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SHORT COMMUNICATION

Litter quality and litter removal by the native fauna in the western Chaco woodland of Argentina

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Most researchers assume litter decomposition to take place at the site where litterfall occurs, mostly by soil micro-organisms and microfauna of less than 1 mm in size. Accordingly, the litterbag method has become the standard technique for evaluating litter decomposition rates (Schlesinger 1985, Wedderburn & Carter 1999). However, there is evidence indicating that at least in tropical arid ecosystems litter can be removed from the site in substantial amounts by animals, including large vertebrates. For example, litter is removed for forage or as building material for nests by ants (particularly leaf-cutting ants) and termites (Bucher 1982, Scholes & Walker 1993). Moreover, ruminant species (including domestic cattle and goats) supplement their food intake by feeding on falling leaf litter during the dry season in African savannas (Owen-Smith & Cooper 1987) and in the Chaco savannas of Argentina (Morello & Saravia-Toledo 1959). These observations suggest that litter removal may be an important component of the decomposition process, particularly in tropical semi-arid environments where lack of soil moisture decreases microbial activity, increasing litter availability for herbivores.

Litter removal may depend not only on its availability, but also on its quality as a food resource, which in turn relates to nutrient content and the presence of anti-herbivore substances. Therefore, litter removal could be greater in those ecosystems where litter has good forage quality, which is usually related to nutrient-rich soils (Tiessen *et al.* 1998).

We assessed litter removal by the native fauna (cattle and goats excluded) in a Chaco woodland of Argentina, using several enclosures of different mesh sizes over the standard 1-mm size used in litterbags, and up to dimensions that allowed large vertebrates to reach the enclosed material. We measured (1) the amount of litter removed annually; (2) seasonal variations in the rate of litter removal; and (3) seasonal variations in the foraging quality of the litter (fibre, nitrogen and phenol concentration).

Our study was conducted at the Chancaní Provincial Reserve (Reserve), Córdoba, Argentina (31°24′S and 65°33′W). Annual rainfall averages 450 mm, concentrated during the summer (October–March). In the dry winter season (April–September) the water balance is negative, resulting in a soil moisture deficit. Mean temperature is 24 °C during the warmest month (January) and 10 °C during the coldest month (July). The local soils (Ustifluvent molico) are of alluvial origin. The main edaphic parameters are pH = 7, organic carbon = 19 g kg^{-1}, extractable phosphorus = 30 mg kg^{-1} and nitrogen content = 2.0 g kg^{-1} (Mazzarino *et al.* 1991).

Vegetation at the Reserve is the typical Western Chaco xerophyllous woodland (Bucher 1982). Woody species are mostly semi-deciduous. The dominant tree species include *Aspidosperma quebracho-blanco* Schlecht. and *Prosopis flexuosa* DC. The dense 2–3-m-high shrub layer is dominated by species of *Larrea*, *Celtis*, *Mimozyganthus* and *Acacia*, with intermingled grasses and herbs.

The experimental design consisted of placing freshly shed litter in metallic cages covered with mesh of different sizes for 1 y (July 1997 to July 1998). Cages were 50 × 50 × 10 cm in size, divided in four sectors of 25 × 25

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cm. The bottom of all cages had a 0.1-cm metallic mesh to prevent material loss. However, we did not expect litter removal from the bottom because earthworms and millipedes do not occur in the area (Mischis & Gleiser 1999). We assumed that litter loss over time in the experimental cages was due to (1) microbial decomposition and (2) removal by animals. We excluded loss from wind because (1) the area is in general not windy (Capitanelli 1979) and (2) the forest in the Reserve has a very dense shrub layer that restricts wind circulation. Loss by running water was also considered very unlikely given that the soil slope is minimal (< 0.5%), and no litter was lost when the cages were exposed to pouring water on them in quantities equivalent to intense local rains.

Each cage sector was filled with 200 g of fresh litter, collected after the first frost when most of the woody plants shed their leaves. Litter composition by plant species was as follows: *Aspidosperma quebracho-blanco* 25%, *Zyzyphus mistol* Griseb. 25%, *Celtis* sp. 25%, *Mimozyganthus carinatus* (Gris) Burk. 10%, *Geoffroea decorticans* (Gill.) Burk. 5%, *Prosopis* sp. 5% and *Acacia* sp. 5%.

To test litter removal we designed the following treatments: (1) cages with a 0.1-cm mesh on all sides and the top (control), where material loss is due to decomposition by soil micro-organisms and microfauna of less than 1 mm; (2) cages with three mesh sizes on all sides and the top: 1-cm, 5-cm and 10-cm treatments. These treatments allow removal from sides and top by relatively small herbivores of different size; and (3) cages with open top and 0.1-cm mesh on lateral sides, that allow removal by large mammal herbivores feeding only from the top.

Treatments (cages) were placed in five 141-m-long transects, located as the NE to SW diagonal in a 1-ha square selected randomly from a grid superimposed on the Reserve map. Five cages (one for each treatment) were located on the ground in a forest opening of at least 2 m in diameter, which were selected at random from those available along each transect. We assumed that access to the cages for large animals (e.g. deer) would be possible only if cages were located in these openings.

Cages were checked at 3-mo intervals from the starting date. We named each period as winter (July–October), spring (October–January), summer (January–April) and autumn (April–July). On each control date, we collected the content of one of the four sectors for analysis. Removal was calculated as the difference in litter mass among treatments and control. We assumed that differences in litter content were due to litter removal by animals.

For chemical analysis, the initial fresh litterfall and the litter collected at the end of each sampling period were oven-dried at 60 °C and weighed. The following techniques for chemical analysis were used: the standard micro-Kjeldahl procedures for total nitrogen (N), the enzymatic gravimetric method (Asp *et al.* 1983) for insoluble fibre content (cellulose and lignin), and the Folin–Denis method (Robertson *et al.* 1999) for soluble phenolic compounds. For each period, we calculated the slope of the linear function defined by the initial and final weight values.

Differences among treatments (cages) and seasons in litter mass and chemical characteristics were analysed by 2-way ANOVA. We tested normality using the Kolmogorov–Smirnov test, and variance homogeneity using the Bartlett test. Means were compared using the least significant difference test (LSD) ($P < 0.05$).

After 1 y of litter decomposition, dry matter loss in all treatments except the 1-cm treatment was significantly higher than in the control (Figure 1). Loss was greatest in cages with the largest lateral mesh size (5 and 10 cm), followed by the open top treatment. Therefore, estimated litter removal was highest in the 10-cm treatment (28%) followed by the 5-cm (26%), the open top (21%) and the 1-cm treatments (11%). Seasonal litter loss differed signi-

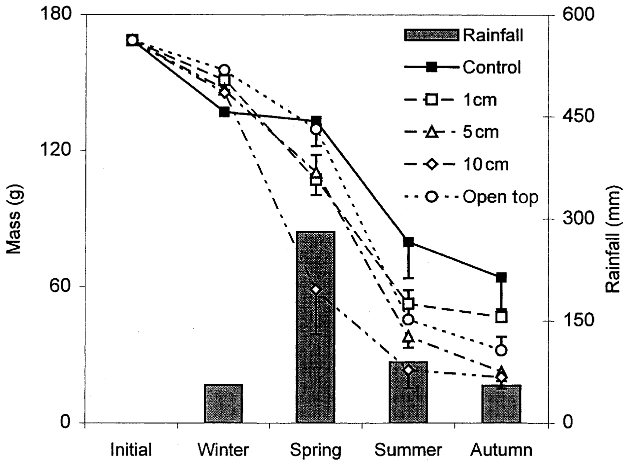

Figure 1. Seasonal litter mass loss (%) for each treatment and rainfall in the study area (data from the Chancaní Reserve Meteorological Station). Error bars correspond to 95% confidence limits.

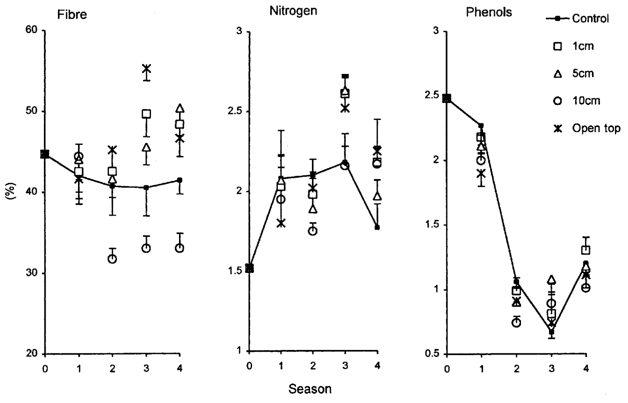

Figure 2. Seasonal variations in fibre, nitrogen and phenols in remaining litter for each treatment. Initial values (0), winter (1), spring (2), summer (3) and autumn (4). Error bars correspond to 95% confidence limits.

ficantly among treatments except in winter. In spring, summer and autumn the largest lateral mesh-size treatment (10 cm) had the lowest values of remaining litter mass (Figure 1).

Seasonal variations in mass loss in control and treatments followed a similar S-shaped pattern. Mass decrease was very small and non-significant during the dry season (winter and spring), peaking significantly in summer for control (linear function slope = −10.5), 1-cm treatment (slope = −10.8), 5-cm treatment (slope = −14.3) and open top treatment (slope = −14.1). However, the 10-cm treatment peaked significantly in spring (slope = −17.1). The mass loss rate decreased significantly in autumn in all treatments, being largest in the open top and control treatments (slope values −2.69 and −2.58, respectively) (Figure 1).

Chemical composition of litter changed during the study period. In control cages, insoluble fibre concentration remained constant, with a slight, non-significant decrease in summer. Nitrogen increased significantly from the initial value, peaking in summer. Soluble phenols showed a considerable decrease in spring and summer, increasing again in autumn (Figure 2).

Seasonal changes in fibre, N and phenols followed a similar pattern to the control in all treatments. Noticeable exceptions were: (1) lower fibre concentration in the 10-cm treatment from spring onwards; (2) higher fibre concentration in the open top treatment in summer; and (3) lower N concentration in the 10-cm treatment in spring (Figure 2). These observed differences in chemical characteristics of the litter among treatments would suggest some degree of selectivity by the removers.

Our results indicate that litter removal by animals larger than 1 mm is a significant process in the Chaco, judging from the fact that removal was significant in all treatments, reaching up to 28% in the 10-cm mesh cages. Consequently, methods for measuring litter decomposition that exclude removal by large animals (e.g. litterbag) might lead to potential underestimation of overall litter degradation and decomposition, at least in tropical semi-arid regions.

Because the amount of litter removed from cages changed as a function of mesh size, time of year, and even litter quality, we believe that more than one species was involved in litter removal. According to indirect evidence from literature and our own observations, potential removers of litter include both invertebrates and vertebrates. Among invertebrates, ants are the primary candidates. Two species known to collect dry leaves from the ground are common in the area: *Acromyrmex striatus* Roger (which forages predominantly on dry material) and *Atta vollenweideri* Forel (Bucher 1982).

Among vertebrates, the most likely candidates include the desert cavy (*Microcavia australis* (I. Geoffrey & d'Orbigny 1833)), the Chacoan cavy (*Dolichotus salinicola* (Burmeister 1876)), the plains vizcacha (*Lagostomus maximus* (Desmarest 1817)), and the grey brocket deer (*Mazama gouazoubira* (G. Fischer, 1814)) (Redford & Eisenberg 1992). The desert cavy is very common in the reserve. Its size would allow easy passage through the 10-cm and even the 5-cm mesh. Given their larger size, the remaining three species would be restricted to open-top cages. Indications suggesting that litter may be consumed by these species include: (1) Branch *et al.* (1996) found that the area around vizcacha burrow entrances is often heavily grazed and sometimes completely denuded of vegetation and litter, as well as a marked increase in dead plant material in vizcacha exclosures; and (2) the grey brocket has been observed feeding on recently fallen leaves (E. H. Bucher, *pers. obs.*).

High nutrient and low fibre and phenol concentration (total N 1.5%, insoluble fibre 44%, soluble phenols 4.5%) were a distinctive characteristic of litter in our study. These values indicate a much better foraging quality than those found in litter of other tropical semi-arid ecosystems like the Chaparral shrubland (0.63%, 52% and 9% respectively) (Schlesinger 1985) and in nutrient-poor savannas of South Africa (1.30%, 87% and 22%, respectively) (Scholes & Walker 1993). Moreover, the nutritional value of the Chaco litter is well within the ranges of optimal values for domestic herbivore food (proteins: 8–16%, maximum insoluble fibre: 70%) (National Research Council 1981). The good nutritional value of the Chaco litter may explain why litter is avidly consumed by cattle throughout the region (Morello & Saravia-Toledo 1959).

High-quality litter in the Chaco may result from (1) a high nutrient and low anti-herbivore chemical content in leaves characteristic of vegetation in nutrient-rich ecosystems (Abril & Bucher 1999, Jaramillo & Sanford 1995, Scholes & Walker 1993); and (2) a defoliation pattern that responds basically to drought or frost in an opportunistic

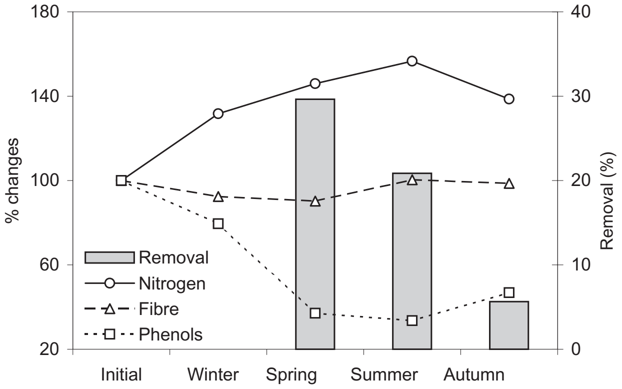

Figure 3. Seasonal changes in litter characteristics (nitrogen, fibre and phenol concentration) and removal rate. Averaged mean for all treatments.

manner (semi-deciduous) (Bucher 1982), without nutrient translocation before shedding.

The relationship between high-quality litter and litter removal rate is also supported by data from African nutrient-poor savannas, where litter tends to accumulate in the soil for more than 4 or 5 y before being completely decomposed, despite a high diversity and abundance of vertebrate herbivores (Scholes & Walker 1993). Such litter accumulation never develops in the Chaco (Abril & Bucher 1999). Moreover, records of litter consumption by native deer in Africa were made in nutrient-rich savannas only (Owen-Smith & Cooper 1987).

The annual pattern of decomposition observed in the 0.1-mm cage is typical of semi-arid regions. Litter remains relatively unaltered (and therefore available for herbivores) during the dry season, being rapidly degraded in the following wet season (Morris *et al*. 1982). With respect to removal, the observed low rate in the dry season could be explained, in the case of ants and other invertebrates, by lack of activity during the cold season (Bucher 1982). Instead, temporal variation in consumption by warm-blooded vertebrates may be the response to a relatively low nutritional value of litter in winter, due to a higher phenol and lower N content (Figure 3). The spring and summer increase in removal could be related to an improvement in the nutritional value of the litter, due to leaching of phenol by rain (Satchell 1974), and an increase in N due to assimilation in the microbial biomass (Schlesinger 1985) (Figure 3). Besides, availability of alternative food is minimal in early spring at the end of the dry season.

Litter removal by the fauna as observed in our study may have important implications in terms of nutrient redistribution because at least some of the nutrients from the litter are dispersed to a considerable distance. Moreover, removal by the fauna accelerates litter decomposition and nutrient turnover, since the material is rapidly processed (Satchell 1974, Yamashita & Takeda 1998). Litter removers can in turn be predated by other species, further extending nutrient dispersion as well as generating new food chains that imply a recycling loop for energy and nutrient flow, before the organic matter becomes completely mineralized. Therefore, it could be expected that semi-arid, tropical ecosystems like the Chaco could sustain a proportionately higher energy and nutrient flow through secondary consumers than tropical rain forest.

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