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Enhancement of soil enzyme activities by the feeding impact of detritivore arthropods on tropical forest tree leaf litters

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Abstract: The detritivore arthropods promote litter decomposition and nutrient release in soil, but their functional role varies depending on feeding habit and the physicochemical properties of plant litter. We compared the feeding impact of *Anoplodesmus saussurei* (Humbert) and *Porcellio laevis* Latraeille, on litter breakdown and soil enzyme activities. These detritivores have contrasting feeding habits - like feeding on semi-liquid portions (*A. saussrei*), and feeding by scrapping soft tissues (*P. laevis*) - and were reared on decomposing leaf litter of two forest tree species, *Cassia siamea* (Lamk.) and *Shorea robusta* (Gaertn. f.) in microcosms. The initial quantities of soluble carbohydrates, cellulose and hemicelluloses were high in the small and fragile *C. siamea* litter, whereas polyphenols, tannin and lignin were initially abundant in the large and hard litter of *S. robusta*. Feeding by *A. saussurei* and *P. laevis* caused significant weight loss of *C. siamea* litter, whereas the weight loss was much less in *S. robusta*. Feeding accelerated the decline of the main chemical constituents in *C. siamea* litter except for lignin. Temporal differences in soil enzyme activities were attributed to differences in litter quality, with *C. siamea* litter exhibiting higher amylase, cellulase and invertase activities than *S. robusta*. Soil enzyme activities were also influenced by the presence of detritivores, and the positive impact of *A. saussurei* was greater than that of *P. laevis* for all the enzymes in *S. robusta* litter. Amylase activity increased in the presence of both arthropods in *C. siamea* and *S. robusta* litters. Cellulase activity was enhanced only by *A. saussurei* in both litters, whereas both detritivore species contributed to higher invertase activity in *S. robusta* litter. The results of our study show a direct and species-specific comminuting effect of detritivore arthropods on physical and chemical breakdown of leaf litters and on biochemical functions, as indicated by enhanced soil enzyme activities.

Resumen: Los artrópodos detritívoros promueven la descomposición del mantillo y la liberación de nutrimentos en el suelo, pero su papel funcional varía dependiendo del hábito alimenticios y las propiedades fisicoquímicas del mantillo vegetal. Comparamos el impacto que tiene la alimentación de *Anoplodesmus saussurei* (Humbert) y de *Porcellio laevis* Latraeille en la descomposición del mantillo y las actividades enzimáticas del suelo. Estos detritívoros tienen hábitos alimenticios contrastantes - por ejemplo, alimentación de porciones semilíquidas (*A. saussrei*) y alimentación por medio de la trituración de tejidos suaves (P. *laevis*) - y fueron criados en mantillo foliar en descomposición de dos especies arbóreas forestales, *Cassia siamea* Lamk. y *Shorea robusta* Gaertn. f. en microcosmos. Las cantidades iniciales de carbohidratos solubles, celulosa y hemicelulosas fueron altas en el mantillo pequeño y frágil de *C. siamea*, mientras que los polifenoles, taninos y lignina fueron abundantes inicialmente en el mantillo grande y duro de *S. robusta*. La alimentación por parte de *A. saussurei* y *P. laevis* causó una pérdida significativa de peso del mantillo de *C. siamea*, mientras que la pérdida de peso fue mucho menor en *S. robusta*. La alimentación aceleró la disminución de los principales constituyentes químicos en el mantillo de *C. siamea*, a excepción de la lignina. Las diferencias

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temporales en las actividades enzimáticas del suelo fueron atribuidas a diferencias en la calidad del mantillo, en donde el mantillo de *C. siamea* exhibió mayor actividad de la amilasa, la celulasa y la invertasa que el de *S. robusta*. Las actividades enzimáticas del suelo también se vieron influenciadas por la presencia de detritívoros, y el impacto positivo de *A. saussurei* fue mayor que el de *P. laevis* para todas las enzimas en el mantillo de S. robusta. La actividad de la amilasa se incrementó en presencia de ambos artrópodos en los mantillos de *C. siamea* y S. robusta. La actividad de la celulasa fue mejorada sólo por *A. saussurei* en ambos mantillos, mientras que ambas especies detritívoras contribuyeron a una mayor actividad de la invertasa en el mantillo de *S. robusta*. Los resultados del estudio mostraron un efecto pulverizador directo y específico de las especies de artrópodos detritívoros sobre la descomposición física y química de los mantillos foliares y en las funciones bioquímicas, tal y como lo indican las actividades enzimáticas mejoradas del suelo.

Resumo: Os artrópodes detritívoros promovem a decomposição da folhada e a libertação de nutrientes no solo, mas o seu papel funcional varia de acordo com hábito alimentar e as propriedades físico-químicas da folhada. Neste estudo comparámos o impacto da alimentação da *Anoplodesmus saussurei* Humbert e da *Porcellio laevis* Latraeillena decomposição da folhada e nas actividades enzimáticas no solo. Estes detritívoros têm hábitos alimentares contrastantes - como alimentarem-secom componentes semi-líquidas (*A. saussrei*), ou por desgaste dos tecidos moles (*P. laevis*) - e foram criados em folhadaem decomposição de duas espécies florestais arbóreas, *Cassia siamea* Lamk. e *Shorea robusta* Gaertn. f. em microcosmos. As quantidades iniciais de carbohidratos solúveis, celulose e hemiceluloses foram altas na pouca e frágil folhada da *C. siamea*, enquanto que os polifenóis, taninos e lenhina foram inicialmente abundantes na abundante e dura folhada daS. robusta. A alimentação na *A. saussurei* e *P. Laevis* provocou uma perda de peso significativa na folhada de *C. siamea*, enquanto que a perda de peso foi muito menor em *S. robusta*. A alimentação acelerou o declínio dos principais constituintes químicos na folhada de *C. Siamea* com exceção da lenhina. As diferenças temporais na atividade de enzimas no solo foram atribuídas a diferenças na qualidade da folhada, com a folhada de *C. siamea* exibindo uma maior atividadequanto à amilase, celulase e invertase do que para a folhada deS. robusta. As atividades enzimáticas do solo também foram influenciadas pela presença de detritívoros, assim como o impacto positivo da *A. saussurei* foi maior do que o da *P. laevis* para todas as enzimas na folhada de *S. robusta*. A atividade da amilase aumentou na presença de ambos os artrópodes nas folhadas de *C. siamea* e *S. robusta*. A atividade da celulase foi intensificada apenas por *A. saussurei* em ambas as folhadas, enquanto que as duas espécies de detritívoros contribuíram para uma maior atividade dainvertase na folhada de *S. robusta*. Os resultados do nosso estudo indicam um efeito direto econtínuo dos artrópodes detritívoros dependente das espécies na decomposição física e química da folhada e nas funções bioquímicas, tal como indicado pelo reforço das actividades enzimáticas no solo.

Key words: Detritivore, litter decomposition, microcosms, secondary metabolites, soil arthropods, soil enzymes.

Introduction

Leaf litter decomposition is necessary for nutrient release and sustained tropical forest productivity. The rate of litter decomposition is controlled by the physical and chemical properties of the litter, the prevailing environmental conditions, and the composition of decomposer biota. The term "litter quality" refers to the intrinsic characteristics of the materials (Swift 1995). High-quality litters are rapidly decomposed, have a high N and P content, high levels of readily-metabolized sugars, and low lignin content. By contrast, low-quality litters are decomposed slowly, have a low N and P content, high levels of lignin and low levels of readily-metabolized sugars. Many plants

contain high concentrations of complex molecules such as polyphenols, tannin and lignin, which may be considered secondary metabolites, non-nutritional, anti-herbivory defense chemicals, or allelopathic compounds. According to Williams & Gray (1974) non-nutritional chemicals, such as phenols, tannins, terpenes, and lipids in leaf litter can inhibit decomposition through decreased microbial and faunal utilization and formation of recalcitrant complexes with other compounds. Swift & Anderson (1989) demonstrated that nutrient-rich leaves with fewer physicochemical defenses are decomposed faster than resistant, nutrient-poor litters. Paustian *et al.* (1997) has defined the quality of litter as its relative ease of mineralization by decomposer organisms. It is known that synergistic interaction between microbes and detritivore soil animals is needed for complete disintegration of physically and chemically stable plant tissues. Thus, any notable variation in the rate of litter degradation between two closely located afforested sites may indicate either a change in the decomposer community or the basic nature of litter resources.

Microbial parameters like soil enzyme activity are ecologically significant indices of organic matter enrichment and stable biological functioning in soil. These parameters have been suggested as sensitive indicators of soil quality, which may be useful to select plants suitable for reclamation of semiarid disturbed areas and to assess the management practices, effects on nutrient cycling, and soil organic matter dynamics (Garcia *et al.* 2000). According to Graham & Haynes (2005) major microbial functional indicators in soil include the activity of extracellular enzymes involved in the transformations of carbon (amylase, cellulase, invertase), nitrogen (protease) and phosphorus (phosphatase); the activity of intracellular enzymes such as dehydrogenase; as well as microbial biomass carbon (MBC) and basal respiration (CO_2 evolution). However, the majority of studies on soil enzyme activities have focused on temperate areas and scant information exists on soil enzyme activities in tropical conditions (Acosta-Martinez *et al.* 2007). One of the main differences between temperate and tropical conditions is the rate of litter decomposition, which is controlled by fluctuating edaphic parameters. Litter production and decomposition in tropical deciduous forests exhibit seasonal trends, with peak litter fall in summer (Singh & Ambasht 1980), followed by rapid decomposition during the wet season (Satchell 1974) and high density of soil arthropods (Reddy 1995), which is controlled by temperature and moisture limitations (Singh & Singh 1975; Lambert *et al.* 1980). The increase in litter moisture content enhances the microbial growth and palatability of litter, which facilitates high density of soil biota during the monsoon and post-monsoon periods in tropical forests. Drastic changes in decomposition may occur within a short time because the distribution of soil biota is affected by extremes of temperature and moisture during the contrasting seasons. Regarding the soil enzyme activity, Mukhopadhyay & Joy (2010) have observed clear differences between leaf litters and seasons. For example, amylase, cellulase, protease, dehydrogenase and acid phosphatase activities were higher in soils containing *Cassia siamea* and *Dalbergia sissoo* litters than *Acacia auriculiformis* and *Shorea robusta* litters, and amylase and cellulase activities reached a peak during rainy season in all the leaf litters. Amylase, cellulase and invertase are fundamental for hydrolyzing the glucosidic linkages of plant carbohydrates. The physicochemical properties of leaf litters that affect food preference and utilization efficiency of soil fauna are also important (Hattenschwiler & Bretscher 2001; Joy & Joy 1991). Large-scale fragmentation of litter during feeding, and a high rate of faecal production by secondary decomposers like earthworms, diplopods and isopods, may influence the activities of microbiota and smaller animals. According to Fioretto *et al.* (2007) microbes require the assistance of soil fauna that modulates litter structure and redistributes organic residues, as "ecosystem engineers".

The objective of the present study was to compare the feeding effect of two detritivore arthropod species, *A. saussurei* and *P. laevis,* on the temporal variation of amylase, cellulase and invertase activities in soil as affected by the resource quality of leaf litters of *C. siamea* and *S. robusta,* trees used for afforestation in tropical wastelands. These litters differ in physical and chemical properties like size and weight, and concentration of nutritional and non-nutritional chemicals. The selected arthropods are characterized by contrasting feeding habits: *A. saussurei* feeds on semi-liquid portions of decomposing litter, whereas *P. laevis* feeds by scraping soft tissues of litter. Thus, species-specific differences are expected in promoting nutrient enrichment and soil enzyme activities.

Materials and methods

Collection and rearing of detritivore soil arthropods

The detritivore soil arthropods *Porcellio laevis* Latraeille (Porcellionidae: Isopoda: Crustacea), commonly termed "woodlice", and *Anoplodesmus saussurei* (Humb.) (Paradoxosomatidae: Polydesmida: Diplopoda), popularly known as the "yellow spotted flat back millipede", were hand-sorted from the litter beds of a reserve forest at Santiniketan in Eastern India (23°29′ North and 87°35′ East). Both species occur in topsoil and decaying litters and are abundant during the monsoon and post-monsoon months (June to November). They were acclimatized in the laboratory on humus-rich soil, and mass-reared in plastic trays containing a 2 cm layer of decomposing litter over a 3 cm layer of washed river sand, under controlled temperature (27 ± 1°C), moisture (~20 % in sand and litter) and photoperiod (14:10 h light: dark cycle) conditions in an incubator, as described by Maity & Joy (1999). Only animals in the same size range (280 - 300 mg live weight and 3.5 - 3.8 cm body length for *A. saussurei;* 6 - 9 mg live weight and 5 - 7 mm body length for *P. laevis)* were used in the experiments. Both are voracious feeders on decomposing litter: *A. saussurei* feeds on semi-liquid portions, whereas *P. laevis* feeds by scraping soft tissues of litter. *A. saussurei* deposits muddy faecal matter, in contrast to the dry faecal pellets of *P. laevis;* however, both are coprophages.

Collection of leaf litter and pit experiment

Freshly fallen senescent leaves were collected from the floor of monoculture stands (approx. 30 years old) of *Cassia siamea* (Lamk.) (Caesalpiniaceae) and *Shorea robusta* (Gaertn. f.) (Dipterocarpaceae) trees during the dry season (February-March), the period of highest litter fall in tropical forests. These trees are preferred for reforestation in the laterite wastelands of Eastern India. The leaves of the native *S. robusta* are large (area = 133.8 ± 12.8 cm^2) and heavy (dry weight 1.7 ± 0.1 g) litter, whereas *C. siamea* is an exotic species with small (size 9.8 ± 0.5 cm^2) and light (dry weight 0.1 ± 0.01 g) leaf litter.

Detritivore soil arthropods may enhance litter decomposition and nutrient release through synergistic and symbiotic relationships with microbes, but no single method is appropriate to isolate and differentiate the faunal impact from the microbial effect. Therefore, experiments were done in litter decomposition pits under field conditions and in microcosms under laboratory conditions to compare major parameters like degradation of litters and temporal variations in soil enzyme activities, with respect to detritivore feeding.

The first experiment was conducted in open field pits during February to May in 2004 to compare the rates of disappearance of major chemical constituents of litters. Each soil pit (120 cm × 60 cm × 30 cm deep) contained 10 kg dry litter, with two replicates for each tree species. The litter in each pit was initially moistened with 10 L of water; thereafter 1 L of water was sprinkled on alternate days to maintain the moisture content at ~ 20 %. The pits were protected from sunlight and rain using plastic sheets during the 90-day duration of the study. From each pit two samples (10 cm × 10 cm × 5 cm) of decaying litter were taken at random at 30-day intervals to determine the concentrations of major nutritional and non-nutritional chemicals. The litter samples were air-dried, pooled, powdered in an electric grinder, sieved (72 mesh-sieve), and stored in a desiccator. All parameters were estimated using six replicates of the pooled sample for each interval and for each tree species.

Laboratory microcosm experiments

Microcosms were used to study the rates of physicochemical breakdown of *C. siamea* and *S. robusta* litters due to feeding activity of *A. saussurei* and *P. laevis.* Air-dried fresh litter was cut into 2 - 3 cm pieces, and five-g cut-up pieces were subjected to decomposition for 7 days in plastic vessels (10 cm × 10 cm × 12 cm height) under the same conditions used for rearing the arthropods. A total of 72 microcosms were prepared, with 12 replicates each for a control treatment and two feeding treatments of *C. siamea* and *S. robusta* litter, respectively. The control treatment (without animals) was used to study the degradation of litter due to microbial activity. Each feeding treatment contained either 10 specimens of *A. saussurei* or 50 specimens of *P. laevis,* drawn from the laboratory stocks. There was negligible mortality of the specimens; yet their numbers were kept the same by removing and replacing dead ones daily. Moisture was maintained by adding distilled water after daily checkups. Triplicate control and feeding treatments were sampled at random at weekly intervals for 28 days. The animals were sorted out and the litter dried at 60 °C

in a hot-air oven for 24 h, stored in a desiccator, and weighed in a microbalance (Sartorius model MC1, accuracy 0.1 mg). Litter was then processed and stored for chemical analysis, as described above.

In a second microcosm experiment, the temporal variations of soil enzyme activities in control and detritivore arthropod feeding treatments of *C. siamea* and *S. robusta* litter were compared at fortnightly intervals for 90 days. A total of 18 microcosms were prepared, representing triplicate control and feeding treatments of *A. saussurei* and *P. laevis* in both litter types. Each microcosm contained a bottom layer of 500 g of washed river sand and an upper layer of 5 g of leaf litter cuttings (2 - 3 cm pieces). Natural soil is unsuitable as a medium to assess the role of detritivores in boosting humification and microbial activities because the presence of high levels of organic matter, nutrients, microbes and enzymes can confound interpretation of the results. Therefore, washed and sterilized river sand was used as a natural medium into which the organic matter and microbial inoculates would be incorporated from the decomposing litter and by the feeding activity of detritivores. The microcosms contained either 10 specimens of *A. saussurei* or 50 *P. laevis,* taken from the acclimatized stocks. Distilled water was added to moisten the litter and sand (~20 % moisture content) and the microcosms were maintained under laboratory conditions as described above. Approximately 10 g of moist sand was scooped out randomly from each microcosm at fortnightly intervals, and samples from each treatment were pooled and stored at 4 °C for enzyme activity studies.

Chemical analysis of leaf litter

The concentrations of major chemical constituents of leaf litter samples were determined by spectrophotometric and gravimetric methods. Total soluble carbohydrate content of litter was measured by the Dubois *et al.* (1956) method, with absorbance of the golden yellow product determined at 490 nm using a spectrophotometer (Model DU 730, Beckman Coulter) using D-glucose as a standard. The method of Updegroff (1969) was employed for estimation of cellulose in litter, with optical density of the green solution measured at 630 nm using cellulose as a standard. Total protein content of litter samples was estimated by the Lowry *et al.* (1951) method, with intensity of the blue color measured at 750 nm using bovine serum albumin as a standard. To measure levels of polyphenols, litter samples were extracted in 50 % aqueous methanol, and optical density of the resultant blue complex was measured at 700 nm using a phenol standard (King & Heath 1967). The Folin-Denis method (Sadasivam & Manickam 1992) was used to estimate tannin content in litter samples, with the color intensity of the blue solution determined at 700 nm, and compared against a standard curve for tannic acid. Hemicelluloses in litter were measured by refluxing samples in neutral detergent (a mixture of disodium ethylenediamine tetraacetate, sodium borate decahydrate, sodium lauryl sulphate, 2-ethoxy ethanol and disodium hydrogen phosphate in distilled water, pH 7.0) and acid detergent (cetyl trimethyl ammonium bromide dissolved in 1N H_2SO_4) solutions, which allowed us to calculate the difference in weight between neutral detergent-fiber and acid detergent-fiber (Goering & Van Soest 1970). The total lipid content of leaf litter was measured by extraction in petroleum ether, followed by evaporation and drying to a constant weight (King & Heath 1967). The lignin and ash contents of litter were determined by refluxing the samples in acid detergent solution, with the resulting fibrous residue treated with concentrated sulphuric acid, weighed and ashed in a muffle furnace at 550 °C (Brauns 1952).

Estimation of soil enzyme activities

The temporal variations in amylase, cellulase and invertase activities in the microcosms were estimated following the methods described by Mishra *et al.* (1979). Fresh sand samples were incubated with Sorensen's buffer (disodium hydrogen phosphate dihydrate and potassium dihydrogen phosphate dissolved in distilled water, 0.06M, pH 5.5) and respective substrate solution (starch for amylase, carboxymethyl cellulose for cellulase and sucrose for invertase) at 30 °C for 24 h. The suspension was then centrifuged and the supernatant solution reacted with dinitro salicylic acid (DNSA) reagent, and heated in a boiling water bath. The optical density of the resulting solution was measured at 540 nm using a spectrophotometer (Model DU 730, Beckman Coulter) using D-glucose as a standard.

Statistical analysis

The statistical analysis and graphical representation of experimental data was performed using Microsoft Excel (Windows 2003), SPSS (version 10.0) and Origin Lab (version 6.1)

Table 1. Degradation (% loss after 90 days) of the main chemical constituents of leaf litter of *C. siamea* and *S. robusta* trees in litter decomposition pits under field conditions. Values are means ± standard error.

Chemical constituent	*C. siamea*		*S. robusta*	
	Initial concentration (mg g^{-1} dry weight)	% loss after 90 days	Initial concentration (mg g^{-1} dry weight)	% loss after 90 days
Soluble carbohydrates	205.77 ± 9.61	89.29	164.80 ± 9.04	88.14
Total proteins	39.08 ± 3.92	58.20	45.94 ± 3.31	48.79
Cellulose	112.5 ± 6.46	64.44	42.5 ± 7.14	35.29
Hemicelluloses	24.59 ± 2.51	74.54	5.58 ± 0.69	100.00
Total lipids	34.5 ± 1.84	80.08	26.43 ± 2.11	43.80
Polyphenols	42.95 ± 1.7	93.41	72.13 ± 1.56	92.40
Tannins	14.0 ± 1.63	96.14	48.82 ± 1.2	89.32
Lignin	321.83 ± 14.62	-44.63	536.52 ± 16.6	-28.17
Ash content	45.03 ± 2.99	32.67	31.53 ± 3.34	40.00

software programmes. The error values of replicates at different intervals of estimation were included for comparing the mean values of different experimental sets. A paired t-test was used to compare the statistical significance of variations between the concentrations of chemical constituents of litter, and between the rates of soil enzyme activity in control and feeding treatments at > 95 % confidence level ($P < 0.05$). The overall differences in soil enzyme activities in the microcosm sets of *C. siamea* and *S. robusta* litters with respect to detritivore feeding and intervals were determined using a two-way repeated measured analysis of variance.

Results

Degradation of chemical constituents of litter

Comparison of the initial levels of major chemical constituents (Table 1) showed large differences between *C. siamea* and *S. robusta* litters. The initial concentration of soluble carbohydrates was higher in *C. siamea* than in *S. robusta,* and *C. siamea* litter contained higher initial levels of cellulose and hemicelluloses than *S. robusta* litter. However, both litters had similar concentrations of total lipids and total proteins. In contrast, *S. robusta* contained higher levels of polyphenols and tannins than *C. siamea,* and the initial lignin content of *S. robusta* was higher than in *C. siamea,* although the ash content was higher in *C. siamea* litter than in *S. robusta.* Temporal trends in the degradation of major chemical constituents of *C. siamea* and *S. robusta* litters in decomposition pits showed a fast initial decline of water-soluble items (soluble carbohydrates, 89.3 % and 88.1 %; polyphenols, 93.4 % and 92.4 %; tannins, 96.1 % and 89.3 %, respectively). The hemicelluloses exhibited a 74.5 % loss in *C. siamea* litter, with levels in *S. robusta* that were below the detection limit within 90 days. On the other hand, losses of total proteins, cellulose and total lipids were faster in *C. siamea* (58.2 %, 64.4 % and 80.1 %, respectively) than in *S. robusta* litter (48.8 %, 35.3 % and 43.8 %, respectively). The lignin content of both litters appeared to increase during the experiment, reaching values of 144.6 % and 128.2 % of initial levels in *C. siamea* and *S. robusta* litters, respectively, by the end of the experiment. The average decrease in ash content was 32.7 % in *C. siamea* litter and 40 % in *S. robusta* for the litter residue remaining after 90 days (Table 1).

Detritivore feeding effect on physicochemical degradation of litter

Fig. 1 depicts the weight loss of *C. siamea* and *S. robusta* litters due to feeding by *A. saussurei* and *P. laevis* in microcosms. The control treatment showed weight loss due to microbial decomposition only, whereas the feeding treatments showed weight loss due to microbial activity and feeding by the animals. Microbial decomposition accounted for 11.9 % and 14 % weight loss of *C. siamea* and *S. robusta* litters, respectively, during 28 days. *C. siamea* litter was preferred by *A. saussurei* and *P. laevis,* leading to 42.2 % and 43.3 % weight loss, respectively. As such, feeding accounted for the degradation of more than 30 % of *C. siamea* litter.

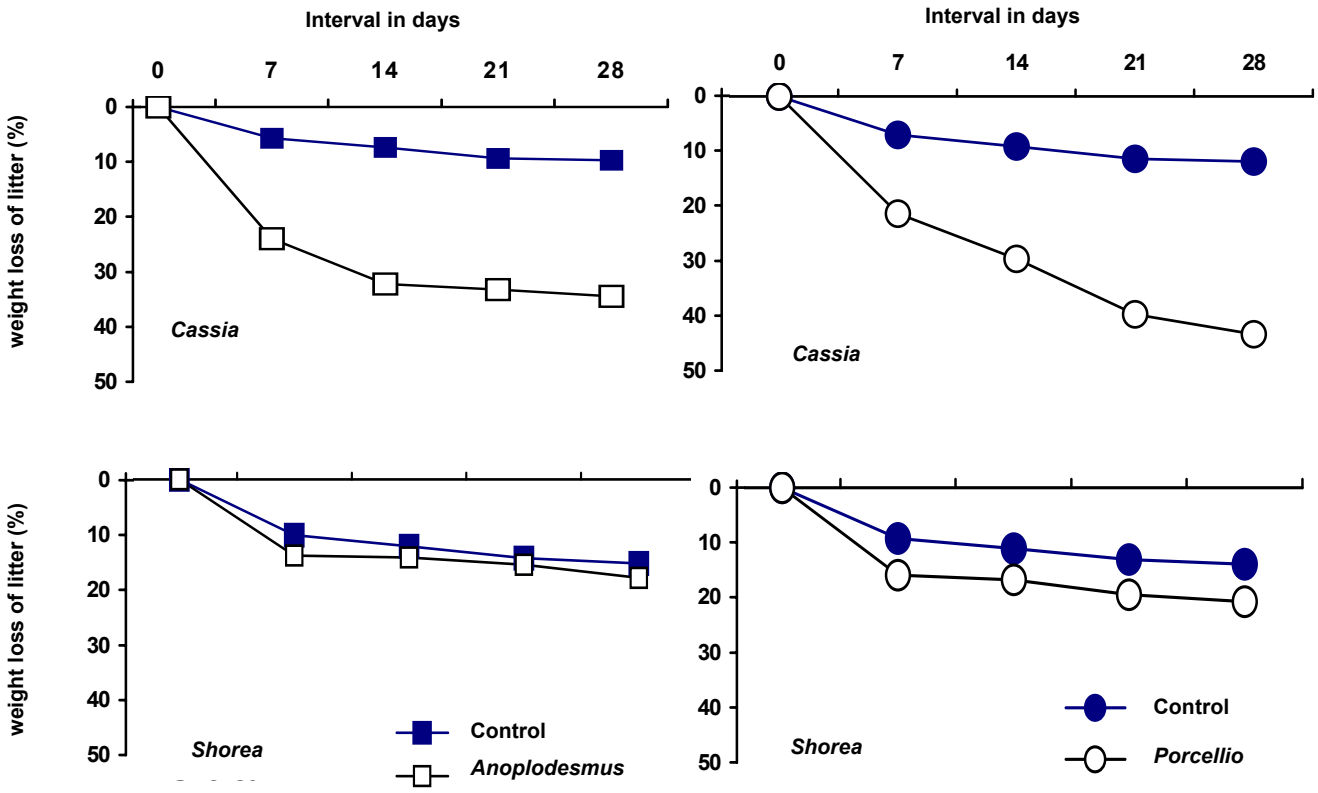

Fig. 1. Temporal variations in the weight loss (%) of *C. siamea* and *S. robusta* litters under microcosm conditions in control (microbial activity only) and feeding (microbial activity and arthropod feeding) treatments containing *A. saussurei* or *P. laevis*.

By contrast, there was a negligible impact of *A. saussurei* and *P. laevis* on *S. robusta,* with a total weight loss of 16.3 % and 20.8 %, respectively, such that feeding by *A. saussurei* and *P. laevis* was responsible for only 2.3 % and 6.8 % weight loss, respectively, showing that *S. robusta* litter was not palatable to these detritivores.

The feeding effects of detritivore arthropods on the degradation of the main chemical constituents of *C. siamea* litter were evident from the differences between the control and feeding treatments (Table 2). Comparison of the residual quantities of major constituents in the control treatment with the initial concentrations showed sharp decline of soluble carbohydrates, cellulose and hemicelluloses within 28 days. Feeding by *A. saussurei* and *P. laevis* further decreased levels of these compounds significantly. Comparison between the feeding treatments showed a higher impact of *A. saussurei* on the degradation of chemical constituents of litter. There was no decline in total protein content in litter in the control treatment, but significant decreases were noticed in the feeding treatments for both detritivores. Total lipids exhibited a slow rate of degradation in the control litter (from 34.5 ± 1.8 mg g^{-1} dw to 26.1 ± 2.3 mg g^{-1} dw). By contrast, there was a significant decline in lipid content of *C. siamea* litter due to faunal feeding. Similarly, the degradation of polyphenols was slow in the control treatment, whereas levels of polyphenols declined sharply in the feeding treatments of *A. saussurei* and *P. laevis*. The tannin content of *C. siamea* litter decreased similarly in control and feeding treatments. The feeding effect of *A. saussurei* was more prominent on the degradation of all these chemical constituents. By contrast, the lignin content apparently increased above initial levels, such that the differences between control and feeding treatments were not significant. The ash content of *C. siamea* litter showed a slow rate of decline in the control treatment, whereas feeding by *A. saussurei* and *P. laevis* decreased ash content significantly.

Detritivore feeding effect on soil enzyme activities

Figure 2 shows the temporal variations in soil enzyme activities under *A. saussurei* and *P. laevis*

Table 2. Concentration of major chemical constituents remaining after 28 days in control (microbial activity only) and feeding (microbial activity and detritivore feeding) treatments of *C. siamea* leaf litter under microcosm conditions, and comparison of differences between control and feeding treatments (paired t test).

Chemical constituents	Concentration (mg g^{-1} dry weight) of chemical constituent remaining in:		
	Control treatment	*A. saussurei* treatment	*P. laevis* treatment
Soluble carbohydrates	134.38 ± 3.30	57.14 ± 6.53***	72.32 ± 6.10***
Total proteins	43.66 ± 1.50	28.03 ± 1.16***	30.58 ± 2.48***
Cellulose	63.75 ± 3.77	36.75 ± 3.50***	45.00 ± 3.56***
Hemicelluloses	14.03 ± 1.33	8.09 ± 1.03***	10.08 ± 1.28**
Total lipids	26.13 ± 2.30	16.25 ± 2.81***	20.63 ± 1.42***
Polyphenols	27.88 ± 0.66	5.94 ± 0.88***	11.50 ± 1.17***
Tannins	10.00 ± 1.08	5.46 ± 0.75***	7.88 ± 0.85**
Lignin	476.63 ± 12.42	467.75 ± 6.46 n.s.	437.75 ± 6.59 n.s.
Ash content	42.69 ± 5.60	17.81 ± 2.25***	22.94 ± 2.05***

Note: Initial concentrations of chemical constituents are given in Table 1.
Paired t - test , df = 17 , ** = $P < 0.01$, *** = $P < 0.001$, n.s. = not significant.

Table 3. Comparison of overall differences in soil enzyme activities between control (microbial activity only) and feeding (microbial activity and detritivore feeding) treatments of *C. siamea* and *S. robusta* litters under microcosm conditions.

Soil enzymes	Litter types	Experimental sets	Overall average		Differences	t stat	*P*
			X_1	X_2			
Amylase activity (µg glucose g dry $soil^{-1}$ h^{-1})	*C. siamea*	Con vs. Ano	29.38	39.19	+ 9.81	5.937	< 0.001
		Con vs. Por	29.38	37.58	+ 8.2	3.527	< 0.001
		Ano vs. Por	39.19	37.58	- 1.61	1.288	n.s
	S. robusta	Con vs. Ano	16.77	61.51	+ 44.74	5.02	< 0.001
		Con vs. Por	16.77	25.49	+ 8.72	1.909	< 0.05
		Ano vs. Por	61.51	25.49	- 36.02	6.151	< 0.001
Cellulase activity (µg glucose g dry $soil^{-1}$ h^{-1})	*C. siamea*	Con vs. Ano	8.31	12.39	+ 4.08	1.821	> 0.05
		Con vs. Por	8.31	10.79	+ 2.48	1.366	n.s
		Ano vs. Por	12.38	10.79	- 1.59	0.147	n.s
	S. robusta	Con vs. Ano	9.63	27.07	+ 17.44	5.574	> 0.001
		Con vs. Por	9.63	10.64	+ 1.01	1.032	n.s
		Ano vs. Por	27.07	10.64	- 16.43	5.811	> 0.001
Invertase activity (µg glucose g dry $soil^{-1}$ h^{-1})	*C. siamea*	Con vs. Ano	85.42	32.66	- 52.76	5.575	> 0.001
		Con vs. Por	85.42	70.44	- 14.98	1.535	n.s
		Ano vs. Por	32.66	70.44	+ 37.84	3.635	> 0.001
	S. robusta	Con vs. Ano	44.52	109.75	+ 65.23	5.781	> 0.001
		Con vs. Por	44.52	77.75	+ 33.23	4.023	> 0.001
		Ano vs. Por	109.75	77.75	- 32.00	4.716	> 0.001

Note: X_1 and X_2 represent the two treatments used for paired t-test. Con = Control, Ano = *A. saussurei* feeding, Por = *P. laevis* feeding. N = 24 in all treatments.

in microcosms containing *C. siamea* and *S. robusta* litters. There was a high amylase activity for the first 30 days of the experiment in the control and feeding treatments containing *C. siamea* litter; thereafter, enhanced amylase activity relative to the control was observed in the feeding treatments of both detritivores up to 60 days. For *S. robusta* the control treatment had the highest amylase activity for the first 15 days, but in the feeding treatments amylase activity remained high for 60 days, particularly for microcosms containing *A. saussurei*. An overall comparison of amylase activity between control and feeding treatment using a t-test (Table 3) showed a significant posi-

tive effect of both arthropods for *C. siamea* and *S. robusta* litters. In *S. robusta* the impact of *P. laevis* was less, such that the difference between the feeding treatments was significant. Comparison of total variations of amylase activity in control and feeding treatments of *C. siamea* and *S. robusta* litters using repeated measures ANOVA (Table 4) indicated significant differences with respect to detritivore feeding and intervals of time. Higher *F* values during intervals indicated the main effect of time as the cause for variations in both litters.

Feeding by *A. saussurei* and *P. laevis* on litter enhanced the cellulase activity in the sand layer of the microcosms (Fig. 2). In *C. siamea* control treatment, cellulase activity slowly decreased from 0.6 ± 0.01 to 0.2 ± 0.02 μg glucose g^{-1} dry soil h^{-1} after day 15. However, in the feeding treatments cellulase activity increased sharply after incubation for 45 days, and maintained high levels until the end of experiment. For *S. robusta* litter, the faunal effect on cellulase activity was more prominent for *A. saussurei* than for *P. laevis*. Cellulase activity was significantly lower in control than in feeding treatments of *A. saussurei* for both litters, but the differences between control and feeding treatments of *P. laevis* were not significant (Table 3). Moreover, the differences between feeding treatments were significant for *S. robusta* litter only. The repeated measures ANOVA also showed significant variations in cellulase activity in both litters with respect to detritivore feeding and duration (Table 4). In *C. siamea*, the higher *F* value indicated the main effect of time intervals, whereas a higher *F* value in *S. robusta* litter showed the main effect of feeding by arthropods.

Soil invertase activity (Fig. 2) increased in the control treatment of *C. siamea* litter, reaching its highest value in 75 days. By contrast, in the control treatment of *S. robusta* litter, the invertase activity remained low throughout the experiment. For *C. siamea*, the invertase activity declined in all the feeding treatments, whereas in *S. robusta*, feeding by *A. saussurei* and *P. laevis* enhanced the enzyme activity. Invertase activity in the feeding treatments of *A. saussurei* on *C. siamea* litter differed significantly from the control and the feeding treatment of *P. laevis* (Table 3). However, in *S. robusta* litter high invertase activity in the feeding treatment was significantly different from the control. Repeated measures ANOVA confirmed the highly significant differences in invertase activity with respect to feeding treatments and time (Table 4). In *C. siamea* litter, the higher *F* value showed the main effect of variations between the sets, whereas in *S. robusta* the *F* values were similar for treatments and time intervals.

Discussion

Degradation of chemical constituents of litter

The leaf litters of different plant species do not decompose at the same rate even under similar environmental conditions. This is due to differences in the structure and composition of the leaves, and is evident from the present results. Comparison of the chemical composition of litters showed higher initial quantities of soluble carbohydrates, cellulose and hemicelluloses in *C. siamea* litter, whereas polyphenols, tannins and lignin were more abundant in *S. robusta* litter. Our results also showed a rapid decline in the levels of water-soluble constituents in both litters, although the lignin content of litter residues showed an apparent increase with incubation time and an inverse relation with the carbohydrates, cellulose, hemicelluloses, polyphenols and tannins. Carbohydrates degrade faster than proteins because microbes utilize the soluble and easily assimilated carbon sources during the initial stages of litter decomposition. According to Williams & Gray (1974), carbon is used as energy source by decomposers while nitrogen is assimilated into proteins, so a high initial nitrogen content in the material promotes decomposition at least during the initial stage.

Our findings on changes in the chemical composition of litter in the pit decomposition experiment are in agreement with the general trend of decline of litter components, which follows the order: sugars > amino acids > hemicelluloses > cellulose > lignin, as noted by Deka & Mishra (1984) and Shukla & Singh (1984). The hemicelluloses are polysaccharides of about 50 to 150 sugar units that are susceptible to attack by microbes, whereas cellulose is a larger polymer of 1,000 to 10,000 sugar units, which is much less susceptible to microbial degradation (Gray & Biddlestone 1974). The rate of decrease of total lipids was faster in *C. siamea* than in *S. robusta* litter. Joy & Joy (1991) also showed a rapid rate of decline of lipids in *C. siamea* litter, whereas in *S. robusta* more than 50 % of the initial amount remained even after decomposition for 8 weeks. The protective action of fats, waxes, terpenes and steroids may inhibit microbial decomposition of plant residues, such that the rate of decline of ether-extractable products of litter may be consi-

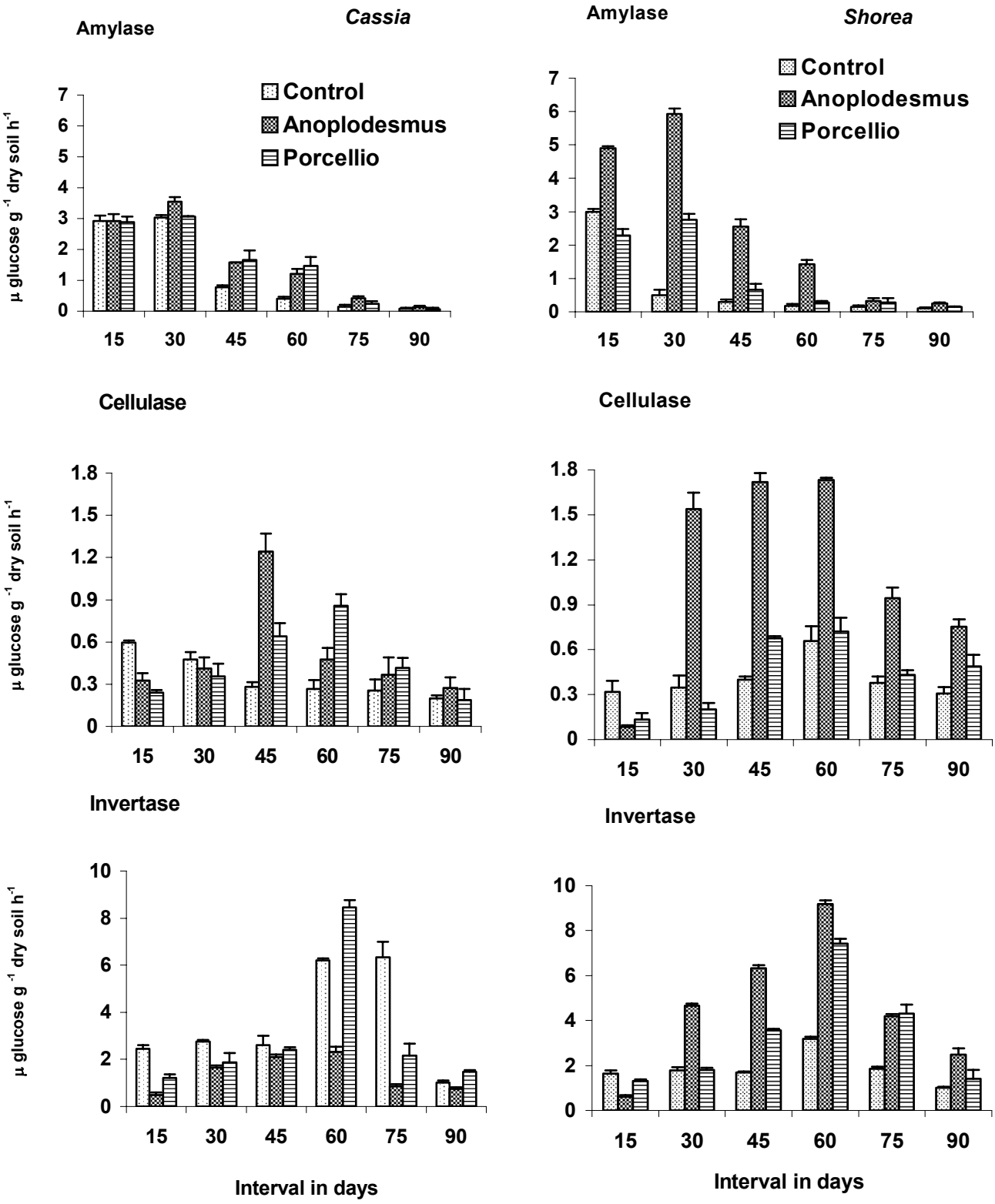

Fig. 2. Temporal variations in amylase, cellulase and invertase activities in the sand medium of control (microbial activity only) and feeding (microbial activity and arthropod feeding) treatments of *C. siamea* and *S. robusta* litters under microcosm conditions (values are mean ± S.E. with six replicates for each interval).

Table 4. Summary of results of a 2-way repeated measures-ANOVA (tests of within-subjects effects) on soil enzyme activities in control (microbial activity only) and feeding (microbial activity and detritivore feeding) treatments of *C. siamea* and *S. robusta* litters under microcosm conditions with respect to treatments (three experimental treatments) and time intervals (six fortnightly estimations).

Soil enzymes	Leaf litter	Source of variation (sphericity assumed)	Df	Sum of squares	Mean square	*F* value	Significance
Amylase activity	*C. siamea*	Treatments	2,6	2.32	1.16	240.82	$P < 0.001$
		Intervals	5,15	103.86	20.77	3606.85	$P < 0.001$
		Treatments*intervals	10,30	2.93	0.29	54.22	$P < 0.001$
	S. robusta	Treatments	2,6	46.63	23.32	4236.57	$P < 0.001$
		Intervals	5,15	122.53	24.51	4368.49	$P < 0.001$
		Treatments*intervals	10,30	43.12	4.31	1632.95	$P < 0.001$
Cellulase activity	*C. siamea*	Treatments	2,4	0.27	0.13	69.59	$P < 0.01$
		Intervals	5,10	1.34	0.27	150.66	$P < 0.001$
		Treatments*intervals	10,20	1.98	0.20	214.42	$P < 0.001$
	S. robusta	Treatments	2,4	6.01	3.00	2544.11	$P < 0.001$
		Intervals	5,10	4.28	0.86	1216.26	$P < 0.001$
		Treatments*intervals	10,20	3.29	0.33	310.37	$P < 0.001$
Invertase activity	*C. siamea*	Treatments	2,6	61.61	30.80	1849.94	$P < 0.001$
		Intervals	5,15	164.16	32.83	1358.32	$P < 0.001$
		Treatments*intervals	10,30	93.02	9.30	634.05	$P < 0.001$
	S. robusta	Treatments	2,6	88.65	44.33	908.60	$P < 0.001$
		Intervals	5,15	224.90	44.98	908.97	$P < 0.001$
		Treatments*intervals	10,30	75.66	7.57	239.73	$P < 0.001$

Note: The df column contains numerator and denominator degrees of freedom for *P* values.

dered as an index of litter quality to decomposers. The lignin content was higher in *S. robusta* than in *C. siamea* litter, and lignin and ash represented the non-degradable organic and inorganic residues. Odiwe & Muoghalu (2003) suggested that a high lignin content makes the litter unattractive to decomposers and resistant to decomposition. According to Jalota *et al.* (2006) and Hobbie *et al.* (2006), the lignin content is an excellent index to predict the rates of weight loss and decomposition of litter across forest tree species, and litter with high lignin content decomposes more slowly. The ash content represents inorganic constituents of plant tissue, which includes silicates and oxides. Jenson (1974) proposed that estimation of ash content provides information on the hard and soft nature of angiosperm tree leaf litters. Berg & Mc Claugherty (2003) noted that the ash content of litter varied between litters and over time; in sugar maple litter the initial ash content of 11.3 % of dry matter increased to 19.55 % after one year of decay. Our results showed a similar trend of increase of lignin content with respect to the unit weight of leaf litter residue collected from the decomposition pits, probably due to continuous loss of water soluble and easily degradable components of litter over time.

Detritivore feeding effect on physicochemical degradation of litter

Our microcosm experiments showed species-specific differences in the feeding effects of *A. saussurei* and *P. laevis* on the degradation of tropical forest litters. Previous work by Pramanik *et al.* (2001) found greater feeding impact of *A. saussurei* in mobilizing calcium, nitrate and organic carbon from decomposing leaf litter than *P. laevis*. According to Werner & Dindal (1987), diplopods and isopods are panphytophages that feed voraciously on decomposing litter and enhance their digestion and absorption rates through coprophagy. Both species accelerated the physical breakdown of *C. siamea* litter, whereas *S. robusta* litter was much less palatable. Das & Joy (2009)

showed that the high quantity of polyphenols, tannins and lignin in *S. robusta* litter could decrease the growth and fecundity of Collembola. The presence of structural materials like lignin and a waxy outer coating in litter affects feeding by small animals, as well as the rate of decomposition (King & Heath 1967). According to Hassall & Rushton (1984), the feeding preferences of isopods are related to the type of anti-herbivory defenses present in plants. David & Gillon (2002) observed higher assimilation efficiency of the millipede *Glomeris marginata* on freshly-fallen Holm oak leaf litter, but they consumed decomposed leaves preferentially, despite lower digestibility, because litter becomes more palatable after some weeks of weathering. Feeding by *A. saussurei* and *P. laevis* may have enhanced the degradation of carbohydrates, proteins and lipids of *C. siamea* litter. Chatterjee & Joy (1990) also reported that feeding by *Lancetoppia* sp. (Cryptostigmata) decreased the level of carbohydrates, proteins and lipids in *C. siamea* leaf litter. The role of polyphenols in reducing palatability and microbial conditioning by acting as feeding deterrents, toxins and binding agents was demonstrated by Appel (1993). However, mass loss of litter due to feeding by detritivores, together with leaching of soluble and easily degradable constituents, led to the decrease of polyphenols, tannin and ash content. Microcosm experiments by Roy & Joy (2009) showed high rates of colonization, feeding preference and assimilation of *A. saussurei* in *C. siamea* litter when compared to low rates in *S. robusta* litter, indicating that the nutritional quality to detritivores may influence the rate of litter degradation.

Impact of litter quality on microbial enzyme activities in soil

Soil enzyme activities are ecologically significant indices of organic matter dynamics and microbial activities in soil. Plant litter is the major energy resource to soil microbes, which is evident from both extensive colonization and high activity rates at least during the initial stage of decomposition (Dilly & Munch 1996). This was apparent from the high enzyme activities in the inert sand medium within 15 days of litter decomposition. These enzyme activities reflect the trends of major biochemical processes in soil. Enzymes like amylase, cellulase, invertase and protease are important in the degradation of organic residues (Mishra & Sahoo 1989). According to Dilly *et al.* (2007) amylase, cellulase and invertase activities indicate the potential to degrade carbon polymers, whereas protease activity represents the release of amino acids and ammonia. Fontaine *et al.* (2003) showed that addition of organic carbon could induce enzyme production due to stimulation of microbial biomass and to a positive relationship between carbon and carbon-hydrolyzing enzymes. Acosta-Martinez *et al.* (2007) compared glycosidase, acid phosphatase and arylsulphatase as affected by soil order, land use within a watershed in north central Puerto Rico, and reported that higher enzyme activities were related to higher organic content of soil. Plants that are used to establish a cover in soils under semiarid climatic conditions influenced the chemical, physical, and biological properties of soil, microbial activity and plant debris, which differ from among species to other (Garcia *et al.* 2005). Our results showed a strong impact of litter quality on soil enzyme activities. The amylase and cellulase activities gradually declined with time in the soil of *C. siamea* litter, but in *S. robusta* treatments, amylase activity declined to insignificant levels within 15 days, whereas cellulase gradually increased to reach peak after 60 days. By contrast, invertase activity showed an increasing trend in the soil of *C. siamea*, but in *S. robusta* litter it remained low throughout the experiment. Ushio *et al.* (2010) showed that trees could regulate nutrient cycling in forest ecosystem through their effects on substrate quality, soil physicochemical properties and microbial community. Mukhopadhyay & Joy (2010) compared nutrient status of soil during short-term incubation of different leaf litters in decomposition pits, and found that *C. siamea* litter increased soil pH, organic carbon, nitrate and available phosphorus relative to *S. robusta* litter. This aspect is ecologically significant due to the practical importance in selecting trees for reclamation of disturbed semiarid lands. Our results demonstrate several inferior qualities of *S. robusta* litter relative to *C. siamea* litter as a carbon and nutrient source for the soil foodweb, like higher quantities of non-nutritional components, slow physicochemical degradation, reduced activity of microbial enzymes, and low preference to detritivores. Singh *et al.* (1999), in a comparison of litter decomposition and nutrient release patterns in a mine spoil habitat, showed higher return of total nitrogen to soil by *Dalbergia sissoo* than *S. robusta*. Krivtsov *et al.* (2010) made an assessment of fungal and bacterial biomarkers in the soil of different forests and suggested that a

correct understanding of site-specific peculiarities of ecological patterns is important for the improvement of biodiversity of woodland and forest ecosystems.

Detritivore feeding effect on soil enzyme activities

The catalytic role of soil fauna in litter decomposition is a significant feature of biological activity in soil. For example, fragmentation and humification of litter by diplopods, isopods and earthworms enhance microbial activity and decomposition. However, the direct influence of detritivore soil arthropods on microbial functions is not clearly understood in tropical forest ecosystems. Our microcosm studies showed significant differences in soil enzyme activities with respect to feeding by *A. saussurei* and *P. laevis*. Comparison between control and feeding treatments showed overall parity in the temporal and sequential changes in soil enzyme activities, which indicated close dependence of the detritivores and microbes in utilizing the resources of decomposing litter. Similarly, Fioretto *et al.* (2007) reported peak activities of enzymes involved in soluble saccharide degradation early in the decomposition, which then declined markedly; whereas the activity of cellulase generally peaked about midway through litter decomposition. In our study, amylase, cellulase and invertase activities increased significantly in the detritivore feeding treatment, and the impact was much greater for *A. saussurei*. Species-specific difference in the feeding habits of the two detritivore species influenced physicochemical degradation of litters and soil enzyme activities. The faunal effect was prominent in the *A. saussurei* treatments, especially in the hard *S. robusta* litter. On the other hand, the drastic decline of invertase activity observed in the soil of *C. siamea* may be due to large-scale scrap feeding by the detritivores on a litter with low quantities of non-nutritional components. Microbes and detritivores may also have exhausted a large portion of the easily digestible *C. siamea* litter, in contrast to *S. robusta* litter, a large portion of which was available for enhanced microbial activity through the feeding effect of detritivores. Mikola *et al.* (2002) concluded that the direct contribution of soil fauna to energy flow and mineralization is low, but indirect effects on litter decomposition through fragmentation and modification of structure and on the activities of microorganisms are very significant. For example, Seeber *et al.* (2006) showed that macro-decomposer millipedes significantly decreased microbial biomass during litter decomposition in mesocosm conditions. However, biodegradation of plant litter is influenced by its chemical composition (Almendros *et al.* 2000), particularly the non-nutritional components that can inhibit microbial utilization and form recalcitrant compounds (Williams & Gray 1974). Others have shown that the release of phenolic acids and flavonoids from leaf litter can regulate the soil arthropod community in tropical forests (Ananthakrishnan & Raman 1993). Moreover, these secondary metabolites act as allelochemics against heterotrophs and accumulate in soil (Ananthakrishnan 1996).

Conclusions

Field and laboratory studies showed notable differences in the physical and chemical qualities of leaf litters of *C. siamea* and *S. robusta* trees. The levels of soluble carbohydrates, cellulose and hemicelluloses were high in the small and fragile *C. siamea* litter, whereas tannin, polyphenols and lignin were abundant in the large and hard litter of *S. robusta*. The litter quality was a determinant of decomposition and feeding by detritivore arthropods. Water-soluble compounds degraded rapidly in both litters, but the decline in levels of proteins, cellulose and lipids were slower in *S. robusta*. Microcosm studies showed enhanced weight loss of *C. siamea* litter in feeding treatments containing of *A. saussurei* and *P. laevis*, whereas *S. robusta* litter was not fed upon by either arthropod. Feeding enhanced degradation of the main chemical components of *C. siamea* litter, and *A. saussurei* had higher impact on the loss of these constituents. Significant temporal variations occurred in soil enzyme activities with respect to leaf litters and detritivore feeding. Amylase, cellulase and invertase activities were higher for *A. saussurei* than *P. laevis*, probably due to increased fragmentation and humification of litter. Persistent high levels of soil enzyme activities in the feeding treatments demonstrated the catalytic effect of detritivores, especially in the hard litter of *S. robusta*. Our results show that the comminuting effect of detritivores and their relationships with the microbial community can influence litter decomposition and soil enzyme activities in tropical forests.

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