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Light- and nutrient-limited periphyton in low order streams of Oahu, Hawaii

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Abstract

To date, most studies of light- and nutrient-limited primary productivity in forested streams have been carried out in deciduous forests of temperate, continental regions. Conceptual models of light and nutrient limitation have been developed from these studies, but their restricted geographic range reduces the generality of such models. Unlike temperate continental streams, streams on tropical high islands are characterized by flashy, unpredictable discharge and riparian canopies that do not vary seasonally. These contrasting conditions suggest that patterns of light and nutrient limitation in tropical streams may differ from those in temperate streams. The effects of light, and nitrogen and phosphorus availability on periphyton accrual (measured as chlorophyll *a* per unit area) were investigated using field experiments in 4 low-order streams on the island of Oahu, Hawaii. Levels of chlorophyll *a* in partially-shaded stream pools were significantly greater than in heavily-shaded pools, and nutrient-enrichment increased the level of chlorophyll *a* in partially-shaded pools but not in heavily-shaded pools. In each stream, phosphate enrichment resulted in an increase in the level of chlorophyll *a*, but nitrate enrichment had no effect. Spates following rainstorms occur frequently in these streams, and may increase periphyton productivity by increasing the flux of nutrients to algal cells. However, differences in inorganic nitrogen and phosphorus concentrations measured during spates and baseflow were small, and during some spates, concentrations of these two nutrients declined relative to baseflow concentrations. These observations suggest that phosphorus limitation was not alleviated by spates.

Introduction

Rates of stream periphyton productivity are controlled to a large degree by the availability of light and limiting nutrients (Borchardt, 1996; Hill, 1996). In streams beneath dense riparian canopies, productivity is directly related to light availability, and the severity of light limitation decreases with decreasing canopy cover (Hill & Knight, 1988; Feminella et al., 1989; DeNicola et al., 1992; Dodds et al., 1996; Lamberti & Steinman, 1997). Results of factorial experiments in which light and nutrient levels were manipulated simultaneously suggest that light is more severely limiting than nutrient availability in heavily-shaded streams; more variation in periphyton productivity is explained by light level than by nutrient level (Triska et al., 1983; Hill & Knight, 1988). In the absence of riparian canopies (e.g. in desert and prairie streams), and beneath canopy gaps or clear-cut areas, light limitation is alleviated and nutrient limitation can be more severe (Lowe et al., 1986; Dodds et al., 1996).

In many cases, dissolved nitrogen (N) and phosphorus (P) have been identified as the nutrients that

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limit periphyton, although trace metal and vitamin limitation has been detected (Borchardt, 1996). The extensive body of research on nutrient limitation that exists for North American streams has generated some broad geographic and geological patterns. Boreal and temperate eastern and central streams are generally P-limited (Peterson et al., 1983; Newbold et al., 1983; Pringle & Bowers, 1984; LaPerriere et al., 1989), while temperate western and southwestern streams in landscapes of volcanic or tectonic origin are generally N-limited (Grimm & Fisher, 1986; Hill & Knight, 1988; Peterson & Grimm, 1992). There are numerous exceptions to this pattern (e.g. Stockner & Shortreed, 1978; Bothwell, 1985), but it is remarkably general considering the large spatial scale, and the many factors controlling nutrient availability.

Compared to temperate streams, periphyton productivity in tropical streams is poorly studied and generalizations about light and nutrient limitation have yet to emerge. Spatial and temporal patterns in nutrient availability, riparian canopy structure and discharge in tropical forest streams can be very different from those in higher latitude streams (e.g. Sanford et al., 1986; Triska et al., 1993; Lesack, 1993a). As a result, patterns of light and nutrient limitation of periphyton productivity may also differ.

Tropical high island streams are often located in steep-sloped watersheds with high infiltration capacity. Consequently, discharge in these streams is responds very rapidly to the onset and cessation of precipitation. In non-monsoonal areas where brief rainstorms dominate the precipitation pattern, day-to-day variation in stream discharge exceeds monthly or seasonal variability (Bright, 1982; Maciolek & Ford, 1987; Resh & De Szalay, 1995; Yule, 1996). Hydrographs of such streams have multiple narrow peaks corresponding to frequent short-lived spates. Temperate streams with similar hydrographs are restricted to those few in arid regions with high subsurface flow (Poff & Ward, 1989). The rates and ratios at which nutrients are supplied to periphyton may be highly variable in flashy tropical streams (e.g. Lewis, 1986; Newbold et al., 1995). Nutrient-rich surface and subsurface runoff and mobilized channel sediments cause some nutrients to increase in concentration during spates, while dilution reduces the concentrations of other nutrients (Casey & Farr, 1982; McDiffett et al., 1989; Hill, 1993; Lesack, 1993b; Newbold et al., 1995). Sediment scouring during spates can remove periphyton, but increased availability of nutrients may enhance productivity during sub-scouring spates (Humphrey & Stevenson, 1992; Peterson et al., 1994). Among the few experimental studies of nutrient limitation in tropical streams, two reported that periphyton was P-limited (Pringle & Triska, 1991; Ghosh & Gaur, 1994), one reported N limitation (Grobbelaar, 1983), one reported micronutrient limitation (Pringle et al., 1986), and one reported nutrient-saturation (Paaby & Goldman, 1992).

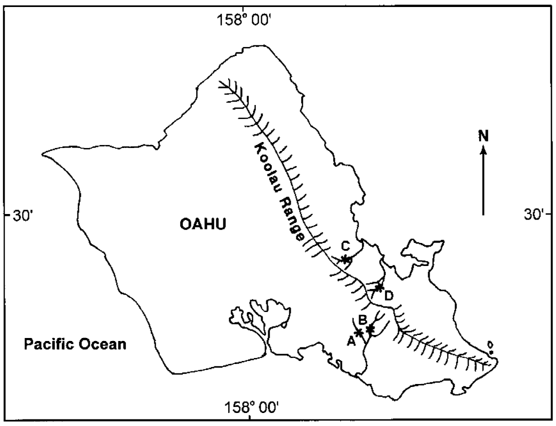

Figure 1. Location of study streams on Oahu, Hawaii. Locations of study reaches are marked with circles. (A) Aihualama Stream, (B) Waiakeakua Stream, (C) Waianu Stream, (D) Haiku Stream.

In this study, we conducted field experiments to determine the effects of light, and N and P availability on periphyton accrual in four streams on the island of Oahu, Hawaii (21° 30′ N, 158° 00′ W). On the basis of a correlation between periphyton chlorophyll *a* density and total N concentration in 11 Hawaiian streams, including four on Oahu, LaPerriere (1995) predicted that N availability limits periphyton productivity in Hawaiian streams. The effects of variation in light and nutrient availability on periphyton have not been examined in Hawaiian streams, however, and the identities of limiting nutrients have not been determined directly. Our experiments were intended to test the prediction that periphyton is N-limited and test for interactions between light and nutrient availability.

Study areas

Experiments were conducted in four streams draining the Koolau Mountain Range, which extends approximately 60 km along the long axis of the island of Oahu (Figure 1). The crest of the Koolau Range runs NW–SE, normal to the direction of prevailing NE trade winds, and divides the island into a wet windward side and a drier leeward side. Two study streams, Aihualama and Waiakeakua, are on the leeward side, and two, Haiku and Waianu, are on the windward side. Aihualama is a first-order stream; the others are second-order. The study reaches at Aihualama, Waiakeakua and Haiku Streams were in forested watersheds under conservation zoning, with minimal upstream development. The Waianu Stream study reach was located downstream from several small farms in a watershed used for agriculture. Shallow (30–50-cm depth) pools were chosen for field experiments within each stream; single pools were used in Waiakeakua, Haiku and Waianu Streams, and six pools were used along a 500-m reach in Aihualama Stream to take advantage of naturally-occurring variation in canopy cover. Three of the six pools in Aihualama Stream were beneath closed riparian canopy and were heavily shaded throughout the day, the other three were beneath canopy gaps and received several hours of direct sun daily. The study reaches at Waiakeakua and Haiku Streams were under large riparian canopy gaps, and received at least 6 h of direct sun daily. There was no riparian canopy over the Waianu Stream reach, but a banana plantation along one bank shaded the study reach at this stream in late afternoon. Study reaches at Aihualama, Waiakeakua and Haiku Streams had steep, boulder and cobble-lined channels. The Waianu Stream reach had a lower gradient and cobble and gravel substrata. Each of the streams had highly variable daily discharge. Long-term discharge data for gauged, low-order streams in Hawaii indicate that stormflows can occur in any month in response to torrential rainstorms (United States Geological Survey, 1998). The study sites at Waiakeakua and Haiku Streams were 5 and 90 m upstream from USGS stream gages No. 16240500 and No. 16275000, respectively.

Methods

Measurements of physical and chemical conditions

Water temperature and conductivity at the study sites were measured with a YSI model 33 SCT meter. Irradiance (photosynthetically active radiation) was measured just beneath the water surface in each study pool at Aihualama Stream using a Biospherical QSL-100 meter with a 4 π sensor. To estimate daily irradiance levels in the study pools, instantaneous measurements (μE m^{-2} s^{-1}) made between 0700 and 1900 hrs were plotted against time of day. Parabolic curves were then fitted to the plots, and the area below each parabola was integrated and expressed as daily irradiance (E m^{-2} d^{-1}). The instantaneous measurements were made on 40 dates between May and October 1995, under a range of weather conditions.

Streamwater samples were collected from each stream within 2 m of the experiment site under baseflow conditions before, during and after the periphyton experiments for determination of inorganic nutrient concentrations. Numerous spates occurred during the study and additional water samples were collected during some spates. All water samples were collected from below the water surface in HCl-washed jugs. The samples were filtered (Whatman GF/F) into HCl-washed Nalgene bottles, and frozen within 1 h of collection. Phosphate, nitrate+nitrite, ammonium and silicate concentrations in all water samples were measured at Analytical Services, University of Hawaii, using a Technicon continuous flow autoanalyzer.

Periphyton experiments

Nutrient enrichment experiments were conducted in each stream to determine whether periphyton accrual was N- or P-limited. The experiments took place during March, April and May 1995 (Aihualama Stream); December 1995 (Waiakeakua Stream); April and May 1997 (Haiku Stream); and November and December 1997 (Waianu Stream). Because the experiments were conducted at different times, we did not make between-site comparisons. Before the start of each experiment, 10–25 nonglazed porcelain tiles (6.45 cm^2 $\times$ 0.5 cm thick) were placed in each of 3 or 4 hardware cloth (0.25 cm^2 mesh) cages, and the cages were attached to steel stakes that held them suspended in the stream pools, about 10 cm above the substrate. The cages were shifted every 2–4 d to minimize position effects. Caged tiles were maintained in the stream pools for periods ranging from 20 d (Waiakeakua Stream) to 48 d (Aihualama Stream) to accumulate periphyton before the nutrient treatments were started. The longer accumulation period at Aihualama Stream was required for visible levels of periphyton to develop in shaded pools. At the end of the accumulation period, 12 tiles were removed from the cages at Haiku and Waianu Streams to determine chlorophyll *a* densities before enrichment treatments began. There were too few tiles in the experiments at Aihualama and Waiakeakua Streams to determine starting chlorophyll *a* densities; this precluded the calculation of periphyton growth rates for each stream. Therefore, comparisons between treatments were made on the basis of final chlorophyll *a* densities, rather than growth rates. The starting and final chlorophyll *a* densities on the control tiles (nonenriched streamwater) from Haiku and Waianu Streams were compared to ensure that periphyton continued to accumulate on tiles during the 7–10-d nutrient treatment periods and was not senescent or sloughing off.

The remaining tiles in each cage were assigned at random to nutrient treatments. These treatments consisted of 14 l of nutrient-enriched or non-enriched stream water in 16 l plastic tubs. Three treatments were used at Aihualama and Waiakeakua Streams: Nitrate-enriched, phosphate-enriched and nonenriched. At Haiku and Waianu Streams, we included an additional nutrient treatment, nitrate + phosphate-enriched. Enrichment levels were calculated to increase nitrate and phosphate concentrations to approximately 5 times the concentrations measured during periods of baseflow. Water samples were taken from experimental containers during each experiment to determine actual enrichment levels. Fresh nutrient solutions were prepared daily by adding 2 l of stock solution (reagent grade K_2HPO_4 or $NaNO_3$ in deionized water) to 12 l of stream water. Each morning during the experiments, the mesh cages holding the tiles were transferred to the plastic tubs of nutrient solution. The tubs were then placed in shallow water near the stream bank to maintain the treatments at the same temperature as the stream, and circulation was provided with battery-powered air pumps. Tiles were held in the nutrient solutions for 4–9 h per day for 7–10 consecutive days (7 days for Aihualama and Waiakeakua Streams, 10 days for Haiku and Waianu Streams). In each stream, the total time of exposure to the nutrient solutions was approximately 55 h. At the end of each daily nutrient treatment, cages were replaced in the stream pools until the following morning. Despite some drawbacks, the use of enriched streamwater in closed containers was chosen as the method of nutrient augmentation in this study in favor of open enclosures (e.g. flow-through tubes or troughs) to reduce the risk of loss during spates (see ‘Discussion’).

On the last day of nutrient treatments, tiles were removed from the cages, placed in separate 20 ml opaque plastic containers, transported on ice to the laboratory, then stored at 0 ° C until extraction. To extract chlorophyll from periphyton, 15 ml of chilled 90% acetone was added to the tile in each plastic container; this volume completely covered the tile. After a 48-h extraction period, chlorophyll *a* concentrations in 3-ml samples from each container were measured with a Hewlett-Packard 8452A diode array spectrophotometer. The same acetone used for extractions was also used for blanks, and commercial (Sigma) chlorophyll *a* was used for calibration standards. A pilot study indicated that longer extraction periods did not yield increased chlorophyll *a* concentrations, and that filtering the extracts had no detectable effect on chlorophyll *a* measurements. Two or three scans were made of each sample, then the absorbance values were averaged and chlorophyll *a* concentrations were calculated following the procedure of Jeffery & Humphrey (1975), and converted to densities (mg chlorophyll *a* m^{-2}).

In addition to nutrient enrichment, light availability was used as an experimental treatment at Aihualama Stream. Light levels corresponded to the two types of pools (partially-shaded and heavily-shaded) in which the tiles were maintained. The experiment at Aihualama Stream was therefore factorial in design, with three nutrient treatments and two light levels. Experiments at Haiku and Waianu Streams were also factorial, with two levels of nitrate enrichment and two levels of phosphate enrichment. The experiment at Waiakeakua Stream did not include a nitrate+phosphate treatment, and so was not factorial. Chlorophyll *a* densities were log-transformed to reduce heterogeneity of variance. Treatments were compared using factorial analyses of variance (Aihualama, Haiku and Waianu Streams), or a one-way analysis of variance followed by Tukey multiple comparisons (Waiakeakua Stream).

Results

Physical and chemical conditions

Mean dissolved inorganic nitrogen (DIN) and phosphate concentrations were low (DIN < 8 μM, phosphate < 1 μM), and mean DIN:phosphate ratios ranged from 10.6 at Waianu Stream to 47.3 at Aihualama Stream (Table 1). Among the forested streams, we observed consistent differences in baseflow nutrient levels: Aihualama Stream had the lowest concentrations of phosphate, nitrate + nitrite and silicate, followed by Waiakeakua and Haiku Streams. Waianu Stream, which is bordered by mixed forest and agricultural land, had the highest concentrations of nitrate + nitrite and phosphate. Ammonium concentrations were $< 15\%$ of nitrate + nitrite concentrations in

Table 1. Physical and chemical parameters of streams under baseflow conditions and during spates. Baseflow values are means ± 1 SD, sample sizes in parentheses. Spate values are ranges,sample sizes in parentheses. NM: no measurements made. No spates occurred at Waianu Stream during the study. N:P ratios are based on concentrations of nitrate+nitrite, ammonium and phosphate

Stream	Conductivity (μS)	Temperature (°C)	PO_4 (μM)	NO_3+NO_2	NH_4 (μM)	Si (μM)	N:P (μM)
Aihualama, baseflow	NM	19.9 ± 1.1	0.04 ± 0.04	1.79 ± 0.75	0.19 ± 0.10	266.8 ± 29.2	47.3
		(17)	(9)	(9)	(9)	(9)	(9)
spates	NM	19.0 – 20.5	0.11 – 0.32	1.22 – 6.16	0.25 – 0.57	163.8 – 197.0	13.8 – 35.9
		(3)	(3)	(3)	(3)	(3)	(3)
Waiakeakua, baseflow	113 ± 9	20.8 ± 0.7	0.25 ± 0.15	3.51 ± 0.82	0.21 ± 0.14	315.1 ± 45.7	14.88
	(14)	(12)	(4)	(4)	(4)	(4)	(4)
spates	110 – 118	20.0 – 22.0	0.09 – 0.28	3.68 – 4.05	0.18 – 0.30	204.6 – 296.6	13.8 – 48.3
	(2)	(2)	(2)	(2)	(2)	(2)	(2)
Haiku, baseflow	135 ± 9	20.5 ± 0.8	0.49 ± 0.09	6.67 ± 1.23	0.24 ± 0.15	411.9 ± 29.4	14.1
	(20)	(27)	(15)	(15)	(15)	(15)	(15)
spates	125 – 159	22.0 – 22.5	0.20 – 0.75	6.05 – 10.27	0.05 – 0.59	188.6 – 460.2	10.7 – 60.7
	(6)	(6)	(6)	(6)	(6)	(6)	(6)
Waianu, baseflow	113 ± 2	21.1 ± 0.7	0.74 ± 0.06	7.67 ± 0.30	0.15 ± 0.06	400.9 ± 83.9	10.56
	(7)	(7)	(6)	(6)	(6)	(6)	(6)

all samples. Differences in baseflow nutrient concentrations at the four streams may have been confounded by sampling in different seasons, which precluded statistical comparisons between streams. The study streams were stenothermal during baseflow; differences between minimum and maximum temperatures at each stream were less than 3 °C (Table 1).

Numerous spates occurred at Aihualama, Waiakeakua and Haiku streams during the study. Hydrographs for Waiakeakua and Haiku Streams indicated that, while spates were short-lived (1–8 d in duration) and the streams were at baseflow for most of the study, maximum discharge during spates was up to 30 times greater than baseflow (Figure 2). Spates had small and inconsistent effects on temperature and conductivity (Table 1). Compared to the mean baseflow values, roughly half of the temperature and conductivity measurements made during spates were higher, and half were lower, for each stream. Dissolved nutrient concentrations in water samples collected during spates are shown in Table 1. In Aihualama Stream, phosphate and DIN concentrations during spates were usually greater than concentrations during baseflow. At Waiakeakua and Haiku Streams, we found no consistent patterns in phosphate or DIN concentration during spates. Silicate concentrations decreased during each spate in each stream, compared to concentrations measured during baseflow.

Daily irradiance levels in Aihualama Stream were approximately 1.6 E m^{-2} d^{-1} in partially-shaded pools beneath canopy gaps, and approximately 0.2 E m^{-2} d^{-1} in heavily-shaded pools beneath closed canopies. These estimates were based on 40 d of instantaneous irradiance measurements at each pool (Figure 3). The polynomial regression calculated from the irradiance data for each pool was significant ($p < 0.01$), and R^2 values ranged from 0.20 to 0.43 for partially-shaded pools and from 0.25 to 0.61 for heavily-shaded pools. High variability in irradiance measurements was due in part to day-to-day changes in cloud cover.

Periphyton experiments

Nutrient concentrations measured in the experimental containers at the start of a daily treatment period at each study stream are shown in Table 2. Enriched phosphate concentrations were 5–30 times greater than in the nonenriched controls, and enriched nitrate + nitrite concentrations were 3–10 times greater than in the controls. Differences in enrichment level between streams were due in part to differences in

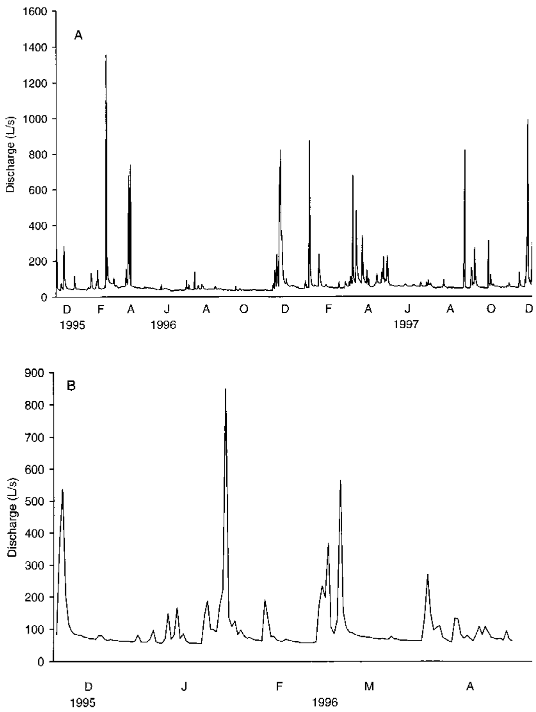

Figure 2. Hydrographs of Haiku Stream (A) and Waiakeakua Stream (B) for the periods during which the streams were monitored and experiments were conducted. Data for United States Geological Survey stream gages 16275000 (Haiku) and 16240500 (Waiakeakua) are from the USGS surface water retrieval database <http://h2o.usgs.gov/swr>.

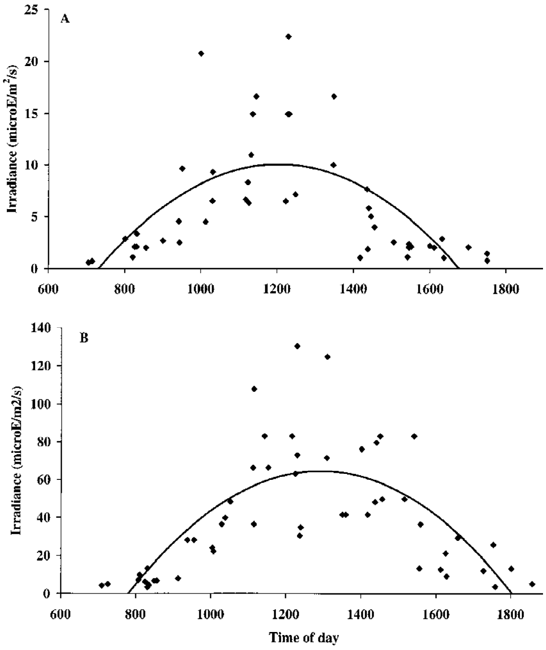

Figure 3. Irradiance (photosynthetically active radiation) measurements made on 40 dates in a heavily-shaded pool (A) and a partially-shaded pool (B) at Aihualama Stream. Lines indicate the second order polynomial regression fitted to the data for each pool, used to estimate daily irradiance levels. Heavily-shaded pool: R^2 = 0.40, estimated daily irradiance 0.2 E m^{-2} d^{-1}. Partially-shaded pool: R^2 = 0.54, estimated daily irradiance 1.6 E m^{-2} d^{-1}.

ambient nutrient concentrations at the four streams (Table 1). At Waianu Stream, nutrient concentrations in experimental containers were measured on a single date at the beginning and end of a treatment period to gauge the depletion of nutrients by periphyton uptake during the day. These measurements indicted that nitrate + nitrite and phosphate concentrations in the enriched treatments decreased by 25% and 12%, respectively. In the control treatment, the nitrate + nitrite concentration decreased by 50%, and the phosphate concentration decreased by 14%.

Periphyton on the experimental tiles from sunlit pools (Waiakeakua, Haiku and Waianu Streams) was dominated by basal cells and short tuffs of the chlorophyte *Stigeoclonium* sp., and pennate diatoms. Periphyton on tiles in the shaded pools at Aihualama Stream was dominated by pennate diatoms and the rhodophyte *Hildebrandia* sp.

At the end of the periphyton accumulation period, and before nutrient treatments began, the mean (± SD) chlorophyll *a* densities on tiles from Haiku and Waianu Streams were 2.0 ± 0.8 and 2.2 ± 1.4 mg m^{-2}, respectively. Accumulation periods were 28 d for Haiku Stream and 24 d for Waianu Stream. At the end of the nutrient enrichment period, mean (± SD) chlorophyll *a* densities on nonenriched control tiles from Haiku and Waianu Streams were 3.3 ± 1.3 and 3.0 ± 1.2 mg m^{-2}, respectively. Differences between these starting and ending chlorophyll *a* densities indicated that periphyton continued to grow on the tiles during the 7–10-d nutrient treatments.

After 48 days of periphyton accumulation and 7 days of nutrient treatments, chlorophyll *a* densities on tiles from partially-shaded pools in Aihualama Stream were greater than those on tiles in heavily-shaded pools (Table 3). Light level had a significant positive effect on chlorophyll *a* densities across the nutrient treatments (Table 4). The main effects of nitrate and phosphate enrichment were not significant, but the phosphate × light interaction was significant, indicating that phosphate enrichment enhanced chlorophyll *a* accrual in partially-shaded pools, but not in heavily-shaded pools. The nitrate enrichment effect was not significant at either light level.

Table 2. Nutrient concentrations in experimental containers. A single water sample was collected for nutrient analysis from each experimental container at the start of each daily treatment period. All concentrations in μM

Stream and treatment	PO_4	NO_3+NO_2	NH_4
Aihualama			
PO_4-enriched	2.44	1.99	0.22
NO_3-enriched	0.07	19.56	0.16
Control	0.09	2.06	0.26
Waiakeakua			
PO_4-enriched	2.76	4.26	0.19
NO_3-enriched	0.38	21.39	0.27
Control	0.29	4.16	0.23
Haiku			
PO_4-enriched	3.01	5.67	0.27
NO_3-enriched	0.52	32.83	0.24
NO3+PO4-enriched	2.75	34.00	0.21
Control	0.47	7.01	0.33
Waianu			
PO_4-enriched	2.86	8.54	0.31
NO_3-enriched	0.48	26.05	0.28
NO3+PO4-enriched	3.15	25.28	0.29
Control	0.68	8.68	0.61

Table 3. Aihualama Stream. Chlorophyll *a* densities (mg m^{-2}) on experimental tiles following 48 days of periphyton accumulation and 7 days of nutrient treatments. Values are means $\pm$ 1 SD Sample sizes in parentheses

Light level	Nonenriched	Phosphate-enriched	Nitrate-enriched
Partially-shaded	6.5 ± 2.5 (18)	11.3 ± 5.3 (20)	6.2 ± 2.8 (19)
Heavily-shaded	4.5 ± 2.1 (13)	3.1 ± 2.7 (16)	2.0 ± 1.9 (15)

In Waiakeakua, Haiku and Waianu Streams, chlorophyll *a* densities on tiles from the phosphate enrichment treatments were greater than those from either the nitrate enrichment or the control treatments (Table 5). For Haiku and Waianu Streams, the main effect of phosphate enrichment was significant, the main effect of nitrate enrichment was not significant, and the nitrate $\times$ phosphate interaction was not significant (Table 6). The lack of significant interactions indicated that nitrate and phosphate did not have mutually inhibitory or synergistic effects on chlorophyll *a* density. Chlorophyll *a* densities from the phosphate enrichment treatment at Waiakeakua Stream were significantly greater than either the nitrate enrichment or control treatments ($p < 0.001$ for the Tukey test in both cases); chlorophyll *a* densities from the nitrate enrichment treatment were not significantly different from the controls. Comparisons of chlorophyll *a* densities could not be made between the study streams due to differences in accumulation periods, enrichment periods, enrichment levels and seasons in which the experiments were conducted.

Table 4. Aihualama Stream. Summary of factorial ANOVA of chlorophyll *a* densities on tiles from the nutrient enrichment experiment

Source	df	MS	*p*
Light	1	30.5	< 0.001
Phosphate	1	0.9	> 0.05
Nitrate	1	1.6	>0.05
Light × Phosphate	1	6.0	< 0.001
Light × Nitrate	1	1.4	>0.05
Error	95	0.4	
Total	100		

Discussion

Light availability had a significant positive effect on chlorophyll *a* density; the average chlorophyll *a* density on tiles from partially-shaded pools in Aihualama Stream was nearly 3 times that on tiles from heavily-shaded pools. Results of studies of periphyton photosynthesis-irradiance relationships in temperate streams indicate that irradiance levels between 100 and 400 μE m^{-2} s^{-1} are saturating (Hill, 1996). This range is well above the average irradiance levels measured in both partially-shaded and heavily-shaded pools at Aihualama Stream. Irradiance rarely exceeded 100 μE m^{-2} s^{-1}in partially-shaded pools, and never exceeded 25 μE m^{-2} s^{-1} in heavily-shaded pools. This comparison suggests that periphyton productivity in Aihualama Stream may be light-limited much of the time, and that P may be limiting only under the highest available light conditions. As determinants of periphyton productivity, light limitation overrides nutrient limitation; nutrient availability can only affect productivity under conditions of near-saturating irradiance (Triska et al., 1983; Hill & Knight, 1988; Borchardt, 1996). Daily irradiance levels in well-lit stream reaches such as those used in Waianu and Haiku Streams are much greater than those at Aihulama Stream (author's unpublished data), and light limitation may be less severe at these well-lit sites. A corollary to the prediction that light limitation is less severe in well-lit reaches is that P-limitation may be relatively more severe at these sites, compared to shaded reaches such as those in Aihualama Stream.

On the basis of a positive correlation between chlorophyll *a* density and total N concentration, LaPerriere (1995) predicted that periphyton in Hawaiian streams is N-limited. This prediction is not supported by the results of the present study. Rather, periphyton in each study stream was P-limited. Phosphate concentrations in most of the streams monitored by LaPerriere were greater (0.7–6 μM) than in the streams in this study (0.04–0.7 μM), and periphyton in LaPerriere's study may have been P-saturated. Saturating concentrations of phosphate reported for North American streams vary by two orders of magnitude, from 0.1 to 2.0 μM (Borchardt, 1996). Thus, it is difficult to predict the phosphate concentration at which periphyton growth in Hawaiian streams might become P-saturated and shift to limitation by another nutrient. Such predictions are particularly difficult because nutrient availability is not a simple function of concentration; it is also affected by periphyton morphology and water flow (Borchardt, 1996). N:P ratios in streamwater or algal tissues have been used in lieu of experiments to evaluate nutrient limitation, but this method is not very reliable. Optimal streamwater N:P ratios vary between species, and at a given N:P ratio, some species in a periphyton assemblage may be N-limited while others are P-limited (Borchardt, 1996). Additionally, it is seldom clear whether algal tissue N:P ratios reflect nutrient storage capacities or nutrient requirements for growth (Lobban & Harrison, 1994). Field experiments using several nutrients at a range of concentrations provide a more reliable method of determining both the identity of limiting nutrients and growth-saturating concentrations.

It is recognized that the nutrient enrichment method used in this study lacked realism due to the absence of flow during nutrient enrichment treatments (4–9 h d^{-1}), and to nutrient depletion by periphyton uptake. This method was chosen as a compromise over two more commonly used methods, nutrient-diffusing substrata and flow-through enclosures (Pringle & Triska, 1996). Nutrient-diffusing substrata simulate naturally enriched substrata such as organic matter-rich sediments. However, channels of steep, Hawaiian streams subjected to frequent spates are lined with boulders and cobbles, and are unlikely to be major nutrient sources. Flow-through enclosures with continuous water column enrichment might have been a more realistic means of enriching the water column, but the risk of spates removing enclosures suspended in stream channels was very high. The weighted tubs used in this study provided a secure means of enriching large volumes of streamwater. Nevertheless, it is possible that the effects of flowing water on nutrient availability, particularly the reduction of boundary layer thickness with increasing flow, would have altered the results of phosphate and nitrate enrichment observed in this study (Borchardt, 1994, 1996). Chlorophyll *a* densities were 50–80% greater on the phosphate-enriched tiles than on the nitrate- enriched tiles (Tables 3 and 5), however, and it is unlikely that increased flow rates would have greatly altered this trend.

In view of the frequency of spates that characterizes Hawaiian streams, the question of whether nutrient limitation increases or decreases in severity during spates is a compelling one. In the streams we studied, phosphate concentrations were greater than baseflow concentrations during some spates and lower during others (Table 1). When phosphate concentrations increased, the changes were small (< 0.3 μM). These observations suggest that P-limitation of periphyton is not alleviated during spates. However, the nutrient data from spates have poor temporal resolution, so accurate predictions about the effects of spates cannot be made. Nutrient concentrations were determined at a single point in time during each spate, and most of these samples were collected on the falling limb of the storm hydrograph. Relationships between nutrient concentrations and rapidly changing discharge during spates are complex, and numerous samples must be collected at short intervals to elucidate those patterns. Not only do nutrient concentrations vary from point to point during individual spates, there is also between-spate variability in nutrient concentrations due to differences in maximum discharge, shape of the storm hydrograph and antecedent events such as flushing flows (e.g. McDiffett et al., 1989; Peterson et al., 1994; Newbold et al., 1995).

Despite recommendations to make productivity and nutrient dynamics in tropical streams a research priority (Bruijnzeel, 1991; Jackson & Sweeney, 1995),

Table 5. Waiakeakua, Haiku and Waianu Streams. Chlorophyll *a* densities (mg m^{-2}) on experimental tiles before and after 7 (Waiakeakua Stream) to 10 (Haiku and Waianu Streams) days of nutrient enrichment treatments. Values are means ± 1 SD Sample sizes in parentheses. NM: not measured

Stream	Before treatments	Nonenriched	Phosphate enrichment	Nitrate enrichment	Phosphate+nitrate enrichment
Waiakeakua	NM	2.1 ± 0.7 (13)	3.9 ± 1.0 (13)	2.6 ± 0.6 (13)	NM
Haiku	2.0 ± 0.8 (12)	3.3 ± 1.3 (12)	4.2 ± 1.4 (13)	2.7 ± 1.4 (12)	4.7 ± 0.9 (13)
Waianu	2.2 ± 0.1 (10)	3.0 ± 1.2 (10)	5.1 ± 1.2 (11)	2.7 ± 1.2 (10)	4.8 ± 1.8 (11)

factors controlling productivity in these streams remain poorly understood. Whether N or P availability limits periphyton in tropical streams has important management implications. The identification of limiting nutrients is required for controlling eutrophication, which is increasing in severity and extent in the tropics (e.g. Dudgeon, 1992; Ellison & Farnsworth, 1996). Limnologists have focussed on P as the primary limiting nutrient in temperate North America, and this has influenced the direction of water quality management (Elser et al., 1990). However, literature surveys indicate that periphyton productivity in many temperate streams is limited by N, rather than P, and this may be true for some tropical streams as well. Both N and P limitation have been reported (Grobbelaar, 1983; Pringle & Triska, 1991; Ghosh & Gaur, 1994). Although P-limitation was observed in four streams in the present study, we hesitate in predicting that all Hawaiian streams are P-limited. There are 366 perennial streams on the high islands of Hawaii, draining watersheds that vary widely in factors that influence nutrient availability, such as land use and soil development. Predictions about the factors limiting periphyton in Hawaiian streams will remain unreliable until additional field experiments have been conducted under a wide range of environmental conditions.

Table 6. Waiakeakua, Haiku and Waianu Streams. Summaries of one-way and factorial ANOVAs of chlorophyll *a* densities from enrichment experiments

Source	df	MS	*p*
Waiakeakua Stream			
Nutrient treatments	2	11.0	< 0.001
Error	36	0.6	
Total	38		
Haiku Stream			
Phosphate	1	27.2	< 0.001
Nitrate	1	0.1	> 0.1
Phosphate X Nitrate	1	4.0	> 0.1
Error	45	1.6	
Total	48		
Waianu Stream			
Phosphate	1	47.4	< 0.001
Nitrate	1	1.0	> 0.1
Phosphate X Nitrate	1	0.0	> 0.1
Error	38	1.9	
Total	41		

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