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Contrasting central Amazonian rainforests and their influence on chemical properties of the cuticle of two millipede species – a first study

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Abstract: The chemical composition of the cuticle of two closely related detritivorous polydesmid millipedes, inhabitants of contrasting forest habitats, was compared for their respective bioelement content (calcium, magnesium, potassium, silicon). No differences were found for the absolute amount of bioelements, but the relative amount was higher in *Pycnotropis tida* (Diplopoda, Polydesmida, Aphelidesmidae) from the inundation forest. *P. sigma* from the upland forest had a higher weight and higher fraction of organic compounds. That might be explained by a substitution of calcium with proteins. Both millipede species strongly accumulated calcium, so that differences in calcium contents of the different trophic levels were reduced within the food chain. The calcium ratio (calcium content in the cuticle to calcium content in wood) was about 50 in *P. tida* and 120 in *P. sigma*. Some adaptive and evolutionary consequences of the different life cycles in relation to the resource quality and species distribution are discussed.

Resumen: La composición química de la cutícula de dos milípedos polidésmidos detritívoros que están muy emparentados pero que viven en hábitats forestales contrastantes, fue comparada en términos de sus respectivos contenidos de bioelementos (calcio, magnesio, potasio, sílice). No se encontraron diferencias en la cantidad absoluta de bioelementos, pero la cantidad relativa fue mayor en *Pycnotropis tida* (Diplopoda, Polydesmida, Aphelidesmidae) proveniente del bosque inundado. *P. sigma*, proveniente del bosque de la meseta, tuvo mayor peso y una fracción mayor de compuestos orgánicos. Esto puede explicarse como una sustitución del calcio por proteínas. Ambas especies de milípedos acumulan calcio fuertemente, de modo que las diferencias en contenidos de calcio de los diferentes niveles tróficos se vieron reducidas en la cadena trófica. El cociente de calcio (contenido de calcio en la cutícula respecto al contenido de calcio en la madera) fue de alrededor de 50 en *P. tida* y de 120 en *P. sigma*. Se discuten algunas consecuencias adaptativas y evolutivas de los diferentes ciclos de vida en relación con la calidad de los recursos y la distribución de las especies.

Resumo: A composição química de duas espécies de milpés detrítivoros muito próximas, em habitats florestais contrastantes foi comparada quanto ao teor dos respectivos bioelementos (cálcio, magnésio, potássio e silício). Não foram encontradas diferenças para os quantitativos absolutos em bioelementos, mas a sua quantidade foi mais elevada no *Pycnotropis tida* (Diplopoda, Polydesmida, Aphelidesmidae) da floresta inundada. A *P. sigma* da floresta das terras altas apresentava um peso mais elevado e uma fracção maior de compostos orgânicos. Isto pode ser explicado pela substituição do cálcio com proteínas. Ambas as espécies de milpés acumulavam fortemente o cálcio para que as diferenças nos teores de cálcio entre os diferentes níveis tróficos fossem reduzidas na cadeia alimentar. A razão de cálcio (teor de cálcio entre as cutículas e o teor de cálcio no lenho) foi de cerca de 50 na *P. tida* e 120 na *P. sigma*. São discutidas al-

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gumas consequências adaptativas e evolucionárias dos diferentes ciclos de vida em relação à qualidade dos recursos e à distribuição das espécies.

Key words: Adaptation, bioelement accumulation, calcium, decomposition, Diplopoda.

Introduction

The Amazonian habitats, non-inundated upland forests (terra firme) and inundation forests, differ significantly. The most important feature is the flood pulse of the Amazon River and its tributaries. It has an average amplitude of 10 m at Manaus and causes regular inundations of vast areas (Junk 1997). Another feature strongly tied to the flood pulse concerns bioelement distribution. The terra firme is poor in bioelements, whereas inundation forests ("várzea") are much richer in bioelements. This is due to the sediment load, especially calcium and phosphorus, carried by so called whitewater rivers (Furch 1997). The differences of bioelement content between terra firme and várzea were greater in bark and leaves than in wood (Furch & Klinge 1989).

This study focuses on two closely related polydesmid millipede species living in these different habitats. (1) *Pycnotropis tida* Chamberlin, 1941 (Polydesmida: Aphelidesmidae), which inhabits the várzea along the Amazon river at least from Iquitos, Peru, to Manaus, Brazil. (2) the very closely related species *P. sigma* Golovatch, Vohland & Hoffman, 1998, which occurs solely on non-inundated terra firme sites at Manaus (Golovatch *et al.* 1998). Both species are believed to have their origin in the Andes and to have dispersed downstream by the Amazon River (Vohland 1998).

This study is constraint by the fact that the population density of terra firme inhabiting *P. sigma* is that low that nearly all specimens ever found and all specimens available for this study were collected from a manured plantation, where bioelement content is not as low as in the surrounding terra firme forest. As a first analysis this study provides an insight into the physiological adaptability and evolutionary competence of Neotropical millipedes which are thought to have their origin in the bioelement rich Andean region and after dispersion downstream now have to cope with an extremely bioelement-poor location. The bioelement content of the cuticle was compared in order to analyse consequences of low bioelement concentration of the food source on species evolution, as indicated by the distribution of the millipede genus *Pycnotropis*.

Materials and methods

Millipede species

Pycnotropis is the only genus of the mostly Andean subfamily Amplininae, which is found throughout the Amazonian region (Vohland 1998). Three out of 26 known species inhabit várzea inundation forests with *P. tida* being one of them, while *P. sigma* represents one of five species found only in Brazilian terra firme rainforests (Golovatch *et al.* 1998).

The univoltine life cycle of *P. tida* is regulated by the flood pulse, i.e. oviposition and maturation of immatures are restricted to the low water period (Vohland & Adis 1999). During the aquatic phase adults survive on and in tree trunks above the water line. In contrast, *P. sigma* has a plurivoltine life cycle with all stages occurring throughout the year. In laboratory experiments, *P. sigma* needed about eight weeks longer than *P. tida* in males (ten weeks in females) to reach the subadult stage. *P. sigma* also attained a larger body length and weight (5.19 ± 0.23 cm and 1192 ± 149 mg in females) than *P. tida* (4.95 ± 0.26 cm and 743 ± 180 mg; Vohland 1999). Both species feed on strongly decomposed wood debris.

Collecting sites

P. tida was collected near Manaus in an inundation forest at Lago Janauarí (03º20′ S, 60º17′ W). This forest is dominated by várzea tree species while only about 4% of the tree species are typical for blackwater inundation forests along the Negro River (Amaral *et al.* 1997). In the várzea, the average population density was about 0.036 individuals m^{-2} (Vohland 1999). *P. sigma* was collected on the terra firme site at an agroforestry experimental station (3°8′ S, 59°52′ W, 40-50 m a.s.l.) of the Brazilian Company of Agriculture (EMBRAPA) in pupunha (*Bactris gasipaes*, Arecaceae) plantations, which were surrounded by primary rain forest (Vohland & Schroth 1999). As both species live in decaying wood, their distribution is patchy. A comparison between logs of the várzea and the terra firme revealed that the percentage of logs inhabited by aphelidesmid millipedes is about ten times higher in várzea than in terra firme forests (Vohland *et al.* 2001).

Due to the extremely low population density of *P. sigma* in the primary rain forest, all animals used for this study were collected in pupunha (*B. gasipaes*) plantations, where population densities were higher. This habitat was not identical with the primary rain forest, for example, due to calcium fertilization.[2] However, analysis of the palm stems, on which *P. sigma* mainly feeds (personal observations), revealed that the calcium content was low and similar to that of other terra firme wood (cf. Table 1).

Chemical analysis of the cuticle

P. tida and *P. sigma* (n = 5 adult males and 5 adult females each) were oven dried at 100 °C to a constant weight. For standardization only the cuticle of midbody segments 6-8 was used in this study and cleaned thoroughly of tissue with forceps and purified water.

The cuticle material was ashed in a quartz crucible for 5 hours at 480 °C using a muffle furnace. The loss of weight was interpreted as organic substance. The remaining ash was digested with concentrated hot hydrochloric acid and filtered through a membrane filter of 0.45 µm pore diameter. The acid insoluble residue was interpreted as silicon dioxide (Eleuterius & Lanning 1987; Tripathi & Singh 1992). Filtrates were diluted with water to a volume of 50 ml. Calcium, magnesium and potassium were determined using a Perkin-Elmer atomic absorption spectrophotometer (AAS).

Results

Absolute amounts

Since the amount of ash in the cuticle (represented by segments 6-8) in both species did not differ significantly, the higher weight of *P. sigma* compared to *P. tida* was caused by the higher amount of organic substances (Table 2). The main fraction of the ash consisted of calcium. Magnesium, potassium, and silicon were found in smaller amounts. Neither the amount of calcium nor the amount of silicon differed between species and sexes. *P. tida* had less magnesium and less potassium in its cuticle segments than *P. sigma*. Females had more potassium in their cuticle than males, but did not differ significantly from males in magnesium content.

Relative amounts

P. tida cuticle had a significantly higher ash content and a significantly lower organic content than *P. sigma* cuticle (Table 3). Calcium content also differed significantly between the two species: measured as % dry weight, the cuticle of *P. tida* was richer in calcium (25.1% d.w.) than the cuticle of *P. sigma* (21.1% d.w.; cf. Table 3). However, measured as % ash, the calcium content was approximately 36% and neither differed significantly

Table 1. Content of bioelements in wood biomass of two central Amazonian rainforest types (Furch & Klinge 1989) and in tree stems of *Bactris gasipaes* (Arecaceae; Wolf 1997).

Forest type	Nutrients ($mg\ g^{-1}$)						
	N	P	K	Na	Ca	Mg	n
Várzea forest*	5.2	0.592	6.58	0.337	4.92	1.527	60
Terra firme forest	4.8	0.126	1.35	0.327	1.78	0.992	224
B. gasipaes	4.34	0.49	3.17	–	1.37	0.63	5

*mean of three sampling sites

[2] Plots with *B. gasipaes* received 200 g dolomitic lime per palm during construction of the planation in 1993 and 2, 1 Mg ha^{-1} dolomitic lime in November/December 1996 (G. Schroth, pers. comm.).

Table 2. Weight (mg) of organic substances, ash, Ca, Mg, K and Si in the cuticle substance of segments 6-8 in *P. tida* and *P. sigma* females (f) and males (m). F-values calculated by a multiple variance analysis. m+f = males plus females.

Species	n	Organic substances (mg)	Ash (mg)	n	Ca (mg)	Mg (mg)	K (mg)	Si (mg)
P. tida (m + f)	10	11.31 ± 1.94	26.31 ± 4.69	8	9.23 ± 1.83	0.33 ± 0.07	0.08 ± 0.02	3.10 ± 0.55
only females	5	12.04 ± 2.39	26.96 ± 5.59	4	9.62 ± 2.24	0.34 ± 0.09	0.09 ± 0.03	2.95 ± 0.55
only males	5	10.58 ± 1.22	25.66 ± 4.15	4	8.83 ± 1.53	0.32 ± 0.08	0.07 ± 0.01	3.34 ± 0.63
P. sigma (m + f)	10	21.41 ± 6.79	28.31 ± 3.84	8	9.97 ± 1.37	0.44 ± 0.06	0.12 ± 0.03	3.56 ± 0.21
only females	5	26.04 ± 3.09	31.14 ± 3.13	4	10.91 ± 1.15	0.47 ± 0.07	0.14 ± 0.02	3.83 ± 0
only males	5	16.78 ± 6.39	25.48 ± 1.81	4	9.02 ± 0.82	0.41 ± 0.05	0.10 ± 0.02	3.47 ± 0.14
MANOVA								
F-species		35.42	1.30		0.93	9.02	16.18	2.31
p		0.000	0.271		0.353	0.010	0.001	0.189
F-sex		9.97	3.93		3.07	1.04	5.19	0.00
p		0.006	0.064		0.105	0.328	0.041	0.956
F-interaction		5.28	1.54		0.52	0.21	0.80	1.26
p		0.035	0.231		0.486	0.654	0.387	0.311

Table 3. Dry weight (mg) of the cuticle segments 6-8 and mg g^{-1} dw of organic substances, ash, Ca, Mg, K and Si in the cuticle of *P. tida* and *P. sigma*. The t-values for data differences between species were calculated. m + f = males plus females.

Species	Dry weight (mg)	Organic substance	Ash	Ca	Mg	K	Si
n	10	10	10	8	8	8	8
P. tida (m + f)	37.62 ± 6.38	301.33 ± 21.40	698.67 ± 21.40	251.0 ± 10.5	8.84 ± 0.93	2.14 ± 0.25	93.84 ± 22.74
P. sigma (m + f)	49.72 ± 9.62	421.43 ± 67.64	578.57 ± 67.64	211.3 ± 21.5	9.30 ± 1.36	2.55 ± 0.34	87.03 ± 11.94
t	3.31	5.35	5.35	4.68	0.78	2.72	0.38
p	0.003	0.000	0.000	0.000	0.448	0.016	0.714

between specis (ANOVA, F = 3.66; P<0.08) nor between sexes (ANOVA, F = 0.81; P<0.38). The cuticle of both species was low in magnesium (about 1% dry weight) and potassium (about 0.2% d.w.) content. Silicon content was about 9% d.w.

Accumulation of bioelements

With respect to alkali and alkali-earth metals studied, the chemical composition of the cuticle was more similar for the two species than expected from the differences in chemical composition of their food. The main fraction, i.e., more than 95% of the alkali and alkali-earth metals of the cuticle of the millipedes, was calcium (Fig. 1).

Both millipede species accumulate calcium and magnesium at high rates (Fig. 2). Taking the average calcium content of wood in the different habi-

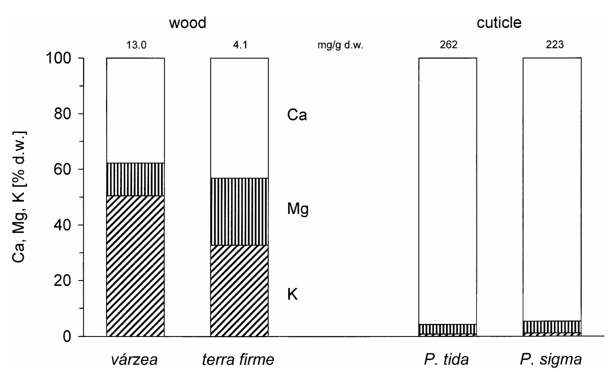

Fig. 1. Chemical composition of the observed alkali and alkali-earth metals calcium, magnesium and potassium of wood (data from Table 1) and cuticle of millipede species (data from Table 4) from contrasting central Amazonian rainforest biotopes.

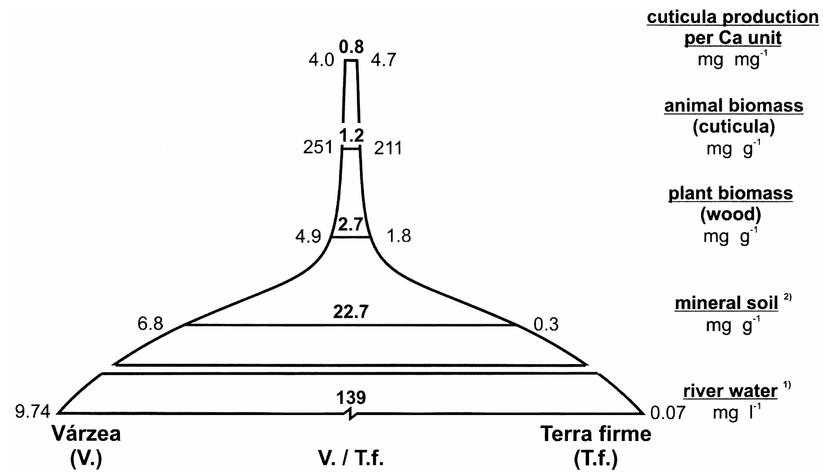

Fig. 2. Calcium content in ecosystem compartments and production of cuticle biomass per calcium unit in the Várzea forest (left) and in the terra firme forest (right). The respective ratios of Várzea to terra firme are shown in the centre. *1 left: calcium content of the Amazon River (Solimões), right: calcium content of terra firme forest streams (Furch & Junk 1997); *2 content of total calcium in the top mineral soil (0-10 cm) according to Furch (2000). Data for wood in Table 1, for cuticle biomass in Table 2, for cuticle production per calcium unit in Table 3.

tats into account (Table 1) the calcium ratio (calcium content in the cuticle to calcium content in the wood) is about 50 in *P. tida* and 110-130 in *P. sigma*. Magnesium was less strongly accumulated in the cuticle than calcium. The magnesium ratio for *P. tida* was 6 and for *P. sigma* 10.

Discussion

Methodological limitations

This study was a first attempt to test the hypothesis that bioelement content of specific habitats (i.e. várzea and terra firme) has impact on millipede species performance. For this, first analysis was done with relatively few (20) animals only, which had to be killed for the study. The age of the animals was not known, but probably it was more conform in *P. tida* than in *P. sigma* as their reproductive cycles were synchronized by the flood pulse (Vohland & Adis 1999). This study may inspire rearing millipedes on substrates with different known calcium concentration and also to observe feeding preferences in relation to resource quality. Observing *P. tida* feeding on dead wood in the field and in the laboratory (Vohland 1999) it was not possible to assign the wood to specific tree species. *P. sigma* fed also on the palm stems as the fibres were observed in the gut (Vohland personal observations).

Bioelements vs organic substances in the cuticle

This study investigated the chemical composition of the cuticle of two millipede species from contrasting habitats. The main result was that both species store the same amount and composition of bioelements in their cuticle segments. But the weight of the cuticle of *P. sigma* was higher than the weight of the cuticle of *P. tida* because of the higher amount of organic substances in the cuticle of *P. sigma*. That means that the bioelements in the cuticle of *P. sigma* were more "diluted" by the higher fraction of organic substances in *P. sigma* compared to *P. tida*.

The main fraction of bioelements consisted of calcium which corresponds with other studies on the chemical composition of the cuticle of millipedes (Ansenne *et al.* 1990; Thorez *et al.* 1992). Calcium is known to have an important function for cuticle stability. As proteins and calcium can substitute each other in their function of hardening the cuticle (Richards 1951 for other calcificating animals), the higher fraction of organic compounds in *P. sigma* may be attributed to a group of proteins substituting calcium as a structure-stabilising element.

Calcium accumulation

The calcium contents of water and soil show considerable differences between várzea (high content) and terra firme (low content). However, trees of the terra firme are able to assimilate calcium from sources of low concentrations resulting in relatively small differences in the calcium content of the biomasses between várzea and terra firme forests: wood of the várzea forest is only about three times richer in calcium than wood of the terra firme forest, compared to a factor of 23 in soils and of 139 in river water (Fig. 2). Furthermore, the two millipede species can extract enough calcium for the production of the calcium-rich cuticle even from wood of very low calcium content. *P. sigma* from the terra firme has a higher calcium use efficiency to produce higher amounts of cuticular biomass per calcium unit than the várzea millipede *P. tida*.

But it should be taken into consideration that decomposing wood differ in its composition from that of the living tree of which the samples were taken to determine bioelement contents (Table 1). There are many factors including temperature, moisture, size of the logs, etc. controlling the decomposition of wood, and even within the same log, there is a mosaic of conditions (Harmon 1986). The rate of decomposition differs between the organic substances and the bioelements (e.g. K is leached out rapidly while P can be enriched by mycorrhizal fungi). But as calcium occurs mainly in the cell walls, decomposition of organic substances and calcium is strongly correlated (Karin Furch, unpublished data), so that in comparison to other resources dead wood can be a calcium-rich resource as shown for the millipede *Pelmatojulus tigrinus* in a gallery forest in Western Africa (Mahsberg 1997).

Animal distribution

The allopatric distribution of the species *P. tida* and *P. sigma* is explained by their different strategies to cope with environmental limitations: *P. tida* experiences severe limitations in its annual life cycle due to the flood pulse which drives the animals out of the logs onto the stems during inundation lasting 5-7 months (Adis & Messner 1997) and forces them to complete development during low water periods (Vohland & Adis 1999). *P. sigma* on the other hand shows a prolonged development time, which might hinder inhabitation of the inundation forest (Vohland 1999). Possibly *P. tida* can only inhabit whitewater inundation forests, because the temporal limitation for foraging is compensated for by a better nutrient quality of the food resources as well as by the smaller size of the animal, whereas *P. sigma* compensates low nutrient quality of the terra firme by a longer development time and higher fraction of organic contents in its cuticle. This view is supported by the fact that forests inundated annually by extremely bioelement poor blackwater rivers (Furch & Klinge 1989) are not inhabited by representatives of the genus *Pycnotropis* at all.

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