



Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina

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Abstract

Litter decomposition, a major determinant of ecosystem functioning, is strongly influenced by the litter quality of different species. We aimed at (1) relating interspecific variation in leaf litter decomposition rate to the functional types different species belong to; and (2) understanding the chemical and/or physical basis for such variation and its robustness to environmental factors. We selected 52 Angiosperms from a climatic gradient in central-western Argentina, representing the widest range of functional types and habitats published so far. Ten litter samples of each species were simultaneously buried for 9 weeks during the 1996 summer in an experimental decomposition bed. Decomposition rate was defined as the percentage of dry mass loss after incubation. Chemical litter quality was measured as carbon (C) content, nitrogen (N) content, and C-to-N ratio. Since tensile strength of litter and living leaves were strongly correlated, the latter was chosen as an indicator of physical litter quality. A subset of 15 species representing different functional types was also incubated in England for 15 weeks, following a similar experimental procedure. Litter C-to-N and leaf tensile strength of the leaves showed the strongest negative associations with decomposition rate, both at the species and at the functional-type level. Decomposition rates of the same species in Argentina and in England were strongly correlated. This reinforces previous evidence that species rankings in terms of litter decomposition rates are robust to methodological and environmental factors. This paper has shown new evidence of plant control over the turnover of organic matter through litter quality, and confirms, over a broad spectrum of functional types, general models of resource allocation. The strong correlations between leaf tensile strength – a trait that is easy and quick to measure in a large number of species – decomposition rate, and C-to-N ratio indicate that leaf tensile strength can be useful in linking plant quality to decomposition patterns at the ecosystem level.

Introduction

Litter decomposition is controlled by three main factors: climate, litter quality and the nature and abundance of the decomposer organisms (Aerts, 1997; Ågren and Bosatta, 1996; Cotrufo et al., 1994; Seastedt et al., 1983; Swift et al., 1979). These

components operate at different spatial and temporal scales, with the dominant factor being climate at a regional scale and litter quality at the local scale (Côteaux et al., 1995; Lavelle et al., 1993). Also, with few exceptions (e.g., Hobbie, 1996), climate appears to be the dominant factor in areas subjected to unfavourable climatic conditions, whereas litter quality largely prevails as the regulator under favourable

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conditions (Côteaux et al., 1995; Lavelle et al., 1993; Swift et al., 1979).

It is well documented that physico-chemical features of leaf litter cause important interspecific variability in decomposition rates (Anderson, 1991; Cornelissen, 1996; Swift et al., 1979). Some of these features may be the legacy of traits of living leaves (Berendse, 1994; Cornelissen and Thompson, 1997; Grime et al., 1996; Wardle et al., 1998). Numerous studies have related decomposition rate to chemical litter quality indices such as total nitrogen (N), carbon-to-N ratio, lignin-to-N ratio (e.g., Cadisch and Giller, 1997; Iritani and Arnold, 1960; Melillo et al., 1982), or sequential extraction of carbon (C) compounds (Palm and Rowland, 1997). The toughness of plant litter, which may be related to anti-herbivore defence of living leaves, can also affect decomposition and nutrient release (Cornelissen and Thompson, 1997; Gallardo and Merino, 1993). In general, more tender leaves are expected to be decomposed faster.

The vast majority of studies on decomposition, however, have concentrated on a relatively small number of species and/or have been restricted to few functional types or taxonomic groups. The recent screening of 125 British plant species by Cornelissen (1996) is one exception to this, but its analyses were restricted to a temperate flora. Very few studies have explored whether these patterns remain consistent in semi-arid and arid ecosystems, and their reports are contradictory. Schaefer et al. (1985) and Cepeda-Pizarro and Whitford (1989) found no correlation between litter quality and mass loss rate. In contrast, Murphy et al. (1998) reported some initial litter chemistry control over decomposition rates. Pérez-Harguindeguy et al. (1997) analysed a wider range of functional types and ecosystems of origin in subtropical Argentina, but no attempt was made to relate decomposition with leaf quality. Comparative approaches to the links between decomposition and traits of living leaves have been scarce in the literature until recently (e.g., Aerts, 1997; Cornelissen and Thompson, 1997; Cornelissen et al., 1999; Wardle et al., 1998). This kind of correlative studies has gained increasing interest in the last years, as part of the efforts towards a better understanding of the effects of individual plant species and functional types on ecosystem processes (Berendse, 1994; Chapin et al., 1997; Hobbie, 1992; van der Putten, 1997).

The objectives of the present study were (1) to relate interspecific variation in leaf litter decomposition rate to the functional types different species belong

to, and (2) to understand the chemical and/or physical basis for such variation and its robustness to environmental factors.

Materials and Methods

Study area

The plant material was collected along a climatic gradient in central Argentina (31°25'–32° S, 64°10'–68°37' W), with a difference in annual precipitation of >800 mm, a difference in mean annual temperature of >11 °C, and a difference in altitude of >1500 m between extreme points. It stretches from the subhumid high plateau of the Córdoba Mountains to the western semiarid-arid plains, which are bordered by the Sub-Andean ranges. Dry and relatively cold winters and rainfall concentrated in the warm season are characteristic of the climate over the whole region (Capitanelli, 1979).

Collection of litter and living material

A total of 52 Angiosperm species were selected (Pérez-Harguindeguy et al., 1997) based on previous studies (Cabido, 1985; Cabido et al., 1989; Cabido et al., 1990; Cabido et al., 1993) considering their abundance along the gradient described above, and trying to include a wide range of plant families and functional types (Appendix 1). Plant functional types were identified following Díaz and Cabido (1997), whose classification is based on species resource allocation to growth vs. storage/defense, size, specific leaf area, plant and leaf life spans, photosynthetic pathway, and shoot phenology.

From November 1995 to October 1996, fresh leaf litter was collected from at least 10 randomly selected individuals of each species in their typical habitats. Senesced photosynthetic tissues (leaf analogues) were collected in the case of leafless species. Fresh leaves (analogues) from the same species were collected in the same period and stored in polyethylene bags at 4°C, for up to 48 h, before being processed.

Litter preparation

Litter samples were sorted and cleaned following Cornelissen (1996). Samples of air-dry litter (1.0 ± 0.1 g) were weighed, 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 considered 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 subsample of each species was air-dried and subsequently oven-dried at 80 °C for the assessment of water content.

Decomposition treatments

All litter samples were remoistened and buried simultaneously in a purpose-built decomposition bed at the experimental area of the Agronomy School, Universidad Nacional de Córdoba, Argentina, on 21 November 1996. The day before the burial, the top 20 cm of soil was removed. The bed measured 4×4 m and was filled with c. 3.5 m³ of mixed litter, leaf-mould at different stages of decay, and soil (for details see Pérez-Harguindeguy et al., 1997). The samples were buried at 10 cm below-ground, and covered with mixed soil and litter in order to homogenise physical conditions, reduce the effect of the unpredictable environment close to the surface, and avoid damage by birds and mammals. The decomposition bed was covered with a metal mesh as protection against animals. There were ten replicates for most species, and at least six were used when material was insufficient. Samples were randomly placed in the decomposition bed and buried for 9 weeks under the natural temperature and rainfall conditions, during the spring-summer season in Córdoba. Monthly mean temperature (20 °C) and total precipitation (636 mm) during the experimental period were very similar to those of the past 10 years.

The 9-week incubation period was long enough for more than 10% of the species to reach c. 90% of litter mass loss. Mass loss after 18 weeks showed a highly significant correlation with the 9-week harvest ($r=0.85$; $p<0.001$, Spearman Rank Correlation test), but in the former case differentiation in decomposition rates among the fast decomposing species had been lost owing to mass losses approaching 100% in a substantial number of species (Pérez-Harguindeguy et al., 1997). Therefore, only data from the 9-week mass loss are presented in this article.

After retrieval, the samples were stored at -14 °C. 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,

then weighed. Decomposition rate was defined as the percentage of weight loss after 9 weeks of burial.

This experiment was not intended to simulate *in situ* decomposition in the habitats of origin. It should be seen as an experiment designed to test the role of different litter qualities under a standard environment. In order to analyse whether the decomposition patterns among species found were relatively independent of the environment, an additional decomposition experiment was carried out in Sheffield, England, which included a subset of 15 Argentine species representative of a wide range of decomposition rates. All samples were processed in the same way as in the first experiment. The day before the burial, the top 10 cm of soil was removed. The bed was filled with c. 1.5 m³ of mixed litter, leaf-mould at different stages of decay, and soil from the area. The samples were buried at 4–5 cm below-ground, and covered with mixed soil and litter in order to homogenise physical conditions and reduce the effect of the unpredictable environment close to the surface. The decomposition bed was covered with a nylon mesh as protection against animals. There were eight replicates for most species, and at least six were used when material was insufficient. Samples were randomly placed in the decomposition bed and buried for 15 weeks under the natural winter temperature and rainfall conditions in Sheffield. Climatic conditions during the burial were not significantly different from historical records (monthly mean temperature=7.7 °C and total precipitation=287 mm, Weston Park Weather Station, Sheffield, U.K.).

Relationships between leaf toughness and litter decomposition rate were also reported by Cornelissen et al. (1999), but these authors used a more simplified and incomplete functional types spectrum and did not explore the chemistry underlying leaf toughness in this context.

Chemical quality

As indices of the chemical quality of the species, measurements of litter total carbon (C) and nitrogen (N) were taken. Total C was estimated as 50% of ash-free biomass (Gallardo and Merino, 1993; McClaugherty et al., 1985; Shlelinger, 1977). Total N was determined by an Autoanalyser RFA 300-Alpken. Six replicates per species were used in all cases.

Physical quality

We measured leaf tensile strength as an index of leaf

physical quality. Measurements of leaf tensile strength (resistance to tearing) were taken following Hendry and Grime (1993) and expressed as force needed per unit of width of a leaf sample rather than per cross-sectional area, thus incorporating leaf thickness as a component of tensile strength. In the case of highly succulent and aphyllous species, a 1-cm² fragment of epidermis and mesophyll (photosynthetic tissue relatively young) was used for the measurements of tensile strength. Six replicates per species were used in all cases. Leaf tensile strength of living leaves was used to represent that of the litter, since the lignin-rich structures providing toughness remain intact during senescence. This was confirmed by the strong correlation found between toughness of litter and living leaves in a subset of 11 contrasting species from our database (Pearson Correlation Coefficient: $r = 0.98$, $p < 0.001$).

Data analysis

Since data distribution was not normal (Hollander and Wolfe, 1972), Spearman Rank correlations were employed to test the relationships between percentage mass loss and leaf (analogue) quality, both at the species level and at the level of plant functional types modified from Díaz and Cabido (1997). Kruskal-Wallis Test and Wilcoxon Ranks Test (Norusis, 1992) were used for comparisons among functional types.

Results

Decomposition rates and leaf quality

Across species, we found highly significant correlations between decomposition rate and the quality of both litter and living leaves (Table 1). Litter C-to-N ratio showed a stronger correlation with decomposition rates than C or N content. Tensile strength was strongly correlated with litter chemical quality and decomposition rate.

The results at the species level were mostly confirmed at the functional type level (Table 1). In few cases (e.g., leaf tensile strength vs. C-to-N ratio), strong and highly significant correlations at the species level corresponded to strong but non-significant or marginally significant correlations at the functional type level. This may be due to the very low number of species within some functional types (Appendix 1). Overall, litter C-to-N and leaf tensile strength showed the strongest association with decomposition rate.

There were significant differences among functional types in all the characters measured (Figure 1). Herbaceous dicots and woody deciduous plants presented the highest mass losses, the smallest C-to-N ratio and the softest leaves. Bromeliads, graminoids, and aphyllous plants showed the slowest decomposition rates, in association with the highest C-to-N ratios and the toughest leaves (or leaf analogues).

Comparison between different decomposition environments

When a subset of 15 species representing all the different functional types were subjected to a decomposition experiment in Britain, involving identical procedures but a different environment, the decomposition rates were consistently lower. However, they were highly correlated with those found in Argentina ($r = 0.98$, $p < 0.0005$; Spearman Rank Correlation Test, Figure 2).

Discussion

Leaf quality and decomposition

Our results supported the hypothesis that the large interspecific variation in leaf traits within the flora of central Argentina, are strongly linked with variations in litter decomposition rate. They also suggest that classifications into functional types proposed in previous work are meaningful for the analysis of decomposition patterns. Our findings give support to the idea that different plant functional types may have distinct effects on major ecosystem processes such as soil organic matter turnover and nutrient availability (e.g., Díaz and Cabido, 1997).

We also confirmed, over the broadest spectrum of life forms published so far, general models of resource allocation (Chapin, 1980; Coley, 1980; Grime, 1979; Herms and Mattson, 1992). According to these models, protective leaf traits against the biotic or abiotic environment (tough tissues and a high C-to-N ratio) are on one side of the fast/slow growth trade off (Chapin et al., 1993; Coley et al., 1985; Grime et al., 1996; Herms and Mattson, 1992; Wardle et al., 1998). In accordance with their predictions, we found that herbaceous dicots and woody deciduous plants (see references above) – with reported high relative growth rates, leaf turnover and palatability in other floras – produce tender, highly decomposable leaf litter with low C-to-N ratios. On the other hand, the

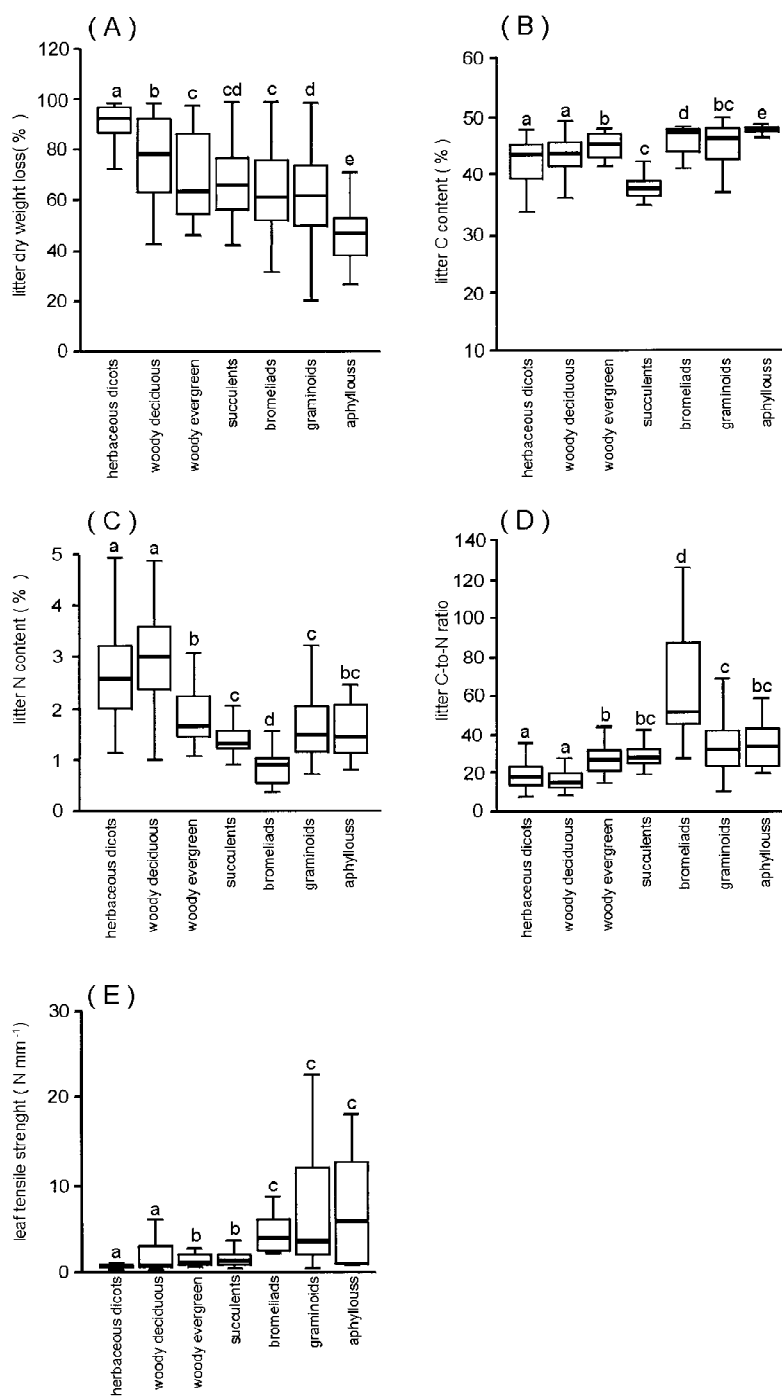


Figure 1. Decomposition rates (A), chemical quality (B, C, D), and physical quality (E) of different functional types of central Argentina. The box-plot shows the distribution of the values by the medians (central line), the quartiles 25 and 75% (box) and the ranges (whiskers). Different letters indicate significant differences between functional types (Kruskal-Wallis and Wilcoxon Rank test).

Table 1. Relationships between decomposition, litter quality, and leaf toughness of 52 Angiosperms of central Argentina, belonging to 7 functional types. Values are Spearman's Rank Correlation Coefficients, with significance level in brackets

	Litter dry weight loss (%)		Litter C content (%)		Litter N content (%)		Litter C:N	
	Species	Functional types	Species	Functional types	Species	Functional types	Species	Functional types
Litter C content (%)	-0.47 ($p < 0.001$)	-0.75 ($p = 0.052$)						
Litter N content (%)	0.48 ($p < 0.001$)	0.68 ($p = 0.094$)	-0.32 ($p = 0.023$)	-0.36 ($p = 0.432$)				
Litter C-to-N	-0.52 ($p < 0.001$)	-0.89 ($p = 0.007$)	0.45 ($p = 0.001$)	0.71 ($p = 0.071$)	-0.99 ($p < 0.001$)	-0.89 ($p = 0.007$)		
Leaf tensile strength (N mm ⁻¹)	-0.58 ($p < 0.001$)	-0.86 ($p = 0.014$)	0.47 ($p = 0.001$)	0.89 ($p = 0.007$)	-0.61 ($p < 0.001$)	-0.32 ($p = 0.482$)	0.64 ($p < 0.001$)	0.64 ($p = 0.119$)

photosynthetic structures of species chronically exposed to potential herbivory – like evergreen plants – or to high environmental stress – like aphyllous plants, most graminoids, bromeliads and succulents – were found to be tougher, and their litter less decomposable, with higher C-to-N ratios. The chemical and physical defences that protect these stress-tolerant functional types seem to persist in their litter, causing slower decomposition (Cornelissen et al., 1999; Grime et al., 1996).

Chemical quality

Nitrogen content, already proposed as a good predictor of leaf quality because of its stimulatory effect on the growth of decomposer communities (Palm and Rowland, 1997), showed a significant positive association with decomposition rates in our experiment. Carbon content was also significantly correlated with decomposition rates, and C-to-N ratio was the best predictor of litter decomposition rate. Similar results have been found (Mtambanengwe and Kirchman, 1995) for 15 litter types of tropical savanna woodland.

Several other leaf (analogue) quality parameters and indexes have been proposed to predict decomposition rate and N release, such as lignin-to-N ratio, or sequential extractions of C compounds (Cadisch and Giller, 1997; Cotrufo et al., 1994; Heal and Ineson, 1984; Melillo et al., 1982; Nicolai, 1988; Taylor et al., 1989). While those parameters sometimes show a higher degree of association with decomposition rate, they require a considerably greater input of time and financial resources. The highly significant association found between litter decomposition and C-to-N ratio in-

dicate that the latter may be a good option, particularly when high numbers of species are involved.

Physical quality

Although leaf toughness is known to enhance resistance to herbivores, pathogens, physical damage (Choong et al., 1992; Choong, 1996; Coley et al., 1985; Wright and Illius, 1995), and soil decomposers (Cornelissen and Thompson, 1997; Cornelissen et al., 1999; Gallardo and Merino, 1993), decomposition studies to a large extent have ignored the effects of physical properties of the leaves. The negative association found between leaf tensile strength and decomposition rate suggest that the structural defences of the living leaves, persisting in litter, could have been responsible for slow decomposition. Carbon-rich structural compounds, particularly lignin, strengthen leaves significantly (Choong et al., 1992; Coley et al., 1985; Wright and Illius, 1995) and litter with high lignin concentration or high C-to-N ratio, in turn, is known to be resistant to decomposition (Gallardo and Merino, 1993; Meentemeyer, 1978; Taylor et al., 1989; Wardle et al., 1998). This is also supported by the strong correlation we found between leaf tensile strength and litter C-to-N ratio at the species level. These associations indicate that leaf tensile strength – a trait easy and unexpensive to measure – can be useful in characterising leaf quality and in predicting litter decomposition at the ecosystem level. Different plant taxa and functional types show different designs to toughen their photosynthetic tissues. Still, our study has shown that in spite of the diversity in leaf design when a great diversity of plant taxa, functional types and habitats of origin are compared, leaf toughness

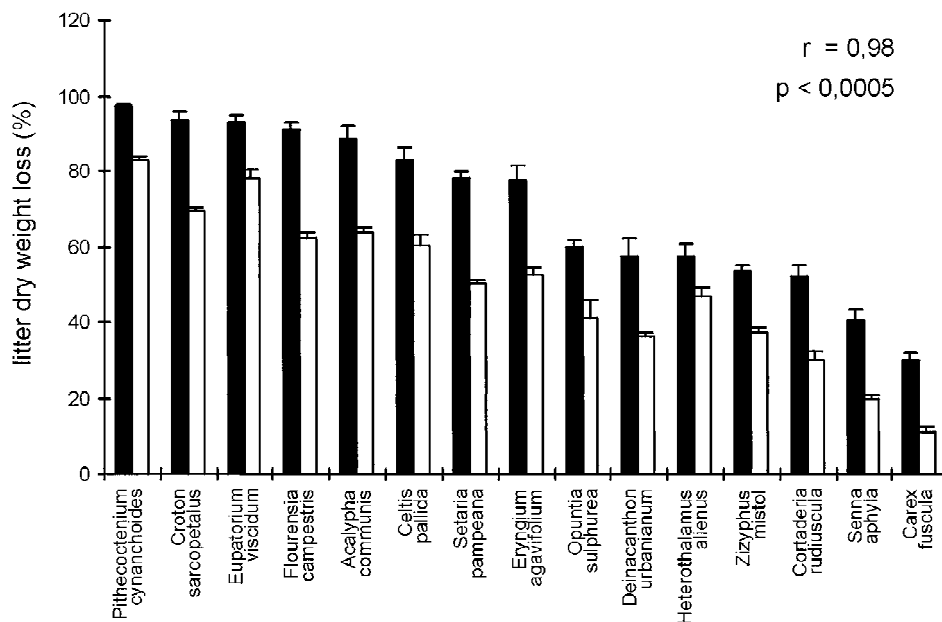


Figure 2. Decomposition rates for 15 Angiosperms from central Argentina, observed in Argentina (solid bars) and Britain (empty bars). Error bars indicate + SE.

remains a powerful predictor of litter decomposition rate.

Environment, leaf quality and decomposition

While biotic and abiotic factors in the litter environment are important determinants of decomposition, it is now widely established that litter quality is also an important driving force of soil processes (Berendse, 1994; Cadisch and Giller, 1997; Hobbie, 1996; Lavelle et al., 1993). Two main conclusions can be drawn from the comparison between decomposition of the same species in Argentina and in England. Firstly, decomposition rate was consistently faster during the hot and humid Austral summer than during the cool and humid temperate winter, illustrating once more the importance of abiotic factors as determinants of decomposition rate (Aerts and De Caluwe, 1997; Swift et al., 1979). Secondly, the strong correlation found between the decomposition rates of species incubated in these contrasting environments reinforces previous evidence that species rankings in terms of litter decomposition rates are robust to methodological and environmental factors (Cornelissen, 1996; Pérez-Harguindeguy et al., 1997). The strong associations found between decomposition rate and traits of living leaves and litter represent further evidence that characters of living leaves, and hence litter quality, are major

drivers of organic matter turnover, even in plants from arid ecosystems.

Overall, our results are in accordance with recent work showing that species and functional-type composition are major determinants of ecosystem processes (Grime, 1997; Hooper and Vitousek, 1997; Tilman et al., 1997; Wardle et al., 1997). This suggests that projected climate- and land-use-induced changes in vegetation (Burrows, 1990; Huntley et al., 1997) may have profound effects on ecosystem functions, such as nutrient cycling, primary productivity, and trophic transfer (Anderson, 1991; Chapin et al., 1997; Norby and Cotrufo, 1998; Vitousek et al., 1997).

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References

- Aerts R 1997 Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449.
- Aerts R and De Caluwe H 1997 Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. *Ecology* 78, 244–260.
- Ågren G I and Bosatta E 1996 Quality: a bridge between theory and experiment in soil organic matter studies. *Oikos* 76, 522–528.
- Anderson J M 1991 The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecol. Appl.* 1, 326–347.
- Berendse F 1994 Litter decomposability – a neglected component of plant fitness. *J. Ecol.* 82, 187–190.
- Burrows C J 1990 Processes of vegetation change. Unwin Hyman, London.
- Cabido M 1985 Las comunidades vegetales de la Pampa de Achala, Sierras de Córdoba, Argentina. *Documents Phytosociologiques* 9, 431–443.
- Cabido M, Acosta A and Díaz S 1989 Estudios fitosociológicos en pastizales de las Sierras de Córdoba, Argentina. *Las comunidades de la Pampa de San Luis. Phytocoenologia* 17, 569–592.
- Cabido M, Acosta A and Díaz S 1990 The vascular flora and vegetation of granitic outcrops in the upper Córdoba mountains (Argentina). *Phytocoenologia* 19, 267–281.
- Cabido M, Manzur A, Carranza M L and González C 1993 La vegetación y el medio físico del Chaco Árido en la Provincia de Córdoba, Argentina Central. *Phytocoenologia* 24, 423–460.
- Cadisch G and Giller K E 1997 *Driven by Nature: Plant Litter Quality and Decomposition*. CAB International-University Press, Cambridge.
- Capitanelli R G 1979 Bosquejo geomorfológico de la Provincia de Córdoba. *Revista del IGM* 5, 66–70.
- Cepeda-Pizarro J G and Whitford W G 1989 Decomposition patterns of surface leaf litter of six species along a Chihuahuan Desert watershed. *Am. Midd. Nat.* 123, 319–330.
- Chapin F S III 1980 The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 2, 233–260.
- Chapin F S III, Autumn K and Pugnaire F 1993. Evolution of suites of traits in response to environmental stress. *Am. Nat.* 142 (Suppl.), 78–92.
- 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.
- Choong M F 1996 What makes a leaf tough and how this affects the pattern of *Castanopsis fissa* leaf consumption by caterpillars. *Func. Ecol.* 10, 668–674.
- Choong M F, Lucas P W, Ong J S Y, Pereira B, Tan H T W and Turner I M 1992 Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytol.* 121, 597–610.
- Coley P D 1980 Effects of leaf age and plant life history patterns on herbivory. *Nature* 283, 545–546.
- Coley P D, Bryant J P and Chapin F S III 1985 Resource availability and plant antiherbivore defence. *Science* 230, 895–899.
- 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 and Thompson K 1997 Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytol.* 135, 109–114.
- 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.
- Cotrufo M F, Ineson P and Rowland A P 1994 Decomposition of tree leaf litter grown under elevated CO₂: Effect on litter quality. *Plant Soil* 163, 121–130.
- Côteaux M M, Bottner P and Berg B 1995 Litter decomposition, climate and litter quality. *Trends Ecol. Evol.* 10, 63–66.
- Díaz S and Cabido M 1997 Plant functional types and ecosystem function in response to global change: a multiscale approach. *J. Veg. Sci.* 8, 463–474.
- Gallardo A and Merino J 1993 Leaf decomposition in two Mediterranean ecosystems of Southwest Spain – influence of substrate quality. *Ecology* 74, 152–161.
- Grime J P 1997 Biodiversity and ecosystem function: the debate deepens. *Science* 277, 1260–1261.
- Grime J P 1979 *Plant Strategies and Vegetation Processes*. J Wiley and Sons, Chichester.
- 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.
- Heal O W and Ineson P 1984 Carbon and energy flow in terrestrial ecosystems: relevance to microflora. *In Current Perspectives in Microbial Ecology*. Eds M J Klug and C A Reddy. pp 394–404. Amer. Soc. Microbiol., Washington.
- Hendry G A F and Grime J P 1993 *Methods in comparative plant ecology: a laboratory manual*. Chapman and Hall, London.
- Hermis D A and Mattson W J 1992 The dilemma of plants: to grow or defend. *Quart. Rev. Biol.* 67, 283–335.
- Hobbie S E 1992 Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* 7, 336–339.
- Hobbie S E 1996 Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* 66, 503–522.
- Hollander M and Wolfe D A 1972 *Non-parametric Statistical Methods*. John Wiley and Sons, New York.
- Hooper D U and Vitousek P M 1997 The effects of plant composition and diversity on ecosystem processes. *Science* 277, 1302–1305.
- Howard P J A and Howard D M 1974 Microbial decomposition of tree and shrub leaf litter. 1. Weight loss and chemical composition of decomposing litter. *Oikos* 25, 341–352.
- Huntley B, Cramer W, Morgan A V, Prentice H C and Allen J R M 1997 *Past and Future Rapid Environmental Changes: the Spatial and Evolutionary Responses of Terrestrial Biota*. NATO ASI Series 1. Springer, Berlin.
- Iritani W M and Arnold C Y 1960 Nitrogen release of vegetable crop residues during incubation as related to their chemical composition. *Soil Science* 89, 74–82.
- Lavelle P, Blanchart E, Martin A, Martin S, Spain A V, Toutain F, Barois I and Schaefer R 1993 A hierarchical model for decomposition in terrestrial ecosystems: applications to soils of the humid tropics. *Biotropica* 25, 130–150.

- 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 over litter decomposition rates. *Ecology* 59, 465–472.
- 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.
- Mtambanengwe F and Kirchmann H 1995 Litter from a tropical savanna woodland (MIOMBO): chemical composition and C and N mineralization. *Soil Biol. Biochem.* 27, 1639–1651.
- Murphy K L, Klopatek J M and Klopatek C C 1998 The effect of litter quality and climate on decomposition along an elevational gradient. *Ecol. Appl.* 8, 1061–1071.
- Nicolai V 1988 Phenolic and mineral content of leaves influences decomposition in European forest ecosystems. *Oecologia* 75, 575–579.
- Norby R J and Cotrufo M F 1998 A question of litter quality. *Nature* 396, 17–18.
- Norusis M J 1992 SPSS for Windows base system user's guide, Release 5.0. SPSS Inc., Chicago.
- Palm C A and Rowland A P 1997 A minimum dataset for characterization of plant quality for decomposition. *In* Driven by Nature: Plant Litter Quality and Decomposition. Eds G Cadisch and K E Giller. pp 379–392. CAB International-University Press, Cambridge.
- Pérez-Harguindeguy N, Díaz S, Cornelissen J H C and Cabido M 1997 Comparación experimental de la tasa de descomposición foliar potencial de especies vegetales del centro-oeste de Argentina. *Ecología Austral* 7, 87–94.
- Seastedt T R, Crossley D A Jr, Meentemeyer V and Waide J B 1983 A two-year study of leaf litter decomposition as related to microclimatic factors and microarthropods abundance in the southern Appalachians. *Holarctic Ecology* 6, 11–16.
- Schaefer D, Steinberger Y and Whitford W G 1985 The failure of nitrogen and lignin decomposition in a North American Desert ecosystem. *Oecologia* 65, 383–386.
- Shlelinger W H 1977. Carbon balance in terrestrial detritus. *Ann. 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.
- Taylor B R, Parkinson D, Parsons W J F 1989 Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Tilman D, Knops J, Wedin J D, Reich P B, Ritchie M and Siemann E 1997 The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302.
- van der Putten W H 1997 Plant-soil feedback as a selective force. *Trends Ecol. Evol.* 12, 169–170.
- Vitousek P M, Mooney H A, Lubchenko J and Melillo J M 1997 Human domination of Earth's ecosystem. *Science* 277, 494–499.
- Wardle D A, Bonner K I and Nicholson K S 1997 Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* 79, 247–258.
- Wardle D A, Barker G M, Bonner K I and Nicholson K S 1998 Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *J. Ecol.* 86, 405–420.
- Wright W and Illius A W 1995 A comparative study of the fracture properties of five grasses. *Func. Ecol.* 9, 269–278.

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Appendix 1. List of the dominant species, families and plant functional types (modified from Díaz and Cabido, 1997) from the flora of central Argentina, included in the decomposition screening. PFTs are FT1=herbaceous dicots, FT2=woody and semiwoody deciduous, FT3=woody and semiwoody evergreen, FT4=leaf and stem succulents, FT5=bromeliads, FT6=graminoids, sedges and other narrow leafed monocots, FT7=aphyllous shrubs

Species	Family	Plant Functional Type (PFT)
<i>Acacia aroma</i> GILL.	Mimosaceae	FT2
<i>Acacia caven</i> (MOL.) MOL.	Mimosaceae	FT2
<i>Acalypha communis</i> var. <i>guaranitica</i> CHOD. et. HASSL.	Euphorbiaceae	FT2
<i>Alchemilla pinnata</i> RUIZ et. PAVON	Rosaceae	FT1
<i>Allenrolfea patagonica</i> (MOQ.) KUNTZE	Chenopodiaceae	FT4
<i>Alternanthera pungens</i> H. B. K.	Amaranthaceae	FT1
<i>Aristida achalensis</i> MEZ	Poaceae	FT6
<i>Aspidosperma quebracho-blanco</i> SCHLECHT.	Apocynaceae	FT3
<i>Baccharis articulata</i> (LAM.) PERSOON	Asteraceae	FT7
<i>Bouteloua aristidoides</i> (H.B.K.) GRISEB.	Poaceae	FT6
<i>Buddleja stachyoides</i> CHAM. et. SCHLECHT.	Buddlejaceae	FT2
<i>Capparis atamisquea</i> O. K.	Capparaceae	FT3
<i>Carduus thoermeri</i> WEINMANN	Asteraceae	FT1
<i>Carex fuscula</i> DUM.-D'URV. Var. <i>distenta</i> (KUNZE) KÜKEN.	Cyperaceae	FT6
<i>Celtis pallida</i> TORREY	Ulmaceae	FT2
<i>Celtis tala</i> PLANCHON	Ulmaceae	FT2
<i>Cortaderia rudiuscula</i> STAPF.	Poaceae	FT6
<i>Croton sarcopetalus</i> MUELL. ARG.	Euphorbiaceae	FT2
<i>Deinacanthon urbanianum</i> (MEZ) MEZ	Bromeliaceae	FT5
<i>Eryngium agavifolium</i> GRISEB.	Apiaceae	FT1
<i>Eupatorium viscidum</i> HOOKER et. ARNOTT	Asteraceae	FT2
<i>Festuca tucumanica</i> E. B. ALEXEEV	Poaceae	FT6
<i>Flourensia campestris</i> GRISEB.	Asteraceae	FT2
<i>Gentianella parviflora</i> (GRISEB.) T. N. HO	Gentianaceae	FT1
<i>Gomphrena pulchella</i> MARTIUS	Amaranthaceae	FT1
<i>Heterothalamus alienus</i> (SPRENG.) O.K.	Asteraceae	FT3
<i>Juncus uruguensis</i> GRISEB.	Juncaceae	FT6
<i>Larrea divaricata</i> CAVANILLES	Zygophyllaceae	FT3
<i>Lithraea ternifolia</i> (GILL.) BARKLEY	Lithraceae	FT3
<i>Maytenus vitis idae</i> GRISEB.	Celastraceae	FT4
<i>Mimozyanthus carinatus</i> (GRISEB.) BURKART	Mimosaceae	FT2
<i>Monanthochloë litoralis</i> ENGELM.	Poaceae	FT6
<i>Muhlenbergia peruviana</i> (BEAUV.) STEUDEL	Poaceae	FT6
<i>Neobouteloua lophostachya</i> (GRISEB.) GOULD	Poaceae	FT6
<i>Nothoscordum inodorum</i> (AIT.) NICHOLSON	Liliaceae	FT6
<i>Opuntia sulphurea</i> GILLIES	Cactaceae	FT4
<i>Pappophorum caespitosum</i> FRIES	Poaceae	FT6
<i>Paspalum quadrifarium</i> LAM.	Poaceae	FT6
<i>Pithecoctenium cynanchoides</i> DC.	Bignoniaceae	FT1
<i>Poa stuckertii</i> (HACK.) PARODI	Poaceae	FT6
<i>Polylepis australis</i> BITT.	Rosaceae	FT2
<i>Prosopis flexuosa</i> DC.	Mimosaceae	FT2
<i>Schinopsis haenkeana</i> ENGL.	Anacardiaceae	FT2
<i>Schizachyrium microstachyum</i> (DESV.) ROSEN, ARRIL. et. IZAG.	Poaceae	FT6
<i>Senna aphylla</i> (CAVANILLES) IRWIN et. BARNEBY	Caesalpiniaceae	FT7
<i>Setaria pampeana</i> PARODI	Poaceae	FT6
<i>Sorghum halepense</i> (L.) PERSOON	Poaceae	FT6
<i>Tephrocactus glomeratus</i> (HAW.) BACK.	Cactaceae	FT4
<i>Tillandsia duratii</i> VISIANI	Bromeliaceae	FT5
<i>Tillandsia capillaris</i> RUIZ et. PAVON	Bromeliaceae	FT5
<i>Trichloris crinita</i> (LAG.) PARODI	Poaceae	FT6
<i>Zizyphus mistol</i> GRISEB.	Rhamnaceae	FT2