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The ecology of the Iberian inland waters: Homage to Ramon Margalef

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The ecology of the Iberian inland waters: Homage to Ramon Margalef

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Ramon Margalef (1919-2004): teacher and researcher

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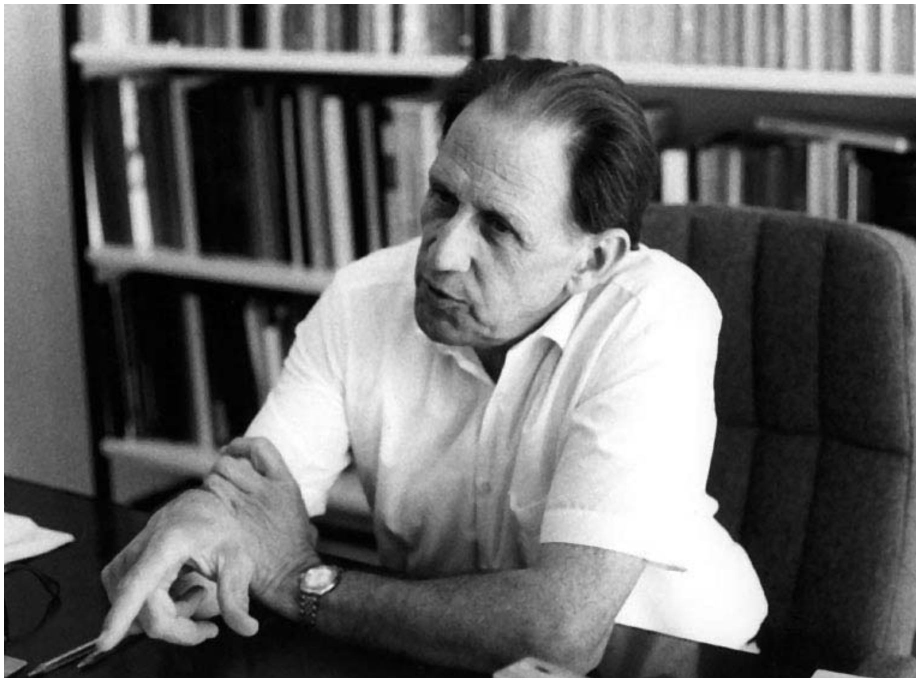

The May 23th, 2004 Professor Ramon Margalef died in Barcelona at the age of 85. While not unexpected, his death equalled his life in simplicity and dignity. The professor had refused to be subjected to a treatment that could artificially prolong his life, wholly in keeping with the tenor of his character. Already in 1979, Margalef presented some very interesting thoughts, still valid today, on r- and K- strategy behaviours amongst human populations, the generational problem and the lengthening of life span in some human populations in the article "El precio de la supervivencia. Consideraciones ecológicas sobre las poblaciones humanas" (Margalef, 1979). In it, there is a sentence which has kept its full force over time, considering the circumstances that led to his death. I remember it quite clearly as, even back then, I found it profoundly disturbing and, quoting from memory, it goes something like:" I would not like to enjoy the privileges medicine granted to Franco and Tito". It looks to me as if this sentence were what we call a living will "*avant la lettre*" and, in it as in so many respects, professor Margalef was way ahead of his time. However, I would not like to dwell on this subject which leads me to very painful recent memories, but to write about his life as a teacher and researcher at the University of Barcelona from the perspective of one of his pupils who got introduced the world of ecology by the hand of professor Margalef and lived side by side with him during part of his "golden years" of scientific research.

Margalef was not especially didactic as a teacher, at least not for those who preferred well organised lectures that allowed the taking of clear and methodical notes, with outlines to complement the explanations in class. We need not forget that until 1974 we cannot talk of a “book on ecology that could complement his lectures”. Until the publishing of *Ecología* (Margalef, 1974), we felt fortunate enough if we had a barely readable cyclostyled copy in thick paper of “Comunidades naturales” (1962), a compilation of some of the lectures he had given at a course on ecology in Puerto Rico which had been published in an unconventional way. His lectures would be a continuous improvisation and, even though there was a well-outlined thread in the syllabus, you could hardly follow it during the lecture on any given day. He followed, or better, pretended to follow some notes he had scribbled on one of those index cards we used to write down bibliographical notes. During the class, however, he would keep bringing up new topics to end up talking about the ones that were of his interest at that moment. More than once, you would write down that there were different ways of facing a specific aspect of an issue only to realise that he expanded on one of them and forgot about the rest. They could of course have been dealt with, or not, but that didn’t seem to worry him at all.

But please do not reach false conclusions from my previous words: his lectures were speeches in the creative sense of the word as he was giving us a state-of-the-art account of key aspects of contemporary ecology, continually updated, as he was leading it himself together with E. Hutchinson, R. H. McArthur, the Odum brothers (Tom and Eugene) and R. Lewontin, amongst others. In his classes, he would bring up the latest books and articles from the latest issues from the most prestigious magazines and he would use them as the backbone of the lesson. I clearly remember as one time, during a lesson on marine plankton, he got sidetracked into talking about a most interesting book he was reading at the moment and about biology of leaves and he started to argue on how many times the surface of the earth could be covered if all the leaves were put one right next to the other one. A kind of biospheric foliar index which led to his reflecting on the idea of why life had not evolved towards one unique species that would cover the whole surface of the Earth, with an autotrophic top layer and an heterotrophic bottom layer, and he even predicted that its thickness would have to be no more than a few millimetres at the most, enough so that there would be a redox potential difference between layers, enough to balance production with respiration. This idea of a planet covered by just one species was the complete antithesis of the concept of biosphere but he used it to stimulate our thinking about what the biogeochemical cycles would be like within a system with no diversity, little biomass, but possibly a lot more efficient in the capture of energy from sunlight through photosynthesis. Margalef underwent cataract surgery in the days before laser surgery and with techniques that were a lot more invasive and required several days in hospital, and therefore we can imagine what it meant for him to spend those days with the eyes bandaged and with nothing else to do but to meditate on some of his favourite subjects. He asked for a cassette player to be brought to him and he recorded a story about a human expedition to a planet that fulfilled the requirements mentioned above, too long to relate now. Unfortunately, the recording is lost, even though it would nowadays be more relevant as a testimony of Margalef’s personality rather than for the subject itself. What we can infer from these anecdotes is that Margalef enjoyed these kind of theoretical approaches similar to Einstein’s *Gedankenexperimente* and the ones by other physicists of his time, although they were not quite the same. I am referring to experiments whose realization is frequently impracticable but which nevertheless lead to reliable results. In Margalef’s case, these mental experiments were not merely theoretical, but were based on a deep and perceptive observation of nature, on simple experiments and the application of regularities he had observed in nature that were based on ecological successions. For Margalef, perfect crime didn’t exist even in nature and the observation of natural phenomena allowed him to detect casual linkages that led him to discover principles that had gone unnoticed until then. That’s why Margalef had always regarded himself as a naturalist. “He dignified the meaning of naturalist”, wrote Joandomènec Ros (Ros, 2004) not too long ago to recall Margalef’s passion for nature, and Margalef himself preferred this term to all others to describe his scientific activities. For this reason, some authors have adopted Josefina Castellví's views that "talking about ecology is talking about Margalef, but talking about Margalef certainly implies a lot more than talking about ecology". With these words, "more than ecology", we mean the observation and study of nature along with deep intellectual interests.

I do not want to expand on the emerging principles of ecology that Margalef developed together with the most prestigious ecologists of his time, Hutchinson, McArthur and the Odums amongst others, or on his lifelong contributions to theoretical ecology as they have been described in detail by other authors (Bascompte and Solé, 2005; Flos, 2005; Walter, 2005). However, I would like to emphasize that, in my opinion, the most relevant article published by Margalef is "On certain unifying principles in ecology" (Margalef, 1963). Very few times more has been said with fewer words. In this paper, Margalef presented a series of emerging principles based on the ecological succession and with them he started dissecting nature. In other words, he started to study and measure all ecosystems, from the least productive seas, such as the Mediterranean, to fertile ones like the Sahara upwelling. Likewise, the Mediterranean forest, the rainforest, the small pond, the biggest lakes or dams, the coral reefs or caves, they all became the subject of his studies. Nothing escaped his ability to discern patterns and the results were spectacular. The best of his comparisons can be found in "Perspectives in ecological theory" (Margalef, 1968), where we are able to realize how powerful the tool he had created was. No wonder this book is one of the top 10 most cited works in ecology and is fully up-to-date. Just to mention a few examples that are far from exhaustive of the application of these emerging principles: Margalef deduced that the natural evolution of lakes was from eutrophic to oligotrophic aquatic systems if the influx of nutrients or organic matter was cut off (Margalef, 1968). He also explained the dynamics of a river population as an equivalent to space succession (Margalef, 1960) and the seasonal dynamics of phytoplankton as a microsuccession (Margalef, 1978). The direct consequence of this last idea led him to develop the concept of biological types of phytoplankton as an adaptation of the species to a double gradient of concentration of nutrients and of turbulent kinetic energy, with his famous mandala model (Margalef, 1980). From those research topics he developed the concept of external or exosomatic energy and its relevance in the organisation of communities. Societies or systems that use more exosomatic energy are the ones that exploit or dominate the other ones. I would suggest a "Gedankenexperimente" to you and to apply this thesis to the present geopolitical situation for the control of the non-renewable natural resources and reach your own conclusions. Margalef used to do it as well, whether to study a coral reef or to analyze any level of organisation of human populations (Margalef, 1992).

And, going back to the topic of Margalef as a teacher, I have to stress that all the advantages and disadvantages I mentioned before helped split his students in two groups: the ones that liked his classes and the ones that didn't, with no intended disrespect towards the latter. Margalef was passionate of natural selection and he considered it could be applied to all aspects of life and at all levels of human organisation. He was, therefore, capable of giving a pass to some students who didn't deserve it while telling them "life will fail you" or "look, I give you a pass but promise me you will never teach the subject or work in anything related to ecology". It is true that he didn't like being too hard on students during exams. He was, however, strict in his selection of the students that deserved the best marks.

Exams are always a source of stress no matter the subject or the professor, but with respect to the exams on ecology, they had the disadvantage they were also atypical as far as the questions were concerned. Many times the problem lay in the way he formulated the questions and not in the subject itself. Margalef was always on the lookout for the bright student who could become a disciple and would show some degree of originality and he would pick the best by asking questions in his particular way. Some questions were handed down from year to year by senior students to the freshmen so that they knew what to expect. The questions might be of the sort: "Why are the taxis in Barcelona black and yellow? They may seem a bit esoteric to the students that are being introduced to the subject for the first time but it would not be an insurmountable obstacle if you knew anything about aposematic coloration. Other questions such as “effect of the Coriolis force in the curvature of the antlers of antelopes, in the growth of branches in the tree trunks, and in the distribution of the genus *Velella*” were meant to sort out outstanding students who could have otherwise remained unnoticed. No matter how hard the exams were, the percentage of passes and failures never changed, with passes to failures at about 2-to-1 ratio. However, many of the students that got a pass were aware of Margalef’s opinion of them when they got back the exam together with a mark which was obviously a fail. The exams of the ones that didn’t pass do not even deserve to be mentioned. Regarding the exams we had to take during our own 1970-1971 ecology course, Margalef suffered from an extra dose of originality as he decided to abolish the traditional Napoleonic exams, with the students locked up in a classroom while they were answering questions. The novelty consisted in a short meeting with all the students early in the morning in the Department library where he hand us two topics to expand upon: we had from 9 a.m. until 4 p.m. when we had to stop by his office and hand him the paper we had written on one of the two topics we had chosen. I have to admit that I had a very bad time over it and many of my classmates shared my feelings due to the difficulty of trying to write something original while having all the notes, books and other means at hand. A few days later he told us we didn’t deserve this kind of exams as we had done so badly in general. To a chosen group of us, who had done well, he let us take a second non-Napoleonic term exam but we had no chance of a third for the final exam and we all went back to the traditional system. I remember that during this first exam four of my classmates handed in an essay which was the result of a joint effort, probably very well thought out as they got an A. They had, however, to share the mark democratically amongst the four of them, with the result of an obvious fail.

I have so far commented on professor Margalef’s teaching career, but he pursued a career in research beyond this aspect of teaching which I would downright call frantic. In the first years of existence of the Ecology Department, Margalef combined his work between the University of Barcelona and the Fisheries Research Institute (IIP) of CSIC. He would go to IIP on Tuesdays and Thursdays and spend the rest of the week at the university. He had his own research team at each one of the centers: the marine biologists Marta Estrada in Barcelona and Miguel Alcaraz and Xavier Niell in Vigo, while at the university, the limnologists Dolors Planas and Rosa Miracle, who were at the time, early 70’s) beginning their research work at the lake of Banyoles plus a group of students who would go during their free time and amongst which I counted myself. Tecla Riera was Margalef’s assistant and was soon joined by Joandomènec Ros and the department became divided into two kind of doctorate students, the marine ecologists and the fresh water ecologists.

The writing of *Ecología* (Margalef, 1974), with its 951 pages, dates from that period. I suppose that, as with anything else, some people are better at writing than others but the way Margalef would write can only be described as extraordinary. His Olivetti typewriter sounded like a machine gun that only stopped when the letters hit the rubber cylinder with a different sound as when there was paper. It was time to stop, pick up the paper from the floor if it was handy or at least the carbon paper, as he used two sheets and some carbon paper to keep a copy. The writing began early in the morning, right after the ecology class, which started at 8 a.m. to allow him more time for his writing. He would seldom have a break, just enough for a coffee and he dealt quickly with any visits. He stopped writing at around 2 p.m., picked up the sheets that might have fallen to the floor, sorted them out, numbered them and piled them up at one end of the table and would call it a day just to continue two days later as if nothing had happened in between. We have to remember that on alternate days he went to IIP and he used the afternoons to attend to other matters. He kept the typed sheets inside a metallic cabinet in brown folders bound with a rubber band. On the cover of the folder he would leave handwritten notes and some of the sheets inside would also be full of them. The 951 pages could easily consist of 3000 or more sheets which made quite a considerable stack. While writing, he would include all the bibliography he remembered and then he would go over the text and insert the missing references by hand. The draft copy was finished in one year. The final writing of the book was not a mere copy of the first one but a full rewriting that took almost as long. If we take a look at Margalef's bibliography during those years, 1971-73 (Ros, 1991), we realise that he had time to write articles on the side that can match the amount of articles published in the previous and later years. The writing of *Limnología* (Margalef, 1983), with its 1010 pages, followed a similar pattern to the one described above and I will obviously not go over it again.

Peter Wangersky, from the University of Halifax, who spent some sabbatical stays in Barcelona, used to say that Margalef could work right through a three-ring-circus show without losing track and being at his most efficient.

Margalef was a person who didn't get out of the office much but his door was always open and students and graduate students alike could visit him there any time we wanted, although we could always tell if he was eager to get on with something else or deeply involved in his thoughts. Tecla Riera was in a way a kind of transmission belt that would keep him connected to the department despite his many other information sources based on his observation skills. He knew what was going on, even though he didn't interfere much. Whenever he proposed a research topic, he felt enthusiastic about it and even anticipated the results he expected if everything turned out well. On many occasions, he would use the pages of his desk calendar to scribble and sketch data to supplement his initial exposition. When he was done, he would tear the page and somehow you would find yourself standing in the corridor, or in the office or the library staring at it, trying to figure out what it said while trying to remember what Margalef had said in relation to what while he was going on about his ideas. We all had to work in a specific taxonomic group and from there we could fit in all the ecology we were able to develop. In those days, the zoological and botanical taxonomists that worked in Margalef's department were equivalent in numbers to the ones that made up the respective departments. Quoting Xavier Ferrer, "he would send us on a single-handed voyage along the seas of research and, as a rule, he wouldn't warn you of any possible dangers" (Ferrer, 2004), always consistent with his belief in natural selection. The results would be uneven and, the same as with his students, some would just disappear discreetly without him losing any sleep over it.

As I have mentioned earlier, he had this incredible capacity for transmitting enthusiasm for the ideas that interested him. You would come out of his office holding the calendar sheets feeling you were going to start a research project that would achieve a major breakthrough in ecology. Other times, he would ask you offhand about your progress and he liked to be shown the results and would get all excited if he considered them relevant and had no qualms about mentioning these results in his papers.

Margalef founded three scientific magazines and he was a regular contributor with his papers *Publicaciones del Instituto de Biología Aplicada* (PIBA), *Investigación Pesquera* (IP) and *Oecologia aquatica*. The issues of PIBA or IP are hard to find and the articles published in them, quite often written by Margalef himself, are very rarely read. Big mistake, as you can find some gems amongst them, as not only would he present and interpret data, but he would also anticipate some of the results and conclusions and formulate hypotheses that he would develop later on. Nowadays this type of approach or projection of the results is called speculative science. "Too much speculative" is the fatal sentence that you can usually find in the letter editors send to reject a paper for publication when you spend too much time on the data assessment or on the conclusion. Margalef was not afraid to expound his ideas even though many times he himself admitted he was not able to prove them at the present stage of information available. Many of the criticisms he received from later ecologists were of the kind that he had this habit of jumping ahead while leaving many gaps to be filled, some of which have already been filled and some are still pending. The wealth of ideas we find in his writings in PIBA or IP can already be found in his earlier works, many of them geared towards the general public. In that sense I can recommend some booklets from the end of the 40's published by Seix y Barral that took up less than a hundred pages and that he wrote as a complement to a meagre salary to help support his family of six. That's why, with a mischievous smile, he used to call these papers "nutritional ecology". The topics, of course, were varied but all juicy nevertheless: *La vida en el mar, Los insectos sociales*, *Las plantas carnivoras* are some of the titles I have been lucky enough to read many years after they were written. One of my favourites has always been the latter as in it he predicted the new food adaptation of carnivorous plants, an example of allotrophy. According to Margalef, this adaptation came about because they had no other chances of obtaining nutrients through more orthodox means. A few years later we had the chance to prove his theory right at the old department in University old building with a specimen of *Sarracenia* he had brought from Canada and which we had kept for a long time in a crystallizer, watering it with distilled water and with regular visits to the genetics department to get a pot full of *Drosophyla* to feed to it.

From the many activities going on at the department, the so-called magic soirees on Thursday afternoon were of special interest. We euphemistically called that to the seminars held by Margalef. They were open activities and they were not based on a previously announced topic; we would just attend and if it was time and nobody came up with a topic, Margalef would stand up and start talking about something that could lead to a discussion, without necessarily having to reach any conclusions. Many of the graduate students at IIP used to take part in those seminars and also many physicists, Jorge Wagensberg amongst others, and many of the physicists involved in the group of complex systems. Jordi Flos was the one that started calling these seminars magic soirees not because of the topics being discussed but for the way the ideas would flow, just like rabbits coming out of a magician's hat. Flos gives a short but interesting account of those seminars in his book *Ecología, entre la magia y el tópico* (Flos, 1984).

Ramon Margalef kept up his activities until his illness prevented him from leaving his house, and that was for a very short time. He kept coming to his office at the department, mostly as an incentive to walk around the libraries of the faculties of Biology, Geology and Physics and Chemistry. He remembered what day the issues from *Science*, *Nature* or many other magazines were expected and there he was, ready to be the first one to read them. His personal evolution during his last years was clearly the one of a K strategist, with a mental lucidity and incredible observation skills which he now used on himself. He didn't mind talking about his illness and how his life had been altered because of it. He used to say he found interesting the way we lose memory, "just like the hard disk of a computer; clusters get deleted without having any links with one another".

He used to come and see us and he liked to stop by for a chat and tell us about his ideas and projects he thought interesting and could no longer embark on. He was concerned about the big man-made changes to the landscape, and he used to call them "the inversion in the landscape topology". At the same time, he was interested in the number of cells of many species from a same taxonomic group that, according to him, was discontinuous at the species level. He used to compare those discontinuities to shoe size, "sort of a quantic cytometry", and was as always worried about nutrients, with a special emphasis on phosphorus. During the opening speech of the Second Iberian Congress of Limnology in Valencia (June 2000), he insisted on his concerns over the pending issues and the relevance of their study in the future. He wrote these words in a short but delightful article, "Cabos sueltos" (2001), published one of the previous volumes of *Limnetica*, and it can be considered as a sort of future projection of his ideas.

He used to enjoy our visits to him at his home. Delivering his mail was always a good excuse; just that many times there were several of us just for a few letters. Even though his memory was failing him, you could immediately tell if the subject caught his attention as he would awaken, his eyes would sparkle and would start up a typical Margalefian discussion. He admitted that our visits helped him while away the "black hours", as he called the hours he spent by himself or in the company of his dear wife Maria. He died as he would have liked, on a Sunday, surrounded by his whole family and able to say his last goodbye to them.

It was then when many of us found out he had been a religious person and were finally able to understand some moments in his life when he had shown extreme fortitude. Pere Ynajara, parish priest from Sta. Eugenia del Congost and a good friend for many years, presided over the funeral service and during the homily he spoke about many aspects of his personality amongst which I would like to single out the sense of irony Margalef would display on many occasions. “He was worried about what would happen to his nutrients”, the priest told us. Which is logical as, being a religious person, he couldn’t have had many doubts regarding more spiritual matters. I can assure you I have no doubts he said it, nutrients being an issue that interested him and one that, once again, he applied on himself. Well then, I can only say that I truly hope his nutrients soon get to an oligotrophic ecosystem, such as the Mediterranean Sea, the waters around Mallorca or the Gulf of Lyons or along the coast of Castellón, the places he studied, described and became the basis of many of his scientific hypotheses. In those waters of great diversity and biodiversity, with low P/B values, with an internalization of the nutrient cycle, great pigment diversity and big sized K- strategist species, there is where I hope he can continue to enjoy the wonderful world he helped us understand.

May he rest in peace.

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Leaf litter processing in low order streams

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ABSTRACT

Forests produce a large amount of detritus, that inevitably end up in streams, subsidizing aquatic systems with organic matter and nutrients. Here we review some of the research carried out at the University of Coimbra with the objective of getting a better understanding of the breakdown process of these materials and its incorporation to secondary production. Litter-fall in deciduous forests in Central Portugal can reach up to 750 g AFDM of leaves m^{-2} yr^{-1}, with 73% of the litter produced between October and December. In several retention experiments, we measured a 90% leaf retention in low order (1^{st}- 4^{th}) streams within 15 – 70 m, and a standing stock of up to 450 g AFDM m^{-2}. The amount of nutrients in the water and the plant physical and chemical defenses can be an indicator of the rate at which plant material is incorporated into secondary production or exported as dissolved and fine particles of organic matter. Respiration rates of decomposing leaves incubated with fungicides were severely reduced, supporting the idea that fungi are very important agents in litter breakdown. The fungi group known as aquatic hyphomycetes are capable of producing enzymes able to cause leaf maceration, and by 2 to 3 weeks, up to 15 % of the decomposing leaf biomass corresponds to fungi. Shredder invertebrates are also biological agents involved in litter breakdown. Given their densities and feeding rates, we measured consumption rates of 12 – 54 g of leaves m^{-2} yr^{-1} in a stream in Central Portugal, corresponding to 2 to 9 times the litter standing stock. Feeding rates were high in nutrient rich leaves and low in chemical and physically protected leaves with low nutrient content. According to several experiments, fungal colonization facilitates the access of invertebrates to the energy trapped in deciduous leaves in streams. Some invertebrates have strategies to cope with low quality food (leaves with low microbial biomass or high chemical defenses). Those include high mobility, small size, compartmentalized digestion in the gut, presence of endosymbionts, and the capability to decrease respiration rates. The relative importance of fungi and invertebrates in the incorporation of plant litter material into secondary production varies across rivers and biomes. Shredder invertebrates seem to play a key role in litter breakdown in headwaters, but their importance appears to decrease downstream. In the same way, some systems where leaves are hard or protected, shredder invertebrates may be less abundant and the energy may be mainly recovered from litter by fungi. Eucalyptus plantations are systems with low diversity of invertebrates and aquatic hyphomycetes. Streams running through eucalyptus plantations seem therefore ideal to experimentally investigate relationships between structural parameters (biodiversity) and function. Finally, our research has been extended to other climatic areas including the Mediterranean and tropical streams. We reported a wide variety of situation in those systems. A general rule applying to all of them is that if leaf litter is abundant and high quality, the incorporation of energy into detrital food webs can be processed very quickly. However, if leaves are well protected and nutrients in the water are low, processing rates are equally very low, independently of the ambient temperatures.

Key words: litter balance, decomposition, fungi, detritivores, Mediterranean and tropical streams.

RESUMEN

Los bosques producen una gran cantidad de detritus orgánicos, que inevitablemente llegan a los ríos, subsidiando los sistemas acuáticos con materiales y nutrientes. Aquí se revisan algunos de los trabajos que se han hecho en la Universidad de Coimbra con el objetivo de entender mejor el proceso de descomposición de este material y su incorporación en producción secundaria. La entrada de hojarasca en bosques caducifolios del Centro de Portugal puede alcanzar hasta 750 g PSLC (peso seco libre de cenizas) m^{-2} año^{-1}, con 73 % de este valor ocurriendo entre Octubre y Diciembre. En varios experimentos de retención medimos que cerca de 90 % hojas que entran en ríos de baja orden (1^a- 4^a) eran retenidas entre los 15 y 75 m, y que la biomasa de hojarasca acumulada era de hasta 450 g PSLC m^{-2}. La cantidad de nutrientes en el agua y las defensas físicas y químicas de las plantas pueden ser un indicador de la tasa a que el material orgánico es incorporado en producción secundaria o exportado como material disuelto o finamente particulado. Las tasas de respiración de hojas incubadas con fungicidas disminuyeron severamente apoyando la idea de que los hongos son agentes muy importantes en la descomposición de hojarasca el los ríos. El grupo de hongos conocido como hifomicetos acuáticos producen enzimas que causan la maceración de hojas, y en 2 o 3 semanas, hasta 15 % de la biomasa de una hoja en descomposición puede corresponder a hongos. Los invertebrados desmenuzadores son también agentes biológicos en la descomposición. Dadas las densidades de desmenuzado-

res y sus tasas de ingestión de alimento, hemos calculado tasas de consumo de hojas en ríos de12 – 54 g m^{-2} año^{-1}, lo que corresponde a 2 a 9 veces la cantidad de hojarasca presente. Las tasas de consumo son generalmente altas en substratos ricos en nutrientes y bajas en hojas pobres en nutrientes o protegidas del punto de vista químico y físico. De acuerdo varios experimentos, la colonización por hongos facilita el acceso de los invertebrados a la energía de las hojas. Algunos invertebrados han desarrollado estrategias para poder vencer la baja calidad de las hojas, incluyendo un alta movilidad, tamaño pequeño, compartimentalización de la digestión en el intestino, presencia de endosimbiontes y la capacidad para disminuir las tasas respiratorias. La importancia relativa de los hongos e invertebrados en la incorporación de la hojarasca en producción secundaria es variable entre ríos y biomas. Los invertebrados desmenuzadores parecen jugar un papel importante en la descomposición de hojarasca en los ríos de bajo orden, pero su importancia parece disminuir rió abajo. Del mismo modo, en algunos sistemas en que las hojas son duras o protegidas, los invertebrados pueden ser menos abundantes y la energía canalizada en producción secundaria principalmente por los hongos. Las plantaciones de eucaliptos son sistemas con una baja diversidad de invertebrados e hifomicetos acuáticos. Los ríos que corren por plantaciones de eucaliptos parecen ser por este motivo sistemas ideales para investigar las relaciones entre parámetros estructurales (biodiversidad) y función. Finalmente, nuestra investigación ha sido extendida para otras zonas climáticas, incluyendo el Mediterráneo y las zonas tropicales. Hemos reportado una gran variedad de situaciones en esos sistemas. Una regla general a todos ellos es que si la hojarasca es abundante y de alta calidad, la incorporación de la energía de las hojas en las cadenas alimentares se procesa de forma muy rápida. Sin embargo, si las hojas están bien protegidas y los nutrientes el agua son bajos, estas tasas son igualmente muy bajas, independientemente de las temperaturas ambientales.

***Palabras clave**: Balance de la hojarasca, descomposición, hongos, detritívoros, arroyos mediterráneos y tropicales.*

ALHOCHTHONOUS ORGANIC MATTER IS AN IMPORTANT ENERGY SOURCE FOR FORESTED LOW ORDER STREAMS

Forests are among the most productive systems on Earth with primary production reaching 1800 g dry mass m^{-2} year^{-1} in the tropics. Even boreal forests are more productive than cultivated lands (850 vs. 750 g dry mass m^{-2} year^{-1}, respectively; Ricklefs, 2000). In forested systems less than 5 % of the primary production will be lost to herbivores (Ricklefs, 2000); this implies that a very large proportion of the energy fixed in forests will end in the detrital pathways (Fig. 1). This is particularly evident in deciduous forests with litter-fall ranging from 300 to 800g dry mass m^{-2} year^{-1}, or with > 1000g dry mass m^{-2} year^{-1} in tropical forests (reviewed Abelho, 2001).

With such an amount of litter production, it is virtually impossible that leaves, fruits, seeds, twigs, and other plant remains, will not end in streams. Moreover, trees in the riparian zones shade the small streams, decreasing in this way the amount of solar energy which could be used by primary producers. Therefore, litter shed by trees is likely to be a key energy source for low order streams running through forests. It is therefore ecologically relevant to understand the fate of energy and nutrients in those systems. At the University of Coimbra, Portugal, we have been addressing several aspects of litter decay in small streams for the last 15 years. Here we review the main findings of our research.

LITTERFALL AND THE DYNAMICS OF ORGANIC MATTER

How are leaves retained in streams? Can we predict decomposition rates of leaves based on their intrinsic characteristics? What is the relative role of the environment in litter decomposition? What are the main agents affecting litter decomposition? To address some of those questions we began measuring litter dynamics in deciduous forests in Central Portugal. In a forest dominated by *Castanea sativa* Mill., annual litter-fall reached 750 g m^{-2} yr^{-1}, with 73 % of litter produced between October and December, which is consistent with other results reported for deciduous forests. Nearly 90 % of the leaves falling into low order streams in Central Portugal were retained in within 10 – 70 meters, with retention decreasing downstream (Canhoto & Graça, 1998). Retained litter accumulates in the stream-bed before being processed or washed away during floods; we measured standing stocks of organic matter of 50 – 450 g AFDM m^{-2} in streams of central Portugal. These values were much higher than the standing stock of periphyton (6 g m^{-2}; Abelho & Graça, 1998) in the same river. Moreover the amounts of coarse particulate organic matter in rivers tend to decrease downstream, whereas the standing stocks of benthic algae tend to increase in the same direction (Cortes *et al*., 1995).

Decomposition is therefore a critical ecosystem process, determining the availability of nutrients for primary producers. Can we predict the rate at which leaves decompose? The answer, to some extent, is yes. We found that decomposition rates increase with nitrogen content of leaves and decrease with the amount of plant chemical and physical defenses (Cortes *et al*., 1994; Canhoto & Graça, 1996). Decomposition rates also tend to increase with nutrient content in the water. This information is important for conservation, restoration and management of riparian zones. "Cleaning" streams by removing wood and other retentive features and removing stream-shading vegetation is a bad environmental practice. Although litter decomposition proceeds until all material is mineralized, this paper will refer to the breakdown of large particles of organic matter and not to the processing of fine particles or dissolved organic matter.

DECOMPOSERS

When leaves enter the streams, their nitrogen content generally increases. This is evidence of microbial colonization, which can be corroborated by the increase of ATP and oxygen consumption of leaves (Abelho *et al*., 2005). Moreover, leaves start loosing mass at a rate proportional to microbial colonization (Suberkropp & Chauvet, 1995); decomposition is therefore a biological process and a measurement of the rate of incorporation of leaf material into secondary production.

Figure 1. Leaf litter accumulated on soil in a Eucalyptus plantation. *Hojarasca acumulada en el suelo de una plantación de Eucaliptus*.

Which are the microorganisms involved in litter decomposition? There is evidence from the literature, that fungi are more important than bacteria in this process in terms of biomass and production (e.g. Pascoal & Cassio, 2004; Abelho *et al*. 2005). In a tropical stream, we found that leaves exposed to fungicides had lower respiration rates and lower microbial biomass than leaves exposed to bactericides. Other authors concluded that even under organic pollution conditions, production of bacteria in leaves is lower than fungal production (Pascoal & Cassio, 2004).

It is also generally accepted that fungal decomposers of leaves are aquatic hyphomycetes (Fig. 2; Gessner & Chauvet, 1994; Gulis & Suberkropp, 2003), since just after submersion a large amount of conidia start detaching from leaves (e.g. Bärlocher, 2000). However, many geofungi have been also isolated from decomposing submersed leaves plated over agar. What is the relative role of both types of decomposers in the decomposition of organic matter in streams? To answer this question we measured the capability of several species of geofungi and aquatic hyphomycetes to cause leaf maceration in water and under laboratory conditions. Only aquatic hyphomycetes caused significant leaf maceration (measured as mass loss and decrease in tensile strength) and had higher enzymatic (xylanase, pectinlyase and polygalacturonase cellulose C1 and Cx) activity in submerged substrates than terrestrial fungi isolated from leaves (Graça & Ferreira, 1995; Rodrigues & Graça, 1997). Softening was correlated with the activity of all enzymes, especially xylanase ($r_s = 0.94$; $P< 0.001$).

Our conclusion is that when falling in the water, leaves are already colonized by terrestrial fungi, but their activity is severely depressed. In the water, leaves are rapidly exposed to thousands of spores of aquatic hyphomycetes (e.g. Bärlocher & Graça, 2002) that germinate and grow into the leaf substrates (Canhoto & Graça, 1999) and produce degrading enzymes (Canhoto *et al*., 2002).

Many of the chemical and physical plant defenses against pathogens and herbivores may remain active after senescence. Thick cuticles may have a two-fold role in plants, by decreasing water losses and retarding fungal attack. One of the explanations for the lower decomposition rates of some eucalyptus leaves in nutrient poor streams is the presence of a thick cuticle. Electronic microscopy observations showed that fungi can only penetrate into the leaf mesophyll of eucalyptus leaves through stomata and cracks at the waxy cuticle (Canhoto & Graça, 1999).

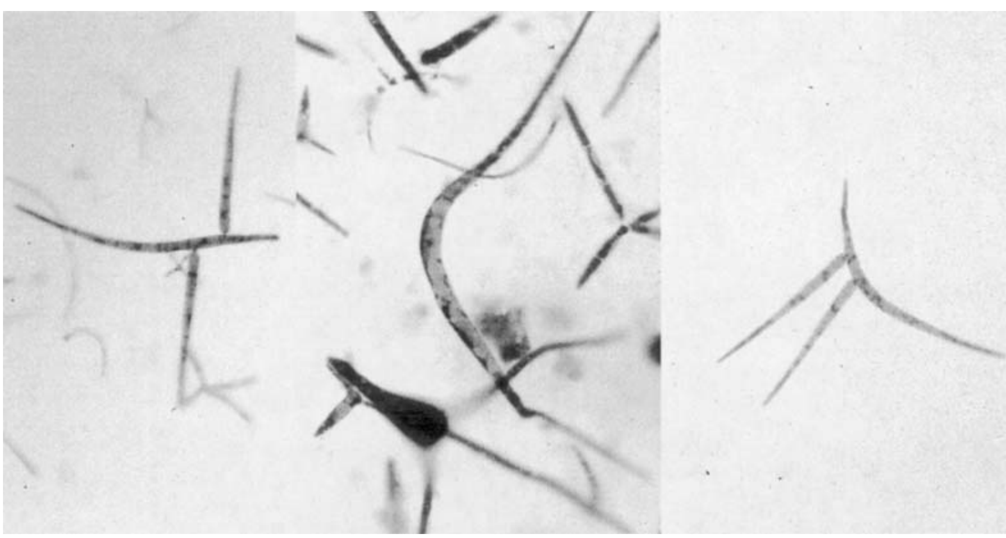

Figure 2. Spores of aquatic hyphomicetes: left and right: *Tricladium splendens*; center: *Clavariopsis aquatica*, *Articulospora tetracladia* and a sigmoid. (Photos by Felix Bärlocher). *Esporas de hifomicetes acuáticos: izquierda y derecha:* Tricladium splendens*; centro:* Clavariopsis aquatica, Articulospora tetracladia *y un sigmoide (Fotos de Felix Bärlocher).*

Another defense of eucalyptus leaves is the presence of oils, allocated in glands. In eucalyptus leaves, oils may account for up to 5 % of leaf mass (Canhoto & Graça, 1999) and they are known to be have antibiotic properties. They were found to also reduce or suppress growth of aquatic hyphomycetes *in vitro* (Canhoto & Graça, 1999) and interfere with microbial enzymes (Canhoto *et al*., 2002). Fungal sporulation from eucalyptus leaves was retarded when compared with other leaves, but the removal of cuticle and oils resulted in accelerated sporulation (Canhoto & Graça, 1996; Bärlocher *et al.,* 1995). The extraction of oils from eucalyptus leaves also resulted in an increase of consumption by the shredder *Tipula lateralis*, whereas the transference of eucalyptus oils to alder leaves resulted in a decrease in food consumption by the same shredder.

DETRITIVORES

Many stream invertebrates use leaf litter as a food resource. Besides incorporating leaf material into secondary production, shredder invertebrates fragment leaves and produce a large quantity of fecal pellets. The result is the transformation of coarse particulate organic matter (C.P.O.M.) into fine particulate organic matter (F.P.O.M.), which may constitute an important food source for other organisms we call "deposit feeders" and "filter feeders".

Feio & Graça (2000), González & Graça (2003), and Azevedo-Pereira *et al.* (2006) calculated for a mountain stream in Central Portugal that the mean annual consumption of leaves by the caddisflies (*Sericostoma vittatum* Rambur and *Lepidostoma hirtum* (Fabricius)) was, respectively, 12 – 22 g m^{-2} $year^{-1}$ and 54 g m^{-2} $year^{-1}$. These values correspond to 2 – 9 times the leaf standing stock of the stream. Shredder invertebrates have therefore a key role in the trophic ecology of low order streams (reviewed Graça 1993, 2001).

Several factors can constrain the access of invertebrates to the energy trapped in leaves. To start with, a reduced number of animals have the enzymatic capability to use the structural compounds of leaves. How do they manage to access the plant energy? We have been studying energy transference from litter pool to invertebrate shredders, using the caddisflies *Sericostoma vittatum* Rambur, and *Lepidostoma hirtum* (Fabricius), as well as the crane fly *Tipula lateralis* Meigen (Fig. 3) as test organisms. Leaves differ in their quality for shredders as asserted from measurements of feeding rates, food choice experiments and growth rates (*e.g.* González & Graça, 2003). The incorporation of leaf material into invertebrate secondary production proceeds at a faster rate in nitrogen rich and soft leaves, when compared with nitrogen poor, chemically protected, hard leaves (Canhoto & Graça, 1995; González & Graça, 2003). The implication is that changes in the frequency of leaf types and therefore forest practices may affect the dynamics of invertebrates in streams. Moreover, litter-fall in temperate areas occurs mainly during autumn, and litter is composed by a mixture of leaves differing in their quality. Leaves of high quality such as alder are quickly consumed, whereas leaves of more recalcitrant species, such as oak, take longer time to be fully colonized and degraded by microorganisms, but they can be a good resource for later in the season. If the mixture of leaves is replaced exclusively by leaves of high quality, it may supply shredders with a large input of high quality food for a short period of time, but energy may lack in later stages. On the other hand, if streams are provided only with low quality resources, food may be scarce early in the season.

Figure 3. Larvae of *Tipula lateralis*, a stream shredder. *Larva de* Tipula lateralis*, un triturador fluvial.*

INTERACTIONS BETWEEN DETRITIVORES AND FUNGI

One common observation on the ecology of shredder detritivores is that they preferentially feed on fungal colonized leaves in laboratory (Suberkropp, 1992; Graça *et al*., 1993b) and field conditions (Graça, 1992). They also feed and grow faster, survive better and have a larger reproductive output when leaves are fully colonized by fongi (Graça *et al.*, 1993b). The reason seems clear: fungal colonization cause leaves to increase nitrogen content (because of fungal biomass) and leaf maceration, benefiting in this way from microbial enzymes (Suberkropp, 1992; Graça *et al*., 1993b; Graça, 1993). Some shredders do selectively consume the leaf patches with high fungal mass or selectively feed on fungal biomass growing on the surface of the leaves (*e.g.* Graça *et al.,* 1993b; Graça *et al*., 2000).

SOME NOTES ON THE ECOLOGY OF SHREDDERS

Fast moving invertebrates are very active visiting patches were litter accumulates and probably remaining for short periods of time in the patches if the food quality is low. For invertebrates with low mobility, high selectivity may not be an option because if they reject less-profitable food they may spend a long time searching before they encounter food again. Invertebrates with low mobility may be more efficient in taking their energetic requirements from low quality food.

Tipulidae larvae are slow moving invertebrates that inhabit streams. Unlike carnivore tipulids, shredder tipulids have an alkaline anterior gut with a pH 10.5 – 11 (*e.g.* Bärlocher & Porter, 1986; Graça & Bärlocher, 1998; Canhoto, 2001). At such a high pH, the gut proteolytic activity of these tipulids remain active and is not affected by polyphenolics from leaf extracts (Graça & Bärlocher, 1998). This strategy therefore, allows for a maximum protein extraction and, at the same time, the plant defenses are overcome. In the posterior section of these tipulids gut, pH values are neutral/alcaline and a high number of endosymbionts seem to have a key role in the digestion of the plant polysaccharides.

In a series of laboratory experiments, we found that *Gammarus pulex* (L.) was able to maintain growth even when low quality food was supplied whereas that did not happen with the less active *Asellus aquaticus* L. (Graça *et al*., 1993a). *G. pulex* compensated for low quality food by reductions in respiration rates. Although another form of compensation may be the increase of food intake to maintain a constant energy / nutrient income (*e.g.* Calow, 1975; Rollo & Hawryluk, 1988), in most cases, shredding invertebrates decrease their energy intake when fed low quality food.

WHAT IS THE RELATIVE IMPORTANCE OF INVERTEBRATES AND FUNGI IN THE INCORPORATION OF LEAF ENERGY INTO FOOD WEBS?

The relative importance of invertebrates and fungi in litter breakdown, and therefore in the incorporation of energy trapped in leaf tissues into food webs has been a matter of debate (see references in Graça, 2001). Apparently, whereas fungi are omnipresent in all flowing waters, the densities of shredder invertebrates can be controlled by other factors, including the quality and quantity of the litter. Therefore, in some systems invertebrates can be considered as unimportant in energy transference in detritus based systems, while in other cases they may be the key elements. For example, Hiebber & Gessner (2002) calculated that, in a stream, fungi were responsible for removing 15 – 18 % of leaf mass, whereas the values for shredder invertebrates were 51 – 64 %. On the other hand, Gonçalves *et al.* (2006) calculated that almost no litter energy in the form of coarse particulate organic matter was taken into secondary production by invertebrates due to the high recalcitrant properties of Savannah Cerrado streams.

As the availability of coarse particulate organic matter tends to decrease downstream and nutrients in the water to increase in the same

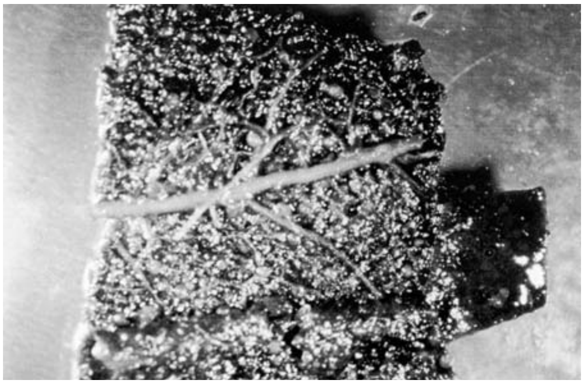

Figure 4. Eucalyptus leaf with oil glands in white. *Hoja de eucalipto con las vesículas de aceite en blanco.*

direction, it is plausible that the role of both types of organisms change along the longitudinal gradient. We tested this hypothesis in a series of streams, ranging from 2nd to 6th order in Central Portugal. Decomposition rates did not differ along the longitudinal gradient (see also Cortes *et al*., 1995). However, microbial role on litter decomposition increased downstream as judged by the difference in mass loss in leaves incubated in coarse and fine mesh bags. Consistently, the density in spores in the water column increased downstream, whereas the density and percentage of shredder invertebrates increased upstream. This relationship was observed only in spring / summer. It is conceivable that during autumn / winter there might be a surplus of energy in the form of leaves and the impact of invertebrate feeding on litter breakdown may then be small (Graça *et al*., 2001b).

STRUCTURAL AND FUNCTIONAL PARAMETERS IN DETRITUS BASED SYSTEMS

Detritus based systems are a ground for testing some ecological theories. For instance, species replacement has been analyzed from the structural point of view but we can learn a lot on the functional changes related to species replacement by invasions. Species invasions have shown to affect community structure, sometimes with the reduction of biodiversity due to local extinctions and the dominance of introduced species (Towsend *et al*., 2000). Given that decomposition is controlled by nutrient related factors and plant defenses, can we predict the ecological effects of species introductions?

If the plant invader is a nitrogen fixing species, then we may expect that the turn over of organic matter to be accelerated. However, if the invaders are chemically or physically protected, decomposition and therefore the rate at which energy re-enters the biota component of ecosystems to be retarded. Invaders are very common in riparian areas (*e.g.* Vitousek, 1996) and we have been testing these assumptions by looking at soil and aquatic systems.

In a series of litter breakdown experiments in which introduced *vs.* native and high quality (N content) *vs.* low quality (high protection) leaves in soils and water were compared, it was found that decomposition rates and associated processes such as microbial and invertebrate colonization were independent of plant origin, but could be explained by intrinsic leaf proprieties (Pinto *et al*., 1997; Pereira *et al*., 1998).

In aquatic systems we compared streams bordered by native deciduous and eucalyptus plantations. Eucalyptus are originally from Australia, but they are nowadays ubiquitous in several parts of the world. Vast areas in the Iberian Peninsula are planted with eucalyptus. This subject was reviewed by Graça *et al.* (2002) and will not be treated in detail here, but we can summarize the changes associated to eucalyptus plantations in the following way:

In eucalyptus plantations the seasonality of litter-fall is altered from an autumn peak to an even litter-fall along the year or a summer peak if the hydrological stress is high. The average standing stock of organic matter was not different between native deciduous and eucalyptus plantations; streams or tended to be higher in eucalyptus plantations, probably because of spates and bark accumulation, which increases litter retention. Fungi accumulate in decomposing leaves at similar rates in both stream types. Eucalyptus leaves are a low quality substrate for shredder invertebrates and fungi, as judged from: (a) their oil content with antibiotic properties (Fig. 4), affecting fungal growth, fungal digestive enzyme activity (Canhoto *et al.,* 2002), and (b) feeding experiments with invertebrates in which there was a decrease in surviving, growth and feeding rates when fed with eucalyptus leaves. Oils inhibit fungal growth and invertebrate consumption *in vitro* (Canhoto & Graça, 1999). Elimination of leaf lipids resulted in faster decomposition and high sporulation by aquatic hyphomycetes (Bärlocher *et al*., 1995).

Maybe for those reasons, invertebrate and fungal richness was low in Portuguese streams running through eucalyptus plantations. Because assemblages of decomposer and detritivore species are poor in eucalyptus streams, we have an ideal model system to investigate relationships between community structure and ecosystem functioning. For instance, Bärlocher & Graça (2002) reported that although streams running through eucalyptus forests had lower number of aquatic hyphomycete species, decomposition rates of chestnut (*Castanea sativa*) were similar (but see Abelho & Graça, 1998).

TROPICAL SYSTEMS

The ecology of low order streams is well established for temperate areas, but scarce in other zones. Most of the literature on the dynamics of litter-fall and the fate of organic matter entering streams is based on research carried out in North America and Europe. A quick survey in the "Web of Science" was run for citations on papers dealing with litter breakdown in streams from 2000 to 2004 and 110 references were found, 44 % from North America, 30 % from Europe, 8 % from the Mediterranean, 8 % from Australia and New Zealand and 2 % for the rest of the world, revealing that patterns of litter dynamics in forested stream systems are based upon research carried out in a restricted geographic area. Do the reported patterns apply to areas with different productivity, seasonality and hydrology? Do invertebrates and microbes play a similar role in other climates?

In a series of feeding trials we found that, as reported for tempered shredder species, tropical shredders also selectively feed on microbial colonized leaves, and there was a tendency for growth rates to be reduced in the absence of microbial assemblages in the leaves. The rate at which leaves are incorporated into secondary production was more variable in the tropical areas than in temperate ones. In experiments carried out in tropical cloudy forests in Venezuela, decomposition rates were fast, with 50 % of leaf mass loss in less than 10 days in leaves of *Hura crepitas* L. The leaves of this species were found to be equivalent to those of *Alnus glutinosa* (L.) in terms of food resources and decomposition rates (Graça *et al*., 2001a and unpublished data). However, in Savannah streams, in Brazil (Cerrado), it took 90 days for alder leaves to loose 50 % of their mass (Gonçalves *et al*., 2006). Apparently, the availability of leaves, their quality, and water chemistry are important factors explaining the differences.

CONCLUSION

Detritus based systems are ideal to test many current ecological theories. They can be studied at community, population, and auto-ecology levels. Litter decomposition is also a research field in which the knowledge of several areas of science (plant ecology, biochemistry, mycology, population ecology, and others) is needed. If organic matter breakdown is an important process in streams, factors interfering with the activities of fungi and invertebrates are likely to affect the functional process of decomposition. Therefore, decomposition rates may be used as indicators of functional status of streams, as proposed by Gessner & Chauvet (2002).

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