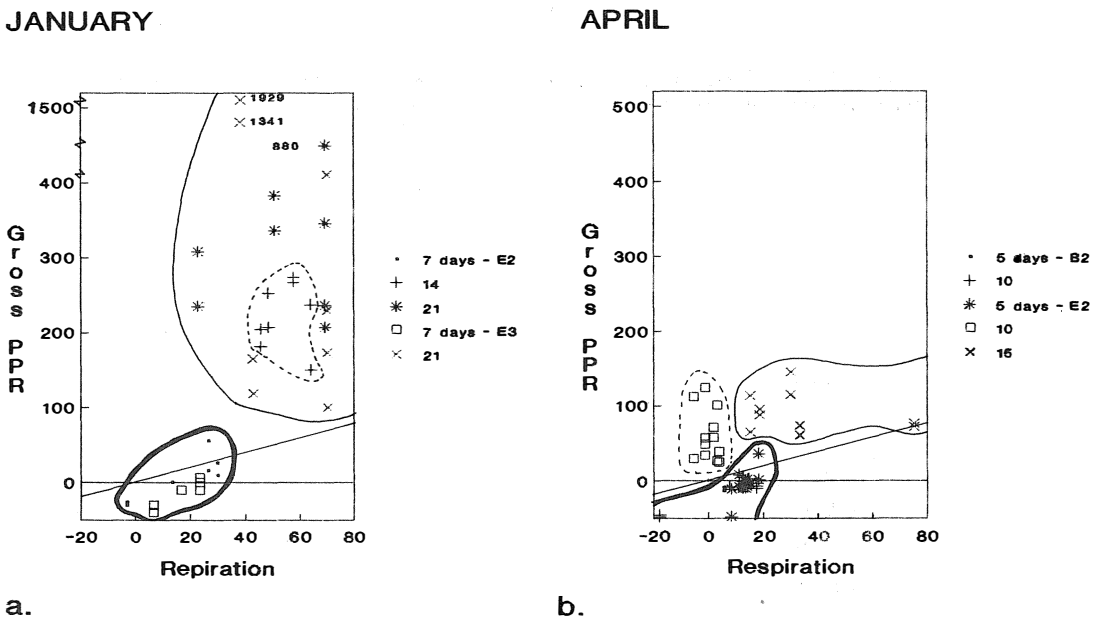

Fig. 4. Gross primary productivity (PPR) / respiration ratios of the periphyton community growing on unenriched and nutrient enriched sand-agar substrata incubated in pasture stream sites E2, E3, B2. a. January bioassay. Thick line: 7 days, dotted line: 14 days, thin line: 21 days. b. April bioassay. Thick line: 5-10 days in B2, dotted line: 10 days in E2, thin line: 15 days in E2. Surá stream, La Selva.

organisms (*e.g.* bacteria and fungi). Overall, these 5,7-day incubation values ranged from near zero to *ca.*= 30 mg O_2 $m^{-2} \cdot h^{-1}$ in January and from near zero to 19 mg O_2 $m^{-2} \cdot h^{-1}$ in April. The Sur stream had a maximum community respiration of 70 mg O_2 m^{-2} h^{-1}.

Because areal net primary productivity (PPR) is underestimated by heterotrophic respiration (i.e. non-algal respiration) it is important that this component increases through time equally across treatments. In January and April an increase in respiration through time was apparent in almost all treatments and all sites (Table 5). For January, a Spearman Rank correlation between chlorophyll *a* and net PPR (algal O_2 productivity minus algal and heterotroph O_2 consumption) resulted in significant ($P<0.05$) coefficients (n=6, r=0.75-0.99). This correlation may indicate that the change in respiration follows algal accumulation. In April, however, the degree of association between algal biomass and net PPR was low (n=4, r=-0.40-0.50, $P>0.05$) in some treatments but high in others (n=4, r=0.80-0.90, $P<0.05$).

Seasonal comparison: In overall, the January colonization bioassay resulted in faster algal accumulation (Fig. 3) than the April bioassay during the first two weeks of incubation ($P<0.05$). The areal net PPR did not differ between seasons until after 2 weeks of colonization when significantly higher values ($P<0.05$) were measured in January (Fig. 5). In contrast, assimilation ratios (Table 4) measured in April resulted in significantly higher values than in January suggesting that faster turnover rates occurred in April.

April received 265 % more rain than did January in the same number of days (*i.e.* 2 weeks), 83 % (105 mm) was concentrated around the second (10 day) and third (15 day) retrieval. In January, 60 % (75 mm) of the total three week precipitation occurred after the retrieval of the second set of substrata (i.e. 14 days). Thus, the difference in periphyton accumulation between the January and April bioassays was probably due to increased April discharge rates and sediment loads accompanied by decreased incident light.

TABLE 5

Respiration rates (mg O_2 m^{-2} h^{-1}) determined during the January and April 1986 bioassays in the Surá stream. Trace mix: Manganese(Mn)+zinc(Zn)+molybdenum(Mo). La Selva Biological Station

January				
Incubation days		7	14	21
Site	Treatment			
E2	Control	13.16	45.70	22.75
	Nitrogen	-3.26	64.20	50.74
	Phosphorus	29.67	57.57	69.44
	Trace mix	26.31	48.37	69.44
E3	Control	16.42	-	38.18
	Nitrogen	23.05	-	42.83
	Phosphorus	6.53	-	70.23
	Trace mix	23.05	-	70.23
April				
Incubation days		5	10	15
B2	Control	14.00	12.57	-
	Nitrogen (N)	11.25	-435.76	-
	Phosphorus (P)	11.25	17.43	-
	N+P	12.50	17.43	-
	Molybdenum (Mo)	15.50	14.57	-
	Mo+N	5.50	7.71	-
E2	Control	18.00	1.50	29.66
	Nitrogen	8.25	-5.50	15.00
	Phosphorus	11.25	-1.30	18.67
	N+P	14.25	3.00	33.00
	Molybdenum	13.50	3.80	104.01
	Mo+N	12.50	-1.30	-

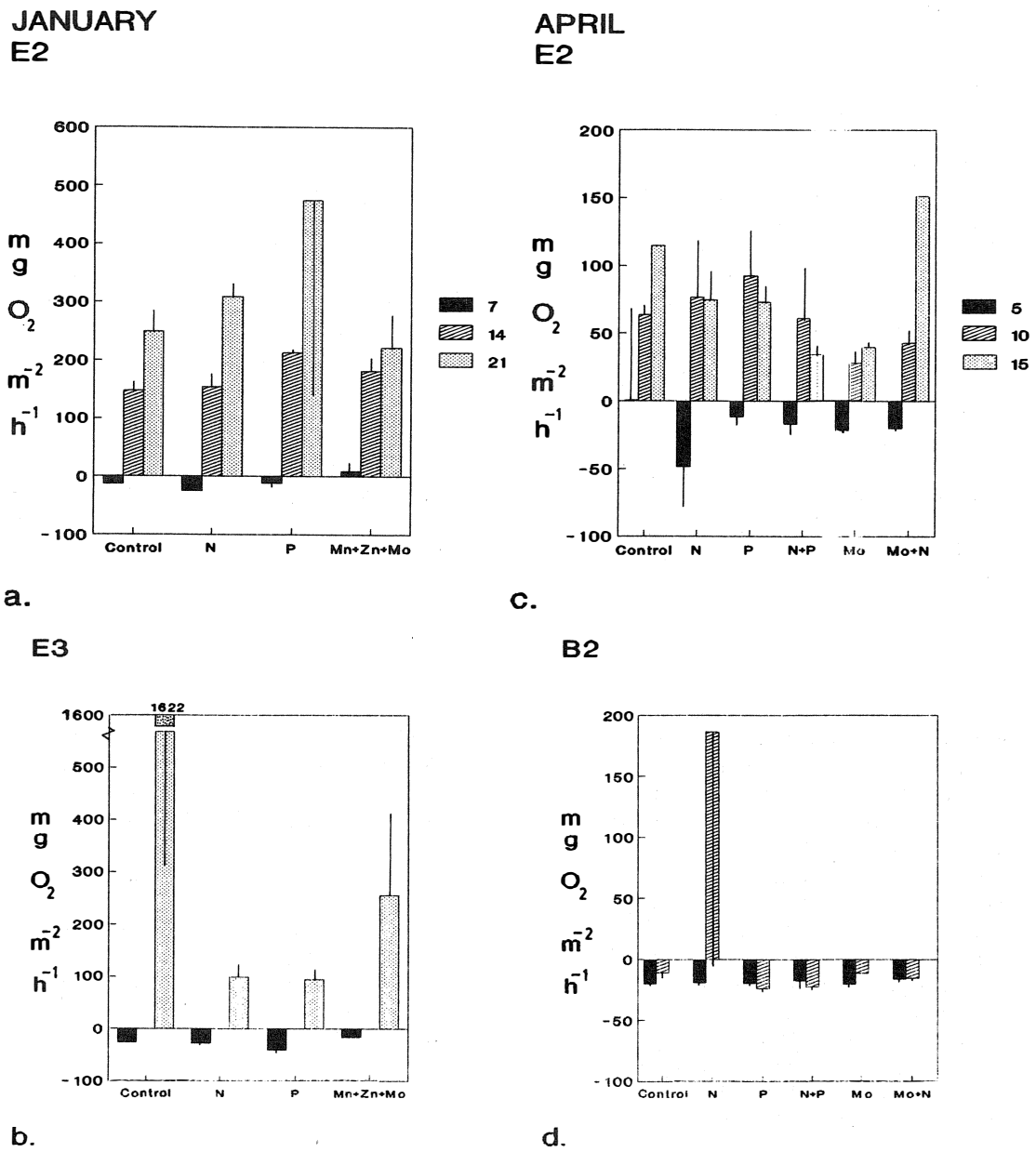

Fig. 5. Net primary productivity (mg O_2 m^{-2} h^{-1}) of unenriched (control) and nutrient (nitrogen:N, phosphorus:P, manganese+zinc+molybdenum:Mn+Zn+Mo) enriched sand-agar substrata incubated in pasture stream sites. a. January bioassays in site E2 incubated for 7,14 and 21 days. b. January bioassays in site E3 incubated for 7,14 and 21 days. c. April bioassay in site E2 incubated for 5,10 and 15 days. d. April bioassays in site B2 incubated for 5,10 and 15 days. Error bars= standard error. Surá stream, La Selva. Note the difference in scale between seasons.

DISCUSSION

Canopy cover and nutrient enrichment: Chlorophyll *a* accumulation on the plates incubated in the forest sites (4.0 mg m^{-2}) was significantly lower than in the open-canopy pasture sites (15-45 mg m^{-2}). Additionally, algal growth was not significant in any of the forest sites after the second week of incubation. Thus, it is evident that the periphyton

accumulation process in this stream is strongly limited by light.

Although phosphorus and nitrogen alone were expected to limit periphyton in various reaches of the Surá stream based on the N:P ratios (Table 1), no nutrient deficiency was evident from the bioassays. These results support the assumption made by Pringle *e t al.*(1986) that absolute macronutrient concentrations were at saturation levels after a non-significant response was obtained from N, P and N+P enrichments in a nearby low N:P stream. Pringle *et al.* documented significant response by the colonizing algal community to a mix of trace element enrichment. The effect of trace element enrichment on net PPR corrected for chlorophyll *a* concentrations was non-significant.

Saturating nutrient levels have been used as an explanation for the lack of a nutrient enrichment response in streams with N:P ratios that deviate from optimal (Grimm & Fisher 1986). In all of those studies, ambient nutrient concentrations were lower than those found during the course of this study (except site B2). Therefore, it is reasonable to assume that macronutrient levels in sites E2 and E3 were sufficient and that periphyton growth was not nutrient limited. In upstream-site B2, however, the phosphorus concentrations were relatively low, with a mean of 6.5 ug l^{-1}. Wurhmann & Eichenberger (1975) and Horner *et al.* (1983) suggested 8 ug l^{-1} and 25 ug l^{-1}, respectively, as phosphorus saturation levels for periphyton algal uptake under flow velocities similar to those measured in this study (0.18-0.22 m s^{-1}). Thus, site B2 should result in algal growth stimulation with nutrient enrichment. Averages, however, are misleading. The large P fluctuations (range= non-detectable to 30 ug l^{-1}) in B2 sometimes surpassed the "saturation values" encountered in some temperate streams (Peterson *et al.* 1983, Bothwell 1985). Thus, intermittent phosphorus increases may have been opportunistically absorbed and stored by the algal community for later use during limiting ambient conditions diminishing the effect of nutrient deficiency. "Luxury uptake" (Gerloff & Skoog 1954) by some or many of the colonizing periphytic diatoms may explain the non-significant growth stimulation by nutrient enrichment in this stream site.

Several studies have shown that standing crop values are not always directly proportional to primary productivity (Lamberti & Resh 1983). Grazing, for instance, may influence the rate at which primary producers incorporate inorganic carbon into organic compounds (Triska *et al.* 1983). In this study, however, grazing was assumed to be minimal, as the substrata were checked daily for invertebrates and no obvious tracks were found from nocturnal activity. Our productivity results were comparable to the chlorophyll *a* results: areal net PPR and respiration rates were not significantly effected by nutrient enrichment.

Tropical context: Studies in tropical streams involving attached microscopic communities are very limited. Most emphasize taxonomy and community structure (Foged 1966,1971, Archibald 1966,1972) rather than functional community characteristics. Only one study of tropical stream periphyton measured chlorophyll *a* concentrations through time and its response to nutrient enrichment (Pringle *et al.* 1986). This work was done in a watershed neighboring the Surá stream. Chlorophyll *a* concentrations determined by Pringle *et al.* (1986) were consistently lower than those obtained in the present study (controls, N, P), probably as a result of lower incident light (forest site) or micronutrient limitation. Chlorophyll *a* levels of periphyton in other tropical streams such as the Gombak River, Malaysia (open canopy) after 48 days of colonization on asbestos tiles (35 mg chlorophyll *a* m^{-2}; Bishop 1973) are comparable to those obtained in January after 14 days of incubation in the present study (Fig. 3).

Tropical PPR rates are largely limited to phytoplankton communities in lakes (Ganf 1975, Henry, Tundisi & Curi 1984, Rai & Hill 1984, Setaro & Melack 1984). Lewis & Weibezahn (1976) made a thorough study of Río Limón's (Venezuela) stream productivity dynamics including benthic primary producers. They obtained a net oxygen production rate as high as 3740 mg O_2 m^{-2} day^{-1} (ca. 605 mg O_2 m^{-2} h^{-1}) and respiration values of 135 mg O_2 m^{-2} h^{-1} which are much greater than the Surá 's January values after 14 and 21 days of periphyton colonization (Table 5, Fig. 5). The study sites in Río Limón only received 6 % of total incident light. Thus, relative to the Surá 's

open canopy sites, the net PPR of Río Limón is many times higher.

In conclusion, the benthic primary producers of the Surá stream are, under closed canopy, light limited and are not limited by macronutrients in open canopy sites. Because the La Selva forest has a very high disturbance rate in the form of new forest gaps (Sanford, Braker & Hartshorn 1986), open areas along forested streams may be a frequent event. Hence, the growth of primary producers in tropical headwaters is possibly more common than is currently thought. Compared to other tropical periphyton studies, the Surá acquires similar biomass levels at similar colonization times. Productivity and respiration rates, however, are lower than other tropical sites. Micronutrient limitation may exist, but could not be demonstrated in our study.

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RESUMEN

En las llanuras del Atlántico norte en Costa Rica, se realizó un bioensayo *in situ* de fertilización con nutrientes inorgánicos en una quebrada de tercer orden que drena bosque primario muy húmedo y pastizales abandonados a la sucesión secundaria. El sustrato artificial de agar con arena se mezcló con nitrógeno, fósforo, N+P, molibdeno, N+Mo y con una combinación de manganeso, zinc y molibdeno los cuales fueron incubados en repeticiones de tres durante 15 y 21 días. el crecimiento de perifiton sobre el sustrato artificial incubado en los sitios escogidos dentro del bosque (4 mg clorofila *a* m^{-2}) mostró una limitación por luz extrema al compararse con el crecimiento en los sitios abiertos en el pastizal (14-45 mg clorofila a m^{-2}) después de 15 días de colonización. La clorofila *a*, la producción y el consumo de oxígeno así como la taza de asimilación no mostraron un efecto significativo por la adición de los nutrimentos, indicando que la concentración de éstos en las aguas de la quebrada se encuentra a niveles de saturación para el crecimiento de perifiton. Perifiton de 10-15 días de edad es autotrófico (P/R>1) en todos los tratamientos. En comparación con otras quebradas tropicales se encontró que esta quebrada muestra tazas de acumulación de clorofila similares pero menores tazas de productividad primaria (<300 mg O^2 $m^{-2}h^{-1}$ y respiración (70 mg O_2 m^{-2} h^{-1})

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