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Natural and Cultural History of the Golfo Dulce Region, Costa Rica

Anton WEISSENHOFER, Werner HUBER,
Veronika MAYER, Susanne PAMPERL, Anton WEBER,
Gerhard AUBRECHT (scientific editors)

HRSG.: Biologiezentrum der Oberösterreichischen Landesmuseen

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Anton WEISSENHOFER, Werner HUBER, Veronika MAYER, Susanne PAMPERL,
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lebensministerium.at
Fakultät für Lebenswissenschaften
OMV
universität wien
Tropenstation La Gamba, Costa Rica

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Due to the orographic formation of its interior and its humid climate, the Golfo Dulce Region is rich with biodiversity, containing very dense flora and fauna. After HOLDRIDGE (1971), the region was subdivided into different zones, including the tropical rainforest, the tropical wetland forest, and tropical premontane rainforest. The biogeographical situation in this area shows many similarities to the flora and fauna in the Amazon and the Colombian Chocó Region and serves as a land bridge with a valuable genetic base between North and South America. After unregulated seizure of land by agricultural settlers, lumberjacks, and large landowners in the 1940s and 1950s, regulated, state-subsidised settlement reform intended to support agricultural exports in the 1960s, and intensification of the livestock industry in the 1970s, primary and secondary forest reserves have shrunk to a minimum. The constant expansion of monocultures on new land has far-reaching consequences for the local ecosystem.

The conservation and sustainable use of tropical forests is established in the Forest Declaration, Convention on Climate Protection, and Convention on the Protection of Species, which demonstrate worldwide concern for these issues. As a regional example, in the 4,304.80 km^2 drainage basin, the ACOSA (Área de Conservación OSA), which covers an area spanning the Cantons Osa, Golfito und Corredores, aims to protect species diversity within the 17 game preserves, which are 44.7% covered by forest, through integration and an alliance with the Parques Nacionales, Vida Silvestres y Forestales (Fig. 2). The main sector of the Corcovado National Park on the Osa Peninsula covers 424 km^2 and the Piedras Blancas National Park covers 148 km^2. The altitude ranges from sea level to 745 m on the Osa Peninsula (Cerro Rincón and Cerro Mueller in the Fila Matajambre) and to 579 m in the Esquinas forest (Cerro Nicuesa). The Golfo Dulce Forest Reserve (592 km^2) was established between the two parks, thereby forming a natural forest corridor.

References

CHINCHILLA V.E. (1987): Atlas cantonal de Costa Rica. — IFAM. San José.

HARTSHORN, G.S. (1983): Plants: introduction. — In: JANZEN D.H. (ed.), Costa Rican natural history. Chicago: Univ. Chicago Press: 118-157.

HERRERA-MACBRYDE O., MALDONADO V. JIMÉNEZ T.R. & K. THOMSEN (1997): Osa Península and Corcovado National Park, Costa Rica. — In: DAVIS S.D., HEYWOOD V.H., HERRERA-MACBRYDE O., VILLA-LOBOS J.& A.C. HAMILTON (eds), Centres of plant diversity. A guide and strategy for their conservation. Vol. **3**. WWF, IUCN.

HERWITZ S.R. (1981): Regeneration of selected tropical tree species in Corcovado National Park, Costa Rica. — Univ. Calif. Publ. Geogr. **24**.

HOLDRIDGE L.R. (1971): Forest environments in tropical life zones. A pilot study. — Oxford.

MALZER O. (2001): Geological History of Central America and the Golfo Dulce Region. — Stapfia **78**: 34-46.

MORA C.S. (1990): La Geología y sus procesos. — San José.

TOSI J.A. Jr. (1975): The Corcovado Basin on the Osa Península. — In: TOSI J.A. Jr. (ed.), Potential national parks, nature reserves, and wildlife sanctuary areas in Costa Rica: a survey of priorities. San José: Centro Científico Tropical. Separate pp. 12.

Addresses of authors:

Anton WEISSENHOFER
Werner HUBER
Department of Palynology and Structural Botany
Faculty Center of Botany
University of Vienna
Rennweg 14
A-1030 Vienna, Austria
E-mail: anton.weissenhofer@univie.ac.at
werner.huber@univie.ac.at

Michael KLINGLER
Workgroup Development Studies
and Sustainability Science
Institute of Geography
University of Innsbruck
Innrain 52
A-6020 Innsbruck, Austria
E-mail: michael.klingler@uibk.ac.at

The river network of the Piedras Blancas National Park, Costa Rica

La red fluvial del Parque Nacional Piedras Blancas, Costa Rica

Julia TSCHELAUT, Christian PICHLER, Anton WEISSENHOFER & Fritz SCHIEMER

Abstract: Research on tropical streams has progressed markedly over the last decade. However, many aspects of biodiversity and functional processes require more detailed attention. The rivers and streams of the Piedras Blancas National Park in south-western Costa Rica provide a unique opportunity to study near-pristine rainforest streams and tropical freshwater ecology. One of the primary objectives of the study was to provide a survey of the river network within the Río Esquinas catchment. Rivers were analysed with regard to abiotic parameters such as morphology, hydrology, hydrochemistry, sedimentology, and to biotic parameters such as canopy cover by the riparian vegetation during the dry and rainy season in 2004. Surveys were carried out on nine streams and rivers, ranging from 1st order to 4th order, which empty into the Golfo Dulce at the Pacific Ocean. The paper discusses differences between sites according to geology and the seasonal hydrological characteristics of running waters within the catchment. The hydrochemical stream signatures indicate different geological sources within the Río Esquinas catchment. High water temperatures (> 25°C) are a permanent feature. The streams and rivers exhibit a high annual variation in discharge, turbidity and hydrochemistry as a result of seasonal rainfall. The mean discharge during the rainy season can be 3 times higher than in the dry season. Detailed morphometric-hydrological measurements at the Quebrada Negra, a 1st order stream, show a clear picture of a highly heterogeneous, dynamic and unregulated stream course with a sequence of pool and riffle sections. Rapid water level fluctuations caused by heavy rains are typical. The abundant riparian vegetation is of major significance for the structure and function of the stream ecosystem. The food web structure and trophic interactions of neotropical streams are analysed, taking the results of the Quebrada Negra as an example.

Key words: neotropical streams, seasonality, hydrology, geomorphology, riparian vegetation, nutrient export, food web.

Resumen: La investigación de cursos de agua tropicales ha aumentado en la última década. Sin embargo, muchos aspectos de la biodiversidad y los procesos funcionales requieren una atención mas detallada. Los ríos y arroyos del Parque Nacional Piedras Blancas, al sudeste de Costa Rica, ofrecen una oportunidad única para estudiar la ecología de los cursos de agua dulce tropicales en estado casi inalterado. Uno de los primeros objetivos del estudio fue estudiar la red fluvial de la cuenca del Río Esquinas. Los ríos fueron analizados teniendo en cuenta factores abióticos como morfología, hidrología, hidroquímica, sedimentología y factores bioticas como capa de vegetación ripariana durante las estaciones seca y lluviosa de 2004. Se realizó un estudio sobre nueve cursos de agua, del primer al cuarto orden, que desembocan en el área del Golfo Dulce, en el Océano Pacífico. El trabajo trata sobre las diferencias entre diversos sitios de la cuenca según factores geológicos y las características hidrológicas estacionales de cada curso de agua. Las características hidroquímicas de los ríos indican diversas fuentes geológicas dentro de la cuenca del río Esquinas. La alta temperatura del agua (> 25ºC) es una constante de los ríos que se describen aquí. Los cursos de agua muestran una gran variación anual en descarga, turbidez e hidroquímica debido a las lluvias estacionales. La descarga promedio durante la estación lluviosa puede llegar al triple de la estación seca. Además se investigaron con mayor detalle las condiciones morfométricas e hidrológicas del Quebrada Negra, un curso de primer orden. Los resultados muestran que se trata de un curso de agua heterogéneo, dinámico y poco regulado, con una secuencia natural de remansos y rápidos. Las rápidas fluctuaciones de nivel causadas por las intensas lluvias son típicas. La abundante vegetación riparia mantiene prinicipalmente a las especies típicas de los cursos de agua de Costa Rica. Se analizan la estructura de la red alimenticia y las interacciones tróficas de los cursos de agua neotropicales – tomando los resultados del Quebrada Negra como ejemplo.

Palabras clave: agua tropicales, características estacionales, hidrología, geomorfología, vegetación riparia, exportación de nutrientes, red alimenticia.

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Introduction

Studies of neotropical streams and rivers have a long history, beginning with early explorers and naturalists who visited these regions and collected aquatic specimens, e.g. von Humboldt and Bonpland (1799-1802), von Spix and von Martius (1817-1820), Bates (1848-1859). Later, more extensive collections were made by professional collectors as well as numerous resident and visiting scientists (see JACKSON & SWEENEY 1995).

There is a growing interest in the study of neotropical lotic systems, and the number of papers published each year that address tropical stream research has increased markedly over the last two decades. Although the advances are evident, JACKSON & SWEENEY (1995) pointed to the pressing need for more research into the ecology of zoobenthos, algal and microbial communities. In particular, there is a strong requirement for research into aquatic system processes and their interaction with the terrestrial environment in a catchment-orientated context.

Tropical streams provide the opportunity to study some general ecological questions e.g. factors that determine patterns of species abundance, distribution and co-occurrence (ARRINGTON et al. 2005). Patterns determined from temperate zones do not necessarily hold for tropical systems because of the greater taxonomic and ecological diversity in the tropics (HOENIGHAUS et al. 2004) and general system differences e.g. in temperature, hydrology and the source of energy for the biota. The effects of disturbance, predation and environmental complexity (e. g. DUDGEON 1993), the structure of tropical food webs (e. g. JEPSEN & WINEMILLER 2002) and the specific role of fish (e. g. FLECKER et al. 2002) represent research questions of a wider ecological scope.

A characteristic feature of tropical rainforests is their high diversity and productivity based on a restricted nutrient supply. One resolution of this paradox is the fast nutrient turnover and high retention capacity. In this respect, rainforest streams can be considered as the export routes of nutrients and thus they can be used to indicate the retention capacities of the system with respect to the nutrient losses that occur. They are therefore good indicators of the retentivity and integrity of the whole rainforest system (e. g. LEWIS 1987).

Tropical streams form aquatic ecosystems which interconnect intimately with the processes in the riparian gallery forests and the hyporheic zones flowing beyond and beside the visible streams. The River Continuum Concept (RCC), introduced by VANNOTE et al. (1980) is a tool for displaying and understanding lotic ecosystem dynamics. It explains changes in the structure and function of communities in low-order rivers and helps predict the way biological communities adapt to such changing geomorphological and hydrological conditions. This concept was the first unified hypothesis about how streams and their watersheds work and has been tested in streams around the world.

This protected area of the Piedras Blancas National Park, Costa Rica, provides a unique opportunity to study near-pristine rainforest streams. A continued program of ecological studies of the Río Esquinas catchment and its aquatic subsystems is in progress.

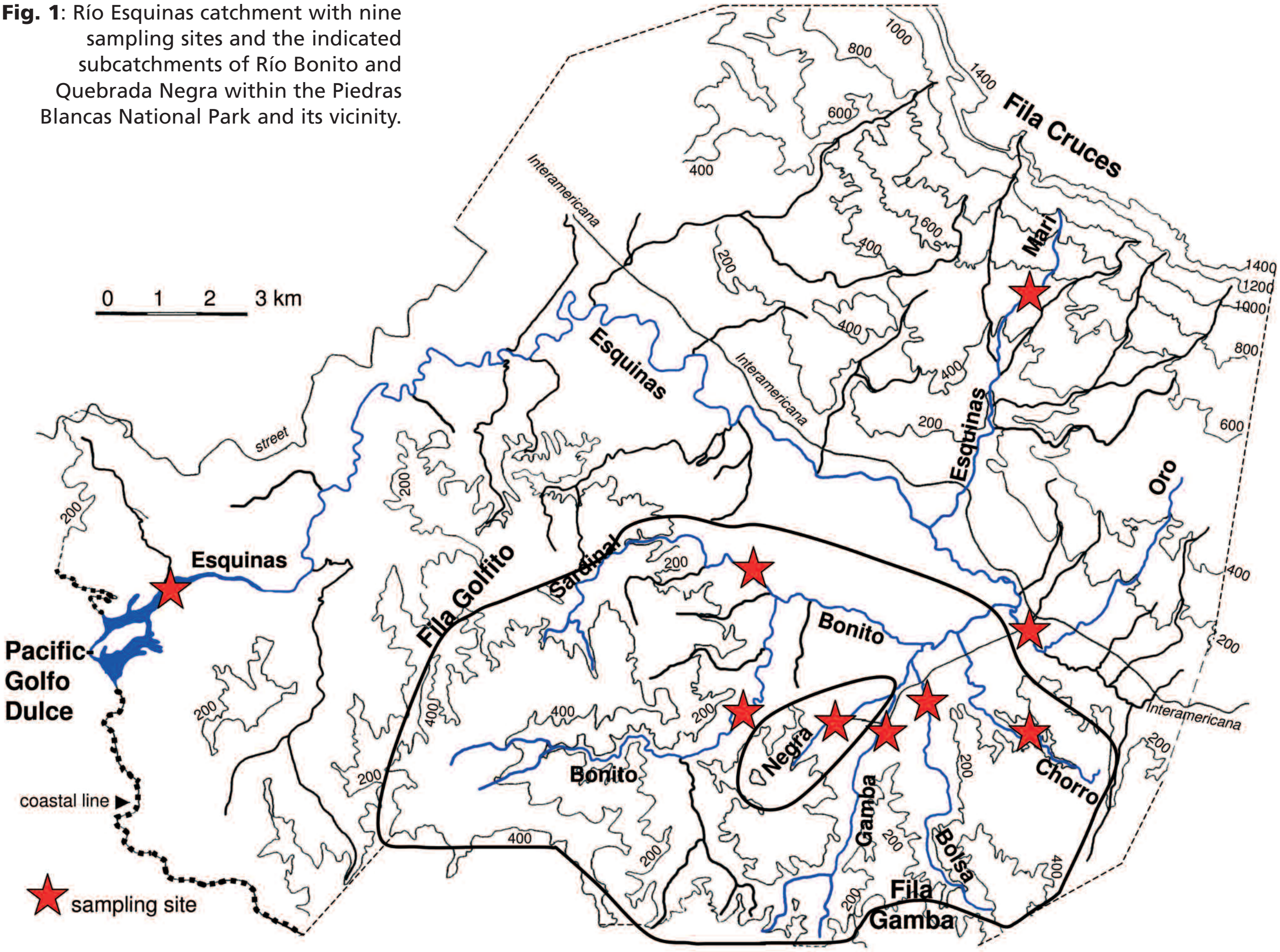
The objective of the present study was to provide an overview of the overall characteristics of the river network within the Río Esquinas catchment (Fig. 1). Rivers were analysed with regard to abiotic parameters such as morphology, hydrology, hydrochemistry, sedimentology and to biotic parameters such as canopy cover by the riparian vegetation. Differences between sites according to geological factors and the seasonal hydrological characteristics of running waters within the catchment have been assessed. Research was carried out at nine study streams and rivers ranging from 1st order streams to the largest river, the Río Esquinas, a 4th order river, that empties into the Pacific Ocean at the Golfo Dulce. Furthermore, the morphometric-hydrological conditions of the Quebrada Negra, a 1st order stream, were investigated in more detail. Streams display a more or less regular alternation between shallow areas of higher current velocity and mixed gravel-cobble substrate (riffles) and deeper areas of slower velocity and finer substrate (pools).

The Río Esquinas catchment

A network of rivers, small streams and drainage channels pass through the national park and its surroundings, which all flow into Río Esquinas (Fig. 1). "Esquinas" means corner and the river is named after its meandering course in its downstream section. The river forms the natural border of the Bosque Esquinas to the north and west of the national park and drains into the Pacific Ocean. Extensive mangrove swamps occur along the tidal estuaries next to its mouth. The banks of the two main rivers passing through the La Gamba valley, the Río Bonito and the Río Esquinas, consist of farmland and secondary forest at different stages of regrowth. Due to logging until the late 20th century, nearly no primary forest is left in the lowland, except small patches along the coast and deep inside the park. However, the up-slope areas within the study catchment show almost no signs of anthropogenic disturbance. Most of the smaller streams lie within primary rainforest.

The river network, especially the Río Bonito, is characterised by an almost unaffected geomorphology.

Fig. 1: Río Esquinas catchment with nine sampling sites and the indicated subcatchments of Río Bonito and Quebrada Negra within the Piedras Blancas National Park and its vicinity.



In its connection with the Río Esquinas, it represents a very interesting, remarkably preserved, undisturbed and fully developed, longitudinal morphological river continuum. The upstream area of the Río Bonito, embedded in primary forest, can serve as a valuable reference section for the investigations of anthropogenic influences for Costa Rican rivers.

Headwater streams, like the Quebrada Mari and Quebrada Negra, are rocky, shallow, narrow and characterised by a dense riparian vegetation. In contrast, the canopy cover of high order rivers such as lower meandering parts of Río Esquinas and downstream parts of Río Bonito is low and the sediments are dominated by mud and sand. Light levels near the bottom zones are reduced due to an increasing water depth and turbidity.

Figure 2 depicts the downstream decrease in slope of rivers along their longitudinal course, with steep headwaters and waterfalls due to the rocky landscape

Table 1: Co-ordinates and brief description of the sampling sites from the nine studied rivers.

river	coordinates	description
Quebrada Mari	-	next to San Miguel, Fila Cruces
Quebrada Negra	N 08° 42,054', W 083° 12,085'	next to the Field Station La Gamba
Quebrada Chorro	N 08° 42,425', W 083° 10,552'	at the waterfall
Quebrada Gamba	N 08° 42,072', W 083° 11,530'	bridge with railing
Quebrada Bolsa	N 08° 42,452', W 083° 11,137'	bridge in La Gamba
Quebrada Sardinal	N 08° 43,407', W 083° 12,773'	500 m before entering into Río Bonito
Río Oro	N 08° 43,004', W 083° 10,033'	bridge on the way from La Gamba to Interamericana (km 37)
Río Bonito	N 08° 43,868', W 083° 17,723'	2,5 km upstream the conference with Quebrada Sardinal
Río Esquinas	N 08° 43,868', W 083° 17,723'	4 km upstream of its mouth before entering into Golfo Dulce

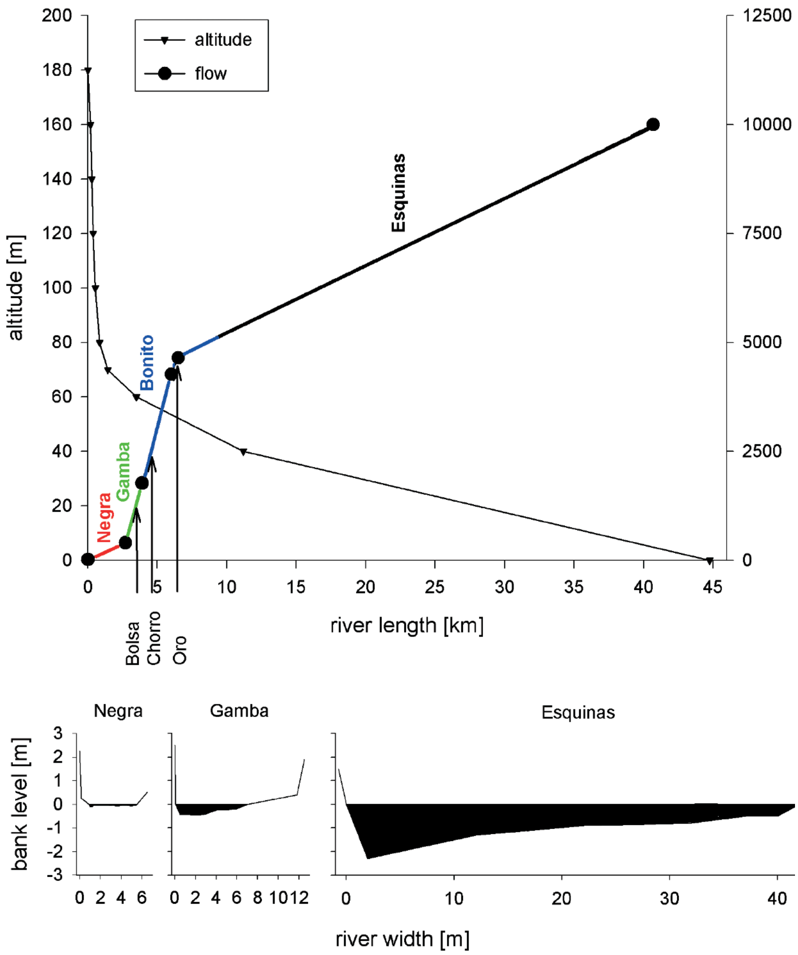


Fig. 2: River length [km] versus altitude [m] and flow [ls^{-1}] during the dry season 2004 of the Quebrada Negra flowing into Quebrada Gamba, Río Bonito and Río Esquinas. Tributaries like Quebrada Bolsa, Quebrada Chorro and Río Oro are indicated.

Fig. 3: Lower Río Bonito.

formation, followed by a decline in lowland sections further downstream. The confluence of various fast-flowing, turbulent mountain streams (e. g. Q. Negra, Q. Gamba, Q. Chorro) results in a fast-flowing river, which corresponds to the piedmont river type with its larger flow, a braided course and high gravel transport (e. g. lower Río Bonito, Fig. 3). The meandering, lower part of the Río Esquinas, winds as a large, smoothly-flowing river through the lowlands to the sea. It is highly influenced by tidal backwaters and the deposition of sand and fine sediments (up to 10 km inland from the Pacific Ocean).

The concave longitudinal profile is evident. Whereas Quebrada Negra shows a steep incline, the slope of Río Esquinas is low. Along the longitudinal course, discharge increases in the dry season from 22.5 ls^{-1} (Q. Negra) to 397 ls^{-1} (Q. Gamba), 4270 ls^{-1} (R. Bonito before the confluence with R. Oro) and 10.000 ls^{-1} (R. Esquinas).

Almost all the characteristics of a river vary with position along its length. In general, discharge increases with increasing stream order, resulting in changes in width, depth and velocity. Particle sizes of river bed material usually shift from an abundance of coarser material upstream to mainly finer material in downstream areas. Sediment size is not only correlated with the stream order, it also depends upon different physical parameters (current velocity, incline) of the stream.

The Golfo Dulce region is one of the most humid areas in Costa Rica, with more than 6.000 mm of precipitation per year. On the Pacific side of Costa Rica, distinct dry (December – March) and rainy (May – November) seasons exist. The heaviest rainfalls occur in September, October and November. February and March are the driest months, when days can pass without rain. As a result of seasonal rainfall, rivers in this region undergo annual changes in water levels. The dry and rainy seasons affect various morphological and hydrological parameters, especially stream width, water depth and discharge. Strong geomorphological changes of the river bed are visible after periods of seasonal flood flow events. In the rainy season, frequent (almost daily) rains and storms can cause bank-full conditions and in some cases flooding (Füreder 1994).

A comparison of cross sections from the dry and rainy season shows the increase in stream width and water depth during the rainy season. Distinct seasonal differences are evident in Figure 4. Río Oro, Quebrada Sardinal and Río Bonito become strikingly larger and deeper during the rainy season.

Streams in Figure 5 are arranged based on Strahler's stream order system starting with 1st order streams (Q. Negra and Q. Mari). Quebrada Chorro, Quebrada Gamba, Quebrada Bolsa, Río Oro and Quebrada Sardinal are 2nd order streams at the respective study sites. Río Bonito was defined as a 3rd order river and Río Esquinas as a 4th order river. The recorded flow at these nine rivers shows a distinct increase from low order streams to rivers with higher stream order. The smallest is the Quebrada Negra with a base flow of 0.031 m^3s^{-1}. The flow of the Río Esquinas was about 300 times as high (10 m^3s^{-1}).

Furthermore, large fluctuations from the dry to the rainy season are a characteristic feature. Data from the Quebrada Mari and the Río Esquinas are not available for the rainy season. Water flow increased in the late rainy season (September, October). Therefore, differences in flow depended on sampling date. Values ranged from 0.094 m^3s^{-1} (Q. Negra) to 1.776 m^3s^{-1} (Q. Sardinal).

Sediment size of the river bed differed markedly between the study sites. At seven rivers within the Esquinas catchment, sediment size was estimated visually in the rainy season (Fig. 6). We used five standard particle size ranges (< 2 mm, 2-6.3 mm, 6.3-20 mm, 20-63 mm, > 63 mm) and noted the proportion of each range in the stream bed sediment. The sites for this analysis were chosen at random. The rivers are thus not comparable, but sediment size ranges can be given. The Q_{25}, the lower quartile, ranged from 1.5 mm to 9.1 mm. This means that 25% of the sediment sizes were less than 1.5 mm at the site with the finest sediment and smaller than 9.1 mm at the site with the coarsest soil. The Q_{50}, the median, ranged from 6.5 mm to 28.9 mm. The Q_{75}, the upper quartile, extends from 28.5 mm to 91.2 mm. The Río Oro showed the smallest sediment size, whereas the Quebrada Bolsa had the coarsest sediment.

Geology and chemistry

Tropical rivers generally have lower concentrations of chemical constituents than temperate rivers, because tropical rivers are mostly precipitation-dominated. However local geology is also important. The chemical composition of stream water reflects and thus reveals geological features of the catchment. The chemical regime of the water, particularly nutrient dynamics and export from catchments, provides insights into major aspects of ecosystem functions (NEWBOLD et al. 1995). The relationship between solute concentration and stream flow can help to explain the interplay among physical, chemical and biological processes within the catchment. The observed physical and chemical differences in solute concentrations among the studied rivers within the Río Esquinas catchment seem largely to be a function of area-specific runoff and geological processes. Chemical data indicate the same source for Río Es-

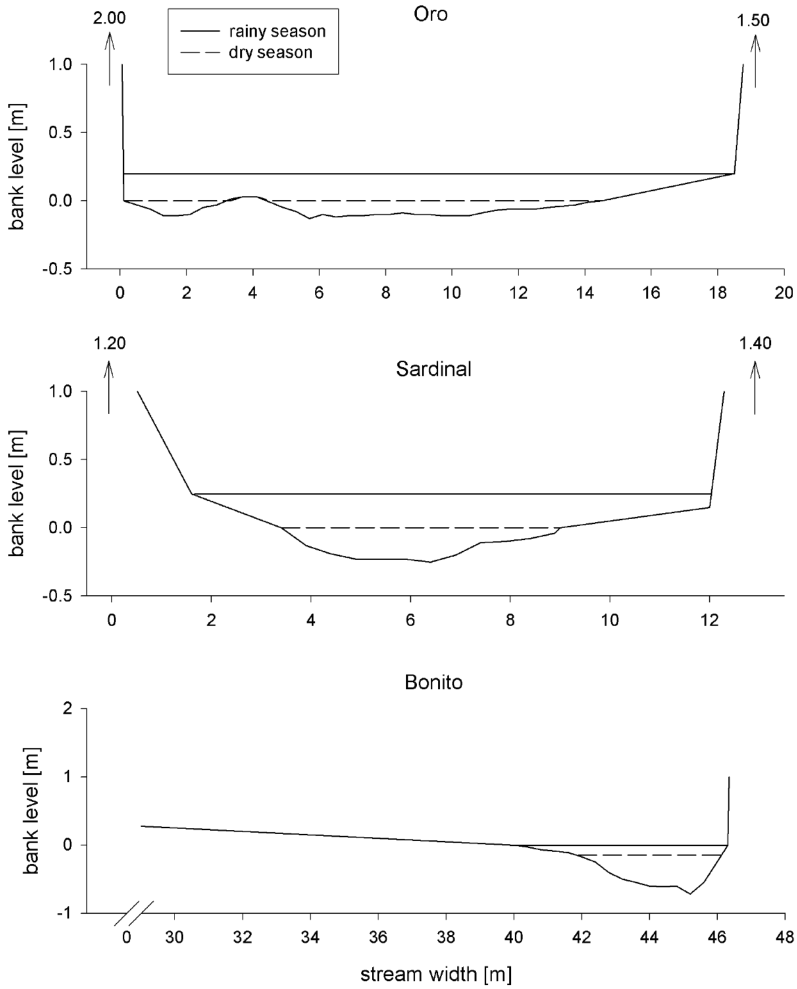


Fig. 4: Cross sections of Quebrada Sardinal, Río Oro and Río Bonito with stream width [m] and water level [m] during the dry and rainy season in 2004. Sampling sites are indicated with red stars in Figure 1.

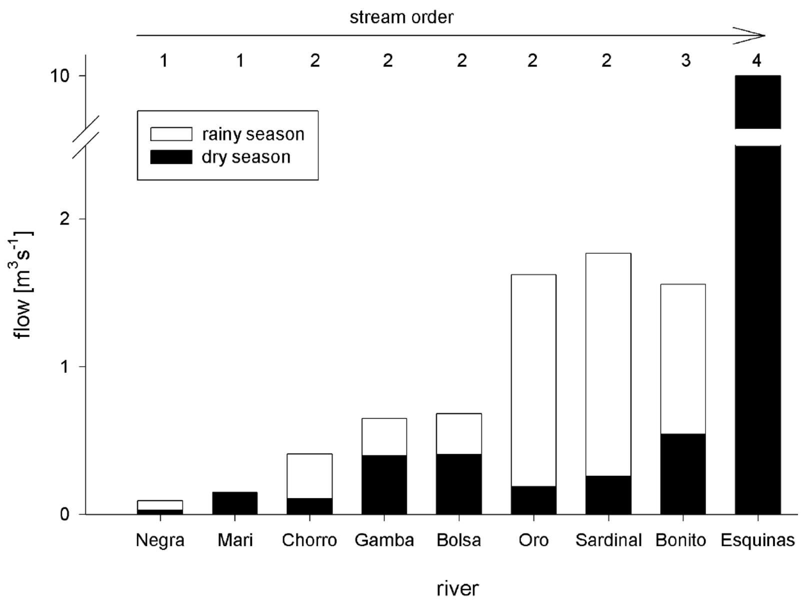


Fig. 5: Comparison of the flow [m^3s^{-1}] from the nine study rivers during the dry and the rainy seasons. Arrangement of rivers according to stream order [1st – 4th]

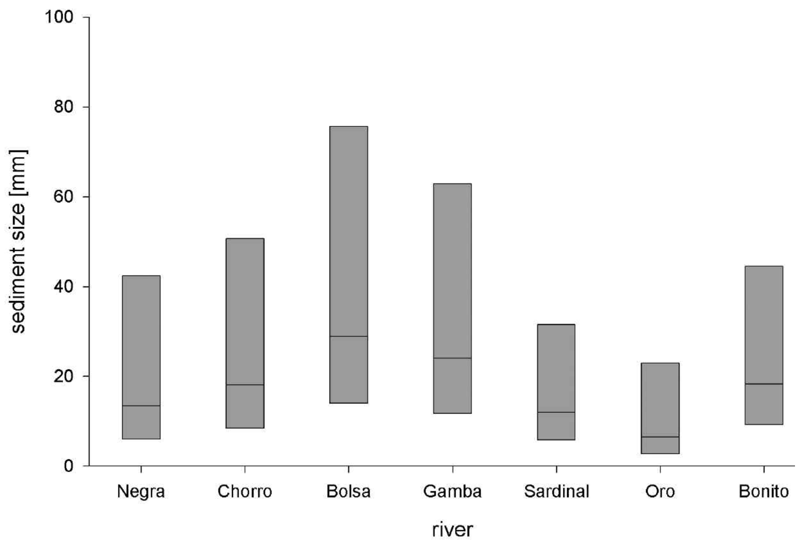


Fig. 6: Comparison of the sediment size [mm] from seven rivers during the rainy season. Arrangement of rivers according to stream order [1^{st} – 3^{th}]. Position of sampling sites is indicated in Fig. 1.

quinas and Río Oro within Fila Costena (Fila Cruces), while all other tributaries originate in Fila Gamba and Golfito (indicated in Fig. 1).

Fila Golfito and Fila Gamba are formed from Late Cretaceous and Early Tertiary rocks of a deep marine sequence of oceanic basaltic flows at the base, followed by deep sea carbonates and volcaniclastics, including some lavas and topped by a volcaniclastic sequence (mainly tuffs) without lava flows. Waterfalls are present here, but are not as characteristic here as they are of the Fila Costena. Sediments of the highest layer of this sequence of the "Golfito Terrane" (Di Marco et al. 1995) are exposed in the Quebrada Bolsa, Chorro and the lower parts of Quebrada Sardinal. Tuffs, siltstones, sandstones, often very coarse breccias, but also thin-bedded (pelagic to hemipelagic) limestones, mudstones and radiolarites (maximum thickness 1 metre, deeply red coloured and sometimes forming jasper) are visible in the profiles. The La Gamba field station and the Esquinas Rainforest Lodge are both located on this unit. Light green tuff crops out on the slope north of the station, whereas fine-grained, medium grey basalt and boulders of basalt breccia are found in the Quebrada Gamba. Layers of grey-green, fine-grained basalt and dykes and sills of dolerite appear in the profiles of Quebrada Bolsa (Malzer 2001).

Quebrada Sardinal originates in the adjoining "Rincon Block", formed almost exclusively by basaltic lavas with only very minor inclusions of radiolarite; this stream enters the Golfito Terrane when discharging into Río Bonito.

The Fila Costena, lying to the north and across an important NW-SE trending fault zone, differs drastically from the Fila Golfito/Fila Gamba area because it belongs to a different megatectonic unit, the "Chorotega Block". It is characterised by shallow marine limestones from the Eocene and shales, sandstones and microconglomerates of Oligocene or Miocene age. There are no major volcanic and volcanoclastic rocks within reach of the investigated rivers. An important feature of the Fila Costena is its steep, rugged, rocky slopes with numerous waterfalls. This catchment area is clearly dominated by carbonate rocks ($CaCO_3$) with possible occurrences of gypsum; high concentrations of $CaSO_4$ are therefore present here.

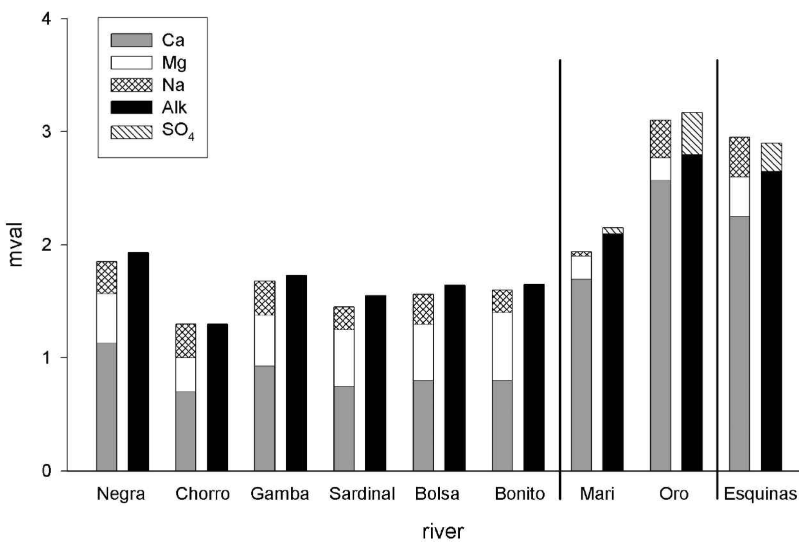


Fig. 7: Ion balances based on concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, alkalinity and SO_4^{2-} [mval] for the nine study streams during the dry season in 2004.

Río Oro and Río Esquinas have the highest alkalinity and concentrations of SO_4^{2-} (Fig. 7). The content of calcium in the Quebrada Negra, Chorro, Gamba, Sardinal, Bolsa and the Río Bonito is between 14.2 and 25.3 mg l^{-1}. Quebrada Mari (34.8 mg l^{-1}), Río Oro (44.4 / 52.4 mg l^{-1}) and Río Esquinas (44.3 mg l^{-1}) show much higher concentrations. Moreover, conductivity of streams originating in the Fila Cruces is also higher (Q. Mari 260 µS cm^{-1}, Río Oro 372 / 314 µS cm^{-1} and Río Esquinas 299 µS cm^{-1}) than in other studied rivers which have their source in the Golfo Dulce area. The reported concentrations of nitrate, phosphate, total dissolved nitrogen and total dissolved phosphorus are clearly correlated with land use. Streams like Quebrada Gamba, Quebrada Bolsa, Río Bonito and Río Esquinas drain agricultural land, which has a strong influence on river chemistry. These rivers are next to plantations (cacao, oil palms and other land use) and have higher nutrient concentrations than those draining forested land. Lowlands are more heavily farmed and settled than upland regions. The pH value of all studied rivers is about 8, in both the dry and the rainy season.

Riparian Vegetation

This species-rich vegetation determines habitat structures, access to light and temperature, provides the organic matter supply (e.g. leaf litter) to the aquatic environment, and reduces the transfer of nutrients and pollutants. These factors have a major influence on the structure and function of fish and macroinvertebrate communities. This special forest type is found along small rivers with adjacent flat terraces. Trees of the riverine vegetation are 35-40 m tall and often have massive trunks with widely spreading buttresses (WEISSENHOFER et al. 2001). The riverine vegetation represents an ecotone — a buffering and intermediate zone between the forest and the aquatic site (SCHIEMER & ZALEWSKI 1992). The abundant riparian vegetation at the Quebrada Negra consists mostly of species typical for headstreams and small rivers in the Golfo Dulce region (see Fig. 8, which represents a vegetation profile at the Q. Negra).

Trees of the canopy layer include *Spondias mombin* (Anacardiaceae), *Cordia cymosa* (Boraginaceae), *Sloanea medusula* (Elaeocarpaceae), *Hyeronima alchorneoides* (Euphorbiaceae), *Lonchocarpus* sp. (Fabaceae), *Carapa guianensis* (Meliaceae), *Castilla tunu* (Moraceae) *Virola koschnyi*, *V. guatemalensis* (Myristicaceae) and *Luehea seemannii* (Tiliaceae).

Prominent species of the mid-canopy layer are *Guatteria chiriquiensis* (Annonaceae), *Welfia regia* (Arecaceae), *Cecropia insignis*, *C. obtusifolia* (Cecropiaceae), *Tetrathylacium macrophyllum* (Flacourtiaceae), *Cupania livida* (Sapindaceae), *Apeiba tibourbou* and *Trichospermum grewiifolium* (Tiliaceae).

The well represented shrub and ground layer contains species like *Dieffenbachia oerstedii*, *Homalomena wendlandii*, *Philodendron* spp., *Spathiphyllum wendlandii* (Araceae), *Asterogyne martiana* (Arecaceae), *Costus pulverulentus*, *C. laevis* (Costaceae), *Carludovica drudei*, *Cyclanthus bipartitus* (Cyclanthaceae), *Episcia lilacina* (Gesneriaceae), various species of Heliconiaceae, *Calathea lutea* (Marantaceae), *Piper auritum* (Piperaceae), *Pentagonia wendlandii*, *Psychotria elata* (Rubiaceae), *Myriocarpa longipes*, *Urera elata* (Urticaceae) and the fern *Nephrolepis* sp. (Oleandraceae).

Epiphytes are common and conspicuous on exposed branches, e.g. *Columnea flaccida*, *C. polyantha* (Gesneriaceae), but lianas are rare.

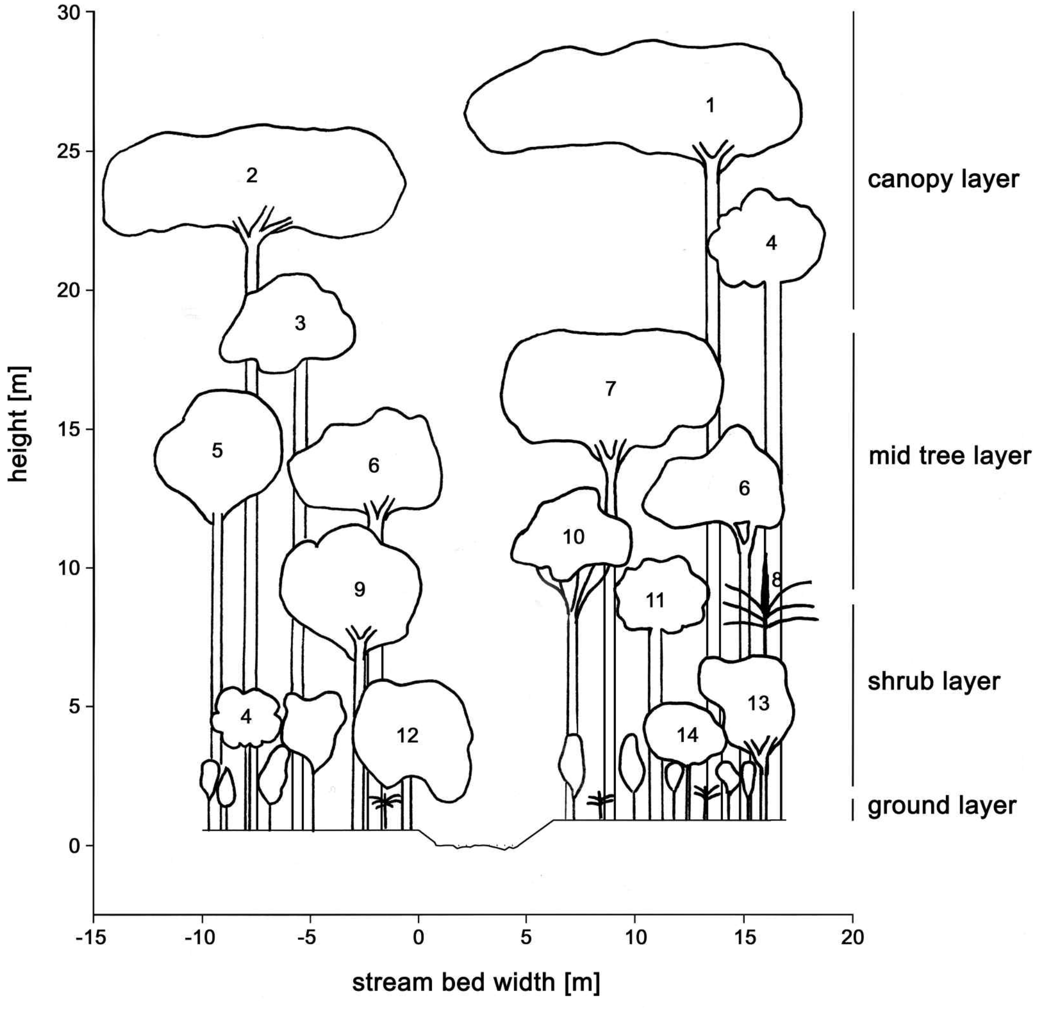


Fig. 8: Riparian vegetation at the Quebrada Negra (~ 300 m downstream from the waterfall and next to the Esquinas Rainforest Lodge). **1**. *Cordia cymosa* (Boraginaceae), **2**. *Carapa guinensis* (Meliaceae), **3**. *Luehea semannii* (Tiliaceae), **4.** *Cecropia obtusifolia* (Cecropiaceae), **5**. *Apeiba tibourbou* (Tiliaceae), **6**. *Tetrathylacium macrophyllum* (Flacourtiaceae), **7**. *Castilla tunu* (Moraceae), **8**. *Welfia regia* (Arecaceae), **9**. *Lonchocarpus* sp. (Fabaceae-Faboideae), **10**. *Virola guatemalensis* (Myristicaceae), **11**. *Cecropia insignis* (Cecropiaceae), **12**. *Acalypha diversifolia* (Euphorbiaceae), **13**. *Myriocarpa longipes* (Urticaceae), **14**. *Alsophila firma* (Cyatheaceae)

At study sites along the larger rivers, the riparian vegetation is often interrupted due to deforestation or logging and therefore adjacent areas are mainly dominated by pasture. These sites (Fig. 1), for example, Río Bonito, Río Oro, Quebrada Bolsa and Río Esquinas, are less shaded than those of headwater streams.

Mangrove forests accompany the sheltered seashore and estuary of the Río Esquinas, where tidal inundation of salt water from the sea occurs. This forest type is floristically poor, thus representing the opposite extreme of the species-rich tropical forest. *Rhizophora mangle* (Rhizophoraceae) and *Pelliciera rhizophorae* (Theaceae) are common and form nearly pure stands.

Quebrada Negra

System-orientated studies concentrated on the Quebrada Negra which is in immediate reach of the Field Station La Gamba. The upper course of the Quebrada Negra is an example of a natural, dynamic and unregulated stream course (see Fig. 9), showing both the mean water depth and the mean current velocity during the dry season.

Streams are highly heterogeneous environments in which habitat characteristics vary drastically over small distances (FENOGLIO et al. 2004). In a naturally flowing river, stream reaches display a more or less regular alternation between shallow areas of higher current velocity and mixed gravel-cobble substrate and deeper areas of slower velocity and finer substrate. Natural dynamics of streams are expressed by these alternating riffle and pool sections. Pool-riffle sequences are the result of particle sorting and require a range of sediment sizes to develop. The intervals of pool-riffle sequences are related to stream width.

The stream is characterised by a wide diversity of habitats with different current velocity, depth and substrate, and represents high heterogeneity. Current velocity, stream depth, stream bed width and sediment size fluctuate within short distances (100 m). Whereas current velocities decrease at pool sequences, riffle sequences are characterised by higher current velocities. Sites where high velocities were recorded have low average depths. In contrast, low velocities occurred at deeper sections (Fig. 10).

Although water depth and current velocity increased during the rainy season in 2004 due to the higher flow caused by heavy rain, the depth and velocity profiles nonetheless resemble those of the dry season. Heavy rainfall during the rainy season caused riverbank erosion, but the pool and riffle sequences showed no major shift between the two seasons within the 100 m course of the Quebrada Negra in 2004.

The hydrograph a continuous record of discharge plotted against time (ALLAN 1995), in Fig. 11 shows the response of the flow of the Quebrada Negra to rainfall from March 2004 to July 2005. With its distinct dry and

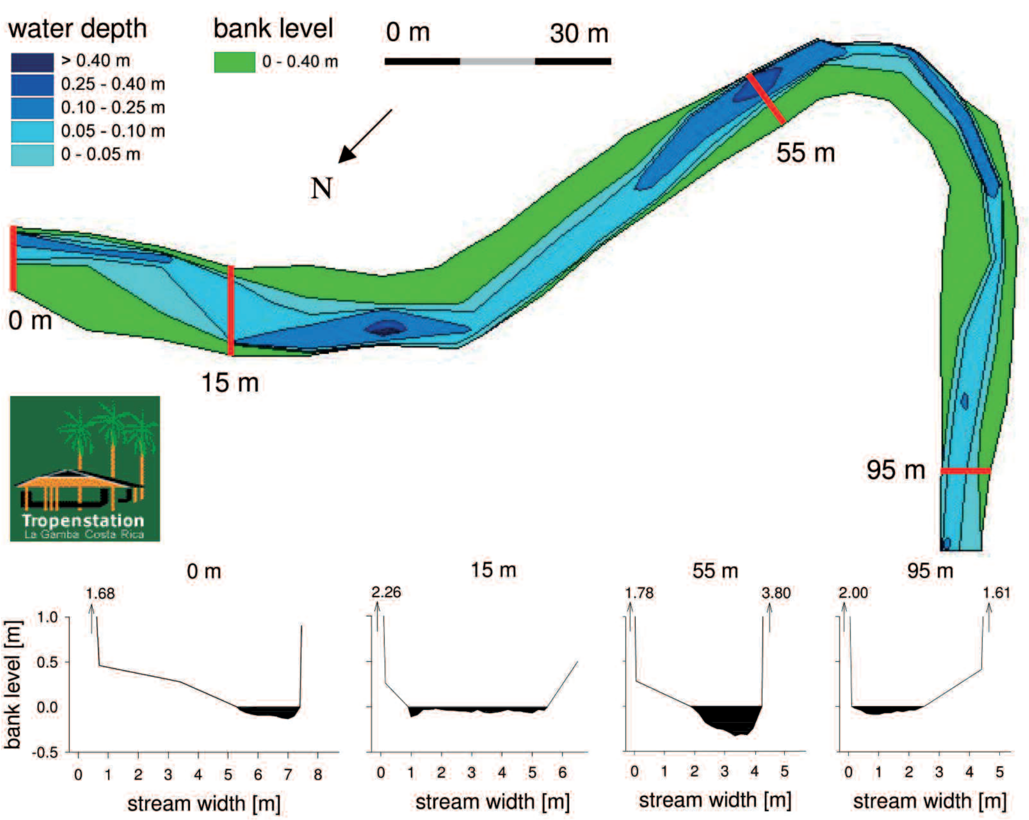


Fig. 9: Course of the Quebrada Negra during the dry season within the 100 m section, with bank level [m] and water depth [m]. Position of the cross sections and the tropical field station are indicated.

rainy seasons, it is a good example for rainforest streams in Costa Rica. Most Central American rivers do not sustain flood conditions for long periods between successive downpours (BUSSING 1993). The water level on 23 February 2004 was defined as a baseline of zero to provide a measure of range and fluctuation in water levels over the observation period. Water level zero has a base flow of 0.020 m^3s^{-1}. Within the sampling time, this was the lowest observed water level. Sudden changes in water level were the rule. High water levels occurred even in the dry season after rain, but water levels were typically higher in the rainy season in months of heavy and continuous rain, when the soil was soaked and runoff was heavy.

The seasonal differences in mean flow discharge are presented in Figure 12. Flow at different water levels was assessed by current velocity measurements along depth profiles at the 55 m cross transect within the 100 m sector. To calculate the mean flow within the two seasons, the average water level of three months of each season was taken. The average water level in the dry season (December, January and February) is 0.4 cm; in the rainy season (August, September and October) the corresponding value is 5.6 cm. This includes average flows of about 22 and 60 ls^{-1}, respectively. High-flow episodes corresponded with a very short time lag to strong rain events. Figure 13 shows that water level fluctuations follow the precipitation. Each peak of heavy rainfall is followed by a rising water level half an hour later. Turbidity generally increased during flooding but cleared quite quickly when rain stopped.

The short-term fluctuations of the Quebrada Negra are very typical and play a more important role than the long-term fluctuations. Water levels rise quickly after the beginning of rain.

Water tends to discharge above ground, and not much water disappears into the hyporheic interstitial (underground). Impermeable rocks or soils with large amounts of clay are one potential explanation for this. These soils absorb moisture very slowly, especially when the soils are deep. A smooth running stream can turn into a torrent very rapidly. Water levels not only rise quickly, but also drop quickly, which can be explained by the high resilience of the rainforest. Sudden changes in water level are the rule for streams and rivers of this region in Costa Rica.

Headwater streams within rainforests, like the Quebrada Negra, receive low irradiance due to the dense riparian vegetation and therefore have a low primary production. Consequently, much of the energy demand by consumers is met from allochthonous sources, especially litter fall. Leaf litter entry into neotropical streams is mostly controlled and often determined by the seasonality of the precipitation. Peaks in leaf fall have been reported during the dry season for Central American forests (DE LA ROSA 1995). Higher leaf fall during the dry season is responsible for the larger litter input into the stream. During the rainy season, most of the leaf litter is transported downstream by flood pulses and higher flow. Riffles and pools show very different leaf accumulations. The former contain more litter because, at shallow sites, leaves accumulate at obstacles and form debris dams.

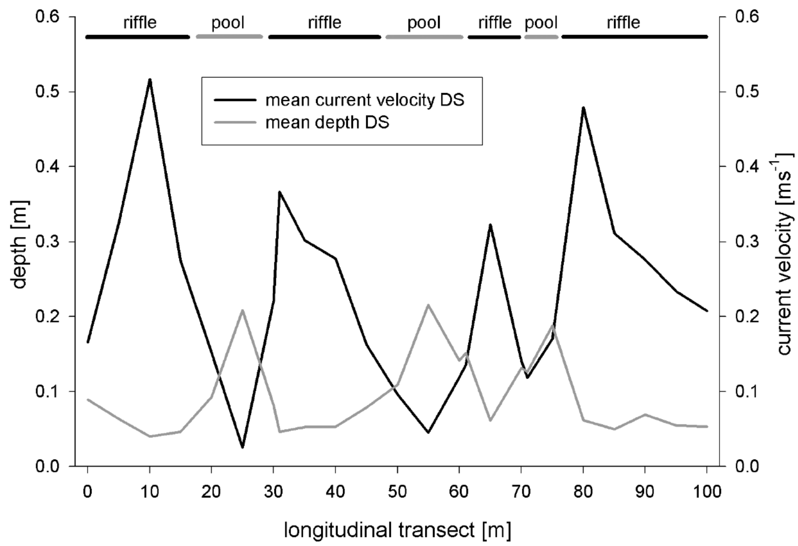


Fig. 10: Mean current velocity [ms^{-1}] and mean depth [m] in the dry season (DS) 2004 within the longitudinal 100 m section.

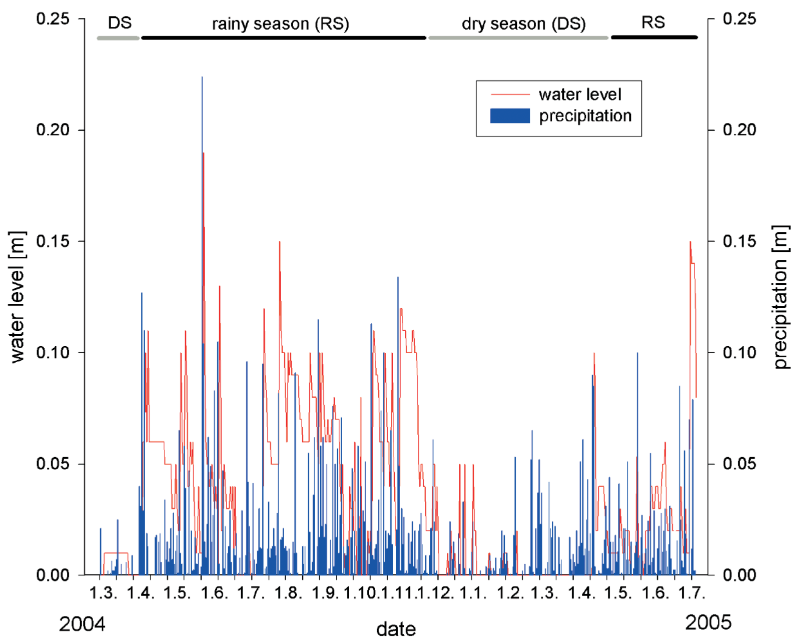


Fig. 11: Water level of the Quebrada Negra and precipitation at the tropical Field Station La Gamba from 23 February 2004 to 1 July 2005.

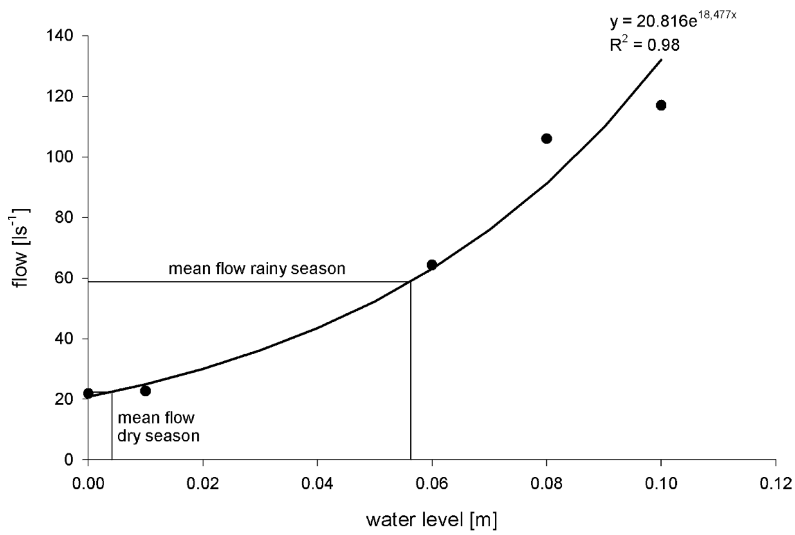


Fig. 12: Measured flow [ls^{-1}] of five different water levels [m] and accounted mean flow [ls^{-1}] of the Q. Negra during the dry and rainy season (based on mean water level for three-month periods).

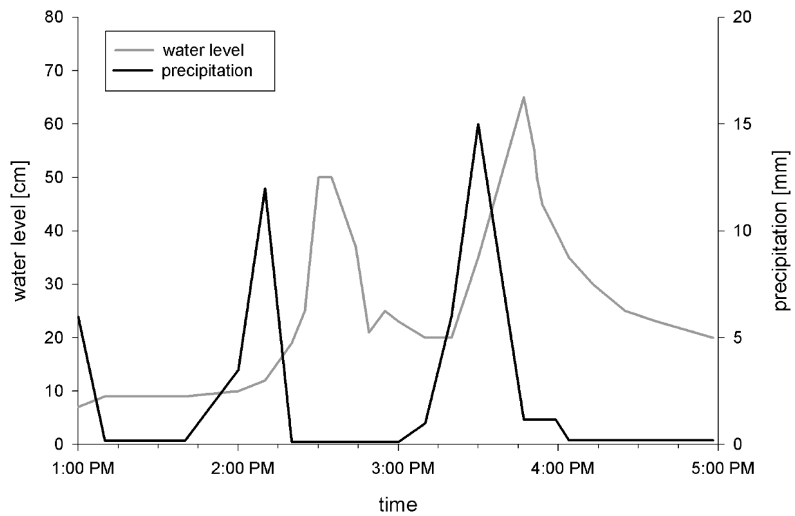


Fig. 13: Short-term fluctuation and detailed recording of the water level and precipitation from 13:00 to 17:00 on 8 August 2004 at the Quebrada Negra.

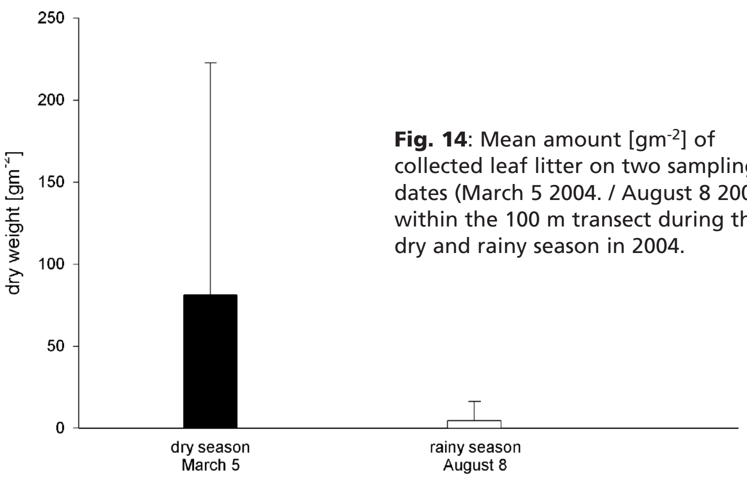


Fig. 14: Mean amount [gm^{-2}] of collected leaf litter on two sampling dates (March 5 2004. / August 8 2004) within the 100 m transect during the dry and rainy season in 2004.

Leaf litter in the Quebrada Negra was recorded as an indicator for the input of organic carbon to the water. Figure 14 shows the huge difference between the two seasons. In the rainy season of 2004, only 4.6 gm^{-2} were recorded versus 81.2 gm^{-2} in the dry season.

The processing of leaf litter in running waters of temperate regions has been the subject of numerous studies, but equivalent tropical ecosystems have received little attention (BENSTEAD 1996). In tropical streams, many leaf types vary in their palatability and tannin levels (DUDGEON & WU 1999). The decomposition and macroinvertebrate colonisation of leaf litter from four different plant species of the riparian vegetation were investigated within the course of the study "Macroinvertebrates and Leaf Litter Decomposition in a Neotropical Lowland Stream, Quebrada Negra, Costa Rica" (TSCHELAUT et al. 2008, RIEMERTH et al. 2008).

Some of the most threatened ecosystems on the planet (e.g. rainforests, coral reefs, freshwater lotic systems) are characterised by extremely complex food webs (LAYMAN et al. 2005). Figure 15 provides an overview of the trophic structure of the rainforest streams of the Esquinas forest. It depicts the trophic interactions and the major trophic pathways based on community composition and the food habits of the major species.

Algae, fine particular organic matter (FPOM), coarse particular organic matter (CPOM) and airborne material are the primary resource basis. The second trophic level is composed of herbivorous macrozoobenthos and fish. Predatory insects, carnivorous and omnivorous fish represent the third trophic level. Piscivore fish are on the top of the trophic pyramid. Many species utilise food from two or more trophic levels.

The abundance of macroinvertebrates provides abundant food for many other predators, including a diverse fish assemblage. Food resources of invertebrate consumers include periphyton and other surface layer complexes, macrophytes, detritus and other animals.

We examined the trophic structure of macroinvertebrates using the system of functional feeding groups (FFG) according to MERRITT & CUMMINS (1996). The classification of the invertebrate consumers of streams into feeding guilds has proved to be very useful for descriptive and analytical purposes (CUMMINS 1973).

The Quebrada Negra invertebrate fauna is, in terms of species numbers, mostly made up of collector-gatherers (53.3%), followed by predators (16.5%), filterers (14.5%), shredders (8.5%) and grazer-scrapers (6.5%). The functional and taxonomic macroinvertebrate composition is quite similar to that reported from other Costa Rican lowland streams (PRINGLE & RAMIREZ

1998, ROSEMOND et al. 1998, RAMIREZ & PRINGLE 2001).

Due to the low periphyton production in the Quebrada Negra, scrapers and grazers were poorly represented and constitute only 6.5% of the macroinvertebrate community.

Ephemeroptera was the most significant group of collector-gatherers, and within this group the Leptohyphidae (20.1%) and Leptophlebiidae (6.9%) were most abundant. Predators were the second major feeding group, dominated by Tanypodinae (7.8%, Diptera, Chironomidae).

Net-spinning caddisflies (Philopotamidae and Hydropsychidae) are passive filter feeders, constructing nets in exposed locations. Larvae of black flies (Simuliidae) are highly specialised suspension feeders.

Major invertebrates that feed on decaying leaves (shredders) in our study stream include crane fly larvae (Tipulidae) and beetles (esp. Ptilodactylidae). Shredders such as Calamoceratidae (caddisflies) were only reported from leaf litter bags within the study "Macroinvertebrates and Leaf Litter Decomposition in a Neotropical Lowland Stream, Quebrada Negra, Costa Rica" (TSCHELAUT et al. 2008).

Fish are conspicuous and important components of tropical river food webs. Fish species almost certainly occupy several of the functional feeding groups and probably exert the greatest impact. Trophic diversification in tropical river fish assemblages is greater than that of in similar habitats of temperate regions that contain less species (WINEMILLER 1991, WINEMILLER & JEPSEN 1998). Compared to temperate river fish, tropical fish show proportionally more herbivorous, detritivorous and omnivorous feeding behaviours (WINEMILLER 1990, 1991; WOOTTON & OEMKE 1992). Seasonality plays an important role in tropical river food webs. Flooding brings fish into contact with a greater abundance and diversity of allochthonous food resources, especially within forested watersheds (GOULDING 1980; HENDERSON 1990). In the Quebrada Negra, population sizes and densities of Poeciliidae decreased from the dry to the rainy season. This

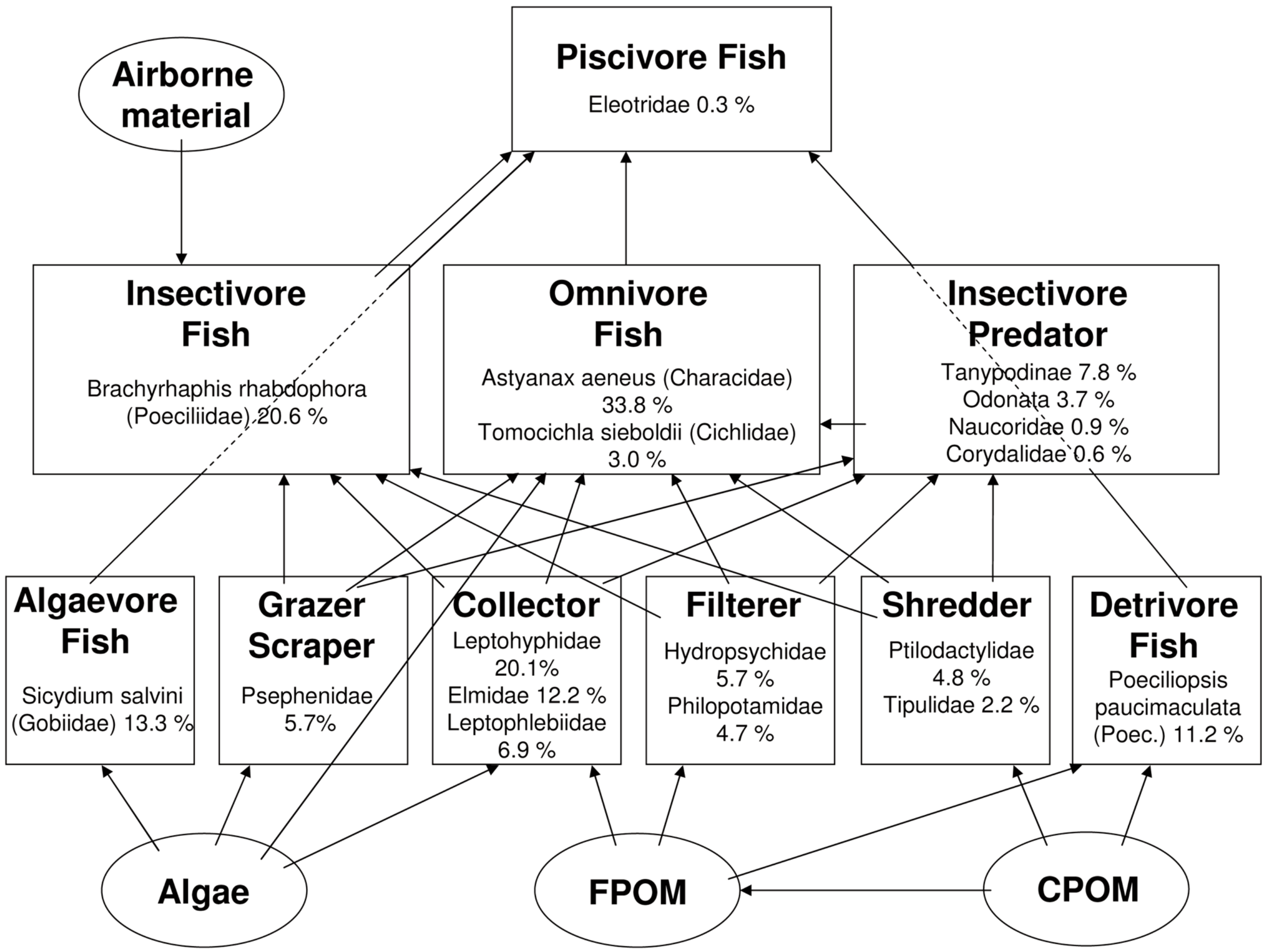


Fig. 15: Simplified food web and major trophic pathways, Quebrada Negra, Costa Rica. Ellipses are the resource basis. Major sampled species/families with their percentage of total numbers (fish: n = 1373; macroinvertebrates: n = 738) are shown.

may reflect seasonal variation in food supply since the availability of algae and detritus is reduced after floods. Periphyton production most likely decreased in the rainy season because of water turbity and decreased light availability. Detrital sources increase in the dry period due to seasonal leaf fall (CHAPMAN & CHAPMAN 1990).

The survey of rivers lays the basis for further research activities on the aquatic habitats within the Piedras Blancas National Park. Promising research avenues will be a test of the ecotone and the River Continuum Concept in tropical lotic systems for their global applicability.

The seasonal climate (dry and rainy season) provides good conditions for testing the food web theory and niche partitioning in neotropical lotic systems. Understanding the ecological energetics will require detailed research on biogeochemical aspects of rainforest river systems, nutrient retention and nutrient spiralling and the role of biofilms.

The Piedras Blancas National Park freshwater invertebrate fauna is largely unsurveyed and undescribed. This protected area in the south of Costa Rica offers an unique opportunity to study the tropical lotic invertebrate community and to identify the relative role of seasonal changes in physico-chemical factors, and in the availability and nature of food resources, in explaining temporal patterns in the functional organisation of macroinvertebrate communities.

Results from such studies can be used to predict taxa distribution at local small scales and to identify factors that can influence micro-distribution patterns in the lotic system.

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References

ALLAN J.D. (1995): Stream Ecology – Structure and function of running waters. — Chapman and Hall.

ARRINGTON D.A., WINEMILLER K.C. & C.A. LAMAN (2005): Community assembly at the patch scale in a species rich tropical river. — Oecologia **144**: 157-167.

BENSTEAD J.P. (1996): Macroinvertebrates and the processing of leaf litter in a tropical stream. — Biotropica **28**: 367-375.

BUSSING W.A. (1993): Fish communities and environmental characteristics of a tropical rainforest river in Costa Rica. — Rev. Biol. Trop. **41**: 791-809.

CHAPMAN C.A. & L.J. CHAPMAN (1990): Density and growth rate of some tropical dry forest trees: Comparisons between successional forest types. — Bull. Torr. Bot. Club **117**: 226-231.

CUMMINS W.K. (1973): Trophic relations of aquatic insects. — Ann.Rev.Entomol. **18**: 183-206.

DE LA ROSA C. (1995): Middle American streams and rivers. — In: CUSHING C.E., CUMMINS C.W. & G.W. MINSHALL (eds). Ecosystems of the world 22 – River and stream ecosystems. Elsevier Science B.V. **7**: 189-218.

DI MARCO G., BAUMGARTNER P.O. & J.E.T. CHANNEL (1995): Late Cretaceous – Early Tertiary paleomagnetic data and a revised tectonostratigraphic subdivision of Costa Rica and Western Panama. — Geol. Soc. Amer. Special Paper **295**: 1-27.

DUDGEON D. (1993): The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream. — Freshwat. Biol. **30**: 189-197.

DUDGEON D. & Y.K.K. WU (1999): Leaf litter in a tropical stream: food or substrate for macroinvertebrates? — Arch. Hydrobiol. **146**: 65-82.

FENOGLIO S., BO T. & M. CUCCO (2004): Small scale macroinvertebrate distribution in a riffle of a neotropical rainforest stream (Río Bartola, Nicaragua). — Carib. J. Science **40**: 253-257.

FLECKER A.S., TAYLOR B.W., BERNHARDT E.S., HOOD J.M., CORNWELL W.K., CASSATT S.R., VANNI M.J. & N.S. ALTMAN (2002): Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. — Ecology **83**: 1831-1844.

FÜREDER L. (1994): Driftmuster in tropischen Bächen am Beispiel Costa Rica. — Dissertation, Naturwissenschaftliche Fakultät der Leopold-Franzens-Universität Innsbruck.

GOULDING M. (1980): The fishes and the forest. Explorations in Amazonian Natural History. — University of California Press, Berkeley.

HENDERSON P.A. (1990): Fish of the Amazonian Igapo: stability and conservation in a high diversity-low biomass system. — J. Fish Biol. **37**: 61-66.

HOENIGHAUS D.J., WINEMILLER K.O. & D.C. TAPHORN (2004): Compositional change in fish assemblages along the Andean piemont – Llanos floodplain gradient of the Río Portuguesa. Venezuela. — Neotropical Ichthyology **2**: 85-92.

JACKSON K.J. & W.B. SWEENEY (1995): Present status and future directions of tropical stream research. — J. N. Am. Benthol. Soc. **14**: 5-11.

JEPSEN D.B. & K.O. WINEMILLER (2002): Structure of tropical river food webs revealed by stable isotope ratios. — Oikos **89**: 46-55.

LAYMAN C.A., WINEMILLER K.O., ARRINGTON D.A. & D.B. JEPSEN (2005): Body size and trophic position in a diverse tropical food web. — Ecology **86**: 2530-2535.

LEWIS W.M. (1987): Tropical limnology. — Ann. Rev. Ecol. Syst. **18**: 158-184.

MALZER O. (2001): Geological history of Central America and the Golfo Dulce Region. — Stapfia **78**: 34-46.

MERRITT R.W. & K.W. CUMMINS (1996): An introduction to the aquatic insects of North America. — Third Edition, Kendall/Hunt Publishing Company.

NEWBOLD D.J., SWEENEY W.E., JACKSON C.J. & A.L. KAPLAN (1995): Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. — J. N. Am Benthol. Soc. **14**: 21-37.

PRINGLE C.M. & A. RAMIREZ (1998): Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. — Freshwat. Biol. **39**: 359-373.

RAMIREZ A. & C.M. PRINGLE (2001): Spatial and temporal patterns of invertebrate drift in streams draining a neotropical landscape. — Freshwat. Biol. **46**: 47-62.

RIEMERTH A., GUSENLEITNER M., DRAXLER G., WANEK W. & F. SCHIEMER (2008): The role of leaf anatomy and tannins in litter decay in a tropical stream. — In this volume.

ROSEMOND A.D., PRINGLE C.M. & A. RAMIREZ (1998): Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. — Freshwat. Biol. **39**: 515-523.

SCHIEMER F. & M. ZALEWSKI (1992): The importance of riparian ecotones for diversity and productivity of riverine fish communities. — Netherlands Journal of Zoology **42**: 323-335.

TSCHELAUT J., WEISSENHOFER A. & F. SCHIEMER (2008): Macroinvertebrates and leaf litter decomposition in a neotropical lowland stream, Quebrada Negra, Costa Rica. — In this volume.

VANNOTE R.L., MINSHALL G.W., CUMMINS C.W., SEDELL J.R. & C.E. CUSHING (1980): The River Continuum Concept. — Can. J. Fish. Aquat. Sci. **37**: 130-137.

WEISSENHOFER A., HUBER W., ZAMORA N., WEBER A. & J.GONZÁLEZ (2001): A brief outline of the flora and vegetation of the Golfo Dulce Region. — Stapfia **78**: 15-24.

WINEMILLER K.O. (1990): Spatial and temporal variation in tropical fish trophic networks. — Ecol. Monographs **60**: 331-367.

WINEMILLER K.O. (1991): Ecomorphological diversification of freshwater fish assemblages from five biotic regions. — Ecol. Monographs **61**: 343-365.

WINEMILLER K.O. & D.B. JEPSEN (1998): Effects of seasonality and fish movement on tropical river food webs. — J. Fish Biol. **53**: 267-296.

WOOTTON J.T. & M.P. OEMKE (1992): Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. — Env. Biol. Fish. **35**: 311-319.

Addresses of authors:

Julia TSCHELAUT
Christian PICHLER
Fritz SCHIEMER
Department of Limnology and Hydrobotany
University of Vienna
Althanstr. 14
A- 1091 Vienna, Austria
E-mail : tschuliebuhlie@yahoo.de
c.pichler@tele2.at
friedrich.schiemer@univie.ac.at

Anton WEISSENHOFER
Department of Palynology and Structural Botany,
Faculty Center of Botany
University of Vienna,
Rennweg 14
A-1030 Vienna, Austria
E-mail : anton.weissenhofer@univie.ac.at

Plate 1: (**a**) Quebrada Negra, (**b**) Quebrada Chorro; (**c-d**) Rio Bonito.

Plate 2: (**a-b**) Quebrada Sardinal; (**c-d**) Rio Esquinas.

Contents/Indice

PLANT BIOLOGY — BIOLOGÍA DE PLANTAS

Ecosystems and vegetation — Ecosistemas y vegetación

Plant diversity — Diversidad de plantas

Life forms — Formas de vida vegetal

Ecophysiology — Ecofisiología

Mammals — Mamíferos

Limnology — Limnología

PLANT-ANIMAL INTERACTIONS — INTERACCIÓNES DE PLANTAS Y ANIMALES

Pollination — Polinización