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Decomposition dynamics and physico-chemical leaf quality of abundant species in a montane woodland in central Argentina

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Abstract

Most studies on decomposition dynamics indicate that the decomposition pattern can be divided in a first rapid phase following a negative exponential model, controlled by nutrient concentration; and a second slow phase controlled by lignified carbohydrates, in which the curve acquires an asymptotic form as decomposition slows down. This pattern has been observed across different floras, but there are still contradictory evidences about which are the most accurate predictors of each decomposition phase. The objectives of this study were: (1) to determine decomposition during the two main phases throughout one year of incubation, of 20 abundant plant species from 7 contrasting plant functional types of a mountain woodland in central Argentina, and (2) to analyse the relationship of decomposition with foliar traits (both of green leaves and litter), in order to identify the more accurate predictors of the first and the second decomposition phases, as well as for annual decomposition. Decomposition was measured as the percentage of remaining dry weight (% RDW) at the end of each phase. As expected, decomposition was much slower (% RDW higher) during the second phase (70–365 days) than during the first one (0–70 days). The % RDW of the first phase was significantly and strongly associated with the % RDW of the whole incubation period. Through a stepwise multiple regression procedure we detected that the best predictors of % RDW for the first phase were the sum of recalcitrant components (lignin, cellulose and hemicellulose) of the litter with a negative relation, and specific leaf area of green leaves with a positive relation ($R^2 = 0.89$). For the whole year incubation results were quite similar to those recorded for the first phase ($R^2 = 0.78$). The second phase was not predicted by any of the traits measured. In general, our results agree with previous studies in which decomposition was tightly related to the physico-chemical characteristics of green leaves and litter. However, our results diverge from the idea that rapid and slow phases are controlled by labile and recalcitrant components, respectively, and suggest that more comparative studies are necessary to find a decomposition model suitable to different floras.

Introduction

Plant litter decomposition is a major determinant of nutrient cycling and soil organic matter turnover in terrestrial ecosystems (Meentemeyer, 1978; Swift et al., 1979). Litter decomposition rate is influenced by environmental conditions, the chemical composition of the litter and the activity of soil organisms. These factors exert a hierarchical control on litter decomposition, operating at different scales in time and space (Aerts,

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1997; Lavelle et al., 1993; Swift et al., 1979). At a local scale, with climate almost constant, decomposition dynamics is strongly affected by the chemical and physical quality of the substrate (Aerts, 1997; Meentemeyer, 1978; Swift et al., 1979). Together with the litter traits that indicate substrate decomposability, there is considerable evidence that many green leaf traits, related to plant resource-use strategies (functional markers *sensu* Garnier et al., 2004), persist in litter influencing on decomposition (Cornelissen and Thompson, 1997; Cornelissen et al., 1999; Pérez Harguindeguy et al., 2000a).

In most studies of decomposition dynamics the pattern of dry weight loss is divided in two phases (Berg, 1986; Berg and Staaf, 1980; Melillo et al., 1989). During the first phase (rapid phase), the dry weight loss is fast, following an exponential model (Aber et al., 1990; Olson, 1963). During the second phase (slow phase), the curve acquires an asymptotic form as decomposition slows down (Berg and Meentemeyer, 2002). Berg (1986) developed a conceptual model that accounts for these two phases. According to this model, in the rapid phase the decomposition of labile fractions prevails, being controlled by nutrient concentration. In the slow phase, the decomposition of lignified carbohydrates is the main process, and is controlled by the concentration of non-labile components in litter. Although the pattern described by this model has been observed across different floras (Gillon et al., 1994; Ibrahima et al., 1995; Loranger et al., 2002), there are still contradictory evidences about which are the most accurate predictors of each decomposition phase. Berg and Ekbohm (1991) and Berg and Tamm (1991) found, for boreal and temperate forests species, that litter initial nutrient concentration (nitrogen content, phosphorous content and water-soluble substances) was tightly correlated with mass loss in the first phase. McClaugherty and Berg (1987) suggested that in temperate forest species, the first phase of decomposition was regulated by the litter initial nutrient content, while the second phase was regulated by the initial lignin content and holocellulose:lignin ratio. For mediterranean species Gallardo and Merino (1993) found that leaf toughness was the best predictor of the first decomposition phase, while the cutin:N and cutin:P ratios were the main controls during the second phase. Other studies found that the best predictors of the second phase were the initial lignin content or the lignin:nitrogen ratio (Fogel and Cromack, 1977; McClaugherty et al., 1985; Meentemeyer, 1978; Melillo et al., 1982).

Although numerous, most of these studies on decomposition dynamics involve a reduced number of species, mainly from temperate or mediterranean ecosystems, or have been restricted to few plant functional types. In this context the aims of our study were: (1) to determine decomposition during the two main phases throughout one year of incubation, of 20 abundant plant species from 7 contrasting plant functional types (from annual forbs to woody evergreen species) of a mountain woodland in central Argentina, and (2) to analyse the relationship of decomposition with foliar traits (both of green leaves and litter), in order to identify the more accurate predictors of the first and the second decomposition phases, as well as for annual decomposition.

Materials and methods

Study area and species selection

The species were collected close to Cuesta Blanca locality (31°30′ S, 64°35′ W), in the Córdoba mountains of central Argentina. The vegetation of the area belongs to the woodland belt of the Mountain Chaco Phytogeographical District (Luti et al., 1979). The area is at 880 m a.s.l. and the mean annual rainfall is 830 mm (1994–2004), concentrated mainly during the warm season. The winter is relatively dry and cold (frost are common from May to September), with a mean annual temperature of 16.5 °C (1994–2004). Precipitation and temperature during the experiment (from December 2001 to December 2002) were similar to the historic records for the study site (892 mm and 16.2 °C respectively).

Species selection was based on species abundance and plant functional type composition. We selected the 20 most abundant species from the 7 more common plant functional types present in the area (annual forbs, perennial forbs, deciduous shrubs, evergreen shrubs, deciduous trees, evergreen trees, and perennial graminoids; Díaz and Cabido, 1997; Gurvich, 2005, Appendix).

Litter preparation

Litter of all species was collected from May to October 2001, depending on the litter fall peak of each species. For each species, 10 replicates were collected, each replicate consisting in litter from at least one individual. Litter was prepared following the widely used litterbag technique (Bocock and Gilbert, 1957). Samples of air-dried litter (1.0 ± 0.1 g) from each replicate were weighed, and then sealed into tube-shape nylon bags of 0.3 mm mesh size. Although this mesh size does not allow the invertebrate mesofauna to contribute to the decomposition process, their effect is small compared with that of bacteria, protozoa and fungi (Cornelissen, 1996). In order to convert air-dry mass of the samples before the burial to true dry mass, a sub-sample of each species was air-dried and subsequently oven-dried at 80 °C during 48 h, for the assessment of water content. For each selected species, 2 bags were prepared from each replicate totalling 20 bags per species. Additionally, and in order to control the stage of decomposition, we prepared 30 litter-bags of a fast-decomposing species (*Bidens pilosa* L. var. *pilosa*) and of a slow-decomposing species (*Stipa eriostachya* H.B.K), selected on the basis of previous studies (Cornelissen et al., 1999; Pérez Harguindeguy et al., 2000a).

Decomposition treatments

All litter samples were buried simultaneously in a purpose-built decomposition bed of 3×3 m placed at the same location where the litter samples had been collected. Before the burial, the top 10 cm of soil was removed and the bed was filled with mixed litter, leaf-mould at different stages of decay, and soil collected from the same site. The samples were buried at 5 cm below-ground, and covered with the litter and soil mixture in order to homogenise physical conditions, reduce the effect of the unpredictable environment close to the surface, and avoid damage by birds and mammals. Samples were randomly placed in the decomposition bed and buried for a maximum of one year under the natural temperature and rainfall conditions of the area. The decomposition method (burial) has been commonly used in recent comparative studies (Cornelissen, 1996; Cornelissen and Thompson, 1997; Cornelissen et al., 1999; Pérez Harguindeguy et al., 2000a). Although this method could overestimate or underestimate decomposition rates compared to those in (*in situ*) non-burial or shallow burial incubations, we assumed the relative patterns among species to be largely similar between incubation depths and sites.

For the two control species (*Bidens pilosa* and *Stipa eriostachya*) two litterbags per species were retrieved each 15 days. Then, based on the plot of the percentage of remaining dry weight (% RDW) against date, we visually determined the first retrieval date (corresponding to the end of the first decomposition phase) when the curves of % RDW against time became asymptotic (about 70 days after incubation). Although the decomposition rates of these species are markedly different (Blundo, 2002), both curves showed a similar pattern, indicating the same date for the end of the first phase. The second period was considered from 70 days to the end of a year of incubation. Even if one year could be considered a short period of incubation for studying the slow phase of decomposition, previous studies under similar environmental conditions, comprising species from the same flora, reported mass losses ranging from 30 to 90% in only 9 weeks (Blundo, 2002; Pérez Harguindeguy et al., 2000a). Thus, we considered that one year is a long enough period to study decomposition in our system.

Once the date for the finalization of the first phase was established, we retrieved 10 samples of each species at 70 days, and 10 samples one year after burying. After retrieval, the samples were stored at −14 °C until processing. Once defrosted, adhering soil, soil fauna and other extraneous material were removed from the decomposed leaf litter by brushing or swiftly rinsing with water. Litter samples were dried for 48 h at 80 °C, and then weighted. Decomposition rate was measured through the percentage of remaining dry weight (% RDW) after each incubation period. For the first phase, the % RDW was calculated on the basis of the initial dry weight, while for the second phase, % RDW was calculated on the basis of the initial weight for the second phase, i.e. the weight remaining at 70 days.

Leaf and litter traits

Since both green leaves and litter traits have been indicated as powerful predictors of decomposition (Cadish and Giller, 1997; Cornelissen et al., 1999; Garnier et al., 2004; Grime et al., 1996; Pérez Harguindeguy et al., 2000a and b), we measured both types of foliar traits in our species set. For all trait measurements we used six replicates that were averaged to obtain a single value for each species.

On green leaves, we measured total C, N and P, specific leaf area (SLA) and leaf tensile strength. Total C was estimated as 50% of ash-free biomass (Gallardo and Merino, 1993; McClaugherty et al., 1985; Schlesinger, 1977) and total N and P were measured using an Autoanalyser (RFA 300-Alpken, Wilsonville, O.R., USA). We also calculated C:N ratio. These chemical traits (C, N and P) were measured in green leaves instead of litter because preliminary data suggested that nutrients in green leaves can be better predictors of litter decomposition rates than the litter nutrient content. Additionally, the green leaves nutrient content is an ecologically meaningful trait that can be used to scale up to ecosystem functioning (Chapin et al., 1997; Lavorel and Garnier, 2002). Leaf tensile strength and SLA are indices of leaf physical quality and were measured following the procedures indicated by Cornelissen et al. (2003). Leaf tensile strength indicates the leaf toughness measured as the force needed to tear a leaf (fragment) divided by its width, expressed in N mm^{-1}. SLA represents the light-intercepting area per dry mass of leaf (m^2 kg^{-1}) and is related to net assimilation rate (Reich et al., 1992) and plant growth rate (Poorter and Garnier, 1999; Reich et al., 1992).

As indicators of the litter chemical quality we measured lignin, celulose and hemicelulose contents following the technique of Goering and Van Soest (1970). We also calculated the total fibre content of litter (LCH = lignin + cellulose + hemicellulose), and the holocellulose: lignocellulose ratio (HLQ = (cellulose + hemicellulose)/LCH), that indicates the proportion of the less recalcitrant non-labile compounds (Berg et al., 1984; Cortez et al., 1996; McClaugherty and Berg, 1987).

Data analysis

We employed Spearman rank correlations to test pair-wise relationships between green leaf and litter traits and to analyse associations between % RDW in the different periods: first phase (1–70 days), second phase (71–365 days) and the whole period (1–365 days). Additionally, we tested associations between foliar traits and % RDW of the different periods.

To analyse how the combination of foliar traits explain % RDW at each period we performed multiple regression analyses with % RDW of each phase and total % RDW as dependent variables, and foliar traits as independent ones. To reduce the number of independent variables, before performing the regression procedure we discarded traits based on pair-wise correlations between them (i.e., when two traits were highly correlated among them, we selected only one; Afifi and Clark, 1984). Then, we performed a forward stepwise regression procedure to select the best combination of traits to explain % RDW for each phase and for the whole year. Once the best model was selected, we checked normality of residuals with Kolmogorov-Smirnov test.

Results

Decomposition dynamics

All species showed a fast weight loss (a low % RDW) at the first phase and a much slower weight loss (a higher or similar % RDW for a longer period) in the second phase (Appendix, Table A1). At the end of the first phase, the % RDW varied from 74% for *Schizachyrium condensatum* to 21% for *Fagara coco*. During the second phase (between 70 and 365 days) the mass loss was much lower and the % RDW ranged from 67% for *Schizachyrium condensatum* to 85% for *Bidens pilosa*. Considering the total period, the % RDW varied from 17% for *Fagara coco* to 54% for *Lithrea molleoides*. The % RDW of the first phase was strongly correlated with the % RDW of the overall period (Figure 1a). In contrast, the % RDW of the second phase was not correlated neither with the %

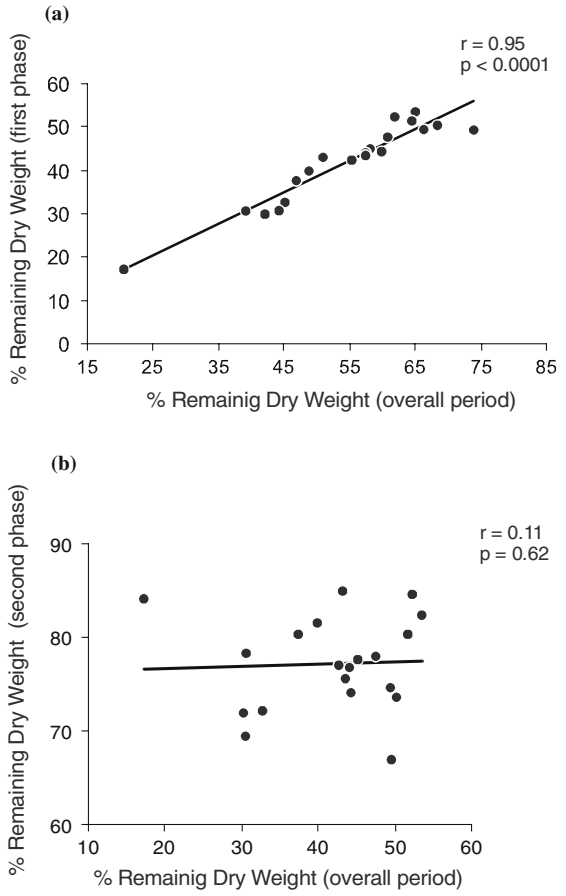

Figure 1. Pair-wise relationships (and Spearman Correlation Coefficients) between the percent of remaining dry weight (% RDW) of the whole period of incubation and (a) % RDW of the first phase, (b) % RDW of the second phase, for 20 plant species from central Argentina.

RDW of the overall period (Figure 1b) nor with the % RDW of the first phase.

Green leaf and litter traits

The C content in green leaves showed little variation (438–474 mg g^{-1}). N concentration varied from 12.2 mg g^{-1} in *Schizachyrium condensatum* to 44.5 mg g^{-1} in *Tagetes minuta*. P concentrations varied from 1.1 mg g^{-1} for *Conyza bonariensis* and *Bouteloua curtipendula* to 5.4 mg g^{-1} for *Acalypha communis* and *Tagetes minuta*. Leaf tensile strength varied from 0.32 N mm^{-1} for *Bidens subalternans* to 14.53 N mm^{-1} for *Schizachyrium condensatum*, and was markedly higher for graminoids than for non-graminoids. Mean SLA varied from 3.3 m^2 kg^{-1} for *Schizachyrium condensatum* to 25 m^2 kg^{-1} for *Bidens subalternans* (see Appendix, Table A2 for more details of green leaf trait values).

Among litter traits, lignin content varied widely, from 55.3 mg g^{-1} in *Celtis tala* to 377 mg g^{-1} in *Acacia caven*. The highest cellulose values were observed in graminoids, 427 and 396 mg g^{-1} for *Stipa eriostachya* and *Bouteloua curtipendula* respectively, and the lowest in *Condalia montana*, *Heterothalamus alienus* and *Lithrea molleoides*. Initial litter hemicellulose content varied from 0–274 mg g^{-1}, being highest in graminoids. Accordingly, this pattern was also followed by HLQ, varying from 0.36 to 0.86, and by LCH varying from 827.7 in *Stipa eriostachya* to 231.1 in *Fagara coco* (see Appendix 1 for more details of litter trait values).

Decomposition dynamics and initial leaf and litter quality

Considering the correlations between independent variables (Table 1) we selected N, C, LCH, HLQ and SLA as the variables to be used for the multiple regression. We discarded C:N ratio, P and leaf toughness because they were highly correlated with N; and cellulose, hemicellulose and lignin because they were highly correlated with LCH or HLQ indices. Additionally, we considered the quadratic term of LCH as another variable, because the direct observation of the scatter plots suggested a non-linear relationship between % RDW of the first phase and LCH (Figure 2a).

For the first phase, the multiple regression procedure selected LCH, LCH^2 and SLA as the best combination of variables for predicting decomposition. LCH + LCH^2 accounted for nearly 74% of the variation in decomposition, SLA for the 15%, and the complete model for the 89% of the variance ($P < 0.0001$ for all the variables and for the whole model). The regression equation was:

$$\%\,\mathrm{RDW\ (first\ phase)} = -19.5 + 0.28 \times \mathrm{LCH} - 2 \times 10^{-4} \times \mathrm{LCH}^2 - 0.90 \times \mathrm{SLA}$$

The regression showed that species with higher content of lignin, cellulose and hemicelulose

Table 1. Spearman's Rank Correlation Coefficients (r) between measured leaf and litter traits of 20 abundant species from Mountain woodlands, in central Argentina

	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C:N ratio	LTS (N mm^{-1})	SLA (m^2 kg^{-1})	Cellulose (mg g^{-1})	Hemicellulose (mg g^{-1})	Lignin (mg g^{-1})	HLQ (mg g^{-1})	LCH
LCH index	0.28	−0.55**	−0.16	0.58**	0.43	0.02	0.65***	0.47*	0.22	0.17	–
HLQ index	−0.05	−0.1	−0.26	0.15	0.33	−0.13	0.43	0.69***	0.89***	–	
Lignin (mg g^{-1})	0.13	−0.11	0.19	0.08	−0.21	0.17	−0.09	−0.49**	–		
Hemicellulose (mg g^{-1})	−0.12	−0.48*	−0.25	0.51*	0.66***	−0.23	0.14	–			
Cellulose (mg g^{-1})	0.23	−0.18	−0.18	0.22	0.12	0.16	–				
SLA (m^2 kg^{-1})	−0.12	0.35	0.13	−0.34	−0.51*	–					
LTS (N mm^{-1})	−0.07	−0.59**	−0.19	0.58**	–						
C:N ratio	0.15	0.99***	−0.56**	–							
P (mg g^{-1})	0.21	0.62**	–								
N mg g^{-1})	−0.11	–									
C (mg g^{-1})	–										

*$P < 0.05$;**$P < 0.01$;***$P < 0.001$. SLA: specific leaf area.; LTS: leaf tensile strength; LCH: lignin + cellulose + hemicellulose; and HLQ: (cellulose + hemicellulose)/LCH.

Figure 2. (a) Quadratic relation (74% of variance explained) between % RDW and LCH index (initial litter lignin + cellulose + hemicellulose content) for 20 plant species from central Argentina; (b) Relationship between the residuals of the first regression (difference between observed values and expected values according to LCH) and specific leaf area (SLA), the second predictor variable. The line indicates the best linear fit between residuals and SLA, explaining an additional 15% of the variance in % RDW. The variance explained by the whole model is 89%.

(high LCH) decomposed slower (higher % RDW) than species with lower content of those compounds. The quadratic term showed that this relation was not linear, being stronger for species with low LCH, and weaker for species with high LCH (Figure 2a). The third term of the multiple regression, SLA, was positively associated to decomposition indicating that, for a given LCH, species with higher SLA decomposed faster (Figure 2b). For the second phase, no variable was selected by the regression procedure to explain % RDW (Table 2). For the whole incubation

Table 2. Correlations between % RDW of the first, second and overall period and initial leaf and litter quality

	% RDW (first phase)	% RDW (second phase)	% RDW (overall period)
C (mg g^{-1})	0.36	0.04	0.33
N (mg g^{-1})	−0.67***	−0.11	−0.62**
P (mg g^{-1})	−0.13	−0.13	−0.1
C:N ratio	0.69***	0.04	0.65**
LTS (N mm^{-1})	0.53*	−0.21	0.45*
SLA (m^2 kg^{-1})	−0.34	0.33	−0.25
Cellulose (mg g^{-1})	0.4	−0.20	0.33
Hemicellulose (mg g^{-1})	0.33	0.01	0.33
Lignin (mg g^{-1})	0.36	−0.05	0.36
HLQ index	−0.08	−0.05	−0.09
LCH index	0.81***	−0.17	0.73***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. SLA: specific leaf area; LTS: leaf tensile strength; LCH: lignin + cellulose + hemicellulose and HLQ: (cellulose + hemicellulose)/LCH.

period, the best combination of predictors was the same as for the first phase (LCH, LCH^2 and SLA). LCH and LCH^2 accounted 68% of the variance in decomposition, SLA for 10%, and the complete model for the 78% ($P < 0.0001$ for each variable and for the model). In this case, the regression equation was:

$$\%\ \text{RDW (overall period)} = -16.5 + 0.22 \times \text{LCH} - 1 \times 10^{-4} \times \text{LCH}^2 - 0.54 \times \text{SLA}$$

These results are in line with the high correlation between the annual decomposition and that of the first phase (see Figure 1a).

Discussion

Decomposition dynamics pattern

For the species included in our study, the rate of weight loss was much slower in the second period than during the first one. Our results are in agreement with the findings by Berg and Ekbhon (1991) and McClaugherty and Berg (1987) who found wider differences in the weight loss of temperate forest species during the rapid phase, a narrower range of weight loss values for the slow phase, and that both phases differed widely in the magnitude of their decomposition rates. These results could be attributable to a two-phase pattern of decomposition, as reported by other authors (Berg, 2000; Gillon et al., 1994; Ibrahima et al., 1995; Loranger et al., 2002; Tietema, 1993; Upadhyay et al., 1989).

The % RDW of the first phase was significantly and strongly associated with the % RDW of the whole period of incubation since, out of the total mass that was lost during one year, the majority (51–96%) was lost during the first 70 days. This indicates that annual decomposition is mainly determined by the decomposition during the first phase, being the latter a good estimator of the former.

Decomposition dynamics and foliar traits

We found that the first phase of decomposition was associated with both green leaf and litter traits. Previous studies for temperate evergreen trees indicated that litter concentration of N, P, K, and water-soluble compounds were the main predictors of initial decomposition rates, while lignin was the best predictor of later phases (Arunachalam et al., 1998; Berg, 1986; Berg, 2000; Berg and Ekbohm, 1991; Berg and Tamm, 1991). For the species considered in our study, the sum of recalcitrant components of the litter (LCH) was the best predictor of decomposition both during the first phase and the whole incubation

period. These results, however, do not discard the importance of labile compounds as determinants of decomposition, since green leaf N concentration was indeed associated to decomposition and also highly correlated to the litter initial sum of recalcitrant compounds (LCH index), our selected predictor. Bollen (1953) suggested that the structural complexity of materials containing lignin and cellulose might exert more control over the rate of decomposition than the N content might indicate. He argued that when weight loss occurs very rapidly in the first phase of the decomposition process, the nutrient-controlled phase is quickly passed; then slowly degrading material dominates the process.

In our study, the second determinant of litter decomposition was SLA, as showed by the multiple regression results. This indicates that, for a given concentration of non-labile compounds (LCH), plants with higher SLA decompose faster. This result is in line with the findings of Cornelissen et al. (1999), Garnier et al. (2004) and Gurvich et al. (2003) who found a positive relationship between SLA and decomposition. The relationship between decomposition and SLA could be direct, as a result of the leaf area exposed to the activity of decomposers (Swift et al., 1979) and similar to the effect of the particle size: an increase in particle size and/or comminution by the soil faunal increase the decomposition rate (Vestergaard et al., 2001). However, the effect of SLA on decomposition could be indirect, since this trait constitutes an expression of other plant characteristics, and is related with the resource-use strategy of a species or its functional role in an ecosystem (Garnier et al., 2004; Lambers and Poorter, 1992).

It is worth noticing that the second phase of decomposition was not related to any of the measured variables, nor to any combination of them. These results do not agree with the findings of other authors, who found that the decay rates in the late stage were strongly related with the initial lignin content, the ratio lignin:N and the content of other slowly degradable compounds such as tannins (Aerts, 1997; Loranger et al., 2002; Meentemeyer, 1978). In our study, the lack of association between second phase decomposition and the foliar traits could be related to the physico-chemical changes produced in litter as decomposition proceeds (mainly affecting the more resistant bounds; Martin et al., 1996). Due to these changes the litter at the beginning of the second phase could have a different (and not correlated) chemistry than the initial litter, and thus decomposition of the second phase could not be predicted by the physico-chemical traits of initial litter.

In conclusion, our results indicate that for our set of 20 species belonging to seven different functional types, the decomposition dynamic can be predicted by the sum of recalcitrant compounds in litter and SLA, a green leaf trait. The variance explained by the combination of both traits was clearly high compared to previous studies. In general our results agree with previous studies in which decomposition is tightly related to the physico-chemical characteristics of green leaves and litter. However, the results diverge with the idea that rapid and slow phases are determined by labile and recalcitrant components, respectively. Our results, together with other studies indicating that the combination of traits determining both phases of decomposition may vary according to the set of species or the ecosystem characteristics, stress the need of comparative studies to find a decomposition model of wider applicability and suitable to floras of different environments.

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References

Aber J D, Melillo J M and McClaugherty C A 1990 Predicting long-tem patters of mass loss, nitrogen dynamics, and soil matter formation from initial fine litter chemistry in temperate forest ecosystems. Can. J. Bot. 68, 2201–2208.

Aerts R 1997 Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystem: a triangular relationship. Oikos 79, 439–449.

Afifi A A and Clark V 1984 Computer Aided Multivariate Analysis. Lifetime Learning Publications. Belmont, California.

Arunachalam A, Maithani K, Pandey H N and Tripathi R S 1998 Leaf litter decomposition and nutrient mineralization patters in regrowing stands of a humid subtropical forest after tree cutting. Forest Ecol. Manag. 109, 151–161.

Berg B 1986 Nutrient release from litter and humus in coniferous forest soils-a mini review. Scand. J. For. Res. 1, 359–369.

Berg B 2000 Initial rates and limit values for decomposition of Scots pine and Norway spruce needle litter: a synthesis for N-fertilized forest stands. Can. J. For. Res. 30, 122–135.

Berg B and Ekbohm G 1991 Litter mass-loss rates decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest. VII. Can. J. Bot. 76, 1295–1304.

Berg B, Ekbohm G and McClaugherty C 1984 Lignin and holocellulose relations during long-term decomposition of some forest litter. Long-term decomposition in a Scots pine forest IV. Can. J. Bot. 62, 2540–2550.

Berg B and Meentemeyer V 2002 Litter quality in a north European transect versus carbon storage potencial. Plant Soil 242, 83–92.

Berg B and Staaf H 1980 Decomposition rates and chemical change of Scots pine needle litter. II. Influence of chemical composition. *In* Structure and Function of Northern Coniferous Forests-An Ecosystem Study. Ecological Bulletins 32. Ed. T. Persson. pp. 373–390. Swedish Research Councils, Stockholm.

Berg B and Tamm C O 1991 Decomposition and nutrient dynamics of litter in long-term optimum nutrition experiments. Scand. J. For. Res. 6, 305–321.

Blundo C 2002 Descomposición de especies pertenecientes a tipos funcionales dominantes en el Bosque Serrano (Córdoba): Efecto de la calidad foliar y la riqueza. Graduate Thesis, Fac. Cs. Ex. Fís. y Nat., U.N.Cba, Córdoba, Argentina.

Bocock K L and Gilbert O J 1957 the disappearance of leaf litter under different woodland conditions. Plant Soil 9, 179–185.

Bollen W B 1953 Mulches and soil conditioners. Carbon and nitrogen in farm and forest products. Agr. Food. Chem. 1, 379–381.

Cadisch G and Giller K E 1997 Driven by Nature: Plant Litter Quality and Decomposition. Department of Biological Sciences Wye College, University of London, London.

Chapin F S III, Walker B H, Hobbs R J, Hooper D U, Lawton J H, Sala O E and Tilman D 1997 Biotic control over the functioning of ecosystems. Science 277, 500–504.

Cornelissen J H C 1996 An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J. Ecol. 84, 573–582.

Cornelissen J H C, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich D E, Reich P B, Ter Steege H, Morgan H D, Van der Heijden M G A, Pausas J G and Poorter H 2003 A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.

Cornelissen J H C, Pérez Harguindeguy N, Díaz S, Grime J P, Marzano B, Cabido M, Vendramini F and Cerabolini B 1999 Leaf structure and defence control litter decomposition rate across species and life forms in regional floras of two continents. New Phytol. 143, 191–200.

Cornelissen J H C and Thompson K 1997 Functional leaf attributes predict litter decomposition rate in herbaceous plants. New Phytol. 135, 109–114.

Cortez J, Demard M, Bottner P and Jocteur Monrozier L 1996 Decomposition of Mediterranean leaf litters: A microcosm experiment investigating relationships between decomposition rates and litter quality. Soil Biol. Biochem. 28, 443–452.

Díaz S and Cabido M 1997 Plan functional types and ecosystem function in response to global change: a multiscale approach. J. Veg. Sci. 8, 463–474.

Fogel R and Cromack K Jr 1977 Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. 55, 1632–1640.

Gallardo A and Merino J 1993 Leaf decomposition in 2 Mediterranean ecosystems of Southwest Spain-influence of substrate quality. Ecology 74, 152–161.

Garnier E, Cortez J, Billès G, Navas M, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C and Toussaint J 2004 Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637.

Gillon D, Joffre R and Ibrahima A 1994 Initial litter properties and decay rate: a microcosms experiment on Mediterranean species. Can. J. Bot. 72, 946–954.

Goering H K and Van Soest P J, 1970 Forage Fiber Analyses. Handbook N° 379, Depatment of Agriculture, USDA, Washington D.C. 20.

Grime J P, Cornelissen J H C, Thompson K and Hodgson J G 1996 Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos 77, 489–494.

Gurvich D E, 2005 Efectos de la remoción de especies y de tipos funcionales de plantas sobre los procesos ecosistémicos en un matorral serrano. PhD thesis, Fac. Cs. Ex. Fís. y Nat., U.N.Cba, Córdoba, Argentina.

Gurvich D E, Easdale T A and Pérez Harguindeguy N 2003 Subtropical montane tree litter decomposition: links with secondary forest types and species' shade tolerance. Austral Ecol. 28, 666–673.

Ibrahima A, Joffre R and Guillon D 1995 Changes in litter during the initial leaching phase: an experiment on the leaf litter of Mediterranean species. Soil Biol. Biochem. 27, 931–939.

Lambers H and Poorter H 1992 Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. Adv. Ecol. Res. 23, 188–242.

Loranger G, Ponce D I and Lavelle P 2002 Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality. Biol. Fertile Soils 35, 247–252.

Lavelle P, Blanchart E, Martín A, Martín S, Spain A V, Toutain F, Barois I and Schaefer R 1993 A hierarchical model for decomposition in terrestrial ecosystem: applications to soils of the humid tropics. Biotropica 25, 130–150.

Lavorel S and Garnier E 2002 Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.

Luti R, Solís M, Galara M, Muller N, Berzal M, Nores M, Herrera M and Barrera J C 1979 Vegetación. *In* Geografía Física de la Provincia de Córdoba. Eds. J Vázquez, J Miatello and M Roque. pp. 297–368. Buenos Aires, Bodt.

Martin A, Gallardo J F and Santa Regina I 1996 Dinámica de las fracciones orgánicas en la descomposición de hojas de rebollos y castaño. Silva Lusitana 4, 199–216.

McClaugherty C A and Berg B 1987 Holocellulose, lignin and nitrogen levels as rate-regulating factors in late stage of forest litter decomposition. Pedobiologia 30, 101–112.

McClaugherty C A, Pastor J, Aber J D and Melillo J M 1985 Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66, 266–275.

Meentemeyer V 1978 Macroclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.

Melillo J M, Aber J D, Linkins A E, Ricca A, Fry B and Nadelhoffer K 1989 Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. Plant Soil 115, 189–198.

Melillo J M, Aber J D and Muratore J F 1982 Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 571–584.

Olson J S 1963 Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331.

Pérez Harguindeguy N, Díaz S, Cornelissen J H C, Vendramini F, Cabido M and Castellanos A 2000a Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. Plant Soil 218, 21–30.

Pérez Harguideguy N, Vendramini F, Díaz S, Cabido C, Cornelissen J H C, Gurvich D E and Castellanos A 2000b Descomposición y caracteres foliares de especies de Pteridófitas y Agiospermas del Chaco Serrano de Córdoba, Argentina. Kurtziana 28, 35–44.

Poorter H and Garnier E 1999 Ecological significance of inherent variation in relative growth rate and its components. *In* Handbook of Functional Plant Ecology. Eds. F I Pugnaire and F Valladares. pp. 81–120. Marcel Dekker, New York.

Reich P B, Walters M B and Ellsworth D S 1992 Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol. Monogr. 62, 365–392.

Schlesinger W H 1977 Carbon balance in terrestrial detritus. Annu. Rev. Ecol. Syst. 8, 51–81.

Swift M J, Heal O W, and Anderson J M, 1979 Decomposition in Terrestrial Ecosystems. Studies in Ecology 5. Blackwell, Oxford.

Tietema A 1993 Mass loss and nitrogen dynamics in decomposing acid forest litter in the Netherlands at increased nitrogen deposition. Biogeochemistry 20, 45–65.

Upadhyay V P, Singh J S and Meentemeyer V 1989 Dynamics and weight loss of leaf litter in central Himalayan forests: abiotic versus litter quality influences. J. Ecol. 77, 147–161.

Vestergaard P, Rønn R and Søren C 2001 Reduced particle size of plant material does not stimulate decomposition, but affects the microbivorous microfauna. Soil Bio. Biochem. 33, 1805–1810.

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Appendix

Table A1. Initial cellulose, hemicellulose and lignin content of litter from the 20 selected species, and mean % RDW of the three periods considered in the decomposition experiment

Species	Cellulose (mg g^{-1})	Hemicellulose (mg g^{-1})	Lignin (mg g^{-1})	% RDW (first phase)	% RDW (second phase)	% RDW (overall period)
Annual forbs						
Bidens pilosa L. var. *pilosa*	245	2.7	214	51.1	85.0	43.4
Bidens subalternans D.C. var. *subalternans*	242	0	254	55.3	77.0	46.2
Conyza bonariensis (L.) Cronquist. var. *bonariensis*	264	0	217	57.4	75.6	43.4
Tagetes minuta L.	201	19.3	161	45.3	72.2	32.7
Perennial forbs						
Acalypha communis Mull. Arg. var. *guaranitica* Chodat & Hassl	179	63	73	42.0	72.0	30.2
Ambrosia tenuifolia Spreng.	237	5	169	44.1	69.5	30.7
Eupatorium argentinum Ariza	182	199	158	46.8	80.3	37.6
Hyptis mutabilis (Rich.) Briq.	236	0	286	64.4	80.3	51.7
Deciduous shrubs						
Acacia caven (Molina) Molina var. *caven*	112	200	377	59.8	74.1	44.3
Condalia montana A. Cast.	81	177	156	58.2	77.6	45.2
Lippia sp	250	80.7	192	57.4	76.8	44.0
Evergreen shrubs						
Eupatorium buniifolium Hook & Arn. var. *buniifolium*	199	0	360	66.3	74.6	49.5
Heterothalamus alienus (Spreng.) Kuntze	97	70.7	165	48.9	81.6	39.9
Deciduous trees						
Celtis tala Gillies ex Planch.	148	97	55.3	39.1	78.3	30.6
Fagara coco (Gillies) Engl.	156	19.7	55.7	20.5	84.0	17.2
Evergreen trees						
Lithrea molleoides (Vell) Engl.	99	124	221	65.0	82.4	53.6
Graminoids						
Bouteloua curtipendula (Michx.) Torr. var. *caespitosa* Gould & Kapadia	396	276	106	62.0	84.6	52.4
Paspalum malacophyllum Trin	387	205	98.3	61.0	77.9	47.5
Schizachyrium condensatum (H.B.K.) Ness	394	274	124	74.0	66.8	49.4
Stipa eriostachya H.B.K.	427	270	131	68.4	73.6	50.4

Table A2. Initial chemical composition (C, N, P and C:N) and physical traits (LTS: leaf tensile strength and SLA: specific leaf area) of the green leaves of the 20 selected species

Species	Family	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C:N (ratio)	LTS (N mm^{-1})	SLA (m^2 kg^{-1})
Annual forbs							
Bidens pilosa L. var. *pilosa*	Asteraceae	459	37.2	4.2	12.4	0.45	17.0
Bidens subalternans D.C. var. *subalternans*	Asteraceae	453	30.6	1.4	14.8	0.32	25.0
Conyza bonariensis (L.) Cronquist. var. *bonariensis*	Asteraceae	467	20.2	1.1	23.1	0.41	12.7
Tagetes minuta L.	Asteraceae	462	44.5	5.4	10.4	0.38	15.2
Perennial forbs							
Acalypha communis Mull. Arg. var. *guaranitica* Chodat & Hassl	Euphorbiaceae	441	45.0	5.4	9.8	0.67	8.0
Ambrosia tenuifolia Spreng.	Asteraceae	450	28.1	1.9	16.0	0.66	11.5

Table A2. Continued

Species	Family	C (mg g^{-1})	N (mg g^{-1})	P (mg g^{-1})	C:N (ratio)	LTS (N mm^{-1})	SLA (m^2 kg^{-1})
Eupatorium argentinum Ariza	Asteraceae	456	26.2	1.6	17.4	0.27	22.8
Hyptismutabilis (Rich.) Briq.	Lamiaceae	466	31.7	3.1	14.7	0.33	12.0
Deciduous shrubs							
Acacia caven (Molina) Molina var. *caven*	Fabaceae	453	27.1	3.1	16.7	6.75	13.6
Condaliamontana A. Cast.	Rhamnaceae	472	23.2	2.1	20.3	0.92	5.9
Lippia sp	Verbenaceae	474	28.7	3.1	16.5	0.42	8.1
Evergreen shrubs							
Eupatorium buniifolium Hook & Arn. var. *buniifolium*	Asteraceae	474	23.7	2.4	20.0	1.67	7.4
Heterothalamus alienus (Spreng.) Kuntze	Asteraceae	452	15.0	1.4	30.4	1.92	9.7
Deciduous trees							
Celtis tala Gilliesex Planch.	Celtidaceae	438	39.7	1.3	11.0	0.63	8.9
Fagara coco (Gillies) Engl.	Rutaceae	468	34.3	1.8	13.7	0.43	11.5
Evergreen trees							
Lithrea molleoides (Vell) Engl.	Anacardiaceae	455	16.7	2.0	27.2	0.86	6.2
Graminoids							
Bouteloua curtipendula (Michx.) Torr. var. *Caespitosa* Gould & Kapadia	Poaceae	456	15.0	1.1	30.6	4.57	14.2
Paspalum malacophyllum Trin	Poaceae	468	27.4	4.1	17.1	4.15	18.7
Schizachyrium condensatum (H.B.K.) Ness	Poaceae	462	12.2	1.3	38.0	14.53	3.3
Stipa eriostachya H.B.K.	Poaceae	459	16.6	1.5	27.7	13.23	4.8