Limnol. Oceanogr., 47(1), 2002, 278–289

Landscape variation in phosphorus concentration and effects on detritus-based tropical streams

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Abstract

Landscape-scale variation in streamwater phosphorus (P) concentration can affect aquatic food webs. Such variation occurs naturally in streams at La Selva Biological Station in Costa Rica due to spatially variable inputs of geothermally modified groundwater. We examined effects of this gradient on detrital food web components at 16 stream sites. The Michaelis-Menten model provided a good fit of the relationship between soluble reactive phosphorus (SRP) and leaf decay rate, fungal biomass, and invertebrate biomass, indicating that these variables were controlled by P concentration and that half-saturation constants were relatively low (7–13 μg L^{-1} SRP). In a subsequent short-term (3 week) whole-stream P enrichment study, we found no effect of P addition on leaf decay rate or on biomass or density of invertebrates. However, laboratory tests of P, N, and Ca concentrations on mass loss of leaves showed detectable stimulation by both N and P after 3 weeks. A fourth study assessed the relative contribution of invertebrate consumption versus P concentration in determining decay rates among streams. The majority of variation was due to P concentration (71%), compared to effects of invertebrates (3%) or invertebrate × P interactions (14%). Overall, we found that a landscape-scale natural gradient in P concentration influenced decay rates of organic matter and biomass of consumers, providing evidence that benthic detrital food webs can be limited from the bottom up by nutrients. Microbial processes appeared to be most important in driving differences in organic matter decay among sites, but invertebrates also contributed to elevated decay rates at high-P sites.

In contrast to our knowledge of nutrient effects in ecosystems where primary producers are a basal resource (cf., Peterson et al. 1993; Brett and Goldman 1997), we know very little about how nutrients function in detritus-based ecosystems (i.e., ecosystems in which most energy is derived from dead organic matter). Food webs of all ecosystems have at least some important detrital component, and the trophic basis of many systems such as wetlands, desert islands, and soils is fueled largely by detritus (e.g., Polis and Hurd 1996). In forested headwater streams, food webs are primarily based on inputs of dead leaves, wood, and associated microbes (Vannote et al. 1980; Hall and Meyer 1998). In such streams, detritus serves as the dominant energy base (Fisher and Likens 1973) and can be positively related to densities and biomass of stream consumers (Darnell 1964; Egglishaw 1964; Minshall 1967; Culp and Davies 1985). Experimental work has shown that detrital carbon can limit stream detritivore biomass and production. Increased coarse particulate organic matter (CPOM) resulted in greater masses and densities of several invertebrate species (Richardson 1991) and exclusion of leaf litter from a headwater stream resulted in reduced secondary production of invertebrates (Wallace et al. 1997).

Nutrients can stimulate microbial activity on carbon substrates and potentially affect availability of detrital carbon to consumers. There is evidence from streams, lakes, and coastal oceans that nutrients can stimulate activity, biomass, or production of heterotrophic microbes (bacteria or fungi) (Pace and Funke 1991; Pomeroy et al. 1995; Suberkropp and Chauvet 1995; Cotner et al. 1997; Grattan and Suberkropp 2001). Studies determining the effects of increased nutrient concentration on decay rates of organic matter in streams (an indirect measure of microbial activity, other losses being equal) have typically shown positive effects (Kaushik and Hynes 1971; Elwood et al. 1981; Meyer and Johnson 1983; Tank and Webster 1998; Grattan and Suberkropp 2001), while others have found no effects of increased nutrients (Triska and Sedell 1976; Royer and Minshall 2001). Nutrient effects may depend on the nutrient composition of organic substrata (Peterson et al. 1993) and/or the relative contributions of nitrogen (N) and phosphorus (P) in stream water (see Elwood et al. 1981 and Newbold et al. 1983). More recent studies have explicitly linked effects of nutrients on increasing decay rates of organic matter to increased microbial activity (Suberkropp and Chauvet 1995; Weyers and Suberkropp 1996; Grattan and Suberkropp 2001).

The extent to which nutrient effects extend beyond stim-

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Acknowledgments

We thank Matt Tolcher, Francisco Rojas, Rick Rosemond, Sarah Dalle, Minor Hildago, Marisol Joseph, Augusta West, Allison Colquitt, Norm Leonard, Mary Ann Daum, Laura England, Jamie March, and Jon Benstead for field and laboratory assistance and Keith Taulbee and Tom Maddox for sample analyses. We are grateful to Jon Benstead for assistance with sample and data analyses and improvements to the manuscript. We thank J. Bruce Wallace for providing *L/W* relationships used for invertebrate biomass determinations, Robert O. Hall for suggesting the use of Michaelis-Menten models, and Mark Hunter for suggesting the variance partitioning procedure. We also thank Mike Vanni and two anonymous reviewers for suggested improvements to the manuscript. Research was supported by National Science Foundation (NSF) grants DEB-9403292 to A.D.R. and DEB-95-28434 to C.M.P. and F.J.T. Synthesis and writing was supported by NSF grant DEB-9806610. We thank the Organization for Tropical Studies and the staff at La Selva Biological Station for facilitating fieldwork.

ulation of heterotrophic microbial assemblages to higher trophic levels in streams has been little studied and may depend on the efficiency of trophic transfer. Increased microbial activity may accelerate respiration and, thus, losses of carbon from the system. Alternatively, increased microbial activity may result in increased detritivore production via increased food quality. If consumers of microbes are of sufficiently large size relative to microbes, the microbial loop may serve as a link, rather than a sink to carbon potentially available to detritivores (Meyer 1994). Pace and Funke (1991) found that nutrient addition stimulated bacterial activity and heterotrophic flagellate abundance in lakes. The extent to which increases in inorganic nutrient concentrations stimulate growth rates of heterotrophic microorganisms and whether those in turn stimulate growth of detritivores in other systems is largely unknown.

This research was aimed at determining P effects on components of detritus-based food webs in streams draining lowland forests in Costa Rica. Specifically, we examined whether there was P limitation of microbes and detritivorous consumers in streams that varied naturally in P concentration. We studied these effects in streams at La Selva Biological Station (Costa Rica), where streams in close proximity exhibit relatively large variation in streamwater P concentration (Pringle 1991; Pringle et al. 1993). Our research consisted of four component studies. The first study was conducted in 16 stream sites at La Selva ranging from 5 to 230 μg soluble reactive phosphorus (SRP), reflecting molar concentrations of 0.15 to 7.12 μM PO_4^{3-}-P, at which we assessed natural P effects on microbial and invertebrate biomass associated with leaves and leaf litter decay rates. The second study was an experimental enrichment of a low-P stream (ca. <5 μg L^{-1} SRP) to concentrations of approximately 200 μg L^{-1} SRP. We examined effects of this relatively short-term (3 week) enrichment on leaf decay rates and invertebrate biomass. In the third study, we conducted a laboratory experiment to determine the separate and interactive effects of P, nitrogen (N), and calcium (Ca) on leaf decay. In the fourth study, we evaluated the relative contributions of microbial degradation and invertebrate consumption in determining decay rate at sites differing in P concentration.

Study site

La Selva Biological Station (10°26′N, 84°01′W) comprises the southernmost extension of a protected land corridor (Braulio Carrillo National Park) that is the last intact tract of primary rainforest on the entire Caribbean slope of Central America that spans elevational extremes. La Selva is located at the base of Volcan Barva of Costa Rica's Cordillera Central mountain range and receives approximately 4 m of rainfall per year, the majority of which falls during the wet season (July–November). Although this volcano is dormant, it is part of an active geothermal system. This system is the source of solute-rich waters that surface at both low (at La Selva) and high elevations on Barva's Caribbean slope. These geothermal waters are high in solutes (Ca, Fe, Mg, Na, Si, Cl, SO_4, and P) but not temperature because they cool during lateral, subsurface transport (Pringle et al. 1993).

Extensive work has been conducted to map the location of solute-rich geothermal inputs at La Selva and to determine long-term trends in nutrient chemistry. Some streams exhibit no geothermal input, while others have multiple inputs from solute-rich seeps (Pringle 1991; Pringle and Triska 1991). Recent work examining temporal variation in streamwater chemistry indicates that most streams at La Selva are consistently either high or low in solutes. However, there is marked year-to-year variation in maximum concentrations (C.M. Pringle unpubl. data).

The food webs in these forest streams appear to be detritally based: there are large inputs of leaf litter but very little algal biomass, and the gut contents of many invertebrate consumers indicate use of detritus (A.D. Rosemond and A. Ramírez pers. obs.). Aquatic consumers in La Selva streams consist of aquatic insect larvae, snails, fishes, shrimps, crabs, turtles, caiman, and otters. Organisms that feed primarily on coarse particulate organic matter are aquatic insect larvae and omnivorous fishes and shrimps (Wootton and Oemke 1992; Rosemond et al. 1998). Collector-gatherers make up the dominant insect functional feeding group in benthic substrata and leaf packs in La Selva streams (Ramírez and Pringle 1998; Rosemond et al. 1998), indicating reliance on fine particulate organic matter as a food resource. Aquatic insect larvae that feed by shredding CPOM are rare in these streams. In contrast to temperate streams, where shredding invertebrates contribute significantly to breakdown of CPOM, this process appears to be driven by macroconsumers (e.g., fishes and shrimps) and microbial and physical processes at La Selva (Rosemond et al. 1998, 2001).

Leaf fall in streams at La Selva is more or less continuous throughout the year, in contrast to more synchronous leaf fall in temperate zone forests. Only 8% of the tree species at La Selva are deciduous (Hartshorn 1983). We selected the fast decomposing, broadleaf *Ficus insipida* Willd. (= *glabrata* Humbolt, Bonpland, and Kunth) (Family: Moraceae) as the focal leaf species used in these studies because it is a dominant riparian species at La Selva (Hartshorn and Hammel 1994), its leaves are observed in accumulations in streams, and enough naturally abscised material could be collected for leaf-pack construction.

Methods

Study 1. P effects on leaf decay rate and microbial and invertebrate biomass at multiple sites—This component of our overall study examined microbial and invertebrate biomass, decay rates of leaves, and measures of litter quality of *Ficus insipida* in 16 sites ranging in P concentration. We determined decay rate, %N, C:N, and fungal and invertebrate biomass from leaf packs placed at these sites and determined relationships with P concentration. We also used multiple regression to determine whether these variables were related to variation in streamwater N concentration, dissolved inorganic nitrogen to SRP ratio by mass (hereafter referred to as DIN:SRP ratio), or current velocity among sites.

Newly abscised leaves were collected and dried at 40°C in March 1994. Initial dry mass (~5 g) of leaves was determined for individual leaf packs. An initial ash-free dry mass (AFDM) to dry mass conversion was determined from a subset of leaf packs. Leaves were placed in litter bags made of commercially available bird netting (mesh size ca. 2 cm). Ten litter bags were placed at each site in depositional areas on 11 April 1994. Single litter bags were collected eight times (days 1, 3, 6, 10, 14, 18, 23, 28) from each site, using a 250-μm mesh dip net to prevent any loss of invertebrates. Leaf packs were refrigerated until they were processed (within 24 h). Invertebrates were rinsed from leaf surfaces and stored in 70% ethanol. Disks were cut from the leaves with a hole punch and preserved for fungal biomass on day 10 (below). A subsample of leaf disks was dried at 60°C to determine the mean dry mass of leaf disks. This mass was added back to the mass of the leaf pack. The whole leaves were then dried to a constant mass at 60°C and a subsample was ashed at 500°C to determine AFDM. Decay rate (k) was determined using the negative exponential model using the natural logarithm of percentage AFDM remaining versus day (from day 0–28) (Benfield 1996).

Invertebrates were identified to the lowest possible taxonomic level (typically genus, except dipterans, which were identified to family or subfamily). Biomass of invertebrates was determined by measuring the length of each individual to the nearest 0.5 mm and estimating biomass from length: mass relationships (Benke et al. 1999) derived from invertebrates of similar morphology and typically from the same family. Invertebrate biomass was normalized by AFDM of leaf packs. We determined the average biomass of invertebrates on leaf packs by averaging biomass/AFDM for a given site (hereafter referred to as average invertebrate biomass) for five dates (days 6, 10, 14, 18, 23). For missing data points for a given site on a given date ($n = 3$), we plotted colonization patterns of biomass versus time and interpolated values.

Water samples were collected five times during the study at 5- to 10-d intervals at all sites. Samples were filtered in the field using prerinsed millipore type HA membrane filters (0.45 μm) and kept cool. Concentrations of SRP were determined within 24 h at the field station laboratory using the ascorbic acid molybdenum-blue method as PO_4^{3-} on filtered samples (Murphy and Riley 1962). Additional samples were frozen and transported back to the University of Georgia for analysis of nitrite + nitrate ($NO_2^- + NO_3^-$) and ammonium (NH_4^+) using an Alpkem RFA 300 Colorimetric analyzer. Current velocity was measured once on day 6 of the study (mean of three readings) at baseflow from the area immediately upstream of the leaf packs using a Marsh-McBirney® current meter.

We quantified %N and C : N and estimated fungal biomass on leaves to determine site effects on these measures of litter quality. Dried leaf packs from days 10 and 18 were ground and subsampled and %N and %C were measured using a Carlo Erba NA 1500 CHN combustion analyzer. We estimated fungal biomass on leaves on day 10 by quantifying ergosterol, a sterol specific to aquatic hyphomycete fungi using methods previously described in Newell et al. (1988) and Paul and Meyer (1996). Ergosterol was expressed as μg g^{-1} AFDM of leaves.

Statistical analyses: We examined whether variation in SRP concentration among sites was related to the dependent variables we measured (i.e., leaf decay rate, fungal biomass, leaf %N, leaf C : N, and invertebrate biomass). In addition, we tested whether other variables we measured at these sites ($NO_2^- + NO_3^-$ concentration, NH_4^+ concentration, DIN : SRP ratio or current velocity) could explain as much or more of the variation in dependent variables as SRP using stepwise multiple regression (SAS 1988). Prior to analyses, tests of normality of the dependent variables were performed using the UNIVARIATE procedure in SAS (SAS 1988). Variables were transformed (using logarithmic transformation for numeric data and arcsin square-root transformation for percentage data) if tests of normality were violated and if transformations improved normality approximations. We then conducted stepwise multiple regression using all sites with those variables that were linearly (or not strongly nonlinearly) related to dependent variables as indicated by bivariate plots (which included all variables except SRP, below). Our sites grouped into two categories, low P ($n = 8$) and high P ($n = 8$), and we also ran stepwise regression separately on these groups (which included all variables).

Relationships between SRP and the dependent variables tested were nonlinear and were fitted using the Michaelis-Menten model of enzyme-catalyzed reactions (Stryer 1981). In the standard application of this model: $V = V_{max}([S]/([S] + K_m))$, where V is the rate of catalysis of an enzyme; $[S]$ is the substrate concentration; V_{max} is maximum rate of catalysis; and K_m is the substrate concentration at which the reaction rate is half the maximum value. For our purposes, this model appeared to be a good descriptor of the relationship between SRP concentration ($[S]$) and the rate (V) of leaf decay, and fungal and invertebrate biomass on leaf packs. We fit the Michaelis-Menten model to raw data using the iterative, least-squares nonlinear fitting function in JMP® (Version 4; SAS 2000). This fitting technique allowed calculation of approximate standard errors for estimates of V_{max} and K_m.

Study 2. P enrichment of a low-P stream—To determine the effects of short-term P enrichment on detrital processing and detritivore biomass, we conducted a whole-stream P enrichment of a low-P stream. In March 1995, we continuously added P to the Piper (which was one of the low-P streams investigated in study 1 and study 4, below) for 3 weeks. Phosphorus concentrations were increased from approximately 15 to >150 μg L^{-1} SRP by continuously dripping dilute phosphoric acid (K_2HPO_4) from a Mariotte bottle (Peterson et al. 1985) into a well-mixed area halfway downstream of a 20-m long run. Mixing of the P solution with stream water was checked with rhodamine dye, and effects of the enrichment on streamwater pH were checked prior to the study. Water samples were taken every 2–3 d during the experiment, both upstream (two samples) and downstream of the enrichment (four samples encompassing the area where leaf packs were placed) and were filtered and analyzed as in study 1.

Leaf packs were constructed using *Ficus insipida* leaves that had been collected from riparian areas at La Selva in May 1994, dried in the sun (in contrast to oven drying in the 1994 study) and placed in dry storage prior to use in this study. Initial dry mass was determined on leaf packs (~5 g). At the onset of the study, leaves were rewetted using stream water and stapled together into packs using a buttoneer fastener (Dennison). Initial AFDM/dry mass conversions were determined from a subset of leaf packs. Four groups of leaf packs were placed upstream of the enrichment, and four groups were placed downstream of the enrichment. One leaf pack was collected from each group after 1, 3, 5, 8, 12, 16, 21 d in situ and processed as in study 1. Invertebrate biomass and density were determined on each date that leaf packs were collected and normalized by g AFDM of leaf material. Mean decay rates were based on decay values calculated for each group of packs (n = 4) from upstream and downstream sites. Differences between upstream and downstream decay rates and invertebrate biomass and density were determined by t-test (SAS 1988).

Study 3. Effects of N, P, and Ca on leaf decay—Results of the Piper enrichment study led to an examination of the singular and interactive effects of N, P, and Ca on leaf decay. Our goal in this study was to determine (1) whether P alone stimulated decay of organic matter in the absence of stream consumers and (2) whether either N or Ca were colimiting to decay processes. We conducted this study at the University of Georgia with leaf litter and water transported from the Piper stream (La Selva Biological Station, Costa Rica). In the lab, we increased P, N, and Ca concentration in a complete factorial design. Water was collected in the field and filtered through Gelman A/E filters. *Ficus* leaves were collected approximately 2 km from the Piper stream. Leaves were oven dried at 30°C and were transported dry. The experiment was initiated on 6 January 1996 with water and leaf material collected on 2 January 1996. Treatments consisted of (1) stream water control and additions of (2) P, (3) N, (4) N and P, (5) Ca, (6) P and Ca, (7) N and Ca, and (8) P, N, and Ca. Our target concentrations were 500 μg L^{-1} SRP, 10 mg L^{-1} DIN (NO_2^- + NO_3^- + NH_4^+-N), and 10 mg L^{-1} Ca. Stock solutions of P and N were made up so that additions to flasks resulted in additions of 0.5 mg of P as KH_2PO_4, 10 mg N, 5 mg as KNO_3 and 5 mg as NH_4Cl per liter of stream water. Calcium was added directly to flasks as $CaCO_3$ at 10 mg per liter of stream water. Three milliliters of a microbial innoculum (made by bubbling stream water from the Piper with leaves collected from the stream) were added to each flask for a total volume of 150 mL. Each treatment combination was replicated (n = 5) in separate acid-washed flasks. Each flask contained a small litterbag made of mosquito netting to which 30 disks of *Ficus insipida* leaves were added. Five initial groups of 30 leaf disks were dried and ashed to determine initial AFDM. Flasks were maintained at approximate stream temperature (22°C, range over the experimental period: 21.8–23°C) and continuously shaken in a shaker/incubator. Part of the water in each flask (100 ml) was emptied every 2 d and replaced with filtered stream water and appropriate nutrient additions. Water sampled from flasks from two dates (8 and 26 January)

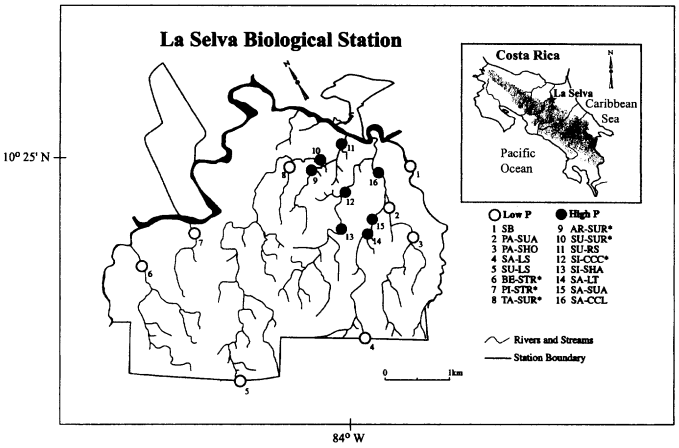

Fig. 1. Map of La Selva Biological Station marked with 16 sites used in study 1 and the sites revisited in study 4. Open symbols indicate low phosphorus sites, and solid symbols indicate high phosphorus sites. Site names are abbreviated stream names hyphenated with the trail crossing closest to the site where leaf packs were incubated. Study sites were within an area of 7.5 km^2.

from one replicate sample of each treatment was filtered using prerinsed millipore type HA membrane filters (0.45 μm) and frozen. Analysis of nitrite + nitrate nitrogen (NO_2^- + NO_3^-) and ammonium (NH_4^+) was conducted using an Alpkem RFA 300 Colorimetric analyzer, and SRP was determined spectrophotometrically using the ascorbic acid molybdenum-blue method (Murphy and Riley 1962). Calcium concentrations were determined by flame atomic absorption spectrometry (direct air-acetylene flame) (American Public Health Association 1992). Mass loss of leaf disks was determined after 3 weeks. Effects of P, N, and Ca on mass loss were determined by three-way ANOVA on percentage AFDM remaining. We also measured pH in stream water at the end of the experiment, as a potential surrogate for changes in respiration, using an Orion pH electrode.

Study 4. P versus invertebrate effects on leaf decay—Six sites that were used in study 1 were examined again in 1996. Our goal was to determine the relative importance of microbial processing and invertebrate consumption in driving differences in decay rate among sites differing in P concentration and to corroborate our results from 1994. Thus, we designed the study to test for P effects on decay rate, invertebrate effects on decay rate (using litterbags with different mesh sizes), and interactive effects. Our a priori hypotheses were that decay rates would be fastest at high-P sites and that effects of invertebrates (i.e., differences in decay rate between large and small mesh) would be greater at high-P versus low-P sites due to increased consumption in response to higher quality food. Leaf packs were constructed as described in study 2 and were placed in six sites on 27 February 1996. Mesh treatments consisted of large mesh (commercially available bird netting as used in study 1, mesh size = 2 cm) and small mesh (Nitex® netting, mesh size = 250 μm). The six sites we chose were three streams high in P (SI-CCC, SU-SUR, AR-SUR) and three streams low in P (PI-STR, TA-SUR, BE-STR) (Fig. 1). Two microsites (areas

Table 1. Mean nutrient concentrations, DIN : SRP ratios, and water velocities at the 16 stream sites used in study 1; ranges in parentheses; $n = 5$. Current velocities were measured ($n = 3$) on day 6 of the study. SRP is soluble reactive phosphorus measured as PO_4^{3-}-P in filtered water samples, DIN : SRP is the ratio by weight of dissolved inorganic nitrogen to SRP. Stream names are as follows: PI = Piper; TA = Taconazo; BE = Bejuco; SU = Sura; PA = Pantano; SB = Sabalo; SI = Saltito; SA = Salto; and AR = Arboleda. Site is where a trail (the name of which is indicated by the suffix, e.g., -STR) crosses the stream. Range in SRP concentrations reflect molar concentrations of 0.15–7.12 μM PO_4^{3-}-P. Range in $NO_2^- + NO_3^-$-N is 0.55–2.66 μM. Range in NH_4^+-N is 0–0.81 μM. DIN : SRP ratios reflect molar ratios of 18.15–0.17.

Site	Nutrient concentration (μg L^{-1})			DIN : SRP	Current velocity (m s^{-1})
	SRP	$NO_2^- + NO_3^-$-N	NH_4^+-N		
PI-STR	5 (5–5)	122 (76–201)	36 (24–55)	71.5	0.06 (0.05–0.07)
TA-SUR	5 (5–5)	143 (28–523)	58 (35–90)	91.0	0.03 (0.03–0.03)
BE-STR	5 (5–7)	39 (12–92)	20 (10–40)	24.8	0.07 (0.06–0.10)
SU-LS*	7 (5–8)	190 (131–321)	33 (18–41)	74.7	0.05 (0.04–0.05)
PA-SHO*	8 (5–14)	81 (55–126)	22 (11–28)	28.1	0.04 (0.03–0.04)
SB	9 (7–12)	54 (21–92)	39 (10–108)	23.1	0.04 (0.03–0.04)
SA-LS*	17 (12–20)	123 (86–142)	9 (0–21)	17.3	0.06 (0–0.13)
PA-SUA	21 (15–30)	60 (20-94)	35 (0–100)	10.7	0.09 (0.04–0.15)
SI-CCC	91 (66–107)	82 (46–180)	14 (0–69)	2.3	0.12 (0.10–0.15)
SI-SHA	117 (77–135)	90 (51–204)	19 (0–75)	2.1	0.06 (0.03–0.08)
SA-CCL*	134 (121–143)	86 (72–102)	0	1.4	0.05 (0.04–0.07)
SU-SUR	154 (146–160)	112 (91–160)	11 (0–50)	1.8	0.08 (0.06–0.12)
SA-SUA	168 (144–224)	76 (65–88)	17 (0–83)	1.2	0.06 (0.04–0.08)
SU-RS	178 (153–188)	110 (82–146)	16 (0–57)	1.6	0.30 (0.29–0.32)
SA-LT	210 (168–236)	60 (44–70)	18 (0–90)	0.8	0.09 (0.07–0.11)
AR-SUR	230 (201–252)	95 (79–133)	2 (0–12)	0.9	0.14 (0.11–0.20)

* $n = 4$.

within 15 m of each other in the same stream reach) were chosen at each site to determine independent k values that were then averaged prior to analyses. Leaf packs of both mesh sizes from both microsites from all streams (total $n = 24$ d^{-1}) were collected after 1, 4, 8, 13, 19, and 25 d and were processed as in study 1. Invertebrate abundance was determined on days 4, 13, and 25. Invertebrates were identified as chironomids (belonging to Family Chironomidae) or as nonchironomids. Invertebrate abundance was normalized for g AFDM of leaf packs to obtain invertebrate density.

Water samples were collected each day the leaf packs were collected and 1 d prior to the study, filtered in the field using millipore type HA membrane filters (0.45 μm), and analyzed for SRP, $NO_3^- + NO_2^-$, and NH_4^+ as in the 1994 study. Minimum and maximum temperatures were recorded on each collection date.

Statistical analyses: We used a general linear model using mesh as a class variable and determined effects of mesh, P, and the interaction between P and mesh effects (P × mesh) on decay rates (SAS 1988). Two decay rates were averaged for each site for each mesh size treatment. To use the information afforded by having two mean rates per site, means were weighted by 1/SD in ANOVA. We fit the Michaelis-Menten model to these data as above and compared the fit of this model to linear relationships between decay rate and SRP concentration. Two-way ANOVAs by date were also conducted on invertebrate density, weighted by 1/SD. We tested treatment effects of P and mesh size on total density, chironomid density, nonchironomid density, and proportion of nonchironomids. Tests of normality and transformations were performed as in study 1. We used a variance partitioning procedure described in Hunter et al. (1997) to determine the relative importance of P concentration and mesh size and their interaction in determining decay rates. This procedure uses type III sums of squares from ANOVA to partition the overall model variance by the factors tested. We have previously used this technique to determine relative contributions of P concentration and large consumers (e.g., fish) to leaf decay rates (Rosemond et al. 2001).

Results

Study 1. P effects on leaf decay rate and microbial and invertebrate biomass at multiple sites—Sites ranged in mean SRP concentration from 5 to 230 μg L^{-1}. Mean nitrate and ammonium concentrations were typical of unpolluted streams ($NO_2^- + NO_3^-$-N < 200 μg L^{-1}, NH_4^+-N < 60 μg L^{-1} on average) (Allan 1995), and atomic DIN : SRP ratios were extremely low (<1) at sites that were relatively high in SRP (Table 1). Although we attempted to place litterbags in depositional areas at all sites (flow <0.10 m s^{-1}), current velocity was somewhat higher for litterbags at three sites (Table 1). There were no major rain events during the study period, and streams remained at baseflow.

To determine the breakdown rate (k) of leaves, we used the negative exponential model, which provided a good fit. For two sites, data from the last day were dropped due to values that were anomalous (site SA-SUA) or zero (site SU-RS). The mean R^2 values for regressions were 0.93 (range, 0.79–0.99).

Plots of relationships between SRP and dependent variables appeared to be nonlinear: they increased with SRP up

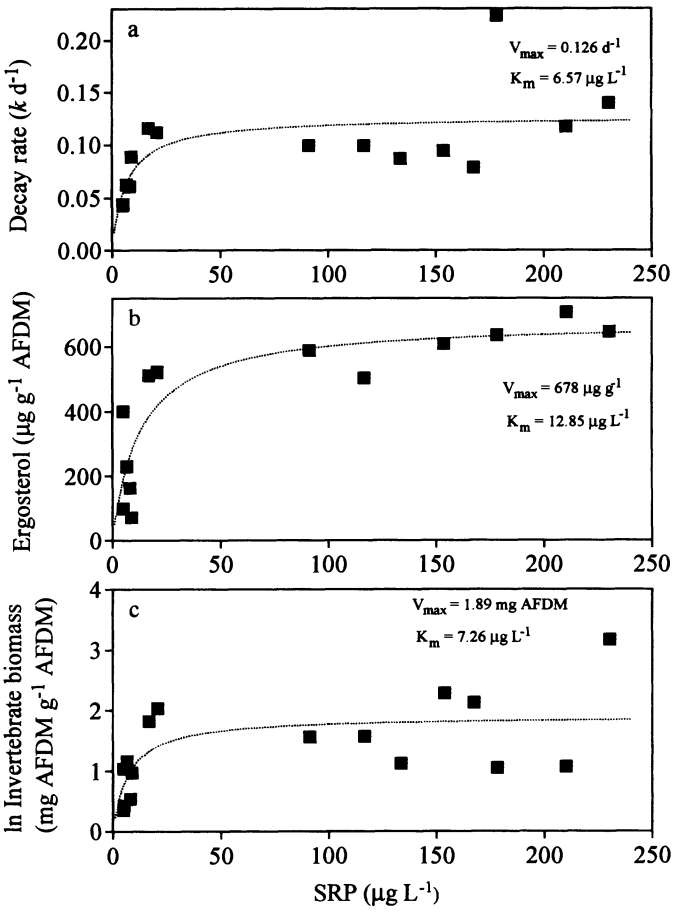

Fig. 2. Relationship between site soluble reactive phosphorus (SRP) concentration and (a) leaf decay rate (k) d^{-1}; (b) fungal biomass (ergosterol) on leaves; and (c) averaged invertebrate biomass. All fitted curves are based on the Michaelis-Menten model ($V = V_{max}([S]/([S] + K_m))$), where in the original application of the model: V is the rate of catalysis of an enzyme; $[S]$ is the substrate concentration; V_{max} is the maximum rate of catalysis; and K_m is the substrate concentration at which the reaction rate is half the maximum value.

to an asymptote. The Michaelis-Menten model of enzyme-substrate kinetics described the relationships between SRP and decay rate (Fig. 2a), fungal biomass (Fig. 2b), and invertebrate biomass (Fig. 2c) fairly well. Half-saturation constants (K_ms) (+1 SE) were similar for each of the variables tested: 6.57 (+3.43) µg L^{-1} SRP for k, 12.85 (±4.72) µg L^{-1} SRP for ergosterol, and 7.26 (+4.37) µg L^{-1} SRP for invertebrate biomass (Fig. 2). Plots of these relationships indicated that saturation of all these processes occurred roughly between 25 and 50 µg L^{-1} SRP (Fig. 2).

The other independent variables we measured were linearly related to the dependent variables and were used in multiple regression analyses. None of the variables entered into models run for invertebrate biomass or fungal biomass over all sites (Table 2). Current velocity was an important explanatory variable for leaf decay rate (as was DIN : SRP) (Table 2). When sites were grouped as low and high P, SRP was the most important explanatory variable over low-P sites for invertebrate biomass and decay rate. SRP did not explain

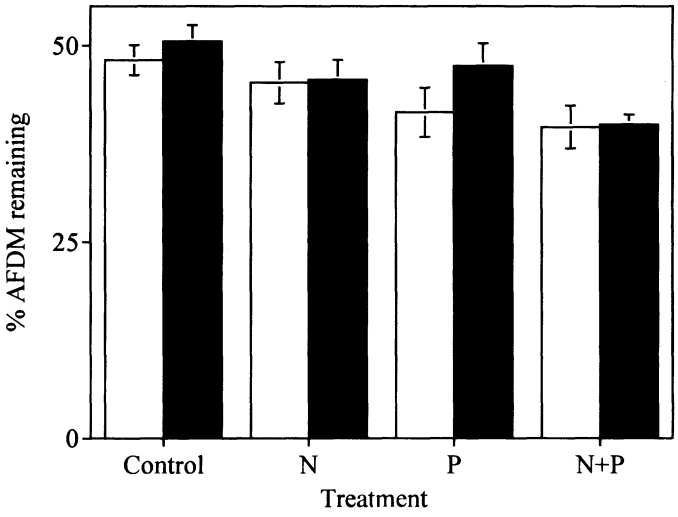

Fig. 3. Percentage ash-free dry mass (AFDM) remaining in treatments from study 3. Treatments consisted of addition of nitrogen (N), phosphorus (P), both N and P, and with (black bars) and without (white bars) added calcium (CA) in a full factorial design (n = 5 replicates). Bars are +1 SE.

significant variation in dependent variables at high-P sites, where there was either a significant relationship with current velocity (decay rate) or no variables (invertebrate biomass, fungal biomass) (Table 2). No independent variables were related to leaf %N, %C, or leaf C : N. The best fit of any of the independent variables to decay, fungal biomass, and invertebrate biomass was with the nonlinear models. Linearization of the Michaelis-Menten models using double-reciprocal plots of SRP concentration and these variables indicated a large amount of variance explained (R^2 = 0.81 for decay rate, R^2 = 0.52 for fungal biomass, and R^2 = 0.78 for invertebrate biomass).

Study 2. P enrichment of a low-P stream—SRP averaged 4 µg L^{-1} upstream and 188 µg L^{-1} downstream during the Piper enrichment (Table 3). The downstream enrichment was maintained consistently, and concentrations were similar in all downstream water samples that encompassed the study area. There were no significant increases in discharge during the experiment.

Mean nitrite + nitrate and ammonium concentrations (+1 SE) during the experiment were typical of other years (NO_2^- + NO_3^- -N = 210 + 3 µg L^{-1}, and NH_4^+-N = 37 + 9 µg L^{-1}, n = 4, samples taken on different dates during the study). We found no significant effect of P addition on decay rate or on density or biomass of invertebrates inhabiting leaf packs (Table 4).

Study 3. Effects of N, P, and Ca on leaf decay—In the laboratory study, N, P, and Ca concentrations were elevated relative to controls (Table 5). Nutrient concentrations in Table 5 represent samples taken from flasks 2 d after nutrients were added or replenished, such that significant uptake by the biota probably occurred. This uptake was greater earlier in the experiment than later. Specifically, only a moderate increase in SRP was observed on day 2 of the study (8

Table 2. Results of stepwise multiple regression analysis from study 1 to determine whether independent variables, mean soluble reactive phosphorus (SRP) concentration, current velocity (CUR), mean nitrate and ammonium concentrations, or dissolved inorganic nitrogen to SRP ratios (DIN : SRP) were related to total invertebrate biomass, decay rate of leaves, or fungal biomass of leaves. SRP was tested as part of a variable set for low P and high P sites but not for all sites (because of nonlinear relationships with dependent variables). F values in parentheses. A plus or minus indicates a positive or negative relationship. Where more than one variable entered the model, R^2 = partial R^2.

Dependent variable	All sites	Low P sites	High P sites
Mean invertebrate biomass	No Variables	(+) SRP† (21.36), R^2 = 0.78	No variables
Leaf decay rate (k)	(+) CUR‡ (29.61), R^2 = 0.68 (−) DIN:SRP* (10.06), R^2 = 0.14	(+) SRP† (33.27), R^2 = 0.85	(+) CUR‡ (71.90), R^2 = 0.92
Fungal biomass	No Variables	(+) CUR† (17.39), R^2 = 0.78	No variables

* $p < 0.01$.
† $p < 0.005$.
‡ $p < 0.0001$.

January), but an increase of ca. 500 μg L^{-1} was observed later (26 January) (Table 5). Concentrations of nitrogen (NH_4^+ and NO_2^- + NO_3^-) in flasks were approximately half of that added to stream water (10 mg L^{-1} total) and were lower earlier in the experiment, indicating greater uptake. Most of the dissolved N was in the form of NH_4^+. Background P concentrations were slightly higher than we would have predicted.

Addition of both N and P accelerated mass loss of leaves. Effects of N and P on mass loss were significant in ANOVA (Table 6), and loss was greatest in treatments with addition of both N and P (Fig. 3). Calcium addition had no effect on leaf mass loss and had positive effects on pH of the incubation stream water (Table 6). Addition of N and P reduced pH of stream water measured at the end of the study (Table 6).

Study 4. P versus invertebrate effects on leaf decay—Phosphorus concentrations in streams in 1996 were similar to concentrations measured in 1994, except SRP was lower in SI-CCC in 1996 than it was in 1994 (Table 7). Mean N concentrations (both nitrite + nitrate and ammonium) were slightly higher in 1996 than in 1994. Ratios of DIN : SRP were slightly higher in 1996 than in 1994 (with the exception of TA-SUR).

Using different mesh sizes to exclude invertebrates was partially, but not totally, successful and resulted in roughly a threefold reduction in invertebrate density in small- versus large-mesh treatments (overall average of mean density from each site: large mesh = 263 g^{-1} AFDM, small mesh = 88 g^{-1} AFDM). Mesh size significantly affected total insect density, with smaller mesh resulting in lower density on all dates (Table 8). Almost all invertebrates in small-mesh treatments consisted of chironomids (which were able to colonize the small-mesh bags), compared to a more diverse assemblage colonizing large-mesh bags. However, small mesh size reduced densities of both chironomids and other taxa (Table 8). Although there was no significant treatment effect on the percentage chironomids by density, they occurred in relatively greater abundance in small mesh and at low P (overall means for all dates of percentage chironomid density: small mesh, low P = 85%; small mesh, high P = 76%; large mesh, low P = 78%; large mesh, high P = 37%). There were some positive effects of P concentration on total insect density (one date only) and on density of nonchironomid taxa (one date only) (Table 8).

Decay rates measured in the 1996 study were slightly lower overall than in 1994, but similar relationships to SRP concentration were observed: decay rates were fastest at high-P sites (Fig. 4, Table 8). Effects of invertebrates on decay rate increased with P concentration as indicated by a significant P × mesh interaction effect in ANOVA (Table 8). The Michaelis-Menten model provided a good fit for both mesh sizes, but a linear model yielded a better fit for large-mesh treatments (R^2 = 0.91 for the linear model). Using constants derived from the Michaelis-Menten model, V_{max} and K_m (+1 SE) were 0.046 d^{-1} and 1.55 (+0.52) μg SRP L^{-1}, respectively, for the small-mesh treatment.

We could account for 88% of the variance in decay rate using P concentration, mesh size, and their interaction (Table 8). The variance partitioning procedure indicated that 71% of the variance in decay rates could be attributed to P effects, 3% could be attributed to mesh effects, and 14% to P × mesh interactions.

Discussion

Evidence for P limitation of detrital processing and detritivore biomass and density—We observed consistent and repeatable relationships indicating phosphorus limitation of leaf decay and microbial and invertebrate colonization over a naturally occurring range in P concentration. In addition, these rates and processes were largely saturated over the

Table 3. Soluble reactive phosphorus concentrations (mean SRP ± 1 SE) in μg L^{-1} from study 2. Means based on n = 4 samples, except ambient samples for which n = 2, unless otherwise noted.

Treatment	11 Apr	13 Apr	15 Apr	17 Apr	19 Apr	21 Apr	24 Apr	28 Apr	1 May
Ambient	5 (5)	0 (n = 1)	5 (5)	4 (4)	4 (3)	5 (n = 1)	3 (n = 1)	2 (n = 1)	6 (n = 1)
Enriched	215 (6)	101 (1)	166 (2)	230 (13)	269 (16)	173 (7)	98 (1.0)	214 (1)	228 (27)

Table 4. Results from study 2. Shown are means (±1 SE) of invertebrate densities (number g^{-1} AFDM) and biomass (mg g^{-1} AFDM) on leaf packs collected on days 5, 8, 12, 16, and 21 of the experiment and mean (±1 SE) of decay rates (k), $n = 4$. In no case were there significant differences between means. +P = P added, C = control, upstream reach.

Day	Treatment	Biomass	Density	Decay rate (all days) d^{-1}
5	+ P	0.36 (0.12)	32.7 (5.6)	0.0531 (0.001)
	C	0.18 (0.02)	21.8 (1.1)	0.0500 (0.004)
8	+ P	3.31 (2.40)	38.1 (3.9)	
	C	0.71 (0.15)	41.8 (2.3)	
12	+ P	1.30 (1.19)	36.1 (2.8)	
	C	0.76 (0.34)	41.1 (12.7)	
16	+ P	1.04 (0.38)	34.3 (6.8)	
	C	0.87 (0.21)	27.1 (8.4)	
21	+ P	0.51 (0.25)	26.9 (10.7)	
	C	0.53 (0.07)	34.2 (7.2)	

range in P concentrations we studied. All aspects of this process, the rate itself, and microbial and invertebrate biomass exhibited a similar relationship with P concentration. Thus, where P concentrations are low (e.g., <10 $\mu g\ L^{-1}$ PO_4^{3-}-P), which is typical of most relatively undisturbed neotropical streams, detrital food web components are likely under bottom-up control and saturate at relatively low concentrations of P. Other studies have similarly shown positive effects of nutrients on detrital processing in streams (Kaushik and Hynes 1971; Howarth and Fisher 1976; Elwood et al. 1981; Meyer and Johnson 1983; Suberkropp and Chauvet 1995; Grattan and Suberkropp 2001). This study and other work we conducted in this system (Rosemond et al. 2001; Ramírez 2001) provide some of the first data to show that nutrients affect detritus-associated microorganisms as well as macroinvertebrate detritivores and detrital processing.

Table 5. Nutrient concentrations from study 3 (note: Ca samples were analyzed on 10 Jan and 22 Jan). Treatment indicates which nutrients were added. SRP = soluble reactive phosphorus measured as PO_4^{3-}-P in filtered water samples. Range in SRP concentrations reflect molar concentrations of 0.68–18.71 μM PO_4^{3-}-P. Range in NO_2^- + NO_3^--N is 0.11–12.8 μM. Range in NH_4^+-N is 1.26–58.1 μM. Range in Ca is 120.2–801.6 μM.

			Mean nutrient concentration		
Date	Treatment	SRP ($\mu g\ L^{-1}$)	NO_2^-+NO_3^--N ($\mu g\ L^{-1}$)	NH_4^+-N ($\mu g\ L^{-1}$)	Ca ($mg\ L^{-1}$)
8 Jan	Control	22	8	90	17
	N	59	906	3,904	17
	P	188	32	136	15
	Ca	42	9	132	20
	N + P	74	891	1,896	20
	N + Ca	49	914	2,580	19
	P + Ca	99	47	158	20
	N + P + Ca	60	891	1,924	19
26 Jan	Control	27	166	158	3
	N	44	898	4,150	3
	P	534	302	506	3
	Ca	30	383	256	12
	N + P	591	891	3,178	3
	N + Ca	24	906	1,106	15
	P + Ca	549	408	150	13
	N + P + Ca	604	906	578	12

Table 6. F values from analysis of variance of weight loss of leaf disks and media water pH taken at the end of study 3. Error degrees of freedom = 32 in each case. Plus indicates greater weight loss or higher pH; minus indicates lower pH.

Factor	df	Weight loss	pH
N	1	(+) 6.02*	(−) 69.15‡
P	1	(+) 9.8†	(−) 16.46†
Ca	1	1.65	(+) 64.95‡
N × P	1	0.05	6.24*
P × Ca	1	0.26	25.68‡
N × Ca	1	1.18	6.51*
N × P × Ca	1	0.27	10.04†

* $p < 0.05$.
† $p < 0.005$.
‡ $p < 0.0001$.

The positive effect of P addition on mass loss of leaves that we observed in the laboratory study supports patterns we observed in cross-site studies implicating P as important in driving differences in decay rate. Temperature was ruled out as a factor in determining differences in decay rate among sites. We measured minimum and maximum temperatures at nine of our 16 sites in 1994 and the six sites used in the 1996 study and found consistently similar temperatures among sites (minimum range: 23–24.5°C, maximum range: 24–28°C, A.D. Rosemond unpubl. data). Several constituents are elevated in geothermally modified groundwater that enters streams (Pringle and Triska 2000) and covary with streamwater P concentrations at La Selva (e.g., Fe, Cl, SO_4, Ca, Na, Mg, and K; Pringle et al. 1990). Although we only tested the effect of one of these (Ca) as part of our laboratory study, we found no effect. Consistent with results from studies 1 and 4, Ramírez (2001) found a positive, asymptotic relationship between respiration rates of leaf packs and SRP across a similar range in sites at La Selva. Ramírez (2001) also found increased respiration of leaf packs due to

Table 7. Mean nutrient concentrations (±1 SE) and DIN:SRP ratios at the six stream sites used in study 4; $n = 7$. Abbreviations and site designations as in Table 1. Range in SRP concentrations reflect molar concentrations of 0.15–6.63 μM PO_4^{3-}-P. Range in NO_2^- + NO_3^--N is 1.54–2.66 μM. Range in NH_4^+-N is 0.20–0.38 μM. DIN:SRP ratios reflect molar ratios of 20.53–0.38.

		Nutrient concentration ($\mu g\ L^{-1}$)		
Site	SRP	NO_2^--N + NO_3^--N	NH_4^+-N	DIN:SRP
PI-STR	5 (±1)	193 (±8)	27 (±2)	98.0
TA-SUR	8 (±4)	132 (±4)	19 (±2)	42.4
BE-STR	6 (±3)	110 (±12)	17 (±2)	49.5
SI-CCC	40 (±5)	128 (±10)	14 (±2)	7.9
SU-SUR	105 (±8)	190 (±10)	18 (±4)	4.4
AR-SUR	214 (±9)	155 (±9)	24 (±11)	1.9

Table 8. Table of F values for analysis of variance of the effects of SRP concentration (P) and mesh size on the total insect, Chironomidae, remaining taxa density, and decay rates in leaf packs on days 4, 13, and 25 of study 4. Plus or minus indicates direction of effect. Negative effects of mesh on invertebrates indicate that densities were reduced by the smaller mesh size. Positive effects of P indicate higher invertebrate density or faster decay rate.

Factor	df	Day 4	Day 13	Day 25	Mean
Total Insects					
R^2		0.62	0.77	0.89	0.88
Mesh	1	(−)7.79*	(−)8.16*	(−)20.94‡	(−)24.33†
P	1	0.56	4.03	(+)7.03*	2.12
P × Mesh	1	0.02	1.19	3.68	0.90
Error	8				
Chironomid density					
R^2		0.60	0.38	0.63	0.69
Mesh	1	(−)7.46*	3.05	(−)9.20*	(−)13.23†
P	1	1.61	0.29	1.46	0.05
P × Mesh	1	0.18	0.03	0.50	0.60
Error	8				
Other taxa density					
R^2		0.52	0.79	0.74	0.76
Mesh	1	4.08	(−)7.37*	3.93	(−)6.26*
P	1	0.26	(+)5.24*	1.57	2.49
P × Mesh	1	0.07	2.50	3.65	0.19
Error	8				
Decay rate					
R^2					0.88
Mesh	1				1.29
P	1				(+)36.85‡
P × Mesh	1				7.25*
Error	8				

* $p < 0.05$.
† $p < 0.01$.
‡ $p < 0.005$.

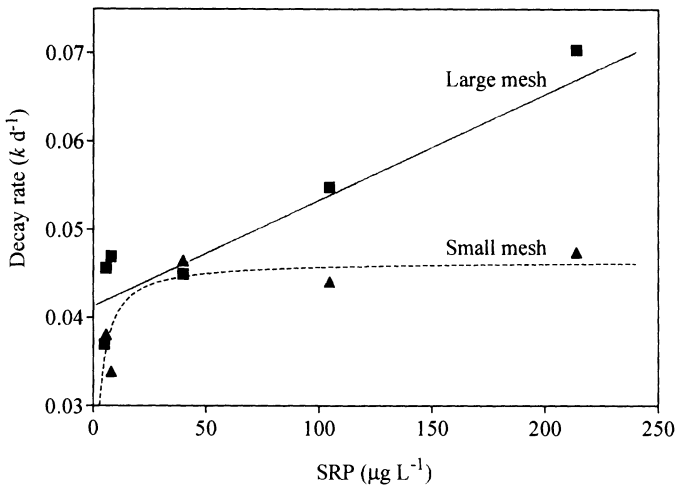

Fig. 4. Relationship between site soluble reactive phosphorus (SRP) concentration and leaf decay rate (k) d^{-1} based on the Michaelis-Menten model (small mesh; triangles) and a linear model (large mesh; squares) from study 4. (for large mesh: $k = 0.0413 + 0.00012$ SRP, $R^2 = 0.91$, $p < 0.005$).

an experimental P enrichment of a low-P stream at La Selva. This is additional evidence implicating P, rather than other constituents in geothermally modified water, in driving differences in decay rate among sites differing in P concentration.

The laboratory study results also showed that N potentially limits decay processes. The extent to which microbial assemblages are colimited by N and P in streams at La Selva is unknown, yet DIN : SRP ratios are relatively high at low-P sites and relatively low at high-P sites (relative to algal-based criteria, Schanz and Juon 1983), suggesting the potential for either P or N limitation at low- and high-P sites, respectively. Addition of N and P in the laboratory experiment also resulted in reductions in pH, suggesting increased respiration. Concentrations of N and P used in the laboratory study far exceeded natural variation in nutrients at La Selva. Thus, the response in mass loss and presumed increase in respiration we observed in the laboratory study indicates that these nutrients were limiting, but is not a good indicator of the concentration that these processes are saturated under field conditions.

Despite positive effects of P in our cross-site and laboratory studies, our experimental P enrichment of the Piper showed no detectable effect on decay rate, nor did a previous 10-d whole-stream enrichment (Rosemond et al. 2001). This may have been due to our inability to detect an effect over short time scales and/or with other variability associated with field conditions. In the laboratory study, which lacked consumers, the effects of N and P addition were significant but were small in magnitude. There was a relatively small increase in AFDM lost because of N or P addition alone (3 and 7% increase in loss, respectively) and a 9% increase in AFDM lost in treatments where they were added together (Fig. 3). We observed a greater P effect in study 1: differences in AFDM lost at 23 d between high and low-P sites were ca. 79% at low-P sites versus 93% at high-P sites (14% difference). The Piper study involved addition of P to a previously low-P stream. The lack of a significant response might be explained in part by a lag in invertebrate response: only a 2% difference in AFDM lost was observed in high-P versus low-P treatments. The way we interpret these results is that nutrients stimulate leaf decay primarily through microbial processes; however, the magnitude of that effect can be small in the absence of detritivores, as evidenced in the laboratory study.

The results of study 4, which tested for the relative effects of microbes and consumers on decay, were largely consistent with this hypothesis. The majority of variance in decay rates among sites was due to P effects alone. However, the significant interaction between mesh treatment and P concentration on decay rate indicated that invertebrates contributed to decay rates more at high-P than at low-P sites. Thus, the lack of an effect of P enrichment of the Piper may have been in part due to a lack of invertebrate response. The hypothesis that N was colimiting in this experiment is unlikely, since N concentrations in the Piper are similar to those at some of the higher P sites (Tables 1 and 7). In addition, results from Ramírez's work, above, suggest that respiration is a more sensitive measure than decay rate of a microbial re-

sponse: he found increased respiration, but not increased leaf decay rates in response to P addition.

The relative contributions of invertebrate feeding versus effects of stream water chemistry on organic matter decomposition in this study were small compared to other studies where their effects have been quantified. For example, Tuchman (1993) found that, in lakes differing in alkalinity, invertebrate shredders accounted for as much as 26% mass loss of leaves, but there was no effect of water chemistry on mass loss. In our study, there was a mean difference of 10.9% mass loss (SE = 1.2%) between mesh treatments among high-P streams and a mean difference of 2.2% (SE = 1.2%) between mesh treatments among low-P streams. These values underscore the relatively greater importance of invertebrates contributing to leaf decay rates at high-P sites. These data also show that invertebrate contribution to leaf decay was lower than in the system studied by Tuchman (1993) and could be extremely low at low-P sites. However, because our invertebrate exclusion was not wholly successful, invertebrate effects on decay have been somewhat underestimated. Generally, our results show that nutrient chemistry (presumably operating via microbial processes) was more important in determining decay rate than invertebrate access and support hypotheses that microbial processes contribute most to leaf decay in tropical streams and that invertebrate processing may be relatively more important with increasing latitude (Irons et al. 1994).

The greater importance of invertebrate contribution to leaf decay at high-P sites could be due to the differential quality of leaves among sites. Leaf-pack dwelling invertebrates feed preferentially on higher quality leaves (Arsuffi and Suberkropp 1984) and consume greater leaf mass with greater microbial colonization (Kaushik and Hynes 1971). Although leaf-pack invertebrate assemblages were dominated by taxa that feed on fine particulate matter rather then larger pieces of leaf material in our study, increased nutrients likely affected fine particulate food resources as well as overall leaf quality. At high-P sites, leaves may have been sufficiently colonized and palatable to attract invertebrate feeding and were less attractive and palatable to invertebrates at low-P sites. Consistent with this hypothesis, we found higher invertebrate density and biomass on leaf packs at high-P sites in both 1994 and 1996. On a whole-stream scale, there may also be greater production of invertebrates supported on higher quality detritus at high-P sites and thus greater consumptive impact. Ramírez (2001) found no differences in total invertebrate biomass and abundance among six sites at La Selva differing in P concentration. However, differences in invertebrate growth rates among sites differing in P concentration (Rosemond et al. 2001) may contribute to differences in invertebrate production.

Landscape patterns in phosphorus effects: at what concentration is P limiting?—As nutrient concentrations become elevated in fresh waters worldwide, it is important to be able to predict their effects on aquatic food webs. Our data suggest that P and N concentrations can limit detrital processing and consumer biomass and lead to predictions that increased nutrient concentrations will change the functioning of detritus-based food webs.

Using Michaelis-Menten models, we were able to calculate half-saturation constants of phosphorus concentrations limiting to components of the detrital food web. These concentrations were roughly similar among different detrital components (2–13 μg L^{-1} SRP) and confidence intervals for estimates of K_m encompassed a similar, relatively low range in concentration (0.5–29 μg L^{-1} SRP). These concentrations do not convey saturation, but examination of plots of relationships with SRP (Fig. 2) suggests that saturation of these variables occurred at <50 μg L^{-1} SRP. Such concentrations are similar to those found to be limiting peak algal biomass in experimental stream channels (28 μg L^{-1} PO_4^{3-}-P; Bothwell 1989), are similar to those associated with maximum algal biomass across a range of 200 stream sites (Dodds et al. 1997), and are in the range of concentrations associated with fundamental changes in food web function in a tundra stream, which primarily occurred through effects on primary producers (Peterson et al. 1985). Thus, these data suggest that autotrophic and heterotrophic processes can be similarly nutrient limited and that limiting concentrations might be in a similar range. These data also illustrate a critical point concerning nutrient effects in low-nutrient aquatic ecosystems: that small increases in nutrient concentration can lead to fundamental changes in ecosystem function.

Geothermally modified waters are a common feature in many volcanic landscapes of Central America (Pringle and Triska 2000). However, different types of geothermal waters vary in pH, temperature, and dominant anions and cations (e.g., Henley 1985) and thus modify receiving surface waters in different ways. Geothermally modified systems can provide insights into how ground and surface water interactions can affect biological function, from benign to dramatic (e.g., hot acidic springs dominated by thermophilic, acid-tolerant algae). The most biologically benign types of geothermal water may be those that have cooled during subsurface transport with solute levels diluted by inputs of meteoric waters, such as the sodium-chloride-bicarbonate type found at La Selva (Pringle et al. 1993). In contrast to most streams in the tropics, which are unaffected by geothermal waters, inputs of geothermal waters (even those with relatively subtle effects) can greatly affect aquatic food webs. For example, previous studies at La Selva have shown that inputs of geothermally modified sodium-chloride-bicarbonate waters are rich in phosphorus and can affect algal biomass, detrital decomposition, and growth of insect consumers in receiving streams (Pringle et al. 1986; Pringle and Triska 1991; Ramírez 2001; Rosemond et al. 2001; this study). The P concentrations over which such changes appear to occur is relatively low (5–<50 μg L^{-1}) and affect multiple components of stream food webs, suggesting that such landscape-scale variation in inputs of solutes can profoundly affect stream ecosystems.

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Received: 23 April 2001
Accepted: 3 October 2001
Amended: 22 October 2001