

**EFFECTOS DE LA FERTILIZACIÓN SOBRE LOS HERBÍVOROS. UNA  
RESPUESTA A LA EUTROFICACIÓN EN UN ARROYO ALTO ANDINO**  
**Fertilization effects on grazers. A response to eutrophication in a high  
Andean stream**

**SILVIA JULIANA MORALES DUARTE**

**UNIVERSIDAD INDUSTRIAL DE SANTANDER  
ESCUELA DE BIOLOGÍA  
BUCARAMANGA**

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**SILVIA JULIANA MORALES DUARTE**

**Trabajo de grado presentado como requisito para optar al título de Bióloga**

**Director**

**JOHN CHARLES DONATO RONDÓN**  
**Dr. en Ciencias Biológicas (Área Ecología)**

**Codirector**

**MARÍA ISABEL CASTRO REBOLLEDO**  
**M.Sc. en Ecología**

**UNIVERSIDAD INDUSTRIAL DE SANTANDER**  
**ESCUELA DE BIOLOGÍA**  
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**Título:** EFECTOS DE LA FERTILIZACIÓN SOBRE LOS HERBÍVOROS. UNA RESPUESTA A LA EUTROFICACIÓN EN UN ARROYO ALTO ANDINO \*

**Autor:** Silvia Juliana Morales-Duarte \*\*

**Palabras clave:** Productividad primaria, biomasa, Andes colombianos, *Tricorythodes* sp., cámaras, enriquecimiento de nutrientes.

Los cambios imprevistos en la disponibilidad de nutrientes son considerados como perturbaciones que modifican las relaciones e interacciones en los sistemas fluviales. Durante los últimos años, tanto el control "Bottom – up", como el "Top – down" son considerados como aspectos funcionales que explican los efectos a través de la cadena trófica en diversos ecosistemas. Mediante la fertilización controlada en un arroyo de alta montaña tropical, se midió la respuesta del suministro de nutrientes sobre la producción primaria y su conexión con la herbivoría, cuantificando la respuesta de *Tricorythodes* sp. La biomasa de los herbívoros aumentó a través de los días del experimento y se comprobaron los efectos sobre la producción primaria. Las concentraciones de clorofila *a* béntica ( $n= 24$ ,  $F= 242.543$ ,  $p<0.0001$ ) como la clorofila *a* liberada del perifiton ( $n= 24$ ,  $F= 52.525$ ,  $p<0.0001$ ) fueron más altas debido al suministro de nutrientes presentando diferencias significativas entre el control e impacto. Estas observaciones indican una regulación simultánea tanto "bottom-up" como "top-down" de la biomasa algal. Se demostró la importancia de llevar a cabo estudios *in situ*, debido a que los niveles de luz y nutrientes son los principales factores limitantes del aumento de la biomasa en los productores primarios, debido a que diferentes variables ambientales pueden influenciar la respuesta de los organismos, como en el presente experimento, donde la luz (factor covariable) genera efectos significativos ( $n= 6$ ,  $F= 4.840$ ,  $p= 0.044$ ) ( $n= 6$ ,  $F= 12.255$ ,  $p= 0.003$ ) en el incremento de la productividad primaria y la biomasa final de *Tricorythodes* sp.

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\* Proyecto de grado

\*\* Facultad de ciencias. Escuela de biología. Director: Dr. John Charles Donato Rondón  
Codirector: María Isabel Castro Rebolledo M. Sc.

## ABSTRACT

**Title:** FERTILIZATION EFFECTS ON GRAZERS. A RESPONSE TO EUTROPHICATION IN A HIGH ANDEAN STREAM\*

**Autor:** Silvia Juliana Morales-Duarte\*\*

**Key Words:** Primary Productivity, biomass, Colombian Andes, *Tricorythodes* sp., chambers, nutrient enrichment.

Unexpected changes in the availability of nutrients inputs can be considered disturbances that modify biological relationships and interactions in river systems. Both "Bottom – up" and "Top – down" explanations consider functional aspects that explain the effects through the food web. Using controlled fertilization in a tropical mountain stream the effect of nutrient supply on primary productivity and its grazing connection was determined. The response of the mayfly *Tricorythodes* sp. was analysed. This grazer's biomass increased throughout the experiment and affected the primary production. The chlorophyll *a* in benthic concentrations ( $n= 24$ ,  $F= 242.543$ ,  $p<0.0001$ ) as in detached periphyton chlorophyll *a* ( $n= 24$ ,  $F= 52.525$ ,  $p<0.0001$ ) were higher because the nutrient supply showed significant differences between the control and the impact. These observations indicate a simultaneous "bottom-up" and "top-down" regulation of the algal biomass. It is important to stand out the ecological relevance of carrying out *in situ* studies. The light and the nutrients levels are the main restrictive factors of biomass growth in primary producers, because different environmental variables can influence organisms response, as in the present experiment, where the light is a covariate factor that generates significant effects ( $n= 6$ ,  $F= 4.840$ ,  $p= 0.044$ ) ( $n= 6$ ,  $F= 12.255$ ,  $p= 0.003$ ) in the increase of the primary productivity and the final biomass of *Tricorythodes* sp.

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## 1. INTRODUCTION

Disturbances in fluvial ecosystems have two sequential events: the application of a force that modifies the physical environment and the response of the biota to the damage made by the disturbance (Lake, 2000; Thomson et al., 2002). These events are common in nature, are responsible for system stage change and are a good tool to understand how the community works (Gafner & Robinson, 2007).

Modification of nutrient availability can be considered as a disturbance, and constitutes one of the main factors that regulate the structure of the communities in the fluvial ecosystems ("Bottom-up" effect) (Biggs & Smith, 2002). During the 70's, it was assumed that biomass and productivity of a certain trophic level were defined by the predation and the grazing at higher levels ("Top-down" effect), although they could be conditioned by other variables, such as the hydrology of the river (Stevenson, 1996; Zapata & Donato, 2005). In recent years, both "Bottom-up" or "Top-down" control of algal communities have been considered important to structure of the trophic chain (McQueen *et al.*, 1986; Hillebrand & Kahlert, 2001; Hillebrand et al., 2002). The predominant control over the distribution and abundance of algae in rivers is given from superior trophic levels (herbivores) to inferior trophic levels (Biofilm, benthic algae); however, this control depends of different concitions (time, place and the environmental ones) (Rosemond et al., 1993; Allan & Castillo, 2008). Diverse experiments established that grazing can significantly affect the structure and dynamics of communities (Lamberti & Resh, 1983; Lamberti & Moore, 1984; Hart, 1987; Hill & Knight, 1987; Liess & Hillebrand, 2004; Peters et al., 2007).

Manipulative experiments carried out on the interaction between herbivorous insects and periphyton in rivers have been limited mainly to the caddisflies (Lamberti & Resh, 1983; McAuliffe, 1984), although Hill & Knight (1987) carried out a study on the interaction between *Ameletus validus* and periphyton in a small

north California stream; all reported a reduction and substantial alteration of periphyton growth, primary production and community structure. Other experiments reported the exclusion of herbivorous insects from periphyton (Lamberti & Moore, 1984; Murphy, 1984; Hart, 1985; Hill & Knight, 1987), and more recent studies have emphasized the effects of both nutrients and herbivores (Hillebrand & Kahlert, 2001; Hillebrand et al., 2002).

The particular response of the biodiversity and structure of communities to nutrient enrichment is largely unknown in tropical rivers in particular in the Andean region. Original forests are fragmented and less than 30% of their original extension remains (Armenteras et al., 2003). On the other hand, the fluvial systems especially those associated to the Andean region, have places with greater population density and they register eutrophication, a rising contamination and are influenced by seasonal flow variations (Donato & Galvis, 2008).

In temperate areas, there are studies that analyze organic matter processing, distribution and energy assimilation of these organisms (McCullough et al., 1979; Kirk & Perry, 1994). In tropical areas most studies of the genus emphasize its taxonomy (Dominguez, et al., 2006; Emmerich, 2007), ecology and bioindication (Roldán, 2003; Liévano & Ospina, 2007). *Tricorythodes* sp. (Ephemeroptera: Leptohiphidae) of the Tota's stream has not been described, despite the dominance of this genus in the system.

Using the effects of the controlled fertilization the main objective of present article is to determine the relationship between the nutrient supply, the primary production and its connection with grazing by *Tricorythodes* sp. nymphs.

## 2. METHODS

### 2.1 Study Area

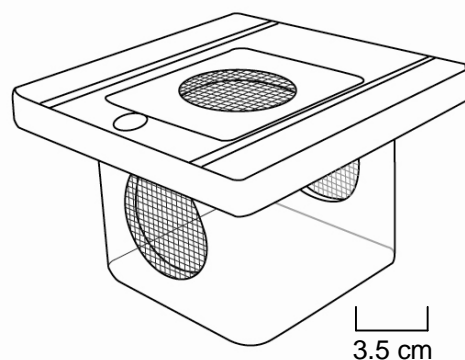
The Tota stream is located in the Colombian Eastern mountain range (5°35' N y 73° 00' W) and its drainage basin has a surface area of 0.034 Km<sup>2</sup>. The average annual temperature and rainfall are 15° C and 730.5 mm respectively. There is a bimodal rainfall regime that is related to the water pattern of the stream. A first rainy period goes from April to May, and the second one goes from October to November. The driest period ranges from December to February. Water flow achieves 1.5- 2 m<sup>3</sup>s<sup>-1</sup> during the rainy periods and 0.1—0.3 m<sup>3</sup>s<sup>-1</sup> during the drier period. Maximum values of water velocity are 0.67 m s<sup>-1</sup> from May to July, and average values between 0.12 ms<sup>-1</sup> to 0.27 ms<sup>-1</sup> in the rainy period, and 0.03 to 0.1 ms<sup>-1</sup> in the drier period. The natural vegetation of the watershed has been replaced by pasture for cattle raising. The predominant riparian plants on the river banks are Alder (*Alnus acuminata*), Eucalyptus (*Eucalyptus globulus*) and Willow (*Salix humboldtiana*) (Castro & Donato, 2008).

### 2.2 Experimental Design

The experiment was carried out in a stretch of 30 m in the middle stream. The first 15 m of the stretch were kept in natural conditions (control site), while in the other 15 m (impact site) we realized the fertilization using a tank of 500 l. In the tank we carried out dilutions of two commercial fertilizers keeping at least the double average of the basal values phosphates concentrations (1.93 µg l<sup>-1</sup>) and the ammonium concentrations (2.31 µg l<sup>-1</sup>) and in the stream. The fertilization was made by daily dripping (90 drops min<sup>-1</sup>) supply of nutrients.

Twenty four chambers were placed in the fertilized site as in the control place. These compartments were of transparent acrylic material with a volume of 343

cm<sup>3</sup>. Each chamber had three circular openings of 3.5 cm of diameter covered with a 0.5 mm mesh, to allow a continuous water flow (Figures 1). Fifteen days before introducing the animals we began the fertilization, and the chambers were placed in the stream to allow the periphyton colonization. In each place, we choose 12 chambers randomly and we introduced into each chamber, 10 *Tricorythodes* sp. nymphs. The *Tricorythodes* sp. were gathered in the study area; their body length was 3.0 mm and the cephalic capsule was 0.5 long by 0.5 mm wide. The herbivores were placed in to the compartments at the beginning of the experiment, when the periphyton colonization period was finished.



**Figure 1. Chamber used as the artificial substrate in the experiment.**

After setting the experiment the sampling was carried out during 3, 10, 17 and 28 days. In each sampling, we took three chambers with nymphs and three with no nymphs as much as in control that in impact.

On the sampled days, *Tricorythodes* sp. nymphs, were taken out of the chambers and immediately measured. Extracted chambers were wrapped up in aluminium paper and moved to the laboratory for the estimation of benthonic chlorophyll a and detached periphyton chlorophyll a (chlorophyll that is detached from the benthonic periphyton and is suspended in the chamber water), using the APHA methods (2005).

### 2.3 Hydrological, physical and chemical variables

We took daily measurements of the current velocity, a Global digital flowmeter and estimated the flow (Q) using the equation of Wetzel & Likens (2000).

Temperature (°C) and dissolved oxygen (mg l<sup>-1</sup> O<sub>2</sub>) were registered daily with a HACH LDO HQ30d oxygen sensor. Conductivity (µm cm<sup>-1</sup>) was measured with a YSI model 556 MPS multiparametric probe and the light values were measured with a Model LI-COR LI-250<sup>a</sup> luxometer. The pH was measured with a SCHOTT pH 11/SET sensor. The ammonium (µg l<sup>-1</sup> NH<sub>4</sub><sup>+</sup>) and the phosphate (µg l<sup>-1</sup> PO<sub>4</sub><sup>3-</sup>), were measured following the techniques described by APHA (2005).

### 2.4 Data Analysis

83 nymphs of *Tricorythodes* sp. were measured for the total body length, length and width of the cephalic capsule. After drying the organisms for 48 hours at 70°C, they were weighed in an electronic scale with a precision of 0.00001 mg. The data obtained were transformed by application of natural logarithm (ln) and were carried out the respective lineal regression analysis with to obtain the equation for the biomass calculation (Burgherr & Meyer, 1997):

$$DM = a * L^b$$

$$\ln DM = \ln a * b \ln L$$

where *a* and *b* are the regression constants, Dry Mass in mg (DM) and the total body length in mm (L).

Using the SPSS 15.0 for Windows, a Multivariate analysis of variance (MANOVA) was carried out to detect significant differences between the to compare fertilized vs. unfertilized and grazing vs. ungrazed), trataments, for environmental variables,

initial and final biomass of *Tricorythodes* sp. nymphs, and benthic chlorophyll *a* and detached periphyton chlorophyll *a*.

### 3. RESULTS

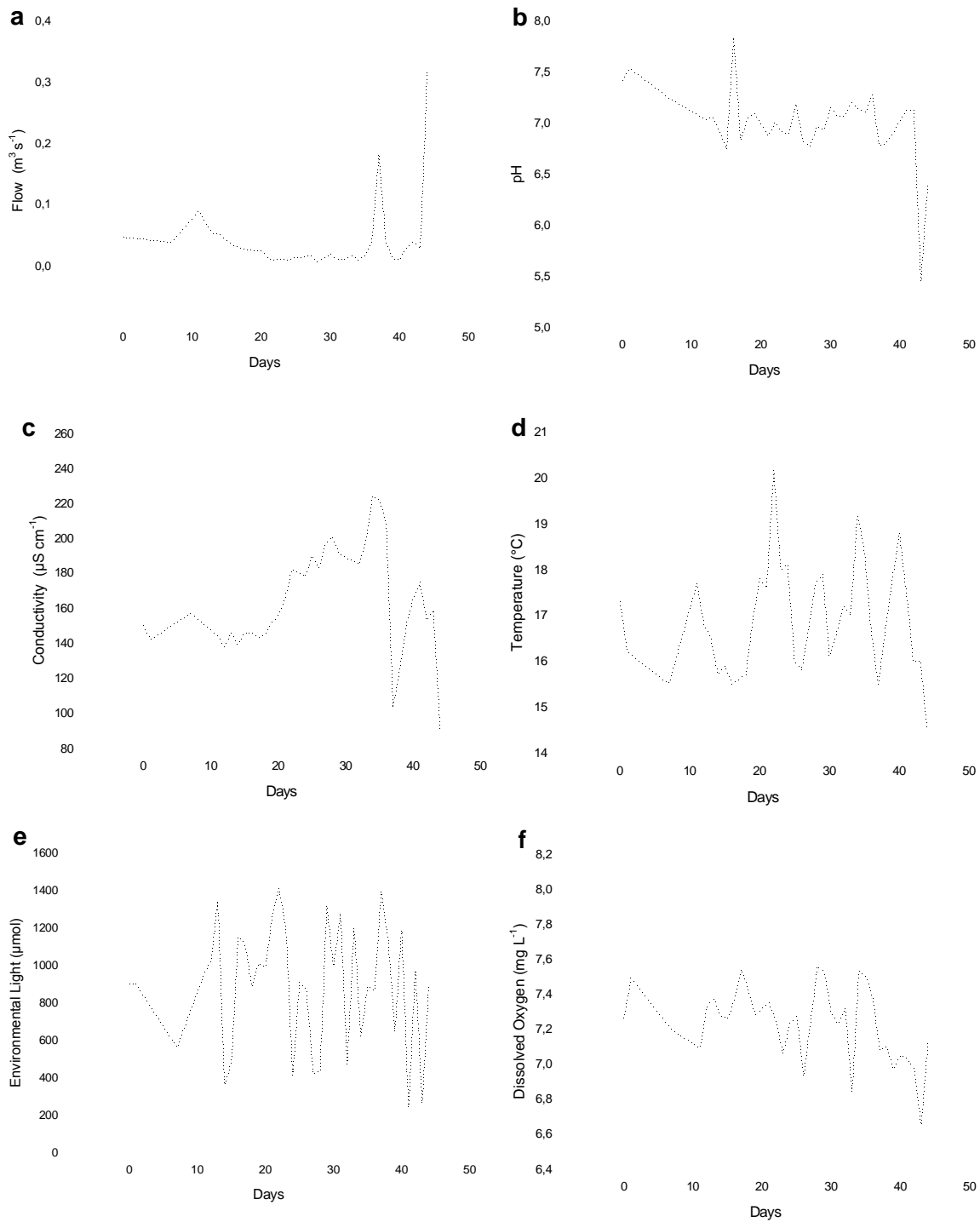
#### Physical, chemical and hydrological variables

In general terms, the experimental conditions kept a uniform environment in light and flow in both control and impact chambers.

The physical variables and the flow measured in the experiment (Figure 2, Table 1) showed significant differences between days, but not between the treatment and the control. Nevertheless, the dissolved oxygen registered significant differences between days and treatments.

**Table 1.** Significance values ( $p < 0.05$ ) among the physical, chemical and hydrological variables between treatments (control - impact) and the sampled days.

	Sites (Impact – Control)		Sample Days	
	F	p	F	p
Flow ( $\text{m}^3 \text{s}^{-1}$ )	0.736	0.394	23.291	<0.0001
pH	1.409	0.239	8.924	<0.0001
Conductivity ( $\mu\text{S cm}^{-1}$ )	0.210	0.648	156.615	<0.0001
Dissolved Oxygen ( $\text{mg L}^{-1}$ )	7.326	0.008	2,915	0.001
Temperature ( $^{\circ}\text{C}$ )	0.022	0.883	31.005	<0.0001
Light ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	0.160	0.691	5.784	<0.0001
$\text{PO}_4^{3-}$ ( $\mu\text{g L}^{-1}$ )	21.496	<0.0001	1.389	0.162
$\text{NH}_4^+$ ( $\mu\text{g L}^{-1}$ )	50.277	<0.0001	0.454	0.990



**Figure 2.** (a) Flow, (b) pH, (c) conductivity, (d) temperature, (e) environmental light and (f) dissolved oxygen values in the sampled days, control (○) and impact (●).

## Fertilization effects

Significant differences were found in  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  we between the treated and control sites (Figure 3, Table 1). Associated with this fertilization, the effect shown by the high concentrations and the significantly greater chlorophyll *a* in benthic ( $n=24$ ,  $F=242.543$ ,  $p=0.0001$ ) as in detached periphyton chlorophyll *a* ( $n=24$ ,  $F=52.525$ ,  $p=0.0001$ ) for the impact treatment (Figure 4).

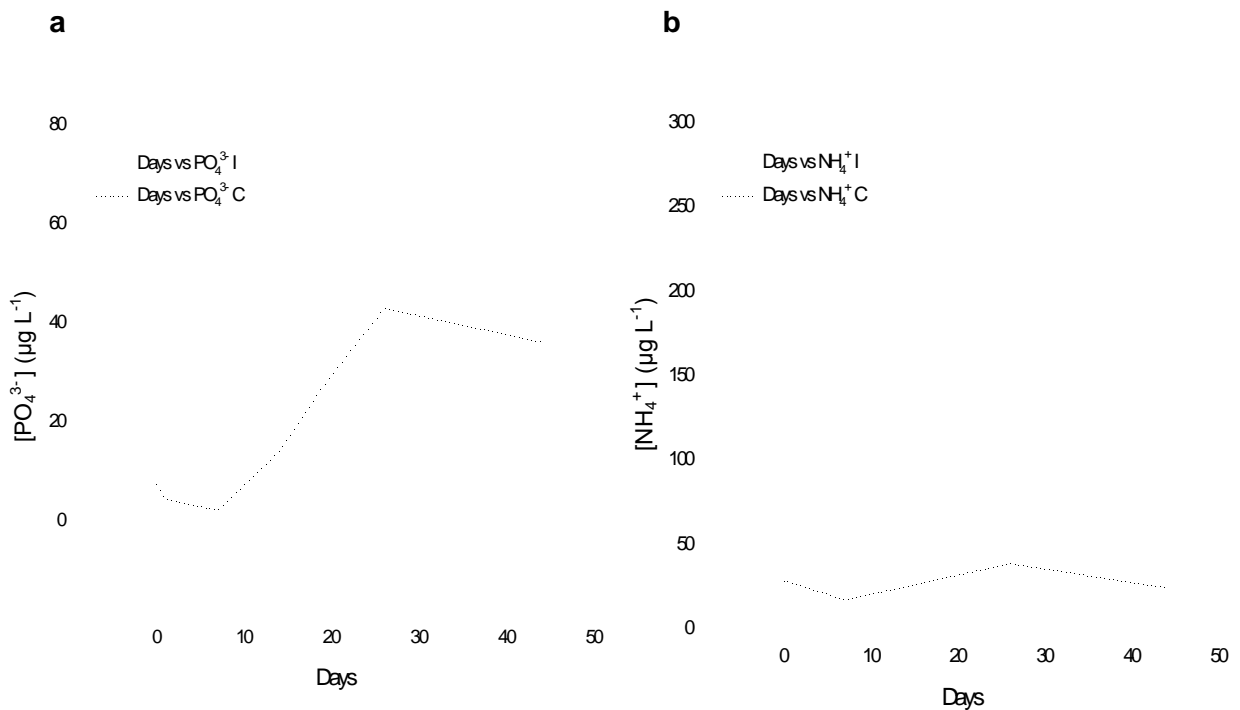


Figure 3. Increment of (a) Phosphate ( $\text{PO}_4^{3-}$ ) and (b) Ammonium ( $\text{NH}_4^+$ ) concentrations in the impact (I) and control (C) during the study days.

## Relationships between *Tricorythodes* biomass, chlorophyll *a* and light

*Tricorythodes* biomass was calculated by means of the equation  $\ln\text{DM} = -7.45 + 4.06 (\ln\text{L})$  ( $n=83$ ,  $r^2=0.66$ ,  $p=0.0001$ ).

The initial mayfly biomass showed significant differences ( $n=12$ ,  $F= 8.130$ ,  $p= 0.009$ ) between sites but not the final biomass ( $n= 12$ ,  $F=0.979$ ,  $p= 0.333$ ).

However, when the mean light value measured in each box was used as a covariate, the initial ( $n= 6$ ,  $F= 4.840$ ,  $p= 0.044$ ) and final ( $n= 6$ ,  $F= 12.255$ ,  $p= 0.003$ ) biomass presented significant differences. When we compared the biomasses between sampling days, we registered differences in the relationship of the final biomass ( $n= 6$ ,  $F= 42.752$ ,  $p= 0.0001$ ), due to rise of the nymphs final biomass in the impact in relation to the control (Figure 5). The values of benthic chlorophyll *a* had significant trends regarding to the initial biomass ( $n= 12$ ,  $F= 5.775$ ,  $p= 0.026$ ) and final biomass ( $n= 12$ ,  $F= 4.985$ ,  $p= 0.037$ ) for the mayfly nymphs.

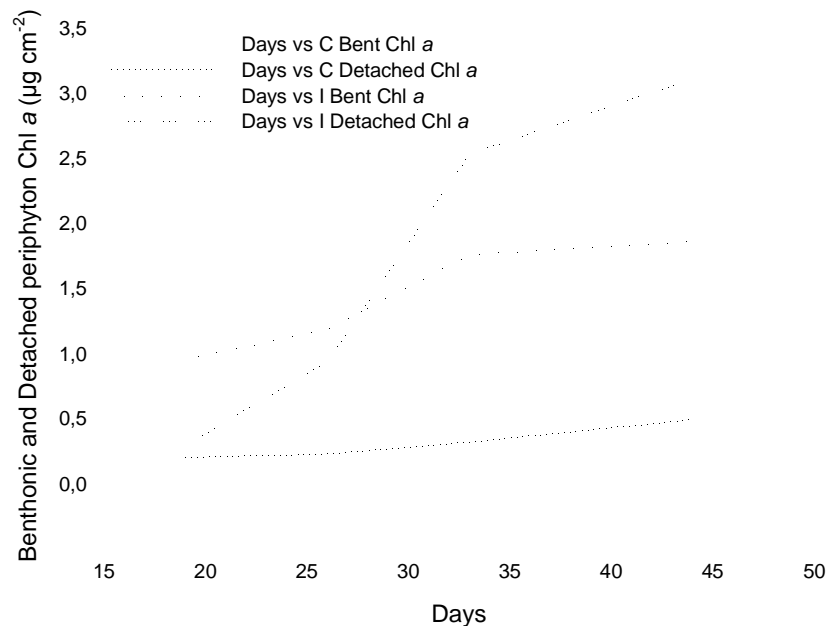


Figure 4. High level concentrations of detached periphyton chlorophyll *a* in the impact ( $\Delta$ ) and control ( $\circ$ ) vs. low level concentrations of benthonic chlorophyll *a* in the impact ( $\blacktriangle$ ) and control ( $\bullet$ ). In general the values concentration of chlorophyll *a* change has a lower variation in the control place that in the impact place.

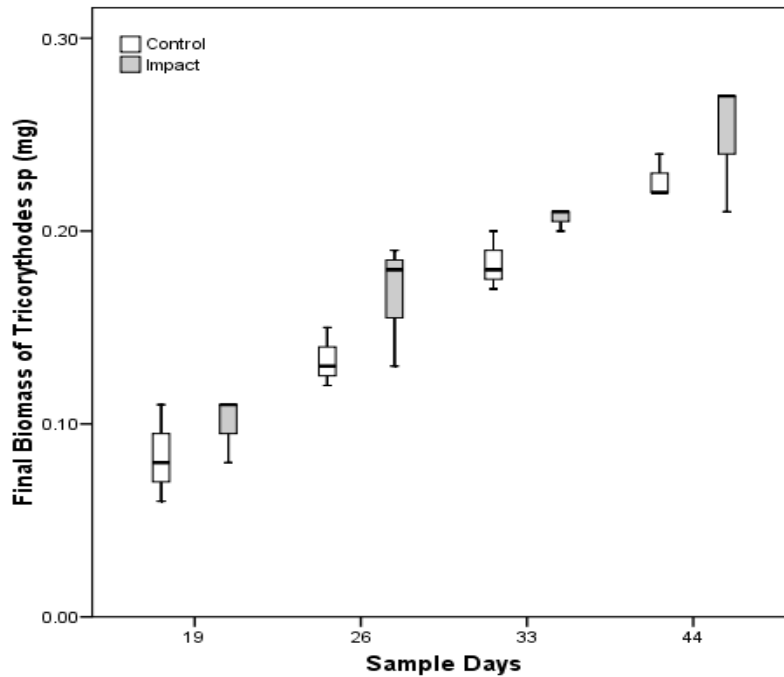


Figure 5. Relationship between final biomass of *Tricorythodes* rise in the treatments (impact and control). The values in the final biomass of mayflies were higher in the impact that in the control in the sampled days.

### Relations between Chlorophyll *a* and *Tricorythodes*

Overall, the detached periphyton chlorophyll *a* was significantly greater in the chambers with mayfly nymphs ( $n= 24$   $F=22.300$ ,  $p = 0.0001$ ). We observed that detached periphyton chlorophyll *a* concentrations are higher for the impact treatments than for those of control. It is important to emphasize that in the treatments with mayfly nymphs presence, the chlorophyll *a* concentrations were lower than in the treatments without the herbivore (Figure 6).

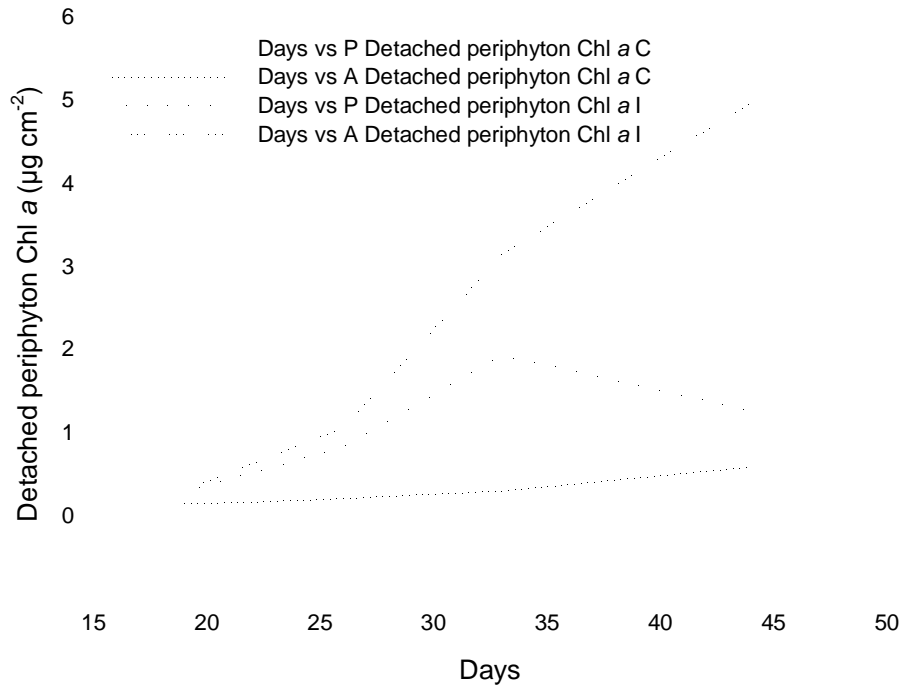


Figure 6. Detached periphyton chlorophyll *a* concentrations reduction in presence of *Tricorythodes* nymphs in the impact ( $\blacktriangle$ ) and control ( $\bullet$ ) and detached periphyton chlorophyll *a* concentrations increment in absence of *Tricorythodes* nymphs in the impact ( $\triangle$ ) and control ( $\circ$ ).

#### 4. DISCUSSION

##### Physical, chemical and hydrological behaviour

The dissolved oxygen values were significantly higher in the impact than in the control site. This is explained by the increase of primary production as a response to the supply of nutrients (Dodds, 2006) and evidences the substantial increments from benthic and detached periphyton chlorophyll *a* in the impact boxes. Dodds (2002) also found positive correlations between the detached periphyton chlorophyll *a* of the water column and nutrients. According to this, the relationship

between nutrient concentration and algal biomass gives a support to model the effects of the nutrients inputs in tropical rivers a good tool to analyze the response to anthropic impacts in biological community and trophic web stability.

### **Response of primary production to the fertilization**

For the selected stretch in Tota's stream, the primary production shows variations and outstanding differences, found in concentrations rise of chlorophyll *a* in the impact place, explained by light, hydrological conditions and nutrient supply. Agree to the study made by Biggs & Smith (2002) that shows us the importance of the supply of nutrients and the relevance in the influence of the periods with hydrological stability over the benthic algae

### **Grazing impact on the primary production**

For the detached periphyton chlorophyll *a* case, the notable effect of "Top-down" regulation would be explained by effects of mayflies on algal biomass (Rosemond et al., 1993; Liess & Hillebrand, 2004; Peters et al., 2007). The analyses maintain the significant relationships between the chlorophyll *a* and the sampling places (impact and control treatments), and to specify the effect of the primary production increase on the herbivores, we show increases of nymphs biomass in the impact chambers with respect to the control ones.

The significant variations in the values rise of final biomass *Tricorythodes* nymphs between impact and control places, keeping in mind the light factor as a covariate, demonstrates a more intense grazing by the herbivores, due to the light influence and nutrients effects in the growth of the periphyton that produce greater food availability for them (Larned & Santos, 2000; Mosisch et al., 2001; Taulbee et al., 2005). In the control chambers, nutrient concentrations declined, producing lower food availability for the nymphs.

In this work we revealed that a decrease in the detached periphyton chlorophyll a concentrations, suggests that *Tricorythodes* nymphs can behave as collectors according to the descriptions given by Merrit & Cummins (1996). The larvae of many mayfly species have gathering collector feeding structures and tend to feed at the outer layers, or loosely attached, portions of the periphyton mat (Steinman, 1996). This contrasts with the reported by Rivera et al. (2008) who for the same Tota stream considers the organisms of this family to be shedders.

It is important to stand out the ecological relevance of carrying out *in situ* studies. Light and nutrients levels are the main restrictive factors of biomass growth in primary producers, because different environmental variables can influence organisms response, as in the present experiment, where the light is a covariate factor that generates significant effects in the increase of the primary productivity and the final biomass of *Tricorythodes*.

In temperate areas the base of the stream trophic web depends of allochthonous material and seasonality, while in the tropical ones it depends on the contributions of algal biomass (Davis et al., 2008) and the intensity of the physical events of hydrological type (Zapata & Donato, 2005). The nutrient rise in a high Andean stream increase primary productivity ("Bottom-Up"), generating herbivores responses that regulated periphyton biomass ("Top-down"). These results are in agreement with those obtained for temperate rivers (Hillebrand & Kahlert 2001; Liess & Hillebrand, 2004; Grafner & Robinson, 2007) and demonstrate the relevance of making this kind of studies in the tropics.

## 5. REFERENCES

Allan, J. D. & M. M. Castillo, 2007. Stream ecology: structure and function of running waters. Springer. Dordrecht, The Netherlands.

Armenteras, D., F. Gast, & H. Villareal, 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation* 113: 245–256.

APHA, AWWA & WEF, 2005. Standard methods for the examination of water and wastewater. The American Water Works Association, Washington D. C., USA.

Biggs, B. F. & R. A. Smith, 2002. Taxonomic richness of stream benthic algae: Effect of flood disturbance and nutrients. *Limnology and Oceanography* 47: 1175-1186.

Burgherr, P. & E. I. Meyer, 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. *Archiv für Hydrobiologie* 139: 101-112.

Castro, M. I. & J. Donato, 2008. El entorno natural del río Tota. In Donato, J. (Ed), *Ecología de un río de montaña de los Andes colombianos (río Tota, Boyacá)*. Universidad Nacional de Colombia. Facultad de Ciencias. Bogotá, Colombia: 73-79.

Davies, P. M, S. E. Bunn & S. K. Hamilton, 2008. Primary production in tropical streams and rivers. In D. Dudgeon (ed), *Tropical stream ecology*, Elsevier Inc. London. UK: 24-37.

Dodds, W. K., V. H. Smith & K. Lohman, 2002. Nitrogen and phosphorous relationships to benthic algal biomass in temperate streams. *Canadian Journal of Fisheries and Aquatic Science* 59: 865-874.

Dodds, W. K., 2006. Eutrophication and trophic state in rivers and streams. *Limnology and Oceanography* 51: 671-680.

Domínguez, E., C. Molineri, M. L. Pescador, M. D. Hubbard & C. Nieto, 2006. Ephemeroptera of South America. In Adis, J., R. Arias, G. Rueda-Delgado & K.M. Wantzen (eds), Aquatic biodiversity of Latin America, Vol. 2, Pensoft, Moscow and Sofia: 1-646.

Donato, J. & G. Galvis, 2008. Tipología de ríos colombianos –Aspectos generales-. In Donato, J. (Ed), Ecología de un río de montaña de los Andes colombianos (río Tota, Boyacá). Universidad Nacional de Colombia. Facultad de ciencias. Bogotá: 27-52.

Emmerich, D. E., 2007. Two new species of *Tricorythodes* Ulmer (Ephemeroptera: Leptohyphidae) from Colombia. Zootaxa 1561: 63-68.

Gafner, K. & C. T. Robinson, 2007. Nutrient enrichment influences the responses of stream macroinvertebrates to disturbance. Journal of the North American Benthological Society 26: 92-102.

Hart, D. D., 1985. Grazing insects mediate algal interactions in a stream benthic community. Oikos 44: 40-46.

Hart, D. D., 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia 73: 41-47.

Hill, W. R. & A. W. Knight, 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. Ecology 68: 1955-1965.

Hillebrand, H. & M. Kahlert, 2001. Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. Limnology and Oceanography 46: 1881-1898.

Hillebrand, H., M. Kahlert, A. L. Haglund, U. G. Berninger, S. Nagel & S. Wickham, 2002. Control of microbenthic communities by grazing and nutrient supply. *Ecology* 83: 2205-2219.

Kirk E. J. & S. A Perry, 1994. Macroinvertebrate production estimates in the Kanawha River, West Virginia. *Hydrobiologia*. 281: 39-50.

Lake, P., 2000. Disturbance patchiness and diversity in stream. *Journal North American Benthological Society* 19: 573-592.

Lamberti, G. A. & V. H. Resh, 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. *Ecology* 64:1124-1135.

Lamberti, G. A. & J. W. Moore, 1984. Aquatic insects as primary consumers. In Resh V. H. and D. M. Rosenberg (eds), *Ecology of aquatic insects*. Praeger Scientific, New York, USA: 164-195.

Larned, S. T. & S. R. Santos, 2000. Light -and nutrient-limited periphyton in low order streams of Oahu, Hawaii. *Hydrobiologia* 432: 101-111.

Liess, A. & H. Hillebrand, 2004. Direct and indirect effects in herbivore-periphyton interactions. *Archiv für Hydrobiologie* 159: 433-453.

Liévano, A & R. Ospina, 2007. Guía ilustrada de los macroinvertebrados acuáticos del río Bahamón. Universidad del Bosque, Bogotá, Colombia.

McAuliffe J. R., 1984. Competition for Space, Disturbance, and the Structure of a Benthic Stream Community. *Ecology* 65: 894-908.

McCullough, D. A., G. W. Minshall & C. E. Cushing, 1979. Bioenergetics of a stream "Collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera). *Limnology and Oceanography* 24: 45-58.

McQueen, D. J., J. R. Post & E. L. Mills, 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Science* 43: 1571-1581.

Merritt, R. W. & K. W. Cummins, 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, USA.

Mosisch, T. D., S. E. Bunn & P. M. Davies, 2001. The relative importance of shading and nutrients on algal production in subtropical streams. *Freshwater Biology* 46: 1269–1278.

Murphy, M. L., 1984. Primary production and grazing in freshwater and intertidal reaches of a coastal stream, Southeast Alaska. *Limnology and Oceanography* 29: 805-815.

Peters, L., H. Hillebrand & W. Traunspurger, 2007. Spatial variation of grazer effects on epilithic macrofauna and algae. *Journal of the North American Benthological Society* 26: 78-91.

Rivera, C. A., E. Pedraza & A. M. Zapata, 2008. Aproximación preliminar a la dinámica del flujo de la materia orgánica. In Donato, J. (Ed), *Ecología de un río de montaña de los Andes colombianos (río Tota, Boyacá)*. Universidad Nacional de Colombia. Facultad de ciencias. Bogotá, Colombia: 145-162.

Roldán, G. A., 2003. Bioindicación de la calidad del agua en Colombia, uso del método BMWP/Col. Universidad de Antioquia. Medellín, Colombia.

Rosemond, A. D., P. J. Mulholland & J. W. Elwood, 1993. Top-down and Bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74: 1264-1280.

Steinman A. D., 1996. Effects of grazers on freshwater benthic algae. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal ecology: Freshwater benthic ecosystems*. Academic Press. San Diego, California: 341-373.

Stevenson, R. J., 1996. An introduction to algal ecology in freshwater benthic habitats. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), *Algal ecology: Freshwater benthic ecosystems*. Academic Press. San Diego, California: 3–30.

Thomson, J. R., P. S. Lake & B. J. Downes, 2002. The effect of hydrological disturbance on the impact of a benthic invertebrate predator. *Ecology* 83: 628-642.

Taulbee, W. K., S. D. Cooper & J. M. Melack, 2005. Effects of nutrient enrichment on algal biomass across a natural light gradient. *Archiv für Hydrobiologie* 164: 449-464.

Wetzel, R. G. & G. E. Likens, 2000. *Limnological Analyses*. Springer. New York, USA.

Zapata, A. M. & J. C. Donato, 2005. Cambios diarios de las algas perifíticas y su relación con la velocidad de corriente en un río tropical de montaña (río Tota-Colombia). *Limnetica* 24: 327-338.