The feeding rates and preferences of a neotropical terrestrial isopod (Oniscidea)

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Abstract

In forest ecosystems, detritivores play a fundamental role in the decomposition of litter through mechanical breakdown and fragmentation of plant materials. The leaf litter properties that are subject to changes during the decomposition process may influence the feeding preferences of terrestrial isopods. Feeding experiments using the leaves of *Syzygium cumini, S. jambos* and *Casearia sylvestris* were conducted to determine the feeding preferences and feeding rates of the terrestrial isopod *Benthana cairensis* Sokolowicz, Araujo and Boelter, 2008 (Philosciidae) throughout the decomposition process. *Benthana cairensis* fed at a higher rate on *C. sylvestris* (66%) when compared to of any of the other litter types. The feeding rates increased with the advancing process of decomposition. The highest consumption occurred when feeding on two- and three-month-old litter, and the lowest when rate occurred when feeding on green leaves. When offered a choice between green, one, two and three month-old litter, individuals of *B. cairensis* preferred the two- and three-month-old litter. The green leaves were also consumed, but to a lesser extent. The feeding preferences of *B. cairensis* are discussed based on the leaf palatability and considering the leaf structure, the secondary compounds present and the nutrient contents.

Key words: feeding preferences, woodlice, Oniscidea, leaf decomposition.

Introduction

The flux of nutrients and energy is one of the fundamental aspects of ecosystem functioning, influencing total productivity and sustainability (Webb, 1977). In terrestrial ecosystems, most of the energy passes through detritivore pathways (Moore *et al.,* 2004). Litter breakdown is influenced by climatic conditions and chemical composition, and increases with the increasing biological activity of the litter-dwelling invertebrate assemblages (Attignon *et al.,* 2004). These litter-dwelling invertebrate assemblages act directly and indirectly at various levels of litter degradation and humus formation (Wolters, 2000), and are often responsible for the mechanical breakdown and fragmentation of a large amount of litter (Webb, 1977; Dangerfield and Milner, 1996; O'Hanlon and Bolger, 1999; David and Gillon, 2002; Quadros and Araujo, 2008).

Understanding the feeding ecology of detritivores is very important at both population and ecosystem levels, as it elucidates which resources influence population processes (*e.g.,* growth, competition). Feeding ecology also highlights the role of each organism in the ecosystem through its pattern of resource utilization. For detritivores, such as terrestrial isopods, the leaf chemistry (Cotrufo *et al.,* 1998), the levels of physical and chemical anti-herbivore defense compounds (Hassall and Rushton, 1984; Zimmer, 2002) and microbial colonization (Gunnarsson, 1987) are thought to

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influence feeding choices. During the course of leaf decomposition, these leaf traits may vary to a substantial extent (McClaugherty *et al.,* 1985; O'Connel, 1988; Ibrahima *et al.,* 1995; McClaugherty *et al.,* 1995; Berg and McClaugherty, 2007). The stage of leaf decomposition is also an important driver of isopod feeding preferences (Soma and Saitô, 1983; Szlávecz and Maiorana, 1990). In the present study, it is proposed that the litter of the same plant species is utilized differently by detritivores over time, as decomposition progresses. This proposition is tested by evaluating the feeding rates and preferences of a terrestrial isopod in relation to the preferred food type through the process of decomposition.

Material and Methods

The locality and the study species

The present study was conducted in Taquara, Rio Grande do Sul, Brazil (20°38'S-50°47'W), in an area measuring 2 ha that is composed of native and exotic trees. The Brazilian pine tree, *Araucaria angustifolia* (Bert.) O. Ktze, was present in the study area. The most common tree species in this ecological community are *Syzygium cumini* (L.) Skeels ("jambolão", Myrtaceae), *Syzygyum jambos* (L.) Alston ("jambo-amarelo", Myrtaceae) and *Casearia sylvestris* Swartz ("guaçatonga", "chá-de-bugre", Salicaceae). Both *Syzygium* species are exotic to South America, while *C. sylvestris* is native to this neotropical region and occurs from Mexico to Uruguay. In Brazil *C. sylvestris* occurs in biomes such as the Amazon forest, the Cerrado and the Atlantic forest, and it is present in all of the forest communities in Rio Grande do Sul (Sobral and Jarenkow, 2006). These three plants have economic importance due to the known pharmacological properties of their extracts (Migliato *et al.,* 2006; Silva *et al.,* 2008; Donatini *et al.,* 2009). The leaf properties of these three plant species, obtained from the literature, are given in Table I.

Benthana cairensis Sokolowicz, Araujo and Boelter, 2008 (Philosciidae) is a neotropical terrestrial isopod species. This isopod species measures up to 12 mm in length and it is found in the leaf litter layer, often under moist, decomposed fallen trunks (Sokolowicz *et al.,* 2008). *Benthana cairensis* is the most abundant isopod in this area of Brazil. Two other species, *Atlantoscia floridana* (van Name, 1940) (Philosciidae) and *Balloniscus glaber* Araujo and Zardo, 1995 (Balloniscidae), are also present in this region.

Feeding essays

Individuals of *B. cairensis* were captured during the autumn of 2006 from the leaf litter layer. The individuals collected from the field were kept the laboratory in a terrarium with soil and leaves taken from the study area one or two days prior to isopod collection. Care was taken to use only *B. cairensis* individuals that were heavier than 18 mg and those that were in a intermoult stage (not in an ovigerous stage) during all of the feeding essays. For all of the essays, 10 control chambers (without isopods) were maintained in the same

Table I. Leaf properties of plants species offered to the terrestrial isopod Benthana cairensis in multi-choice feeding trial. ASF = acid-soluble fraction. References: (1) Leffler and Enquist (2002); (2) Almeida *et al.* (2006); (3) Luz *et al.* (1997); (4) Ramana *et al.* 2000; (5) Mandal (1997); (6) Silva *et al.* (2008); (7) Ostertag *et al.* 2008; * present study.

	Lignin (%)	ASF	C:N	N (%)	Tannin (%)	Toughness (g mm^{-2})	Thickness (mm)	Ref.
Casearia sylvestris						1.03		(1)
		34.9		2.3[a]				(2)
							0.13	*
					3.8-5.2			(3)
Syzygium cumini	27.9	36.6[b]		1.6[a]	2.4[d]			(4)
	9.8	35.8[b]						(5)
	16.4		34	1.3	12.4[c]			(6)
							0.17	*
Syzygium jambos	17	35.7	43	1.2	13.9[c]			(7)
							0.29	*

Remarks:
a. Total N obtained from crude protein with a conversion factor of 6.25.
b. Sum of cellulose + hemicellulose.
c. Tannins accessed by the Folin-Denis method.
d. using Prussian-blue method.

conditions and for the same period of time to estimate the autogenic mass loss of the leaves (Szlávecz, 1985).

To verify whether *B. cairensis* showed preferences towards leaves from one of the three most common plants (*S. cumini, S. jambos* and *C. sylvestris*), litter bags of 1-mm mesh (20 x 20 hm) were filled with leaves collected directly from the trees. These litter bags were left to decompose *in loco* for 14 days. Discs measuring 18 mm in diameter were cut from the leaves and offered to the isopods in plastic chambers. The isopods were provided with water and maintained at 20 ± 1°C, with a 12:12 h photoperiod. There were 20 replicates, each one with three discs of each plant species and one individual of *B. cairensis.* Prior to the experimental trials, the leaves were dried (60°C; 48 h), weighed and then re-moisturized and offered to the isopods. After 10 days, the remaining leaf pieces in the chambers were dried and weighed.

To investigate the influence of the stage of *C. sylvestris* decomposition on the consumption, egestion and assimilation rates of *B. cairensis,* green leaves were placed in litter bags and left to decompose *in loco* as described above. After one, two and three months, a litter bag was transported to the laboratory and used in the feeding trials. Leaf discs were cut, dried and weighed as described above, and offered to *B. cairensis* (30 replicates) for 10 days (green, one- and two-month-old leaves) or six days (three-month-old leaves). After this period, the animals, the remaining leaf pieces and the feces were dried and weighed. During the course of these trials, the feces were not removed from the units, allowing for coprophagy. Additionally, at the start of each month, a new set of litter bags with green leaves were set-up. In this way, after four months, litter bags that had been decomposing for one, two and three months were available for comparison. The leaves at these different stages of decomposition (plus the green leaves) were offered in a multiple-choice trial as described above. For this trial, there were 14 replicates and it lasted for seven days.

Analyses

The feeding preferences in the multiple-choice feeding assays were evaluated by comparing the amount of each plant species consumed at each stage of decomposition, in relation to the total amount consumed in each replicate. Prior to each test, the change in weight observed in the control units (5.4% for *S. cumini,* 3.4% for *S. jambos* and 8.2% for *C. sylvestris*) was discounted from the difference between the initial and final weight of the leaves in each replicate. Preference data from the multi-choice experiments were analyzed through resampling statistics (Roa, 1992), using 9999 iterations, as in Ihnen and Zimmer (2008).

In the no-choice feeding trials, the food ingested in each replicate was calculated as the difference between the initial and final weight of leaves, discounting the average loss in weight observed in the control replicates (17.1 ± 1.2% in green leaves; 12.8 ± 1.8% in one-month-old leaves; 5.8 ± 1.2% in two-month-old leaves; 5.7 ± 0.2% in three-month-old leaves). The relative consumption rate (RCR in mg mg^{-1} day^{-1}) was calculated as RCR = food ingested/(isopod weight x duration of experiment) and the approximate digestibility (AD in %) was calculated as AD = [(food ingested – feces produced)/food ingested] x 100 (Waldbauer, 1968). These variables were log-transformed to ensure homocedasticity, which was further confirmed using a Shapiro-Wilk test ($p < 0.05$). The influence of the type of diet (*C. sylvestris* leaves in different stages of decomposition) on the RCR and the AD was analyzed using an analysis of covariance (ANCOVA), as recommended by Raubenheimer and Simpson (1992). In the case of RCR, the food ingested was used as the dependent variable and isopod dry weight was used as the covariate. For the AD, the difference between the food ingested and the feces produced was considered the dependent variable and the food ingested was the covariate. Comparisons between the diets were made using treatment contrasts. These tests were done using R (http://www.R-project.org).

Results

Feeding preferences among *S. cumini*, *S. jambos* and *C. sylvestris*

When offered a choice between the leaves of three plant species that had been decomposing for 14 days. *B. cairensis* fed preferentially on *C. sylvestris* (66.5% of the total, on average) compared to of *S. jambos* (31.9%), while *Syzygium cumini* was clearly avoided (less than 1% of total consumed) (Fig. 1). All of the comparisons were significant ($p < 0.02$).

The feeding rates with respect to different stages of decomposition in *C. sylvestris*

A summary of the total food ingested, the RCR and the approximate digestive ability of *B. cairensis* throughout the decomposition stages of *C. sylvestris* are given in Table II and the ANCOVA results are summarized in Table III. The highest RCR was observed when *B. cairensis* was feeding on leaves that were three months old, and the lowest RCR was observed on green leaves (Table II). The effects of the treatments and the covariates were significant for both the RCR and the AD analysis, indicating that the RCR and the AD change along *C. sylvestris* decomposition (Table III). During the trials, there was no appearance of feces in the replicates containing the green leaves and feces production in this treatment could therefore not be calculated.

Feeding preferences between leaves of *C. sylvestris* at different stages of decomposition

Regarding the influence of the stage of decomposition on feeding preferences, *B. cairensis* fed more on leaves that were two and three months old (Fig. 2).

Discussion

A number of studies have indicated that terrestrial isopods exhibit feeding preferences when given a choice (Dudgeon *et al.,* 1990; Soma and Saitô, 1983; Hassall and Rushton, 1984; Dias and Hassall, 2005; Catalán *et al.,* 2008). Accordingly, *B. cairensis* clearly showed preferences towards *C. sylvestris* in our study, whereas *S. cumini* was rejected. Compared to the leaves of both *Syzygium* species, *C. sylvestris* leaves were thinner and very soft, with a higher N percentage (Table I). In addition, both of the *Syzygium* species leaves are rich in fiber content and lignin (Table I). These compounds usually confer mechanical protection to the photosisntetic tissue in the living plants, and are associated with slow rates of decomposition in high concentrations (Fortunel *et al.,* 2009). It is worth mentioning that, the leaves were highly fragmented and fragile by the end of three months of decomposition in the field, with a dark-brown coloration, indicating that *C. sylvestris* has a high decomposition rate. Corroborating this, *C. sylvestris* lost more weight than both *S. cumini* and *S. jambos* in all of the control chambers. Terrestrial isopods, as well as other detritivores and herbivores, usualy avoid feeding on leaves that are rich in structural compounds (Cornelissen *et al.,* 1999). Soma and Saitô (1983) and Catalán *et al.* (2008) showed that, when given a choice, isopods always prefer to feed from leaves with a lower fiber content.

Another important leaf trait that influences palatability is the presence and quantity of secondary compounds, especially phenolics. Many species of the genus *Syzygium* (= *Eugenia*) have been reported to be very rich in polyphenols, gallic and ellagic acid derivatives, tannins and flavonol glycosides (Mahmoud *et al.,* 2001). The leaves of *S. jambos* (= *E. jambolana*), for instance, are rich in flavonol glycosides (Mahmoud *et al.,* 2001). The leaves of *S. cumini,* which were rejected by

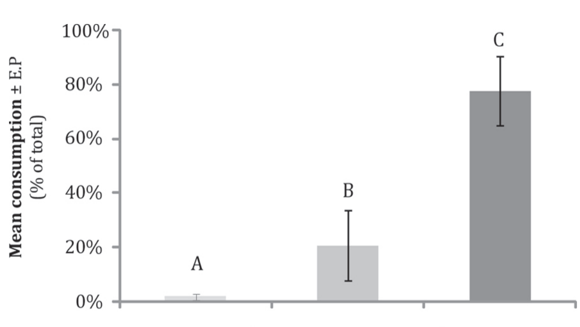

Figure 1. Feeding preferences of *Benthana cairensis* (Oniscidea) when offered a choice between three food types. Different letters indicate significant differences between species, obtaining with resampling statistics after 9999 iterations.

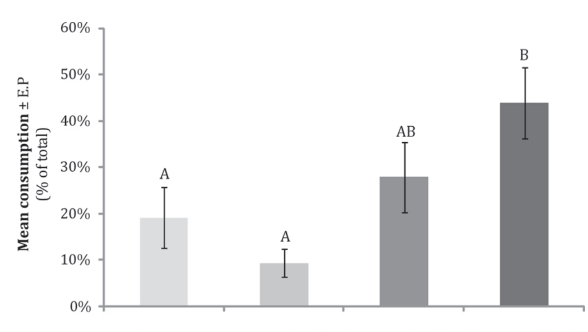

Figure 2. Feeding preferences of *Benthana cairensis* (Oniscidea) when offered a choice among leaves of *Casearia sylvestris* in different stages of decomposition. Different letters indicate significant differences between times, obtaining with resampling statistics after 9999 iterations.

Table II. Nutritional indices for *Benthana cairensis* feeding on different diets (green, one-month-old, two-month-old and three-month-old leaves of *Casearia sylvestris*). The RCR (mg mg^{-1} day^{-1}) = food ingested/(isopod weight x duration of experiment). AD (%) = [(food ingested – feces produced)/ food ingested] x 100. Values are given as mean ± s.e.

Diet type	Food ingested (mg)	Relative consumption rate (RCR)	Approximate digestibility (AD)
Green leaves	1.98 ± 0.13	0.02 ± 0.001	—
One month-old	4.33 ± 0.48	0.05 ± 0.01	58 ± 5%
Two month-old	8.07 ± 0.92	0.08 ± 0.01	19 ± 4%
Three month-old	11.12 ± 1.21	0.14 ± 0.01	39 ± 4%

Table III. The summarized results of analysis of covariance (ANCOVA) on the effects of four diets (green, one-month-old, two-month-old and three-month-old leaves of *Casearia sylvestris*) on the (a) relative consumption rate and (b) the approximate digestibility of terrestrial isopod *Benthana cairensis.*

Source of variation	DF	F ratio	*p*
(a) Relative consumption rate			
Diet	3	34.593	< 0.001
Covariate (weight)	1	3.937	0.050
Residuals	91		
(b) Approximate digestibility			
Diet	2	15.116	< 0.001
Covariate (food ingested)	1	20.174	< 0.001
Residuals	67		

B. cairensis, are rich in tannins and saponins (Lima *et al.,* 2007; Migliato *et al.,* 2006) and their ethanolic extracts were proven to have an anti-bacterial effect towards both gram-positive and gram-negative microorganisms (Loguercio *et al.,* 2005). In addition to being powerful feeding deterrents (Schoonhoven *et al.,* 2005), these compounds act negatively on the microbial community on which terrestrial isopods rely to acquire the digestive enzymes (Zimmer and Topp, 1998). The digestion of recalcitrant plant material by terrestrial isopods is achieved through enzymes that are secreted by the hepatopancreatic symbionts and by the microbes ingested with the food (Zimmer, 2002). Thus, interfering with bacteria, secondary compounds indirectly act negatively on the isopod's digestive processes (Zimmer, 2002). Hassall and Rushton (1984) and Dudgeon *et al.* (1990) have shown that isopods prefer leaves with lower quantities of phenolic compounds.

The presence of secondary compounds may explain why the leaves of *Syzygium* were consumed in very low amounts, in comparison to *C. sylvestris.* However, this plant is also rich in terpenoids, a large group of secondary compounds mainly found as components of essential oils (Schoonhoven *et al.,* 2005), including casearins (diterpenes) and sesquiterpens with high cytotoxic activity (Santos *et al.,* 2007; Silva *et al.,* 2008). Moreover, diterpenes and clerodanes, which are present in *C. sylvestris* leaves, are known to be potent feeding deterrents to many insect species (Gebbinck *et al.,* 2002).

The feeding choices of isopods are influenced by the chemical composition of the litter, which changes according to the decay stage (Van Wensem *et al.,* 1993). Many studies have shown that decayed leaves were more readily eaten by isopods (Rushton and Hassall, 1983a; Szlávecz, 1985), although none have established which changes in the leaves make them more palatable as they decompose. Generally, soluble organic constituents (*i.e.,* polyphenols, carbohydrates and lipids) are lost more rapidly than solid residues (*i.e.,* holocellulose and lignin) (Berg and McClaugherty, 2007). Therefore, decaying leaves might constitute a food source with lower contents of secondary compounds, as well as a nutrient-poor diet. However, as decomposition progresses, the concentration and absolute content of nutrients, such as N and P increases (Gosz *et al.,* 1973), probably due to microbial colonization. The microbial community changes in composition, according to the substrate that was left to decompose, and the microbial biomass is usually higher in decayed leaves (Attiwill and Adams, 1993). In this stage of decomposition, the microbial biomass may compensate for the lack of original nutrients, serving as a valuable food source (Zimmer and Topp, 2003; Ihnen and Zimmer, 2008). Nonetheless, even though consumption and assimilation rates were higher on more decayed leaves (three-month-old), our results suggest that *B. cairensis* would not feed solely on this type of litter in the field. When given a choice among leaves at different stages of decomposition, *B. cairensis* fed more on the most decayed leaves, as was expected, but also complemented its diet by feeding on green and one-month-old leaves. This behavior has already been observed in other terrestrial isopod species (Szlávecz and Maiorana, 1990) and has been suggested as a means of obtaining an adequate balance of nutrients through feeding on a more diverse diet (Rushton and Hassall, 1983b).

Acknowledgements

The authors are grateful to Dr. Georgina Bond-Buckup and Dr. Ludwig Buckup for providing access to Sítio Cairé, where isopods and plants were collected, and to Biol. Jair Gilberto Kray for identification of plant species. An anonymous referee is greatly acknowledged for comments and criticisms, which improved the quality of the manuscript.

References

Almeida, A. C. S.; Ferreira, R. L. C.; Santos, M. V. F. S.; Silva, J. A. A.; Lira, M. A. and Guim, A. 2006. Avaliação bromatológica de espécies arbóreas e arbustivas de pastagens em três municípios do Estado de Pernambuco. *Acta Scientiarum Animal Sciences,* 28:1-9.

Attignon, S. E.; Weibel, D.; Lachat, T.; Sinsin, B.; Nagel, P. and Peveling, R. 2004. Leaf litter breakdown and plantation forest of the Lama forest reserve in Benin. *Applied Soil Ecology,* 27:19-124.

Attiwill, P. M. and Adams, M. A. 1993. Nutrient cycling in forests. *New Phytologist,* 124:561-582.

Berg, B. and Mc Claugherty, C. 2007. Plant litter: decomposition, humus formation, carbon sequestration. Berlin, Springer, 338 p.

Catalán, T. P.; Lardies, M. A. and Bozinovic, F. 2008. Food selection and nutritional ecology of woodlice in central Chile. *Physiological Entomology,* 33:89-94.

Cornelissen, J. H. C.; Pérez-Harguindeguy, N.; Díaz, S; Grime, J. P.; Marzano, B. and Cabido, M. 1999. Leaf structure and defense control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist,* 143:191-200.

Cotrufo, M. F.; Briones, M. J. I. and Ineson, P. 1998. Elevated CO_2 affects field decomposition rate and palatability of tree leaf litter: importance of changes in substrate quality. *Soil Biology and Biochemistry,* 30(12):1565-1571.

Dangerfield, J. M. and Milner, A. E. 1996. Millipede fecal pellet production in selected natural and managed habitats of southern Africa: implications for litter dynamics. *Biotropica,* 28:113-120.

David, J. F. and Gillon, D. 2002. Annual feeding rate of the millipede *Glomeris marginata* on holm oak (*Quercus ilex*) leaf litter under Mediterranean conditions. *Pedobiologia,* 46:42-52.

Dias, N. and Hassall, M. 2005. Food, feeding and growth rates of peracarid macro-decomposers in a Ria Formosa salt marsh, southern Portugal. *Journal of Experimental Marine Biology and Ecolology,* 325:84-94.

Donatini, R. S.; Ishikawa, T.; Barros, S. B. M. and Bacchi, E. M. 2009. Atividades antiúlcera e antioxidante do extrato de folhas de Syzygium jambos (L) Alston (Myrtaceae) *Revista Brasileira de Farmacognosia,* 19(1a):89-94, jan.-mar. 2009

Dudgeon, D.; Ma, H. H. and Lam, P. K. S. 1990. Differential palatability of leaf litter to four sympatric isopods in a Hong Kong forest. *Oecologia,* 84:398-403.

Fortunel, C.; Garnier, E.; Joffre, R.; Kazakou, E.; Quested, E.; Grigulis, K.; Lavorel, S.; Ansquer, P.; Castro, H.; Cruz, P.; Doležal, J.; Eriksson, O.; Freitas, H.; Golodets, C.; Jouany, C.; Kigel, J.; Kleyer, M.; Lehsten, V.; Lepš, J.; Meier, T.; Pakeman, R.; Papadimitriou, M.; Papanastasis, V. P.; Quétier, F.; Robson, M.; Sternberg, M.; Theau, J. P.; Thébault, A. and Zarovali, M. 2009. Leaf traits capture the effects of land use changes and climate on litter decomposability of grasslands across Europe. *Ecology,* 90(3):598-611.

Gebbinck, E. A. K.; Jansen, B. J. M. and Groot, A. 2002. Insect antifeedant activity of clerodane diterpenes and related model compounds. *Phytochemistry,* 61:737-770.

Gosz, J.R; Likens, G. E. and Bormann, F. H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecological Monographs,* 43(2):173-191.

Gunnarsson, T. 1987. Selective feeding on a maple leaf by *Oniscus asellus* (Isopoda). *Pedobiologia,* 30:161-165.

Hassall, M. and Rushton, S. P. 1984. Feeding behaviour of terrestrial isopods in relation to plant defences and microbial activity. *Symposia of the Zoological Society of London,* 53:487-505.

Ibrahima, A.; Joffre, R. and Gillon, D. 1995. Changes in litter during the initial leaching phase: An experiment on the leaf litter of Mediterranean species. *Soil Biology and Biochemistry,* 27(7):931-939.

Ihnen, K. and Zimmer, M. 2008. Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopods: Oniscidea). *Pedobiologia,* 51:335-342.

Leffler, A. J. and Enquist, B. J. 2002. Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: comparison across tropical forests and tree life history. *Journal of Tropical Ecology,* 18:151-159.

Lima, L. A.; Siani, A. C.; Brito, F. A.; Sampaio, A. L. F.; Henriques, M. G. M. O.; Riehl, C. and Silva, A. 2007. Correlation of anti-inflammatory activity with phenolic content in the leaves of *Syzygium cumini* (L.) Skeels (myrtaceae). *Química Nova,* 30(4):860-864.

Loguercio, A. P.; Battistin, A.; Vargas, A. C.; Henzel, A. and Witt, N. M. 2005. Atividade antibacteriana de extrato hidro-alcoólico de folhas de jambolão (*Syzygium cumini* (L.) Skells). *Ciência Rural,* 35(2):371-376.

Luz, S. F. B.; Sato, M. E. O.; Duarte, M. R. and Santos, C. A. M. 1997. Parâmetros para o controle da qualidade de folhas de *Casearia sylvestris* sw. – Guaçatonga. *Revista Brasileira de Farmacognosia,* 7:1-11.

Mahmoud, I. I. Marzouk, M. S. A. Moharram, F. A.; El-Gindi, M. R. and Hassan, A. M. K. 2001. Acylated flavonol glycosides from *Eugenia jambolana* leaves. *Phytochemistry,* 58:1239-1244.

Mandal, L. 1997. Nutritive values of tree leaves of some tropical species for goats. *Small Ruminant Research,* 24:95-105.

McClaugherty, C. A., Pastor, J.; Aber, J. D. and Melillo, J. M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, 66(1):266-275.

Migliato, K. F.; Baby, A. R.; Zague, V.; Velasco, M. V. R.; Corrêa, M. A.; Sacramento, L. V. S. and Salgado, H. R. N. 2006. Ação farmacológica de Syzygium cumini (L.) Skeels. *Acta Farmacéutica Bonaerense,* 25(2):310-314.

Moore, J. C.; Berlow, E. R.; Coleman, D. C.; Ruiter, P. C.; Dong, Q.; Hastings, A.; Johnson, N. C.; Mccann, K. S.; Melville, K.; Morin, P. J.; Nadelhoffer, K.; Rosemond, A. D.; Post, D. M.; Sabo, J. L.; Scow, K. M.; Vanni, M. J.

and Wall, D. H. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters,* 7:584-600.

O'Connell, A. M. 1988. Nutrient dynamics in decomposing litter in karri (*Eucalyptus diversicolor*) forests of south-western Australia. *Journal of Ecology*, 76(4):1186-1203.

O'Hanlon, R. P. and Bolger, T. 1999. The importance of *Arcitalitrus dorrieni* (Hunt) (Crustacea:Amphipoda, Talitridae) in coniferous litter breakdown. *Applied Soil Ecology,* 11: 29-33.

Ostertag, R.; Marín-Spiotta, E.; Silver, W. L. and Schulte, J. 2008. Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. *Ecosystems,* 11:701-714.

Quadros, A. F. and Araujo, P. B. 2008. An assemblage of terrestrial isopods (Crustacea) in southern Brazil and its contribution to leaf litter processing. *Revista Brasileira de Zoologia,* 25(1):58-66.

Ramana, D. B. V.; Singhb, S.; Solankia, S. K. R. and Negi, A. S. 2000. Nutritive evaluation of some nitrogen and non-nitrogen fixing multipurpose tree species. *Animal Feed Science and Technology,* 88:103-111.

Raubenheimer, D. and Simpson, S. J. 1992. Analisys of covariance: an alternative to nutricional indices. *Entomologia Experimentalis et Applicata,* 62:221-231.

Roa, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. *Oecologia,* 89, 509-515.

Rushton, S. P. and Hassall, M. 1983a. Food and feeding rates of the terrestrial isopod *Armadillidium vulgare* (Latreille). *Oecologia,* 57:415-419.

Rushton, S. P and Hassall, M. 1983b. The effects of food quality on the life history parameters of terrestrial isopod (*Armadillidium vulgare* (Latreille)). *Oecologia,* 57:257-261.

Santos, A. G.; Perez, C. C.; Tininis, A. G.; Bolzani, V. S. and Cavalheiro, A. J. 2007. Clerodane diterpenes from leaves of *Casearia sylvestris* Swartz. *Química Nova,* 30(5):1100-1103.

Schoonhoven, L. M.; van Loon, J. J. A and Dicke, M. 2005. Insect-plant Biology. Oxford Univ Press, Oxford.

Silva, S. L.; Chaar, J. S.; Figueiredo, P. M. S. and Yano, T. 2008. Cytotoxic evaluation of essential oil from *Casearia sylvestris* Sw on human cancer cells and erythrocytes. *Acta Amazonica,* 38(1):107-112.

Sobral, M. and Jarenkow, J. A. 2006. Flora Arbórea e Arborescente do Rio Grande do Sul. Porto Alegre, Rima-Novo Ambiente, 350 p.

Sokolowicz, C. C.; Araujo, P. B. and Boelter, J. F. 2008. A new species of Benthana (Crustacea: Isopoda: Philosciidae) from southern Brazil. *Revista Brasileira de Zoologia,* 25(2):314-318.

Soma, K. and Saitô, T. 1983. Ecological studies of soil organisms with reference to the decomposition of pine needles. II. Litter feeding and breakdown by the woodlouse *Porcellio scaber. Plant and Soil,* 75:139-151.

Szlávecz, K. 1985. The effect of microhabitats on the leaf litter decomposition and on the distribution of soil animals. *Holarctic Ecology,* 8:33-38.

Szlávecz, K. and Maiorana, V. C. 1990. Food selection by isopods in paired tests. p. 115-121. *In:* P. Juchault and J. Mocquard (eds), The Biology of Terrestrial Isopods III. Proceedings of Third Symposium on the Biology of Terrestrial Isopods. Université de Poitiers.

Van Wensem, J.; Verhoef, H. A. and Van Straalen, N. M. 1993. Litter degradation stage as a prime factor for isopod interaction with mineralization processes. *Soil Biology and Biochemistry,* 25(9):1175-1183.

Waldbauer, G. P. 1968. The consumption and utilization of food by insects. *Advances in Insect Physiology,* 5:229-288.

Webb, D. P. 1977. Regulation of deciduous forest fitter fecomposition by soil arthropod feces. pp. 57-69. *In:* W. J. Mattson (ed.), The role of arthropods in forest ecosystems, New York, Springer-Verlag.

Wolters, V. 2000. Invertebrate control of soil organic matter stability. *Biology and Fertility of Soils,* 31:1-19.

Zimmer, M. 2002. Is decomposition of woodland leaf litter influenced by its species richness? *Soil Biology and Biochemistry,* 34:277-284.

Zimmer, M. and Topp, W. 1998. Microorganisms and cellulose digestion in the gut of *Porcellio scaber* (Isopoda: Oniscidea). *Journal of Chemical Ecology,* 24:1397-1408.

Zimmer, M. and Topp, W. 2003. Leaf litter-colonizing microbiota: supplementary food source or indicator of food quality for *Porcellio scaber* (Isopoda: Oniscidea)? *European Journal of Soil Biology,* 39:209-216.

Submitted 15/05/2009
Accepted 14/07/2009