ORIGINAL ARTICLE

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Do canopy herbivores mechanically facilitate subsequent litter decomposition in soil? A pilot study from a Neotropical cloud forest

Abstract There is increasing evidence that the above- and belowground components of ecosystems influence one another, thereby controlling key processes such as organic matter decomposition. The aim of this study was to test the hypothesis that leaf herbivory in forest canopies could facilitate subsequent leaf litter decomposition in soils, through changes in leaf quality (i.e., litter palatability) or geometric form (i.e., increased availability of leaf edges made by herbivore damages). In a 9-month field experiment in an Ecuadorian tropical cloud forest, we compared the decomposition rates of entire leaves (EL) and 15 %-damaged leaves (DL) of *Ficus cuatrecasana* showing similar initial leaf chemistry. We found that DL decomposed significantly faster than EL in early stages of decomposition (i.e., between 0 and 38 days). A parallel experiment using cellulose discs on which we simulated different degrees of damages revealed, however, that geometry per se (i.e., increased edge availability) did not influence decomposition rates. We discuss these contrasting results and propose that higher edge availability in damaged leaves may promote the access of microbes and/or macro-detritivores to leaf tissues thereby enhancing the initial stages of leaf decomposition.

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Introduction

It is estimated that, worldwide, 90 % of total plant biomass is not consumed by herbivores and enters the soil system directly as dead organic matter (DOM) (Gessner et al. 2010). Decomposition of DOM relies on several factors, such as climate, the physical and chemical properties of plant litter, and the sequential action of soil invertebrates, fungi and bacteria (Chapin et al. 2002). Several studies have shown that herbivores can play a significant role in litter decomposition by affecting the activity of soil decomposers and detritivores through modification of their biomass distribution (Mulder et al. 2008), and of organic matter input quality and quantity (van Dam and Heil 2011; Wardle et al. 2004), thus affecting nutrient availability and plant productivity (reviewed by Vitousek and Sanford 1986; Hunter 2001; Cebrián and Lartigue 2004). Positive effects of herbivory could be related to a high consumption of net primary production, high return of labile fecal material to soil, and an improvement of litter quality through reduced leaf content of phenolics, lignin and structural carbohydrates (Chapman et al. 2006; Wardle et al. 2004). While herbivores have been shown to increase litter decomposition rates in particular ecosystems such as grasslands, coniferous forests, and semi-arid woodlands (Chapman et al. 2006; Wardle et al. 2004) herbivory-litter decomposition relationships in the tropics remain controversial, with several studies suggesting a weak association between both processes (Didham 1998; Kurokawa and Nakashizuka 2008).

While most attention has focused on the effects of herbivores on resource quality, the importance of their physical modification (fragmentation that modifies organic matter geometric form) for subsequent processing remains poorly studied.

Plant decomposition is generally speeded up by any activity that grinds up and fragments vegetal tissues (Chapin et al. 2002). This process could be referred as to "mechanical facilitation" and fits into the concept proposed initially by Heard (1994): the "processing chain ecology". Heard (1994) argued that resource transformation rate can be regulated by a consumption chain of species adapted to the specific conditions of that resource. For example, resource consumption by species B may depend on pre-treatment of the resource by species A. In such a system, consumers specialize on resources in each condition (e.g., herbivory), influencing the rate at which the resource is transformed between conditions (i.e., to litter). Microcosm studies have shown the synergistic action of different detritivores taxa in leaf litter decomposition (Zimmer et al. 2005; De Oliveira et al. 2010). Other studies have proposed the existence of mechanical facilitation among a variety of consumers, such as stream detritivores that fragment whole leaves and leave behind smaller particles to be exploited by others (Daugherty and Juliano 2002; Flecker 1996; Jonsson et al. 2002), or tuber moth larvae that make holes on the tuber and facilitate the entrance of other burrowers (Dangles et al. 2009). Also, Muller et al. (2002) suggested that feeding Scolytid beetles facilitates fungal colonization in decaying wood. To our knowledge, no analogous studies have been performed using canopy herbivores and soil decomposers as study models in order to test whether the areas opened as a result of the chewing action of herbivores would facilitate litter palatability, accessibility and consumption by decomposers and detritivores.

Fragmentation creates fresh surfaces that increase the proportion of vegetation mass accessible to attack by micro- and/or macro-organisms (Chapin et al. 2002). Accessibility is enhanced greatly by the removal of protective barriers such as cuticle and lignin cell walls, and by increasing the ratio of litter surface area to mass (Chapin et al. 2002). A great variety of leaf damage is caused by insect herbivores due to their different modes of feeding (Mithöfer et al. 2005). In most cases, mechanical damaging by insects (e.g., through holes or scars) removes amounts of plant material and creates new foliar edges (Hargrove and Crossley 1988; R.E.C and O.D., personal observation). These edges may promote the entrance of plant pathogens, such as fungi (Hargrove and Crossley 1988; Moran 2005), which themselves increase the nutritional value of leaf litter and palatability for detritivores (Graça 2001). Leaf edges may also facilitate the action of other macrodecomposers that seem to prefer feeding on leaf edges (e.g., Jonsson et al. 2002).

In this study, by comparing the decomposition rate of entire and damaged leaves, we tested the hypothesis that canopy herbivores facilitate the action of soil detritivores and decomposers via mechanical damage to leaves. We then tested for the role of initial leaf chemical quality versus geometric form in explaining the observed differences in decomposition rates in entire leaves (EL)

versus damaged leaves (DL) using (1) initial leaf chemistry analyses and (2) perimeter/area ratio manipulated cellulose discs. Cellulose disc manipulation was necessary to test whether higher edge availability in damaged leaves can promote the access of microbes and/or macro-detritivores to leaf tissues thereby enhancing leaf decomposition, while eliminating variations resulting from litter quality (Yin et al. 1989).

Methods

Study site

The study was conducted in a tropical cloud forest on the western Andean slopes of Ecuador, at Otongachi Reserve (00°18′60″S, 78°56′53″W, 950 m a.s.l.). The reserve represents a 150 ha patch of primary–secondary forest surrounded by pastures and cattle farms. Seasons in this region can be well separated into a dry (June–November: 65 ± 16 mm per month) and a rainy (December–May: 315 ± 90 mm per month) season (see Appendix 1). The average annual precipitation is about 2,300 mm and the mean temperature ranges between 16.0 and 25.0 °C (see Appendix 1). Soil at the study site had an average slope > 70 %, a root depth (i.e., depth to bedrock) > 100 cm, and a "moderately" thick soil texture (sandy loam, silt loam, sensu AEE 2000). Soil analyses performed at the Center for Environmental and Chemical Services of the Pontifical Catholic University of Ecuador (PUCE) (using ten 1 kg samples collected randomly in the study area) revealed a soil electric conductivity of 42.3 ± 25.7 μS/cm, a moisture of 28.2 ± 5.3 %, a pH of 6.7 ± 0.4, and a C/N ratio of 10.57.

Decomposition of entire versus damaged leaves

In May 2008, 4,000 leaves were picked-out randomly from a single tree as our specific aim was to test for the mechanical effect of herbivory per se on decomposition. The species Ficus cuatrecasana (Dugand) was chosen for our study because of its broad distribution in Ecuador and the Neotropics across a wide altitudinal range (Jørgensen and León-Yánez 1999) and because of the palatability of its leaves for mammals (Castellanos et al. 2005; Giraldo et al. 2007) and insects (R.E.C and O.D., personal observation) in Andean forests. In order to avoid the effect of potential confounding factors (such as age or position in the tree) on leaf chemistry, only green leaves (i.e., neither emergent nor senescent) were picked-out randomly from a single 10-m-high F. cuatrecasana tree. Moreover, all leaves were "shade leaves" as the study tree was located entirely in the forest understorey.

Green leaves were mixed and sorted into "entire" (EL, showing no damage by herbivores) and "damaged" (DL, eaten to some extent by herbivores) (EL:DL in the

tree = 0.67). From the damaged leaves pool, we randomly selected 500 damaged leaves, scanned them (HP Scanjet 4070, Hewlett-Packard, Los Angeles, CA), and quantified eaten areas using imaging software (Scion Image 4.0.2., Frederick, MD). The median damaged surface was 15.2 ± 5 % per leaf (Fig. 1), which corresponded roughly to damaged areas measured on fallen *F. cuatrecasana* leaves collected previously in 1 m² litter traps (18.9 %) in the study area. Two groups of leaves, entire (non-eaten) and damaged (15.2 ± 5 % eaten) were sorted, air-dried to constant weight, and weighed into 7.0 ± 0.1 g portions using an analytical balance (FA2104N, Ningbo Utech International, Ningbo, China). This value was chosen based on data obtained from a litter fall census realized during our experiment, and was sufficient to ensure that a minimum leaf mass would remain at the end of our study period. Using 1 m² litter traps, we indeed measured a mean litter fall input of 292 g m^{-2} day^{-1} of *F. cuatrecasana* leaves (dry weight) at the beginning of the experiment, which corresponds to 6.57 g/0.15 m^{-2} day^{-1}. This estimation did not change significantly over time as we found an annual litter input of 5.34 g 0.15 m^{-2} day^{-1} over the whole study period.

The leaves were remoistened to make them pliant, and enclosed in 15 × 15 cm (0.15 m²) plastic mesh bags. As mentioned above, leaf edge availability may enhance leaf decomposition in soils either through an increased colonization of microbes, the facilitated action of detritivores, or both. In order to assess whether leaf damage would preferentially benefit microbes, micro- or macro-decomposers, we performed our leaf litter decomposition experiment using different types of mesh bags: coarse-mesh (CM, 10 mm mesh size) and fine-mesh (FM, 0.5 mm mesh size). While the fine-mesh bags

Fig. 1 *Histogram* of the leaf damage area of 500 scanned damaged-leaves from a *Ficus cuatrecasana* tree. The *distribution curve* shows damaged area median (= 15.2 %)

excluded macro-detritivores, coarse-mesh bags did not. In total, 240 bags (60 replicates for each of the four treatments) were prepared and placed for decomposition in 24 different sites selected randomly in an area ~2,000 m² around the *F. cuatrecasana* tree. Bags were covered with a handful (~75 g) of forest mixed litter and 10 bags of each treatment were removed every 40 days, from June 2008 to March 2009. In the laboratory, leaves from each litter bag were cleaned gently to remove soil particles, adhering debris, and invertebrates, then dried (60 °C, 48 h) and weighed.

Leaf chemistry analyses

To assess the potential role of leaf chemistry in observed difference (due to herbivory on the tree) between EL and DL decomposition rates, a subsample of both types of leaves (*n* = 5) was used to analyze basic litter components at the beginning of the experiment (0 days of decomposition). Percentages of critical elements, C, N, P and K were measured following Kaspari et al. ([2008](#)) and were performed at the Oklahoma State Soil, Water and Forage Analytical Laboratory (OSU 2009, available at http://www.soiltesting.okstate.edu/). N percentage was estimated from crude protein based on a nitrogen-to-protein conversion factor of 4.4 (Milton and Dintzis [1981](#)).

Perimeter:area ratio manipulation with cellulose discs

We tested the specific effect of edge availability on litter decomposition by manipulating the perimeter:area ratio of cellulose discs. Standard cellulose filter discs (Fisher Scientific, Pittsburg, PA; 28.3 cm-perimeter) were cut using sterilized scissors to simulate a gradient of edge availability corresponding to three different values of perimeter:area ratio (the total damaged area remained constantly equal to 15 %): (1) a ratio of 1.1 obtained by cutting one hole of 3.6-cm diameter, (2) a ratio of 1.6 obtained by cutting two opposite holes of 2.6-cm diameter, and (3) a ratio of 2.2 obtained by cutting four opposite holes of 1.8-cm diameter (see drawings in Fig. [4](#)). Thirty replications of each treatment were decomposed in CM bags for 58 days in the same field area between November 2008 and January 2009. Mass loss was measured as described in the leaf decomposition experiment.

Statistical analyses

We tested for differences between treatments (EL vs. DL) using a one-sample *t* test of DL:EL decomposition ratios (based on mass loss %) versus a theoretical mean of 1 in both types of mesh bags for all dates. In this test, no significance meant that DL and EL decomposed at equivalent rates, so that their ratio = 1 (Carta et al.
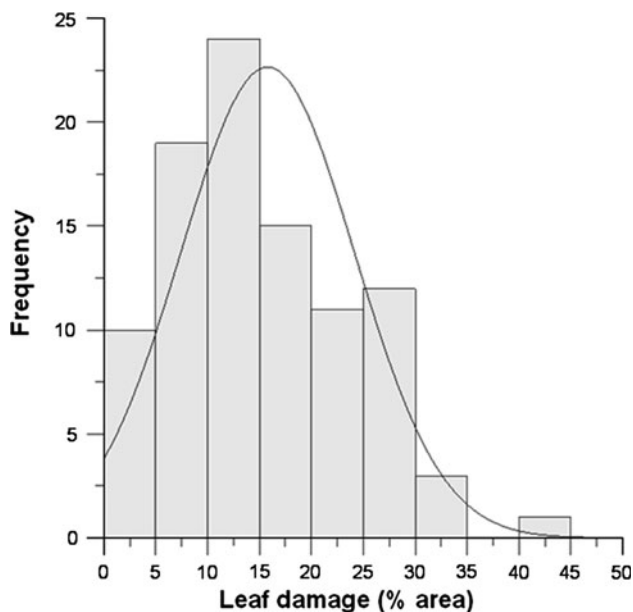
2004). Additionally, the decomposition rate coefficient k was calculated for each litterbag using a negative exponential decay model ($M_t = M_0 \exp^{-kt}$, where M_0 is initial litter mass and M_t is mass remaining at time t), which reflects the most commonly observed functional response for leaf decomposition (Graça et al. 2005). An analysis of covariance (ANCOVA) was used to test for differences in leaf-litter decomposition rates between CM and FM bags (as independent categorical variable) and between EL and DL (the covariate) over time. We used one-way ANOVA to test for differences among both treatments. For the cellulose disc experiment, we used the Anderson–Darling P value (Stephens 1974) (± 95 % confidence intervals) to determine whether the DL:EL discs fitted into a log-normal distribution (as expected for random decomposition). The Anderson–Darling is a goodness-of-fit statistic to test the hypothesis that a random sample $X_1,..., X_m$, with empirical distribution $F_m(x)$, comes from a continuous population with empirical distribution function $F(x)$ where $F(x) = F_0(x)$ (normal distribution) (Stephens 1974; Scholz and Stephens 1986). All the analyses were performed using Minitab 15.1 (Minitab, State College, PA).

Results

Over time, the decomposition rates (k) of leaf litter in CM bags reached 0.0091 ± 0.0015 day^{-1} for EL versus 0.0090 ± 0.0016 day^{-1} for DL. In FM bags, the k values were between 0.0037 ± 0.0005 and 0.0042 ± 0.0013 for EL and DL, respectively. Differences between CM and FM treatments were highly significant (ANCOVA, $P < 0.0001$), with leaf litter mass decomposing ~50 %

slower in FM bags than in CM bags (Fig. 2). When considering the whole study period, we found no significant differences in decomposition rates between EL versus DL within mesh size treatments (ANCOVA, $P_{FM} > 0.05$; $P_{CM} > 0.05$). However, date by date analysis showed that DL from the CM bags treatments decomposed at a significantly faster rate than EL ($\bar{x}_{CM} = 1.31$; $\bar{x}_{FM} = 1.03$) in the early stages of decomposition (0–38 days; $t = 2.42$, $P < 0.05$; Fig. 3). Overall, 8.9 % of leaf biomass was processed more rapidly during the first month of decomposition. There was also a close to significance (although not significant) trend of faster decomposition of DL in the period of day 38–82 ($t = 1.54$, $P < 0.08$). After 82 days, we likewise found no significant difference in the decomposition rates between EL and DL ($P > 0.05$). No differences in decomposition rates were found among dates for the FM bag treatments ($P > 0.05$; Fig. 3).

Overall, we found no differences in the initial leaf quality between EL and DL except with K, which was lower in DL than in EL (t test, $P < 0.05$; Table 1).

With regards to the cellulose disc experiment, no significant differences were found in decomposition rates among the three perimeter:area ratio treatments (one hole, $P = 0.165$; two holes, $P = 0.068$; four holes, $P = 0.104$; Anderson-Darling test, Fig. 4a–c). Comparison of the decomposition rate between leaves and cellulose discs at 58 days (based on decomposition k rate model) revealed that EL decomposed 16.55 % faster than entire discs, and DL decomposed 17.95 ± 3.7 % faster than herbivore-simulated cellulose discs.

Discussion

Our results support previous experiments that showed the importance of a sequence order of consumers on pre-conditioned resource utilization (Heard 1994), but from a new perspective of consumption sequence, from herbivores to detritivore facilitation. Jonsson et al. (2002) and Dangles et al. (2009) evidenced facilitation between consumers that resulted in resource exploitation that was 1.8- to 4-fold more efficient. This suggests that any variation in the sequence of detritivore activity would alter not only the first stages, but the whole decomposition process. This was also supported by the fact that, in the absence of macro-detritivores (i.e., in FM bags), EL and DL always decomposed at similar rates.

At the beginning of the decomposition process (i.e., 0–38 days) DL decomposed significantly faster than EL in CM bags, but not in FM bags, suggesting that leaf edges may facilitate the breakdown action of soil macro-detritivores. As a potential mechanism, higher availability of edges may have promoted the colonization of microbes (e.g., Hargrove and Crossley 1988; Moran 2005) thereby increasing the nutritional value of detritus and their palatability for detritivores (Graça 2001). Leaf edges may have also facilitated the action of some groups of macro-detritivores that seemed to prefer
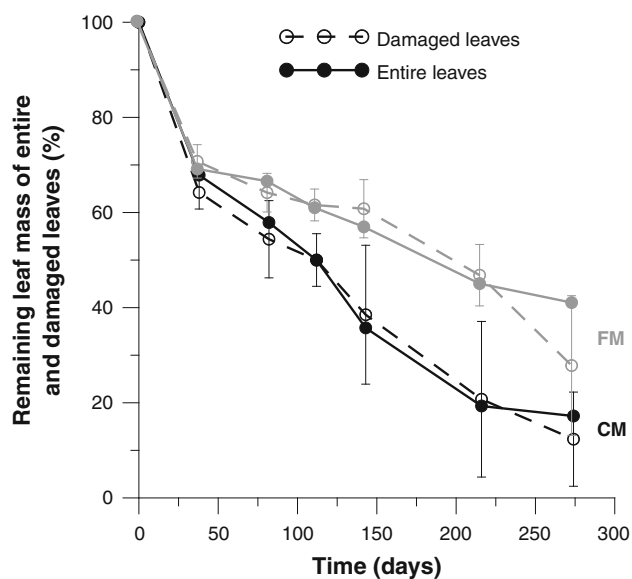
Fig. 2 Decomposition rates (mean values of ten replicates $\pm$ SD) of entire and damaged leaves in coarse (10 mm) and fine mesh (0.5 mm) leaf-bag treatments over the study period. *Open circles* Damaged leaves (DL), *filled circles* entire leaves (EL)
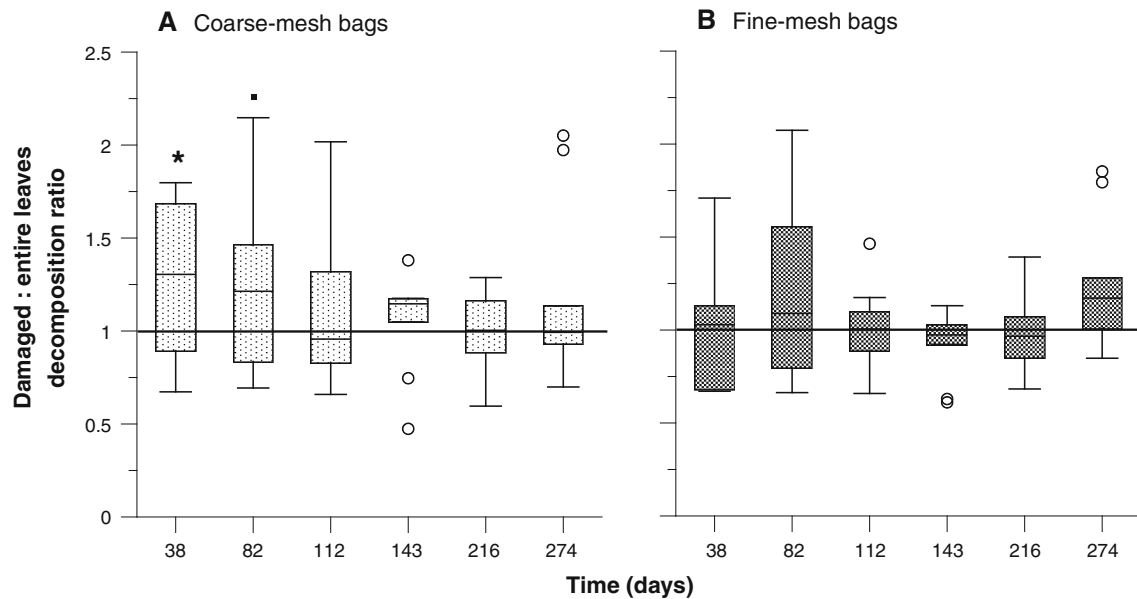
Fig. 3 Damaged:entire decomposition ratio *t* test analysis against a theoretical mean of 1. Outliers are represented by *empty circles*. *Asterisk* Significant at $P < 0.05$; *black dot* near-significance for $P = 0.08$; *no symbols above boxes* no statistical difference. **a** Coarse mesh (CM) bags, **b** fine mesh (FM) bags

Table 1 Initial litter chemistry analyses for green fallen damaged and entire leaves at 0 days of decomposition

	Leaves collected in litter traps (0 days of decomposition)	
	Damaged	Entire
% Crude protein	7.8[a]	6.7[a]
% N	1.77[a]	1.52[a]
% C	44.6[a]	44.1[a]
% P	0.07[a]	0.06[a]
C:N	25.2[a]	29.01[a]
N:P	25.32[a]	25.38[a]
% K	0.73[b]	1.06[a]

Values in rows followed by the same letter were not significantly different (*t* test, $P \geq 0.05$). Entire leaves collected in litter traps presented 68.9 % more K rate than damaged leaves (*t* test, $P < 0.05$)

feeding on leaf edges rather than eating leaves from top to bottom (Jonsson et al. 2002, R.E.C. and O.D, personal observation). The similarity of decomposition rates between EL and DL in fine mesh bags (FM) confirms that the positive effect of higher leaf edge availability on the decomposition process necessarily involves the presence and action of macro-detritivores. Further studies on the evolution of leaf litter quality over decomposition and on the feeding habits of the soil macro-detritivore community would be needed to better understand the mechanisms involved. Hättenschwiler et al. (2008), for example, compared the CNP concentrations of green versus senescent leaves of 45 spp. of Amazonian trees. They found little variation in C concentration between both types; however, N and P concentrations differed significantly. Averaged across all species, N and P concentrations were 30 and 65 % lower, respectively in senescent leaves compared to green ones. This implies demanding components such as N or P are first reabsorbed by plants before abscission. Once on the ground, these scarce components are exploited rapidly by micro-decomposers by lowering their C-use efficiency as suggested by Manzoni et al. (2008) for N. This would imply that, during the decomposition process, the C:N or C:P ratios gradually increase until the whole organic matter is finally mineralized. In this context, we assume microbial colonization might be more intense in the early stages of decomposition because of the higher concentration of soluble organic matter. Besides, macro-detritivores may prefer litter that is in early stages of decomposition both because of the presence of microbes and because of the higher concentrations of labile and essential substances.

Our hypothesis that leaf herbivory in forest canopies could facilitate subsequent leaf litter decomposition by soil macro-detritivores through changes in leaf litter palatability (e.g., via microbial colonization) was not supported when considering the entire study period. Moreover, modifications in the geometric form per se as an effect of changes in the perimeter-to-size ratio did not have an effect on cellulose disc decomposition. Three reasons, not mutually exclusive, may explain our results. First, the filter papers, being a uniform substance, may be poorly attractive to detritivores (and microbial decomposers) in comparison to DL because of the absence of exposed suitable cell layers and fresh surfaces for decomposing colonizers and nutrients (Chapin et al. 2002; Muller et al. 2002). Second, mechanical facilitation through increased leaf edge availability may be less important in terrestrial than aquatic systems where both
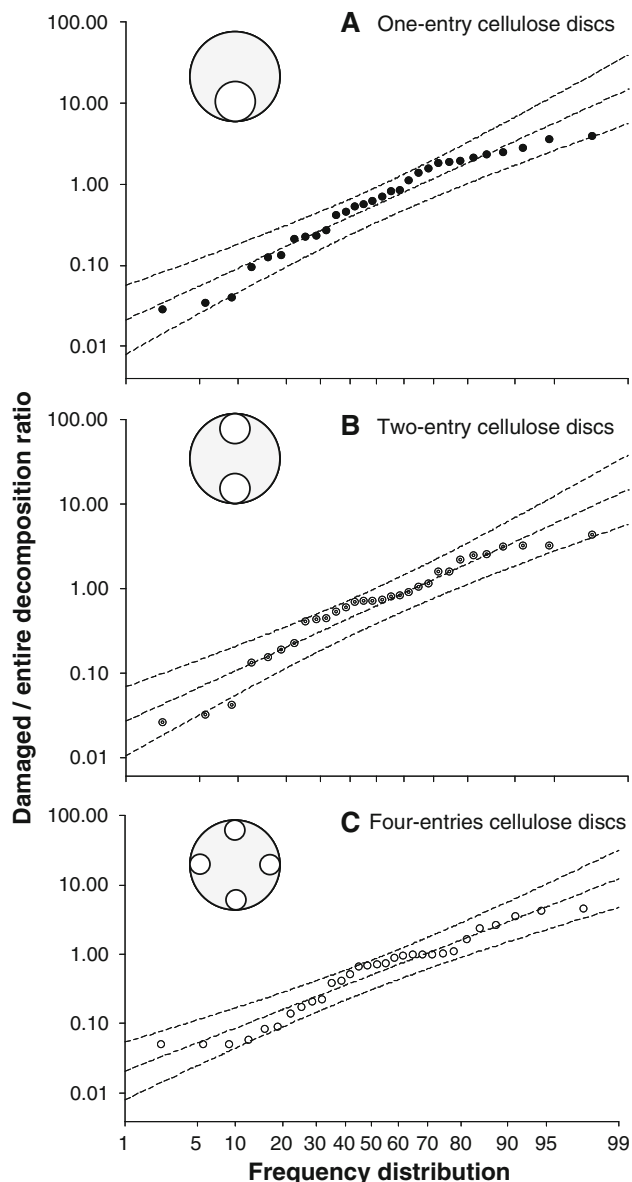
Fig. 4 Decomposition ratio of "damaged" and entire filter paper discs tested against a log-normal distribution model ($n = 30$ for all cases). *Lower* and *upper dashed lines* represent $\pm 95\%$ confidence intervals. **a** One hole (11.31 cm perimeter), $P = 0.165$. **b** Two holes (7.99 cm perimeter each), $P = 0.068$. **c** Four holes (5.66 cm perimeter each), $P = 0.104$

leaf litter material and detritivores are found in patches (see Dangles 2002) thereby promoting niche segregation at the leaf level among detritivore species (Jonsson et al. 2002). Third, decomposition rates may also depend on litter quality parameters, such as secondary compounds induced by herbivory, that were not measured during our experiment (Kurokawa and Nakashizuka 2008). Although not surprising, the fact that both entire and damaged leaf treatments decomposed faster than entire and simulated damaged cellulose discs after 58 days (results not shown), supports the first and third of these explanations.

In conclusion, canopy herbivores seem to mechanically facilitate soil detritivore action at least at the beginning of the decomposition process. Because our results cannot be generalized to the whole litter plant community, further studies could obtain a more general relationship by using a range of tree species that differ in the physical (Kurokawa and Nakashizuka 2008) and chemical (Hättenschwiler et al. 2008; Kagata and Ohgushi 2011) properties of their leaves. In tropical rainforests, leaf herbivory ranges between 25% and 40% (32% in average, Brenes-Arguedas et al. 2008; 68% occurring in young leaves, Coley and Barone 1996). It is therefore likely that soil litter has a higher proportion of damaged leaves in tropical forests than in temperate ones (where herbivory rates range between 22% and 26%, Lowman 1984). The potential role of canopy herbivores in modifying leaf litter quality and geometric form may therefore be crucial to better understand leaf litter decomposition patterns and mechanisms in tropical forest ecosystems.
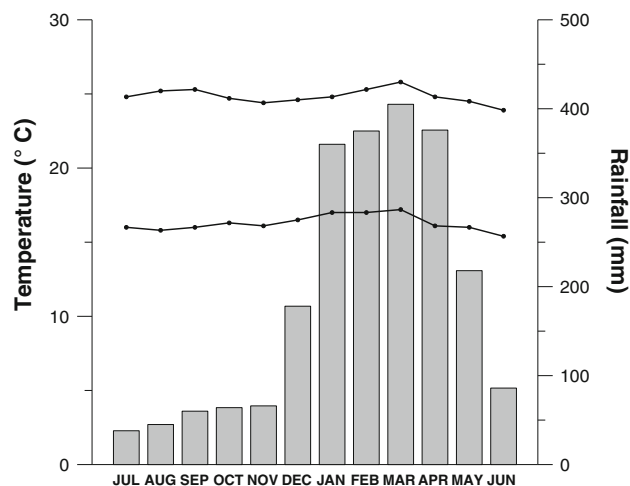
Appendix 1

See Fig. 5.

Fig. 5 Monthly means of temperature range (*solid lines*) and rainfall (*bars*) at the Otongachi reserve based on 30s WORLDCLIM 1.4 shapefile at http://www.diva-gis.org/ (Hijmans et al. 2005)

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