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Leaf litter addition experiments in riparian ponds with different connectivity to a Cerrado stream in Mato Grosso, Brazil*

by

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Abstract

Using standardized artificial substrates (bricks and nylon nets), we analyzed the effect of different treatments on benthic invertebrate colonization in riparian ponds of a Cerrado stream in Mato Grosso, Brazil. Treatments were (1) leaf litter (removal vs. addition of naturally fallen, undecomposed leaves), (2) connectivity (meander pond: direct connection; connected pond: indirect connection; and isolated pond; no connection to the stream) and (3) season (dry vs. rainy season). Benthic invertebrate colonization was generally low. Approximatly 78 % of all animals were chironomids, with microcrustaceans (cladocerans and harpacticoids) together making up nearly 7 %, springtails 3 %, caddisfly larvae 2.1 %, mayfly larvae 1 %. The isolated pond was the least densely colonized habitat, with highly significant lower densities than the two connected ponds (Factorial ANOVAs, $p < 0.0001$). Season had a strong effect on colonization density, which was significantly higher during the rainy than during the dry period ($p = 0.001$). Significant positive effects of the litter addition treatment on invertebrate colonization were only found during the dry season in the meander pond, where invertebrate densities increased about threefold between litter-free and litter-added treatments ($p = 0.03$). All other combinations showed a slightly negative, non-significant effect of litter addition. As only few specimen of shredding invertebrates were found, we concluded that recently fallen leaf litter seems to be more important as a mechanical matrix for colonization, FPOM retention and cover from predators, than as a food source in riparian ponds of Cerrado streams.
Keywords: **Stream, pond, connectivity, riparian zone, leaf litter, Cerrado.**

*Dedicated to Dr. Ilse Walker on the occasion of her 75th birthday.

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Resumo

Utilizando substratos artificiais padronizados (tijolos e redes de nylon), foram analisados os efeitos de diferentes tratamentos em poças de um córrego de cerrado em Mato Grosso, Brazil. Os tratamentos empregados foram (1) serapilheira (ausência vs. adição de folhas naturalmente caídas, porém não decompostas), (2) conectividade (uma poça natural num meandro do córrego com conexão direta, uma poça indiretamente conectada, e uma poça isolada sem conexão com o córrego) e (3) estação (época chuvosa vs. época seca). A colonização por invertebrados bentônicos foi geralmente baixa, sendo que 78.2 % do total corresponderam a Chironomidae, microcrustaceos (Cladocera e Harpacticoida) juntos contribuíram com menos que 7 %, Collembola 3 %; larvas de Trichoptera e Ephemeroptera, 2.1 % e 1 %, respectivamente. A poça isolada foi a menos densamente colonizada, e que demonstrou uma densidade significativamente mais baixa do que as demais (ANOVAs fatoriais, $p < 0.0001$). Verificou-se um forte efeito das estações sobre a colonização, sendo significativamente mais alta durante o periodo chuvoso do que durante o seco. O efeito da adição da serapilheira foi significativamente positivo somente durante a estação seca na poça do meandro, onde a densidade de invertebrados quase triplicou ($p = 0.03$). Todos os outros tratamentos demonstraram efeitos levemente um pouco negativos, porém não significativos com a adição de serapilheira. Considerando que foram encontrados somente poucos individuos dentre os taxons considerados trituradores, é provavel que folhas recentemente caídas possam ser mais importantes como um meio mecanico para colonização, retenção de MOPF e de proteção contra predadores do que como fonte alimentar em poças riparianas dos córregos do Cerrado.

Introduction

In temperate ecosystems, leaf litter consumption by shredding invertebrates is of central importance for the detritus food chain (CUMMINS 1974; WALLACE et al. 1982; CUMMINS et al. 1989; DOBSON et al. 1992), and experimental exclusion of leaf litter inputs causes massive changes in the functioning of stream ecosystems (WALLACE et al. 1999; BAER et al. 2001; EGGERT & WALLACE 2003). Leaf litter is also an important element in tropical low-order streams, either as habitat (HENDERSON & WALKER 1986; WALKER 1992; DUDGEON & WU 1999) or as food (GRAÇA et al. 2001; MATHURIAU & CHAUVET 2002). Here, shredding is often mediated by large benthic omnivores, such as freshwater crabs or shrimps (PRINGLE et al. 1993; CROWL et al. 2001). In Cerrado streams which lack large benthic omnivores (WANTZEN 2003), the consumption of leaf litter by benthic invertebrates appears to be limited. In earlier studies, we either found feeding specialists dwelling in areas where leaf litter is retained for long periods or miners which feed on fresh, green leaves that were torn off and carried into the streams by rainstorm events (WANTZEN & WAGNER 2006). The floristic composition of gallery forests covering the riparian zone of these streams is characterized by tree species from the Cerrado and partly from Amazonia (RODRIGUES & LEITÃO-FILHO 2000), many of which have high phenolic content (RIBEIRO et al. 1999). Riparian wetland ponds are considered to be important turnover sites for biodiversity and for allochthonous particulate organic matter (POM) provided that the POM is either nutrient-rich, or that leaves have passed sufficiently long time in the water so that repellent secondary plant compounds have been leached (WANTZEN & JUNK 2000; WANTZEN et al. 2006a, c). However, riparian ponds are highly dynamic systems which may become completely changed within short time periods, either by drying out (NOLTE et al. 1996), or due to flood events (NOLTE 2001; WANTZEN & JUNK 2006; WANTZEN et al. 2006c). In Amazonia, the assemblages of leaf-dwelling organisms in the stream channel has been studied in detail (HENDERSON & WALKER 1986, 1990; WALKER 1987, 1992, 1994, 1999; RUEDA-DELGADO et al. 2006), as well as in both natural and artificial ponds (NOLTE 2001). Cerrado streams and their riparian wetlands make up a large part of the yet-preserved area of the Cerrado bioma, with the area covering about 20 % of the Brazilian territory (WANTZEN et al. 2006b). In spite of their wide geographic distribution, the riparian wetland zones of these habitats have only been poorly studied yet. The aim of our study was to analyze the effects of (a) presence or absence of leaf litter, (b) connectivity of the riparian habitats with the stream, and (c) season on the colonization of benthic invertebrate in riparian ponds.

Study area

The study site has been previously described in detail by WANTZEN (2003). The experiments took place in the forested headwater zone of the Tenente Amaral stream (15°54'S, 55°10'E; 650 m asl.) about 35 km east of the city of Jaciara, Mato Grosso. The stream flows into the São Lourenço River, one of the feeder rivers of the Pantanal wetland. The climate is seasonal with rainfall occurring mostly between October and April. Annual precipitation averages 1750 mm. Like most Cerrado streams it originates from tertiary sandstones of the Brazilian Shield and is characterized by low conductivity (<10 µS/cm), persistent O_2 saturation, slightly acidic pH, and low variation in average water temperature in the range of 20 to 26 °C (HECKMAN 1995; WANTZEN 2003). Discharge averages 400 to 700 l s^{-1}. Sediments consist of sandstone and medium sand with low content of organic matter.

Materials and methods

For the enrichment experiment we chose three riparian wetland ponds of similar size (1x1 m, 20 cm deep). The 'meander' pond was carved out in a natural stream meander by the scouring activity of the stream during former rainstorm events. It was protected against further scouring by a tree that had fallen into the stream channel some meters upstream. An opening of about 50 cm width and 10 cm depth maintained a permanent exchange of water between stream and pond. The 'connected' pond was a part of a secondary channel that had also developed during former extreme floods and fell dry during the rainless period. We deepened it artificially to 20 cm depth to provide permanent flooded conditions. A small channel (10 cm deep, 1 m long, 20 cm wide) maintained water exchange between the pond and the stream channel. During the experiments there was no overbank flow. Thus, the water source was a mixture of near-surface groundwater dripping into the pond, and stream water from the channel. Both water types had a similarly low conductivity (3-10 µS cm^{-1}). However, the DOC content of the groundwater was higher (WANTZEN, unpublished data). The third site was the 'isolated' pond, about 20 m distant from the stream in an organic soil patch of undecomposed organic matter in the riparian wetland forest (see schematic view in WANTZEN 2003). It exclusively received near-surface groundwater, confirmed by the visibly darkened color of the water (due to humic substances). This pond was man-made but similar to other natural ponds. The artificial pond was chosen as the natural ponds contained large roots that created a strong spatial heterogeneity and may have caused an unwanted bias through providing additional substrate for colonization. In all ponds the natural organic matter layer on the bottom was removed 3 weeks prior to the experiment to create similar habitat conditions, and to allow the development of biofilms on the surfaces. It is important to note that the riparian ponds always remained oxygenated. However, the two stream-connected ponds had higher oxygen concentrations (93 ± 5 % in both ponds) than the isolated one (60 ± 15 %).

In all 3 ponds three replicates of artificial substrates (made from a pair of bricks and a piece of folded, 100 x 10 cm nylon gauze (mesh 1 mm)) were exposed as described in WANTZEN (1998). Before exposure all bricks were allowed to develop biofilms by placing them in a grade on the stream bottom for 4 weeks. They were scrubbed with a brush under current water to remove benthic invertebrates and so reduce any bias between new and reused bricks (WANTZEN & PINTO-SILVA 2006). Substrates were then exposed for another 4 weeks in the ponds for the colonization experiments. Each substrate was fixed on a metal pole, maintaining the bricks and net in position (so that the space between the bricks could be colonized like a crevice), and facilitating sampling. During sampling care was taken not to loose animals by placing a 200 µm-mesh handnet below the substrates before lifting, by pulling it off the pole. Substrate surfaces were carefully scrubbed with a brush, gained organic material stained with bengal rose and then preserved in 70 % ethanol (WANTZEN & PINTO-SILVA 2006) before the samples were taken to the laboratory for identification.

During two seasons (wet season: October to April 2000, dry season: May to September 2001) two experiments per pond were made, one with leaf litter addition, the other without. For the addition of leaf litter we added an amount corresponding to about 500 g dry weight m^{-2} of leaf litter. This amount was sufficient to create a 5 cm thick layer on the bottom of the ponds, as often observed in nature. The dry weight was calculated from wet-weight-to-dry-weight conversion factors from dried subsamples as described in RUEDA-DELGADO et al. (2006). The leaf mixture was collected from the forest floor and showed no signs of physical breakage (estimated age of the leaf litter on the ground: 3-6 weeks) using the following species (in decreasing order of quantity): *Protium almecega* L. MARCHAND - Burseraceae, *Alchornea triplinervia* (SPRENG.) MÜLL. Arg. - Euphorbiaceae, *Protium heptaphyllum* (AUBL.) MARCHAND - Burseraceae, *Guatteria odontopetala* MART. - Annonaceae, *Qualea wittrockii* MALME - Vochysiaceae, *Chrysophyllum marginatum* (HOOK. & ARN.) RADLK. - Sapotaceae, *Olmedia obliqua* HUBER - Moraceae, *Sloanea latifolia* (RICH.) K. SCHUM. - Elaeocarpaceae, *Guarea guidonia* (L.) SLEUMER - Meliaceae, *Xylopia* sp. - Annonaceae, *Inga uruguensis* HOOK. & ARN., *Miconia chamissois* NAUDIN - Melastomataceae, *Nectandra* sp. - Lauraceae, *Hyeronima alchorneoides* ALLEMÃO - Euphorbiaceae. They were washed in the stream prior to the addition thus avoiding carriage of fine particulate organic matter and animals into the ponds. For the "no-litter" treatment no additions were made and fallen litter was removed once a week. The largest part of the pond areas was covered with tent-like emergence traps, based on the construction of the bottom eclector trap (as described in ADIS & SCHUBART 1984; ADIS 1997), which prevented most leaves from falling into the pond. Thus only single leaves that had recently fallen into the uncovered parts of the ponds (20-30 % of the pond area) were present in this treatment. Ponds were not completely covered to allow aerial colonization by aquatic insects. In all statistical tests benthic invertebrate number per artificial substrate unit (composed of two bricks and one nylon net) was the dependent variable, which was tested against the treatments (season, connectivity, or litter addition). Data were tested for normal distribution, and if possible factorial ANOVAs with post hoc TUKEY tests were calculated using the software SYSTAT 11.

Results

In all treatments colonization of the artificial substrates was very low in comparison with earlier findings from current-exposed sites in the same stream (WANTZEN 1998; WANTZEN & PINTO-SILVA 2006). Not more than 1276 animals from 26 higher taxa were found in the whole experimental series. Approximately 78 % of all animals were chironomids. Microcrustaceans (cladocerans and harpacticoids) together made up nearly 7 %, springtails 3 %, caddisfly larvae 2.1 %, mayfly larvae 1 %. The semi-aquatic springtails may have colonized the metal pole that protruded out of the water, or they may have colonized air bubbles that were trapped in the submerged artificial substrates. Astonishingly high were the percentages of adult insects, with 1.3 % dipterans (mostly chironomids which were hatching during sample treatment) and 1.2 % hymenopterans (Table 1). The maximum density found was 131 ind. substrate-1 in the meander pond during the rainy season, when both microcrustaceans and chironomids were abundant.

The isolated pond was the least densely colonized habitat. Densities in this pond were significantly lower compared with the meander pond ($F = 21.979$, $df = 1294$, $p < 0.0001$) and the connected pond ($F = 16.113$, $df = 1294$, $p < 0.0001$). Differences between the meander and connected ponds were not significant ($F = 0.730$, $df = 1294$, $p = 0.393$). On average the colonization density (Fig. 1) was much higher during the rainy season than during the dry season, with highly significant differences ($F = 11.334$, $df = 1941$, $p = 0.001$).

Significant positive effects of the litter addition treatment were only found during the dry season in the meander pond, where invertebrate densities increased about threefold between litter-free and litter-added treatments ($F = 4.756$, $df = 322$, $p = 0.03$). Patchy occurrence of microcrustaceans can be excluded as a cause for this difference because densities of these taxa were much higher in the no-leaf than in the leaf litter addition treatment. In the connected pond there was a small increase due to litter addition during dry season, this was however not significant ($F = 0.717$, $df = 322$, $p = 0.398$). All other combinations showed a slightly negative, but non-significant effect of litter addition.

Discussion

The limited number of repetitions and low density of the invertebrates in our experiment do not allow generalized statements on the ecosystem functions of Neotropical streams. However, we can draw some cautious conclusions for the Tenente Amaral stream. The significantly lower density of animals in the isolated pond may have been caused by the lower oxygen concentration and by potential negative effects from dissolved organic substances, as already described for ponds that develop in the channels of temporary streams in Australia (BUNN & DAVIES 1990). Another probable reason may be the more difficult colonization of the isolated pond. This habitat can be reached only by flying adults and by migration of crawling life stages of aquatic invertebrates across the moist zone of the thick organic layer. We found a number of aquatic insect larvae in moist leaf litter of this area (mostly ceratopogonids and chironomids; WANTZEN et al. unpubl. data) however these were obviously not able to contribute significantly to the colonization of the isolated pond.

During the dry season the connected pond did not show significant differences between treatments with and without litter addition. Invertebrate densities in the addition treatment were much lower than in the meander pond. In this period we observed several specimens of small (3-4 cm) rivulid fish patrolling in the pond and in the connection channel. It can be assumed that a combination of poor accessibility and a lack of shelter against predators in the channel have reduced the colonization of the pond during the dry season, irrespective of the litter treatment. The permeability of migration pathways is crucial for the colonization of habitats by aquatic invertebrates (BOULTON et al. 1991).

In the meander pond, however, which had a broad opening to the stream, the litter addition coincided with a significant increase in the total colonization. Although this cannot referred to a direct relation between litter amount and colonisation, the density increase of taxa depending particularly on organic matter, e.g. in dipterans, beetles, mayflies and caddisflies, suggests that the litter addition enhanced their survival. Benthic microdetritivores such as the encountered microcrustaceans were not positively affected by the leaf litter. Three effects of the litter are possible:

Firstly, a mere mechanical effect, i.e. the leaf litter acted as a sediment trap for organic matter deriving from the inflowing stream water. During the rainy season when the density was generally much higher in the two connected ponds than in the isolated one (irrespective of the leaf addition), we observed an increased amount of fine particulate organic matter in the ponds. In addition, the amount of small organic particles in the samples of the standardized artificial substrates was visibly higher than during the dry season (however this was not quantified).

Secondly, the leaves may have protected the invertebrates from predation by rivulids. These were observed to pick food from the surface of the uppermost leaf layer but did not actively penetrate the dense sections of the leaf packs, as several highly specialized Amazonian fish species do (WALKER & HENDERSON 1996).

Thirdly, the leaf litter served as a direct food source for invertebrates. As observed earlier in Hong Kong streams (DUDGEON & WU 1999) this last effect seemed to be of lower importance, as neither invertebrate shredders nor their feeding marks were abundant. Single specimens of two taxa were encountered that are known to shred leaves (the calamoceratid caddisfly genus *Phylloicus*; GRAÇA et al. 2001; WANTZEN & WAGNER 2006; RINCÓN, pers. commun.), or to mine in the conditioned mesophyll (*Stenochironomus*, Chironomidae; WANTZEN & WAGNER 2006).

The generally higher abundances during the rainy season in the connected and in the meander pond may also have been influenced by the hydraulic conditions, i.e. that the ponds have become more "stream-like" and attractive for rheophilic species. This has been observed for the periodical colonization of secondary channels by main channel species in a large Neotropical river system (MARCHESE et al. 2002). Typical rheobionts such as stonefly larvae only occured in these ponds during the rainy season, but numbers were too low to test assumptions about hydrological effects on colonization in the directly connected pond. We suppose that drifting organisms in general may have used the connected ponds as shelter from abrasion during the stronger flow conditions of the rainy season.

In conclusion, our experiments have shown that connectivity is a decisive variable in the colonization of riparian floodplain ponds in a similar pattern to that of large river-floodplain systems (AMOROS & ROUX 1988; WARD & STANFORD 1995; JUNK & WANTZEN 2004). Recently fallen leaf litter seems to be more important as a mechanical matrix for colonization, FPOM retention and cover from predators than as a food source in riparian ponds of Cerrado streams.

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Table 1: Sums of colonization of 3 artificial substrates per treatment in 3 different ponds, during the dry and the rainy season, and with leaf litter (500 g dw m^{-2}) added (add.) or not (not).

	Meander pond				**Connected pond**				**Isolated pond**			
	dry		**rainy**		**dry**		**rainy**		**dry**		**rainy**	
	not	**add.**	**not**	**add.**	**not**	**add.**	**not**	**add.**	**not**	**add.**	**not**	**add.**
Diptera (Chironomidae) larvae	37	139	191	208	20	45	187	147	5	-	9	10
Diptera (Ceratopogonidae) larvae	-	1	5	-	2	-	-	2	-	-	1	-
Diptera (others) larvae	1	-	2	-	1	1	-	-	-	-	-	-
Diptera adults	3	4	1	2	3	-	-	1	-	-	2	-
Collembola (Entomobryidae)	1	18	4	-	-	6	-	1	-	-	-	-
Collembola (others)	-	3	-	-	-	2	-	-	-	-	3	1
Ephemeroptera	-	5	3	1	-	-	2	-	-	2	-	-
Trichoptera	-	-	14	5	-	-	2	3	-	-	2	1
Plecoptera	-	-	1	-	-	-	-	1	-	-	-	-
Odonata	-	1	-	-	-	-	-	-	-	-	-	-
Sialidae	-	1	-	-	-	-	-	-	-	-	-	-
Gyrinidae	1	-	1	-	-	-	-	-	-	-	-	-
Hymenoptera (Formicidae)	2	7	-	5	-	-	-	-	-	-	1	-
Hymenoptera (others)	1	-	2	-	1	-	-	-	-	1	1	-
Coleoptera larvae	1	1	1	-	-	-	1	2	-	-	-	-
Coleoptera adults	-	1	2	-	5	-	3	-	-	-	-	1
Orthoptera	-	-	1	-	-	-	-	-	-	-	-	-
Thysanoptera	-	1	-	-	-	-	-	-	-	-	-	-
Psocoptera	1	-	-	-	-	-	-	-	-	-	-	-
Homoptera	-	-	-	-	-	-	-	1	-	-	-	-
Isoptera	-	-	-	-	-	-	-	-	1	-	-	1
Araneae	-	3	-	-	-	-	-	-	2	-	-	1
Acarina	-	1	3	1	-	-	-	1	-	-	-	-
Copepoda	-	-	-	3	-	-	27	8	-	-	-	-
Cladocera	-	-	1	-	-	-	32	19	-	-	-	-
Oligochaeta	1	-	-	-	-	-	-	-	-	-	1	-
indet.	-	1	-	-	-	1	-	8	-	-	-	1
Sum	49	187	232	225	32	53	259	193	9	1	20	16

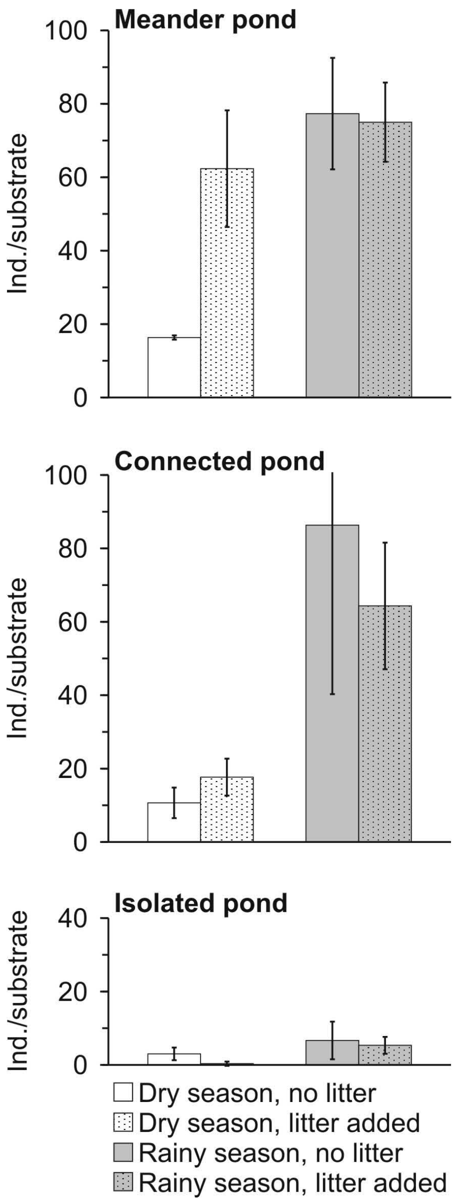

Fig. 1:
Average colonization density of the artificial substrates during the dry and the wet season.