

A TEST OF TOP-DOWN AND BOTTOM-UP CONTROL IN A DETRITUS-BASED FOOD WEB

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Abstract. In food webs based on primary production, biomass of organisms within trophic levels can be simultaneously controlled by resources (bottom-up) and consumers (top-down). In contrast, very little is known about top-down and bottom-up control in detritus-based food webs. Here, we tested whether exclusion of macroconsumers (fishes and shrimps) and/or phosphorus (P) addition affected insect detritivore biomass and decay rate and quality of leaf detritus in a tropical stream. Four treatments were established in a third-order stream in Costa Rica: (1) macroconsumers present, ambient P; (2) macroconsumers excluded, ambient P; (3) macroconsumers present, P added; (4) macroconsumers excluded, P added. Biomass of insect larvae inhabiting leaf packs and mass loss of leaves were measured after 7 and 10 d in situ. After 10 d, biomass and density of insect larvae increased as a result of both P addition and exclusion of macroconsumers. Chironomids (Diptera, Chironominae) were the dominant detritivores in leaf packs, comprising 51–80% of total invertebrate biomass and were responsible for the observed treatment effects. Mass loss rates of leaf packs were accelerated by the presence of macroconsumers but not by P addition. Positive effects of P on insects presumably occurred through increased microbial carbon relative to leaf carbon. However, percentage nitrogen (N), C:N, and fungal biomass of leaves were not affected by either experimental treatment. Laboratory growth studies corroborated positive effects of P on chironomids: growth rates were higher in high-P treatments (high-P stream water and low-P stream water with P added) vs. low-P stream water. However, no differences in the in situ growth rates were observed between a high- and a low-P stream.

The relative importance of top-down and bottom-up effects was evaluated using several indices. Loss rates of organic matter were affected more by top-down effects of macroconsumers than by bottom-up effects of P. Macroconsumers had negative effects on two trophic levels, contrary to food-web theory predicting alternating negative and positive effects. Positive bottom-up effects of P on insect biomass were greater than negative top-down effects of macroconsumers. In addition, P effects on invertebrates were similar in direction but greater in magnitude than previously published effects of nutrients on consumers in food webs based on primary producers. These results suggest that the impacts of nutrient enrichment on detritivores may be as great or greater than those previously observed on herbivores.

Key words: *bottom-up (resource) control; consumers; detritivores; detritus processing in streams; La Selva, Costa Rica; macroconsumer control in streams; nutrient limitation in streams; phosphorus; stream invertebrates; top-down vs. bottom-up control of stream food web.*

INTRODUCTION

Ecologists have investigated how species and populations are distributed within food webs to understand what factors determine biomass and productivity within a trophic level (Elton 1927, Lindeman 1942, Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981). Today, these studies have contributed to understanding of global patterns in marine, freshwater, and terrestrial production (Carpenter and Kitchell 1988, McNaughton et al. 1989, Granéli et al. 1990). Much of what ecologists have learned about controls on trophic-level biomass has come from assessing grazing-based food webs (Hunter and Price 1992, Power 1992b). Many experi-

mental analyses of resource and consumer control on populations and trophic levels have involved manipulations of dissolved nutrients to assess resource limitation of primary production and/or manipulations of predator biomass to determine effects on prey and possible cascading effects on basal food resources (see references in Persson et al. [1996]). When resources and consumers were manipulated in lake ecosystems, both factors typically impacted the biomass of primary producers and herbivorous consumers (Brett and Goldman 1997). The impact of fish predation or nutrient limitation on trophic-level biomass or production may depend on the proximity to the manipulated trophic level. Nutrient additions to lake mesocosms had the strongest impact on primary-producer biomass, while exclusion of planktivorous fish was the strongest determinant of zooplankton biomass (Brett and Goldman

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1997). Understanding that consumer and resource limitations may simultaneously play an important role and that the intensity and influence by “top-down” and “bottom-up” factors (sensu McQueen et al. 1986, Carpenter et al. 1987) varies with trophic-level position has augmented and revised earlier concepts predicting alternation of controls by consumers and resources within grazing-based food webs (e.g., Hairston et al. 1960, Fretwell 1977).

Very few studies have addressed whether these same processes are important in detritus-based food webs (but see Batzer 1998, Mikola and Setälä 1998a, b), despite the fact that approximately 70–90% of global primary production enters detrital food webs (O’Neill and Reichle 1980, Pomeroy 1991, Wetzel and Ward 1992). Although detritus has long been recognized as an important energy source to consumers (Wiegert and Owen 1971), we presently lack an understanding of resource and consumer control of detritus and detritivores (but see Wallace et al. 1999).

Detritus consists of a nonliving carbon substrate and its associated microflora. The relative importance of microbial and substrate carbon (C) may change depending on ecosystem properties. Pelagic and soil ecosystems are typically dominated by size-structured feeding interactions in which microbivores are the dominant first-order detritivores (Pace and Funke 1991, Mikola and Setälä 1998a). In such systems, transfer of detrital C takes place primarily through consumption of microbes (bacteria and fungi). In contrast, there are typically fewer size-structured feeding interactions in benthic systems and more taxa that directly consume particulate C (Wallace et al. 1997, Batzer 1998). In benthic systems, the fate of particulate C, in addition to microbial C, may assume greater importance in supporting biomass of consumers and in ecosystem functioning than in systems where there are specialized microbivores (Meyer 1994). Thus, it is important to determine the fate of both microbial and substrate C for ecosystems of this type.

Detritus and primary producers may differ in how they respond to food-web manipulations due to differences in their rate of renewal. For many ecosystems the detritus renewal rate is typically controlled from outside the system, whereas the renewal rate of primary producers is controlled within the system (extrinsic vs. intrinsic control, sensu Persson et al. 1996). On a proximal scale, responses of detrital vs. primary-producer standing crops may respond differently to gradients in limiting resources. For example, carbon from primary production may increase across gradients in nutrient concentrations or light levels (Oksanen et al. 1981). However, we hypothesize that total detrital C (substrate C + microbial C) may become depleted across gradients of limiting resources. Specifically, as microbial activity increases (e.g., in response to a limiting nutrient), substrate C is lost as microbial C and respired CO₂. The microbial C component of detritus-based

food webs and primary-producer biomass may respond similarly to gradients in limiting resources (e.g., increase in response to limiting resources), while substrate C may decrease over the same gradients. Models addressing grazing-based food webs that predict how the respective biomass of several different trophic levels should change across gradients in productivity (e.g., Oksanen et al. 1981) may not be useful for detrital-based food webs for this reason. There has previously been little treatment of how food-web manipulations, including impacts of consumers and resources, affect total detrital resources.

There is increasing evidence that organisms in detrital food webs can be resource limited (Wallace et al. 1999). However, predictive models of how limiting resources affect detrital food webs are currently lacking. Resource limitation has been shown via experiments in which the biomass of detritivores changed in response to manipulations of the quantity of particulate (Culp and Davies 1985, Richardson 1991, Wallace et al. 1997, Batzer 1998), or microbial (Mikola and Setälä 1998a) carbon. In systems in which particulate C is utilized, colonization and growth of detritivores can be affected by both the quantity and quality of detritus (Cummins 1974, Lawson et al. 1984). Nutrient addition to streams has resulted in increased detrital quality, measured as increased microbial biomass and activity (Suberkropp and Chauvet 1995), but the influence of nutrient addition on higher trophic levels of the detritus-based food web characteristic of streams has not been addressed. We hypothesize that nutrient enrichment can positively affect detritivore biomass via increases in detrital quality, but at the same time may lead to depletion of substrate C.

While predators may affect prey similarly, regardless of the consumers’ source of food (e.g., grazing vs. detrital based), subsequent effects on basal C resources may differ. On one hand, extrinsically controlled detrital standing stock may be more susceptible to consumption due to a lack of compensation response characteristic of many primary producers (Gaedke et al. 1996). Alternatively, detritivore populations may have weak direct effects on detritus compared to herbivore effects on producers due to the prevalence of omnivory in detrital-based food webs (Polis 1991). Results from previous studies are equivocal. Oberndorfer et al. (1984) showed that predators produced effects that cascaded to food resources in detritus-based streams by reducing abundance of detritivores, resulting in greater availability of detrital C. Studies of soil systems, however, showed that predators reduced microbivore biomass, but had no subsequent effects on soil microbes (Mikola and Setälä 1998b). The strength of trophic cascades (sensu Carpenter and Kitchell 1988) in detrital-based systems has not been well studied and remains an area of great interest to ecologists studying food-web dynamics and organic-matter processing.

In this study, we investigated both top-down and

bottom-up control of detritus and detritivores in a stream food web. We studied effects of macroconsumers (sensu Pringle and Hamazaki 1997) that have been shown to reduce abundance and biomass of lower-order consumers (Pringle and Hamazaki 1997, 1998, Rosemond et al. 1998) and potentially affect decay rates of organic matter (Rosemond et al. 1998). First, we simultaneously tested top-down effects of macroconsumers and bottom-up effects of P addition in situ by experimentally manipulating the presence or absence of macroconsumers (fishes and shrimps) and stream water P concentrations. A second set of experiments was conducted to test the bottom-up effects of P concentration on invertebrate growth rates. In these experiments we measured growth rates of chironomids in stream water that differed in P concentration, both in situ and in the laboratory. We determined the relative importance of top-down and bottom-up control by quantifying the biomass of detritivorous insect larvae and detritus mass loss in response to experimental manipulations and compared our results with similar analyses from grazing-based food webs of aquatic and terrestrial ecosystems.

STUDY SITE

La Selva Biological Station (area: ~1600 ha, 62% in primary forest) is located on the Caribbean slope of Costa Rica in Central America along the southern boundary of Braulio Carrillo National Park (area: >45 000 ha). La Selva receives ~4-m annual precipitation, with peak precipitation occurring in June–July and November–December (Sanford et al. 1994).

Streams at La Selva Biological Station in Costa Rica exhibit a wide range in inorganic phosphorus (P) concentrations (<5 to >250 $\mu\text{g/L}$ soluble reactive phosphorus [SRP]) due to variable inputs of geothermally modified groundwater (Pringle 1991, Pringle and Triska 1991). Groundwater comes into contact with geothermally active areas at high elevations, cools as it travels down slope, and enters lowland streams enriched in various chemical constituents, including P. Some streams at La Selva receive geothermally modified groundwater, while others do not, resulting in spatially variable P concentrations (Pringle et al. 1993b).

Data on water chemistry of streams at La Selva collected over several years indicate that streams are typically consistently either high or low in P (Pringle 1991). This study involved three streams: the Sabalo, the Taconazo (both low P, SRP < 20 $\mu\text{g/L}$) and the Arboleda (high P, SRP > 250 $\mu\text{g/L}$) (Fig. 1). Minimum and maximum water temperatures in these streams are consistently ~22–26 °C during March and April (A. D. Rosemond and C. M. Pringle, unpublished data).

In addition to potential bottom-up limitation of invertebrates resulting from P limitation, omnivorous fishes and shrimps at La Selva exert top-down control on the abundance and biomass of insect larvae (Pringle and Hamazaki 1997, 1998). In many tropical lowland

streams, macrobiota are abundant and diverse. Twenty-six species of fishes from three families (Characidae, Cichlidae, and Poeciliidae) have been recorded from the Sabalo (Burcham 1988), where the majority of this work was conducted. Many of these fishes are omnivorous (Burcham 1988, Bussing 1994), feeding on more than one trophic level. In addition to fish, three species of nocturnally active omnivorous shrimps inhabit the Sabalo: *Macrobrachium diqueti*, *M. faustinum*, and *M. heterochirus* (Pringle and Hamazaki 1998).

Our P \times macroconsumer study was conducted in April 1995, a period of time when precipitation is typically low (80–160 mm/mo; Sanford et al. 1994) in the Sabalo, a third- to fourth-order stream on the eastern boundary of La Selva (Fig. 1). Most of the catchment is composed of tropical wet forest (Hartshorn and Peralta 1988), but actively grazed pasture lies on the eastern side of lower reaches of the Sabalo where we ran our experiment. Riffle substrata were medium-sized cobbles and gravel, while substrata in runs contained finer sediments and accumulations of organic matter. Further description of the site can be found in Pringle and Hamazaki (1997).

The growth studies conducted in March 1996 were either in situ, or in the laboratory with stream water from the Taconazo and Arboleda. The Taconazo and Arboleda are second- and third-order streams, respectively, located in close proximity to each other within the boundaries of La Selva and their watersheds consist largely of primary forest (Fig. 1). The Arboleda receives geothermally modified groundwater inputs that are high in SRP, and the Taconazo has no geothermal input and is low in soluble reactive phosphorus (SRP) (Pringle 1991, C. M. Pringle, unpublished data).

METHODS

P \times macroconsumer study

We experimentally manipulated the presence or absence of macroconsumers (fishes and shrimps) and stream water P concentrations in the Sabalo from 10 April to 20 April 1995 to determine their relative effects on biomass and density of leaf-pack-dwelling invertebrates and rates of detrital decay. We established four treatment combinations to test these effects: (1) macroconsumers present, ambient P (MAC) (ambient conditions); (2) macroconsumers excluded, ambient P (NOMAC), (3) macroconsumers present, P added (MAC+P); (4) macroconsumers excluded, P added (NOMAC+P). Phosphorus was increased from ~15 to >100 $\mu\text{g/L}$ SRP by a continuous addition of dilute phosphoric acid (K_2HPO_4) into the middle of a 40-m run. Water samples were taken every 2–3 d during the experiment both upstream ($n = 2$) and downstream of the enrichment at $n = 4$ “corners” that encompassed the group of experimental treatments. Concentrations of SRP were determined at the field-station laboratory using the as-

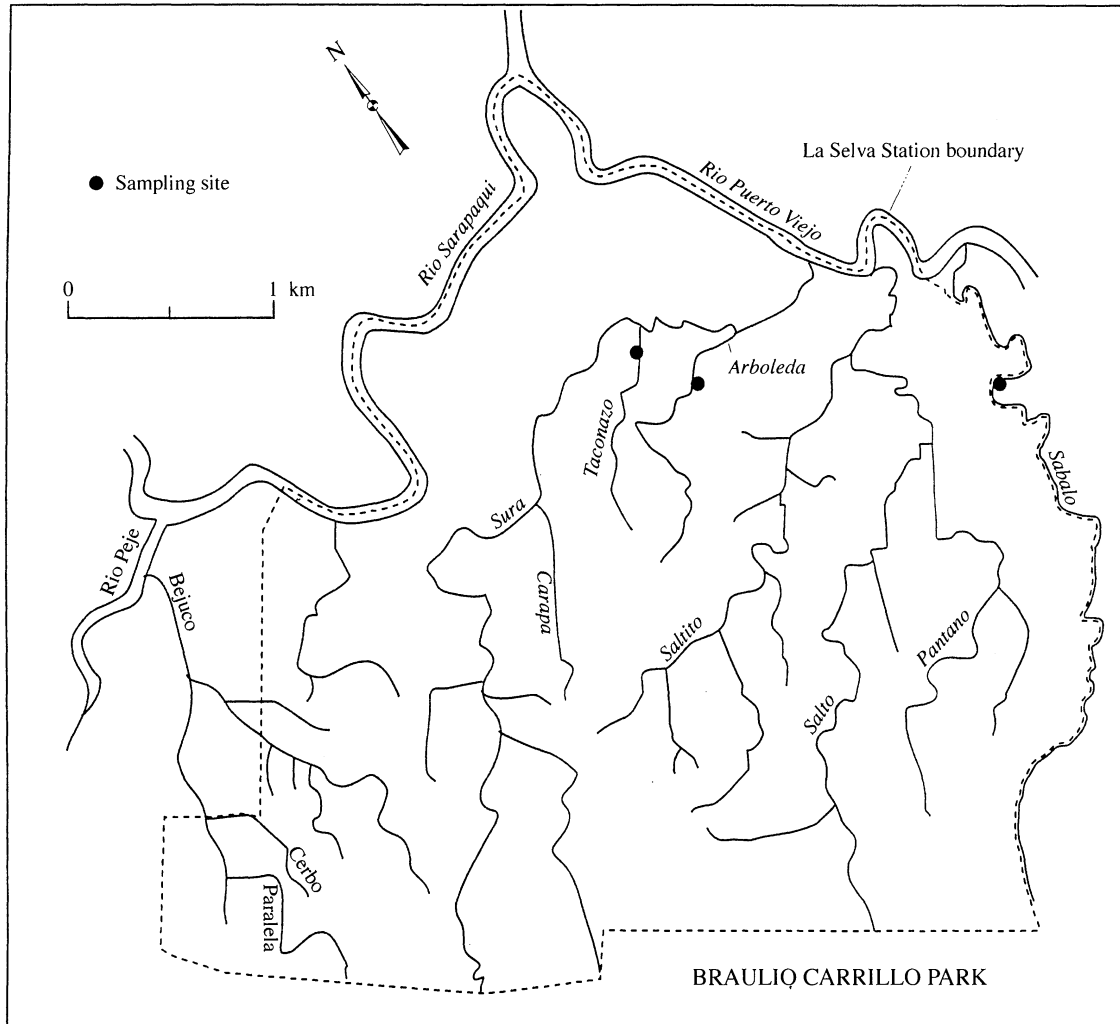


FIG. 1. Map of La Selva Biological Station, Costa Rica, indicating the location of the three streams used in this study: the Sabalo (low P), the Arboleda (high P), and the Taconazo (low P).

corbic-acid molybdenum-blue method (Murphy and Riley 1962). Additional samples were frozen and transported back to the University of Georgia (Athens, Georgia, USA) for analysis of nitrate nitrogen ($\text{NO}_3\text{-N}$) and ammonia nitrogen ($\text{NH}_4\text{-N}$) using an Alpkem RFA 300 Colorimetric analyzer (IRAMA Corporation, Milwaukie, Oregon, USA) (APHA 1992).

Our experimental units consisted of 16 quadrats made of 45×45 cm polyvinyl chloride (PVC) frames fitted with 12-gauge copper wire on 5-cm legs, to raise them slightly above the substratum. Frames were installed either upstream ($n = 8$) or downstream ($n = 8$) of the enrichment. We used an electric field to exclude macroconsumers from half of the experimental units. This technique has been used previously to exclude fishes and shrimps effectively in the Sabalo (Pringle and Hamazaki 1997, 1998) and in other streams (Pringle and Blake 1994, Pringle et al. 1999). Extensive

observations and other experiments in the study stream (e.g., Pringle and Hamazaki 1997, 1998, Rosemond et al. 1998) indicate that insects (< 1 cm) are not excluded by the electric field. From each group of eight quadrats, four were randomly selected and attached to a power source (12-volt solar-powered electric cattle-fence chargers). Access by fishes and shrimps was allowed to the other four control quadrats, which were not attached to a power source. We treated our overall design as a factorial ($P \times$ macroconsumers; $n = 4$ for each treatment combination).

Current velocity and water depth were measured at each corner of each quadrat prior to the experiment (5 April 1995) and any differences between treatment groups were determined by analysis of variance (ANOVA) (SAS 1988). Discharge was measured daily, based on water depth at a permanent staff gauge using a developed rating curve (Gordon et al. 1992).

For all quadrats, we measured insect colonization

and breakdown rates of *Ficus insipida* Willd. (= *glabrata* HBK) leaf packs. *Ficus insipida* is a dominant riparian tree of rivers in Central America including La Selva (Stout 1980, Hartshorn 1983) and is found on the banks of the Sabalo. We collected newly abscised leaves, dried them at $\sim 40^{\circ}\text{C}$ and grouped them into packs of ~ 5 g. At the beginning of the experiment, leaves were re-wetted using stream water, and were "stapled" together using a buttoneer fastener (Dennison Corporation, Farmington, Massachusetts, USA). Leaf packs were individually marked and tethered within each quadrat (2 packs/quadrat) with monofilament line.

Leaf packs were retrieved after 7 and 10 d using a 250- μm mesh net and were refrigerated until processing (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 analysis of fungal biomass (below). A subsample of the leaf disks was dried at 60°C to determine the mean dry mass of leaf disks, and was added back to estimate the total mass of the leaf pack. Leaves were then dried to a constant mass at 60°C and a subsample was ashed at 500°C to determine ash-free dry mass (AFDM). Invertebrates were identified to the lowest possible taxonomic level (typically genus, except dipterans, which were identified to family or subfamily). Biomass was determined by measuring the length of each individual to the nearest 0.5 mm and estimating biomass from published length:mass relationships (Benke et al. 1999) derived from invertebrates of similar morphology, and typically from the same family.

Invertebrate biomass and density were normalized by AFDM of leaf packs. We also calculated the biomass of two subsets of invertebrate taxa: chironomids (all individuals in subfamily Chironominae) and predatory invertebrates (e.g., odonates, predatory trichoptera). We also determined the average individual mass as the ratio of invertebrate biomass to density, to assess whether there were any overall differences in size of invertebrates, and determined the percentage and mean size of chironomids in leaf-pack samples.

We quantified the percentage of N, C:N, and fungal biomass on leaves to determine treatment effects on leaf quality. Percentage N and C:N were determined from dried leaf packs, which were ground, subsampled, and processed using a Carlo Erba NA 1500 CHN combustion analyzer (CE Instruments, Milan, Italy). We estimated fungal biomass on leaves by quantifying ergosterol, a sterol specific to aquatic hyphomycete fungi, using methods previously described in Newell et al. (1988) and Paul and Meyer (1996). Leaf disks were cut from leaf packs as they were processed, placed in scintillation vials with 20 mL reagent-grade methanol and refrigerated (4°C). Ergosterol was extracted in methanol and potassium hydroxide, separated, and measured with high performance liquid chromatography using a LiChrosphere 100 RP-18 10- μm particle

column (Merck and Company, Whitehouse Station, New Jersey, USA). Ergosterol was measured at 280 nm with a Shimadzu chromatograph and an HP3394 integrator.

Two-way analysis of variance (ANOVA) with interaction was used to determine effects of P and macroconsumers on invertebrate biomass, mass loss of organic matter, and leaf quality. To normalize distributions and equalize variance, invertebrate biomass was log-transformed, and percentage mass loss and leaf % N were arcsine square-root transformed prior to analysis. Although our P treatment was pseudo-replicated (sensu Hurlbert 1984), we felt that two-way ANOVA was an appropriate analysis, with conservative interpretation of P effects, as it allowed us to compare relative strengths of top-down and bottom-up control. In addition, our growth studies were conducted to corroborate results of P enrichment.

Analysis of relative top-down, bottom-up control

We used previously published techniques to compare the relative control of top-down and bottom-up forces on losses of organic matter and biomass of invertebrates. Brett and Goldman (1997) determined the relative magnitude of nutrient and fish manipulations in a meta-analysis of top-down and bottom-up effects in lake food webs. To do so, they compared the logarithmic ratio of zooplankton and phytoplankton biomass in controls vs. treatments, in which either consumers or nutrients were manipulated (response = $\log(\text{treatment mean}/\text{control mean})$). To compare our results to those of Brett and Goldman (1997), we determined log-transformed ratios of mean treatment biomass, due to either P addition or macroconsumer manipulation, divided by mean control biomass. Our control was defined as macroconsumers absent, ambient P. Hunter et al. (1997) examined long-term population data of forest lepidopterans and partitioned variance according to tree and year effects in two-way ANOVA. The relative roles of top-down and bottom-up forces were determined by dividing treatment sums of squares by error sums of squares. Overall variance in tree effects was related to variance in budburst phenology, a measure of bottom-up plant quality, and overall variance in year effects was related to estimates of pupal predation to estimate top-down effects. Likewise, we used sums of squares from our two-way ANOVA to determine the relative impact of the top-down and bottom-up forces, and could directly do so in this case (in contrast to relating the ANOVA factors to more direct measures of top-down or bottom-up control) because the variance was associated with measurements of response to experimental manipulations of top-down vs. bottom-up factors (M. D. Hunter, *personal communication*). We also used a top-down index (TDI) to determine the relative importance of top-down and bottom-up control (Rosemond et al. 1993). The TDI is a ratio of treatment mean of a top-down manipulation minus the control

mean to the treatment mean of a bottom-up manipulation minus the control mean. When $TDI = 1$, top-down and bottom-up factors are equivalent, values $>$ or < 1 indicate greater top-down or bottom-up control, respectively.

Growth studies

Growth studies were used to further test the effects of P in affecting detrital food quality, as a mechanism by which higher abundances and biomass of invertebrates might be observed in the field. We tested whether differences in stream water P concentration could result in differences in detritivore growth rates, when the number of detritivores was kept constant. We used chironomids (subfamily: Chironominae), which were the dominant detritivores found in leaf packs in our previous studies at La Selva (Rosemond et al. 1998, A. D. Rosemond, C. M. Pringle, A. Ramírez, M. J. Paul, and J. L. Meyer, *unpublished data*), and in the P \times macroconsumer study described here. Chironomids for the growth experiments were picked from leaf packs found in the Sabalo, briefly chilled, and measured to the nearest 0.1 mm with an ocular micrometer at 8–20 \times magnification using a Zeiss SV11 dissecting microscope (Zeiss, Thornwood, New York) to determine initial size and biomass. Two studies were conducted. In the in situ study, growth rates were measured in both the low P Taconazo (TA) and the high P Arboleda (AR) streams. We selected these streams because they are in close proximity to each other but differ in P concentrations (Pringle 1991). We separated effects of P from other constituents in stream water by including a treatment in which we added P to low-P stream water in the laboratory portion of these studies. The laboratory study was conducted using stream water from (1) the TA, (2) the AR, and (3) the TA, to which additional P was added. The laboratory study was conducted twice in order to increase sample size.

Laboratory growth studies.—For the laboratory studies, stream water was collected on the day experiments were initiated and passed through coarse filter paper to remove large particles. Four liters of stream water were added to each of 6 acid-washed plastic tubs and aerated. Two containers had stream water from AR, two had stream water from TA, and two had stream water from TA to which $\sim 250 \mu\text{g/L}$ P (as potassium phosphate) was added. Chironomids were placed into Toby Teaboy, which are commercially available small plastic baskets lined with 224- μm mesh polyester netting (Aldridge Plastics, Aldridge, UK). We added 90- μm mesh Nitex netting to the inside of the teaboy for the growth experiments. Thirty pre-conditioned and 30 unconditioned *Ficus insipida* leaf disks were placed in the teaboy with the chironomids. Leaves were conditioned by incubating them in the source stream for 5 d prior to the experiment: disks used in the TA+P treatment came from TA. The 30 unconditioned leaf

disks were added to provide unlimited carbon substrate during the study period.

Our replicated unit for measuring growth rates was individual teaboy. In the first laboratory study, which ran 4–8 March 1996, we used five to three chironomids per teaboy, six teaboy per treatment ($n = 18$). We obtained average growth per teaboy in 12 of the 18 teaboy; in others, all individuals were lost to pupation or metamorphosis. Water samples were taken once from each tub for analysis of SRP, $\text{NO}_3\text{-N}$, and $\text{NH}_4\text{-N}$. The second laboratory study was run from 13–16 March using 36 teaboy containing either one or two chironomids. From these, roughly half (those that did not pupate during the study period) could be used in our analysis. Air temperature in the laboratory was kept constant during the studies, resulting in average water temperatures of 22.5°C (range: $21\text{--}23.75^\circ\text{C}$, with no difference between treatments). At the end of the second laboratory study, we placed all leaf disks from the growth studies in methanol for subsequent determination of fungal biomass (see *Methods: P \times macroconsumer study*, above).

We determined instantaneous growth rates (IGRs) using equations described in Huryn and Wallace (1986). Growth rates were negatively correlated to initial length of individuals, as is typically found in studies of organisms over a range in size (Stites and Benke 1989, Huryn 1990). Thus, we used analysis of covariance (ANCOVA) to determine treatment differences in IGR, with initial length used as the covariate (SAS Institute 1988). Data from all surviving individuals from the two laboratory studies were used together in ANCOVA, with the exception of three data points, which were determined as outliers based on residuals and jackknife distances using SYSTAT (Wilkinson et al. 1992). We compared IGR least-squares means (LSM) (i.e., means adjusted for the covariate) of each treatment using a matrix of all P values for the null hypothesis that each pair of LSMs were equal (SAS Institute 1988).

In situ growth studies.—The in situ study was run from 12–15 March 1996 using one or two chironomids per teaboy, 12 teaboy per treatment with *F. insipida* disks that had been pre-conditioned in each stream for 4 d prior to the study. Data from $n = 9$ (TA) and $n = 11$ (AR) teaboy could be used in our final analysis; the rest contained individuals lost to pupation or metamorphosis. Temperatures in the AR and TA were similar during the study period and were similar to those in the laboratory studies (medians of min-max temperatures ranged from 22.2° to 24.0°C in the TA and from 23.5° to 23.7°C in the AR from 13 through 15 March). IGRs were determined and LSMs compared as in the laboratory growth studies above. No data points from the in situ study were removed based on lack of fit.

TABLE 1. Nutrient concentrations and atomic N:P ratios from the 1995 Sabalo P × macroconsumer study.

Nutrient	Date					
	7 Apr	10 Apr	13 Apr	15 Apr	17 Apr	19 Apr
SRP ($\mu\text{g/L}$)						
Ambient	11 (4)	15†	35 (16)	11 (1)	14 (1)	8 (1)
Enriched	124 (88)	216 (176)	151 (11)	117 (39)	84 (23)	142 (43)
NO ₃ -N ($\mu\text{g/L}$)	139 (2)	135 (1)	120 (3)	148 (0)	197 (45)	150 (1)
NH ₄ -N ($\mu\text{g/L}$)	19 (4)	50 (25)	20 (2)	37 (8)	17 (3)	22 (5)
N:P						
Ambient	31	27	9	38	34	45
Enriched	3	2	2	4	6	3

Note: Values are means with 1 SD in parentheses; means are based on $n = 2$ samples, except for the soluble reactive phosphorus (SRP)-enriched samples for which $n = 4$, unless otherwise noted.

† $n = 1$ sample.

RESULTS

P × macroconsumer study

The experiment took place in a relatively shallow run, and mean water depth among treatments ranged from 26 to 48 cm at baseflow while current velocity ranged from 0.13 to 0.30 m/s. There were no consistent differences in depth of experimental units (i.e., quadrats) based on treatment assignments. However, current velocity was higher ($P < 0.01$) in quadrats that were located in the upstream part of the run (low P), relative to downstream (high P). The mean, standard deviation, and range of current velocities, respectively, of the four treatments were: MAC (0.24 m/s, 0.06 m/s, range: 0.15–0.30 m/s), NOMAC (0.24 m/s, 0.05 m/s, range: 0.16–0.28 m/s), MAC+P (0.16 m/s, 0.01 m/s, range: 0.15–0.16 m/s), NOMAC+P (0.17 m/s, 0.05 m/s, range: 0.13–0.24 m/s). Discharge throughout the study period ranged from 0.08 to 0.18 m³/s.

Ambient P concentrations in the Sabalo remained low throughout the study period ($<15 \mu\text{g/L}$), but were slightly elevated on one sampling date (Table 1). P concentration in the enriched stream section was 6–15 fold greater than ambient concentrations. Nitrate (135–197 $\mu\text{g/L}$) and ammonia (19–50 $\mu\text{g/L}$) were at moderate concentrations relative to other streams (Table 1). Except for one date, N:P ratios in the unenriched stream section were >25 , indicating potential P limitation (Schanz and Juon 1983). P enrichment reduced N:P ratios to ≤ 6 .

The electric-exclusion technique was successful at excluding macrobiota. No macroconsumers were observed in exclusion treatments when we quantified fish visitation on 18 April 1995, nor at any other time during the experiment. Over 90% of the fishes moving through control treatments during our observation period were the omnivorous species *Astyanax fasciatus* and *Cichlasoma septemfasciatum* (Burcham 1988, Bussing 1994, C. M. Pringle, unpublished data). In addition, *Alfaro cultratus*, *Neetroplus nematopus*, and lesser numbers of *Poecilia gilli* were observed during the study period. No quantified observations were made of

shrimps, which are nocturnally active; however, we observed several in the study area (typically under rocks).

Biomass of insect larvae inhabiting leaf packs was increased by P addition and macroconsumer exclusion after 10 d (Table 2, Fig. 2). Similar effects were observed on insect density (Table 2). We found no treatment effects on the mean mass of individuals, calculated by dividing biomass by density, using two-way ANOVA with interaction, indicating that changes in total biomass were driven largely by changes in density, rather than changes in size of individuals.

Phosphorus addition and macroconsumer exclusion significantly increased chironomid biomass, but did not alter biomass of other taxa (Table 2). There was no shift in the proportion of chironomids, which comprised 51–80% biomass across treatments, nor were there differences in chironomid size among treatments. The biomass of insect larvae that were classified as predators (Order: Diptera, Tanypodinae, Ceratopogonidae and Order: Odonata) averaged $\sim 10\%$ of samples by biomass and did not differ due to treatment effects (Table 2).

Macroconsumers accelerated the loss rates of leaves after 7 and 10 d (Table 3, Fig. 3). P addition did not significantly affect loss rates of organic matter.

Leaf quality was not affected by P addition or macroconsumer exclusion (Table 4). Estimates of fungal biomass from ergosterol extraction were variable and similar at 7 and 10 d. Percentage N was similar among treatments and did not increase in response to P addition. Ratios of C:N also did not differ significantly among study treatments.

Top-down vs. bottom-up control

We partitioned changes in trophic-level biomass due to top-down and bottom-up factors using the methods of Brett and Goldman (1997). We found that, for reduction in leaf-pack mass, macroconsumer effects were greater than effects of P addition (Table 5). For invertebrate biomass, the reverse was true: P had greater positive effects than the negative effects of macroconsumers on insect biomass. This same result was ob-

TABLE 2. Table of *F* values for ANOVA on the effects of macroconsumers and P on biomass and density of invertebrates inhabiting leaf packs on days 7 and 10 of the experiment.

Source of variation‡	df	All invertebrates				
		Total biomass (mg AFDM)	Total density (mg AFDM/g AFDM leaf litter)	Biomass		
				Chir.	Other	Pred.
Day 7						
MAC	1	0.60	3.14	2.74	0.52	0.60
PHOS	1	3.23	4.99*	89.4*	0.32	0.08
MAC × PHOS	1	0.00	0.00	0.18	0.05	1.22
Error	12					
Day 10						
MAC	1	4.55†	6.71*	8.31*	0.07	0.14
PHOS	1	12.64**	26.41***	13.88**	2.27	1.53
MAC × PHOS	1	0.19	0.72	0.06	0.03	0.32
Error	11					

Note: AFDM = ash-free dry mass; "Chir." includes all chironomids in the subfamily Chironominae, "Other" includes all taxa other than Chir., and "Pred." includes all invertebrates classified as predators.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; † $P = 0.056$.

‡ MAC = macroconsumer treatment, PHOS = P-enrichment treatment.

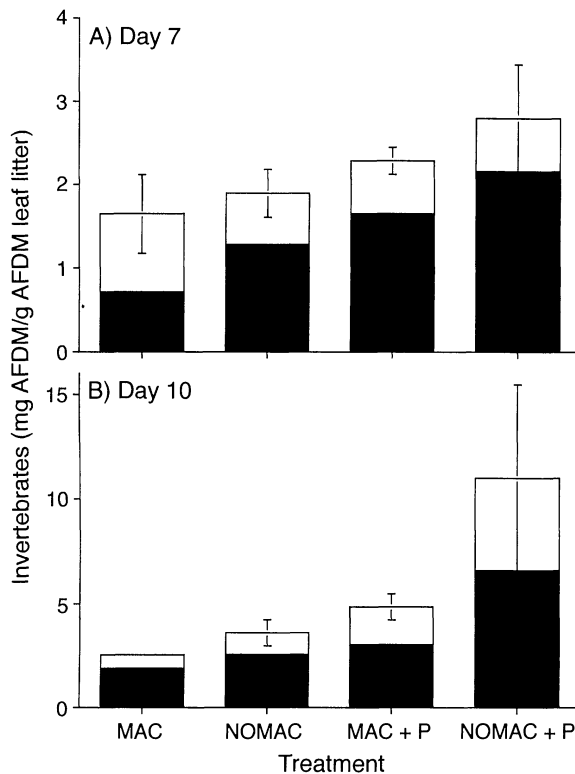


FIG. 2. Invertebrate biomass in ash-free dry mass (AFDM) normalized for AFDM of leaf packs from the four treatments established in the 1995 Sabalo study on (A) day 7 and (B) day 10. Data are means \pm 1 SE; black areas of bars indicate chironomid biomass, and white areas indicate biomass of all other invertebrate taxa. The four treatments were: (1) macroconsumers present, ambient P (MAC); (2) macroconsumers absent, ambient P (NOMAC); (3) macroconsumers present, P added (MAC+P); and (4) macroconsumers excluded, P added (NOMAC+P). Note the different y-axis scales.

served using the partitioning of variance procedure (Hunter et al. 1997): top-down effects were greater than bottom-up effects for organic matter and bottom-up effects were greater than top-down effects for insect biomass (Table 6).

The top-down index (TDI) results were consistent with our other analyses, above. TDI for invertebrate biomass indicated relatively greater bottom-up limitation ($TDI < 1$, $TDI = 0.37$ on day 7 and 0.54 on day 10). In contrast, organic matter was under relatively greater top-down control ($TDI > 1$, $TDI = 1.93$ on day 7 and 2.26 on day 10).

Growth studies

Laboratory growth studies.—In growth experiments, we obtained measurable changes in the size of chironomids after 3–4 d. P concentrations were higher in the AR (Arboleda) and TA (Taconazo) +P treatments than in stream water from TA (Table 7), allowing us to compare growth rates in high-P stream water (AR) to those in low-P stream water (TA). While nitrate and ammonia concentrations were similar among treatments, they were lower in the first laboratory study than in the second laboratory study and in situ. It is unknown why

TABLE 3. Table of *F* values for ANOVA of the effects of macroconsumers and P on percentage mass loss of leaf packs. Abbreviations are as in Table 2.

Source of variation	df	AFDM remaining	
		Day 7	Day 10
MAC	1	27.27***	12.23**
PHOS	1	3.28	0.00
MAC × PHOS	1	0.22	1.31
Error	12 (day 7) 10 (day 10)		

** $P \leq 0.01$; *** $P \leq 0.001$.

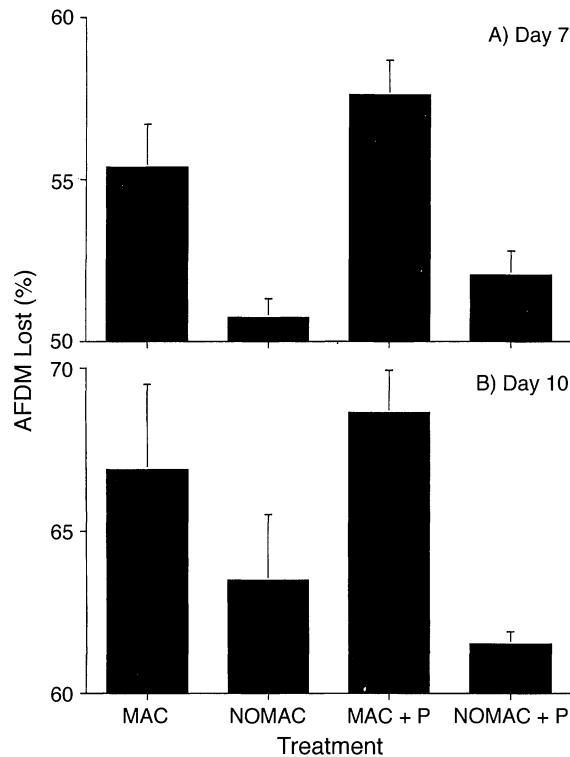


FIG. 3. Percentage ash-free dry mass (AFDM) lost from leaf packs in the 1995 Sabalo study on (A) day 7 and (B) day 10. Data are means and 1 SE; treatments as in Fig. 2.

nitrate concentrations were so low in the TA+P treatment of the first set of laboratory studies.

Instantaneous growth rates (IRG) and the initial length of chironomids were highly correlated within treatments and thus could be compared among treatments in the laboratory study. Lines describing the relationship for each treatment are as follows (where length = length of invertebrates in millimeters): AR, $IGR = -0.1175(\text{length}) + 0.9024$, $R^2 = 0.88$ ($n = 8$ samples); TA+P, $IGR = -0.13719(\text{length}) + 0.97747$, $R^2 = 0.90$ ($n = 10$); TA, $IGR = -0.12937(\text{length}) + 0.85938$, $R^2 = 0.83$ ($n = 11$). ANCOVA of growth rates among the three treatments (AR, TA+P, and TA) indicated a significant treatment effect ($F = 9.17$, $P < 0.001$). Comparison of the least-squares means (LSM) of growth rates from the different treatment combinations indicated that growth rates were significantly higher in the AR and TA+P treatments than the TA treatment (Fig. 4). Ergosterol quantities extracted from leaf disks (mean μg ergosterol ± 1 SE) used in the second laboratory study did not differ among treatments (TA, 22.63 ± 9.47 μg ; TA+P, 16.44 ± 4.84 μg ; AR: 12.77 ± 3.64 μg).

In situ growth studies.—For the in situ studies, P concentrations were very different between streams (Table 7), and nitrate and ammonium concentrations were similar. Growth rates were slightly lower than in

TABLE 4. Macroconsumer and nutrient impacts on different measures of organic-matter quality.

Treatment†	%N	C:N	Ergosterol ($\mu\text{g/g}$ AFDM)
Day 7			
MAC	1.82 (0.04)	19.93 (0.73)	208.74 (152.91)
NOMAC	1.82 (0.08)	20.14 (1.39)	44.52 (13.68)
MAC + P	1.77 (0.04)	19.76 (0.58)	58.19 (35.13)
NOMAC + P	1.86 (0.04)	20.07 (1.07)	25.76 (41.37)
Day 10			
MAC	1.51 (0.14)	24.01 (3.48)	111.84 (37.12)
NOMAC	1.58 (0.16)	22.46 (2.20)	33.45 (20.79)
MAC + P	1.54 (0.08)	22.84 (1.93)	65.58 (78.54)
NOMAC + P	1.67 (0.04)	20.45 (0.98)	59.12 (72.05)

Note: Values are means with 1 sd in parentheses.

† MAC = macroconsumers present, ambient P; NOMAC = macroconsumers absent, ambient P; MAC + P = macroconsumers present, P added; NOMAC + P = macroconsumers absent, P added.

laboratory studies and although there was a predictive equation between length and IGR for AR, there was no such relationship for TA [TA: $IGR = -0.0263(\text{length}) + 0.3544$, $R^2 = 0.05$ ($n = 9$); AR: $IGR = -0.06711(\text{length}) + 0.5397$, $R^2 = 0.62$ ($n = 11$)]. Thus, we did not conduct ANCOVAs based on initial length. In situ growth rates (mean ± 1 SE) derived from the two streams were not different by t test (AR = 0.207 ± 0.038 ; TA = 0.238 ± 0.051).

DISCUSSION

Evidence for top-down, bottom-up control in a detritus-based food web

We found that P influenced the biomass of higher trophic levels in a system where the energy base for trophic interactions was clearly detrital, through a presumed increase in detrital quality. Whereas nutrient enrichment has predictable positive effects in primary-producer-based systems, relatively few studies have previously tested the effects of nutrient addition in heterotrophic systems (see e.g., Pace and Funke 1991). Our P \times macroconsumer study also showed that detritivores and detrital processing were simultaneously controlled from the top down by macroconsumers.

TABLE 5. Comparison of log-transformed ratios of treatment means divided by control means for both macroconsumer (MAC) and P (PHOS) manipulations.

Factor	Organic-matter mass		Invertebrate biomass	
	Day 7	Day 10	Day 7	Day 10
MAC effect	-0.0400	-0.0428	-0.0583	-0.2246
PHOS effect	-0.0167	+0.0266	+0.1716	+0.4843

Notes: This analysis was done for invertebrate biomass as well as means of leaf-pack mass. The greater the number, the greater the increase (+) or decrease (-) in biomass that occurred in response to the experimental manipulation (P addition in the absence of macroconsumers, macroconsumers present vs. absent).

TABLE 6. Percentage of variation in biomass explained by macroconsumers (MAC) or P (PHOS) based on sums of squares in the ANOVA.

Factor	Organic matter mass				Invertebrate biomass			
	Day 7		Day 10		Day 7		Day 10	
	%	ss	%	ss	%	ss	%	ss
Total		0.0164		0.0230		1.2322		4.2666
MAC effect	64.0	0.0105	51.7	0.0119	3.8	0.0481	16.0	0.6839
PHOS effect	7.3	0.0012	~0		20.4	0.2572	44.5	1.900
Error	28.0	0.0046	42.6	0.0098	75.8	0.9566	38.8	1.6537

Thus, processes operating in these detritus-based food webs are similar to those that have been observed in primary-producer-based systems (e.g., Hunter and Price 1992, Power 1992b, Rosemond et al. 1993).

The mechanisms by which bottom-up and top-down factors affected biomass of detrital carbon and detritivores requires consideration of different parts of the system. We hypothesized that nutrient (in this case, P) addition would result in increased microbial vs. substrate carbon. Specifically, we predicted that P addition would stimulate production of microbial C, resulting in a reduction in leaf (substrate) C. Our results provide weak support for this aspect of a conceptual model representing the dynamics of this detrital-based food web (Fig. 5). Measurements of leaf quality in the P × macroconsumer study did not change as a result of P enrichment. Fungal biomass on leaf disks used in the growth studies also showed no relationship with P concentration. The lack of a measurable microbial response in this study may have been due to the response variable measured (microbial biomass vs. activity). In our study we did not control for consumption of leaf microflora,

and thus did not test directly all aspects of microbial response to P addition. Consumption of increased microbial production by microheterotrophs (e.g., ciliates, flagellates) or insect larvae could have maintained low microbial biomass in all treatments, regardless of nutrient addition (Newell and Bärlocher 1993). Alternatively, stimulation of invertebrate growth and biomass may have also occurred primarily through a bacterial response, not addressed by ergosterol analysis, and this response may have been too small to detect as measurable changes in percentage N. Inadequate methodologies may also have contributed to our inability to determine changes in leaf quality due to changes in P concentration. For example, samples for fungal biomass analysis were stored for ~3 yr prior to analysis. The effects of such extended storage on ergosterol have yet to be assessed, but may have influenced results. In addition, microbes other than ergosterol-containing hyphomycete fungi (e.g., oomycetes) may have responded to P addition and would not have been detected by our methods. In contrast, previous work has shown that nutrient (N and P) addition stimulated fungal biomass and activity on leaves in streams (Suberkropp and Chauvet 1995) and increased bacterial numbers and activity, and flagellate abundance in lake water (Pace

TABLE 7. Nutrient concentrations from the 1996 growth studies.

Date	Treatment†	Nutrient concentration (µg/L)‡		
		SRP	NO ₃ -N	NH ₄ -H
Laboratory growth studies§				
5 March	AR	187 (19)	31 (16)	23 (1)
	TA	5 (2)	91 (6)	12 (4)
	TA + P	212 (1)	1 (1)	9 (1)
13 March	AR	232 (3)	173 (2)	71 (11)
	TA	8 (1)	136 (1)	34 (3)
	TA + P	125 (113)	129 (2)	44 (8)
16 March	AR	177 (7)	117 (10)	125 (21)
	TA	8 (1)	98 (4)	56 (15)
	TA + P	181 (3)	61 (2)	65 (4)
In situ growth studies				
11 March	AR	232	141	81
	TA	6	132	16
17 March	AR	246	127	30
	TA	10	110	19

† AR = Arboleda; TA = Taconazo + P = nutrient enrichment.

‡ SRP = soluble reactive phosphorus. Data are means with 1 SD in parentheses.

§ Means are based on $n = 2$ samples (one from each tub).

|| Single samples were taken from each stream.

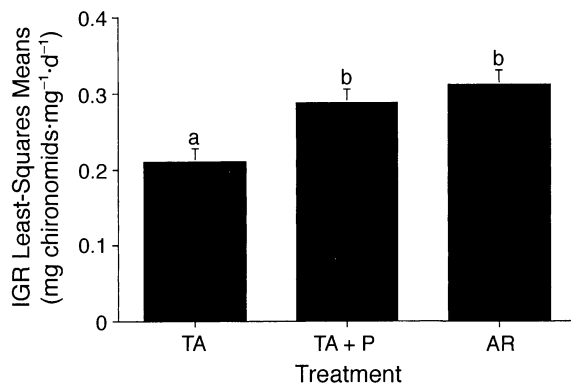


FIG. 4. Least-squares means of instantaneous growth rates (IGRs) of chironomids grown in three different media in the laboratory: (1) stream water from the Arboleda (AR), which is high in P; (2) stream water from the Taconazo, which is low in P, to which P was added (TA+P); and (3) stream water from the Taconazo (TA). Data are means and 1 SE. Treatments bars with different lowercase letters are significantly different at $P < 0.05$.

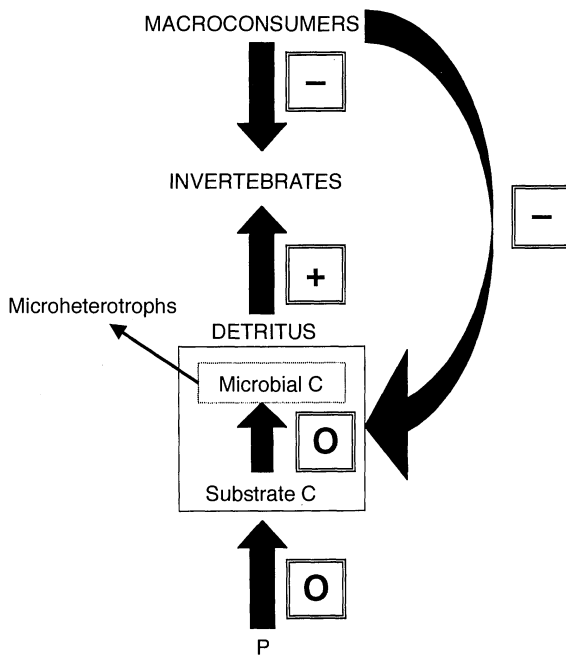


FIG. 5. Hypothesized pathways by which P addition and the presence of macroconsumers affect the detrital stream food web studied here. Phosphorus (P) addition was predicted to stimulate conversion of substrate C to microbial C. Arrows pointing up indicate bottom-up effects, and arrows pointing down indicate top-down effects. Symbols in boxes beside the arrow lines indicate the direction of the effect, if tested (+, positive effect; -, negative effect; 0, no detectable effect); no symbol indicates that the pathway was not tested as part of this study.

and Funke 1991). Other work has shown that nutrient enrichment stimulated decay rates of organic matter, as a presumed or demonstrated result of increased microbial biomass or activity (*sensu* Howarth and Fisher 1976, Meyer and Johnson 1983, Grattan and Suberkropp 2001). However, because we did not observe positive effects of P addition on leaf quality and organic-matter loss rates, we lack evidence for a microbial mechanism to explain increased growth rates and biomass of invertebrates.

Despite a lack of evidence to support a microbial mechanism, we did observe positive effects of P addition on detritivore biomass in our factorial experiment (Fig. 5) and also observed increased growth of invertebrates in the laboratory related to P concentration. Since invertebrate biomass was greater in the high P treatment of the P \times macroconsumer study, but was not accompanied by increased loss rates of leaf C, we hypothesize that organisms may have been feeding on fine particulate organic matter (FPOM) trapped in the leaf packs. This external source of C may have been of higher quality in P-enriched sections of the stream, supporting higher invertebrate biomass. This food resource would have been readily utilized by collector gatherers, the dominant functional feeding group found

in leaf packs. Increased invertebrate biomass in the factorial experiment occurred as a result of increased biomass of chironomids. Chironomids have some of the fastest growth rates and shortest life histories among aquatic insect larvae (Wallace and Anderson 1996) and thus may have been able to respond quickly to changes in food quality. The positive response of chironomids may have also been due to their colonization ability. Chironomids are an "early colonizing" species and may have been able to colonize high-P or macroconsumer-exclusion treatments faster than other taxa. Our data indicate that increased biomass was due to increased numbers of invertebrates, rather than increased invertebrate size. This supports the hypothesis that the increased biomass observed in the P \times macroconsumer study was due to increased colonization and was driven by the response of chironomids.

Differences in current velocity between upstream and downstream reaches may have affected loss rates of leaves, deposition of FPOM in leaf packs, and/or colonization rates of invertebrates. Current velocity, which may contribute to decay of organic matter in streams (D'Angelo and Webster 1992), was significantly higher in the upstream part of our study reach in the P \times macroconsumer study. Thus, leaf decay would be predicted to be higher in the upstream part of the stream compared to downstream and this influence would have been the reverse of the predicted effects of P (where enrichment should have accelerated loss rates in leaf packs in the downstream section). However, we found faster decay in treatments with macroconsumers present, regardless of upstream or downstream location. Current velocity may also have caused differences in the deposition of FPOM or invertebrate colonization if differences in current velocity between treatments were of sufficient magnitude. However, exclusion of macroconsumers and P addition both had effects on invertebrate biomass that were largely additive. It would have been difficult to observe this pattern if there had been an overriding factor such as current velocity that was driving differences in invertebrate colonization based on position in the stream.

The results of our laboratory growth studies showed that growth rates of chironomids, which were the dominant invertebrates in our leaf packs, can also be stimulated by increased P concentration. This provides indirect support for our field observations of higher density and biomass in leaf packs. Under food-limited conditions in the field it is unlikely that the number of animals remains constant and individuals grow larger, as we observed in the growth experiments, but rather that more animals would colonize areas of higher food quality (e.g., Hart 1981), as we observed in the whole-stream enrichment. The growth rates of chironomids that we observed were much higher than those reported for temperate streams (Huryn and Wallace 1986) and higher than would be predicted by temperate-stream models based on chironomid size and stream temper-

ature (Huryn and Wallace 1986), but were roughly similar to values obtained from a blackwater, subtropical river for chironomids of similar length and mass (Hauer and Benke 1991). It is noteworthy that such high rates of chironomid growth (e.g., $\sim 0.4 \text{ mg} \cdot \text{mg}^{-1} \cdot \text{d}^{-1}$ for chironomids $\sim 4 \text{ mm}$ in length) were obtained on a food supply that consisted solely of terrestrial leaf material and associated microbes. Such high growth rates, combined with quantitative biomass measurements, have been used to estimate extremely high production of chironomids in blackwater rivers (Benke 1998). Benke's (1998) findings emphasize the potential importance of primary consumers such as chironomids, which have rapid growth rates and turnover of biomass, on the food-web dynamics of rivers. The increase in growth rates of chironomids we observed with increased P concentration suggests that variation in P among streams at La Selva likely affects production of these consumers.

Positive effects of P on chironomid growth rates were observed in laboratory studies, but not in situ. In both studies, leaf disks came from leaves that had been conditioned in situ. In the laboratory studies, surfaces of leaf disks appeared to stay relatively "clean" (free from sedimentation), but silt accumulated in the chironomid enclosures in situ, which may have resulted in a lower quality food resource. The fact that growth rates were lower and more variable in situ than in the laboratory is consistent with this hypothesis. It should be noted that the quantity of deposited particles in chironomid growth enclosures used in situ was much greater and apparently different in quality than FPOM accumulation in leaf packs in the P \times macroconsumer study (A. D. Rosemond, *personal observation*).

Macroconsumers affected the biomass of both consumers and basal carbon resources (Fig. 5). These results contrast with theoretical predictions that top-down effects alternate between trophic levels (Hairston et al. 1960, Power 1990a, Brett and Goldman 1997), but are consistent with findings from other tropical rivers. Various studies of tropical streams have shown that macroconsumers affect many components of river food webs. Their consumption can control the mass or abundance of periphyton, inorganic and organic sediments, aquatic insect larvae, and coarse particulate organic matter (Power 1990b, Winemiller 1990, Flecker 1992, Wootton and Oemke 1992, Pringle et al. 1993a, 1999, Pringle and Blake 1994, Flecker 1996, Pringle 1996, Pringle and Hamazaki 1997, 1998, Rosemond et al. 1998). In most of these studies, macroconsumers reduced invertebrate abundance or biomass as well as basal resources (both algal and detrital) through feeding or physical disruption, which could not be distinguished in this study. Thus, the fate of detrital C affected by macroconsumers is unknown. Macroconsumer effects on two trophic levels contrast with findings from many temperate systems that show effects of macroconsumers on single trophic levels or food types

(e.g., Carpenter et al. 1987, Osenberg and Mittelbach 1990, Power 1990a, Brönmark et al. 1992). The effects we observed may be due in part to omnivory, feeding on both of these resources, and thus preclude predictions that their effects should alternate between trophic levels (Strong 1992). Omnivory may also be generally common in detrital food webs: detritus is a relatively poor-quality food resource and many organisms that feed on detritus may also feed on other trophic levels (Polis 1991). Thus, our observations of similar effects of macroconsumers on contiguous trophic levels may apply to other systems in which top consumers are omnivorous (see Diehl 1993, 1995).

Relative effects of top-down and bottom-up factors

Top-down effects of macroconsumers on organic matter were relatively greater than the bottom-up effects of P. Here, the overriding negative effects of macroconsumers on organic-matter loss rates outweighed any potential positive cascading effect they may have had via consumption of smaller detritivores such as insect larvae and subsequent effects on leaf C. Top-down effects may be particularly pronounced in detritus-based food webs because detrital biomass is more susceptible to top-down control than biomass of primary producers. Intrinsically controlled renewal rates of primary production can swamp consumptive effects in some cases (e.g., Power 1992a), in contrast to extrinsically controlled rates of renewal of detritus, which are not linked to consumptive effects. In this study, top-down effects were driven by large omnivores. First-order detritivores apparently did not affect loss rates of leaves, as mass loss was greater in treatments with reduced biomass of detritivores (MAC [macroconsumers present] vs. NOMAC treatments). The relative importance of top-down and bottom-up factors in this system can also be scale dependent. Feeding effects by macroconsumers can be immediate, but increased leaf decay due to nutrient enrichment is a process that occurs over a longer period of time. Additional studies we have conducted in La Selva streams indicate a positive correlation between stream water P and decay rate of leaves (A. D. Rosemond, C. M. Pringle, A. Ramírez, M. J. Paul, and J. L. Meyer, *unpublished manuscript*). We suspect that a longer period of time was needed in this study to see a significant bottom-up effect of P on leaf C loss.

Our results illustrated relatively greater bottom-up than top-down effects on invertebrate biomass in leaf packs. This finding contrasts with food-web theory indicating that top-down control is more important higher in the food web and bottom-up control is more important lower in the food web (McQueen et al. 1986, Brett and Goldman 1997). For example, macrobiota (fish) effects were greater (approximately -0.50) than nutrient effects (approximately $+0.10$) on zooplankton in Brett and Goldman's (1997) study, compared to our study where effects of macroconsumers (-0.22) were

less than effects of P addition (+0.48) on invertebrates. Also, in our study the overall impact of P addition on insect biomass was greater than the impact of nutrient addition on zooplankton in studies summarized by Brett and Goldman (1997). The magnitude of the strength of bottom-up forces also exceeded that observed by Hunter et al. (1997) for forest Lepidoptera. Although our study was of much shorter duration than that of Hunter et al., and involved experimental manipulation of top-down and bottom-up factors, the range of P concentrations we used was within the range of natural variation observed among streams at La Selva and adjacent regions in lowland Costa Rica. While variation in P concentration accounted for up to 44.5% of variation in invertebrate biomass in our study, bottom-up forces explained only 17.2% and 35.1% of variance in population of two species of terrestrial insect herbivores (*Operophtera brumata* (Lepidoptera: Geometridae) and *Tortrix Viridara* (Lepidoptera: Tortricidae), respectively; Hunter et al. 1997).

Our results have important implications for the study of food webs. Top-down effects were consistent with other studies showing that large omnivorous consumers obviate cascading effects in food webs (Diehl 1993, Pringle and Hamazaki 1998). Our results also suggest that bottom-up limitation of consumers can be of greater importance in detrital vs. primary-producer-based food webs. Thus, nutrient availability may be a critical factor influencing the flow of C into detritivores in detrital systems. In this way, nutrients may be more important and effective in facilitating energy flow in detrital food webs than from primary producers to herbivores in grazing-based systems. Many of the obvious effects of anthropogenic nutrient enrichment involve algal blooms (Carpenter et al. 1998); however, there may also be important effects of nutrient enrichment on detritivore pathways. A true understanding of ecosystem-level effects of nutrient enrichment will require determination of the conditions under which nutrients affect detritivores, and the relative effects of nutrients on detritivores and herbivores. Additional studies of the actual and comparative effects of nutrients on a variety of basal C sources will increase our ability to predict how increased nutrient concentrations will affect food-web structure and ecosystem function in both autotrophic and heterotrophic systems.

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