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 (Côuteaux 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 (Côuteaux 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 m^3 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 intented 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 m^3 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-cm^2 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). Kruskall-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
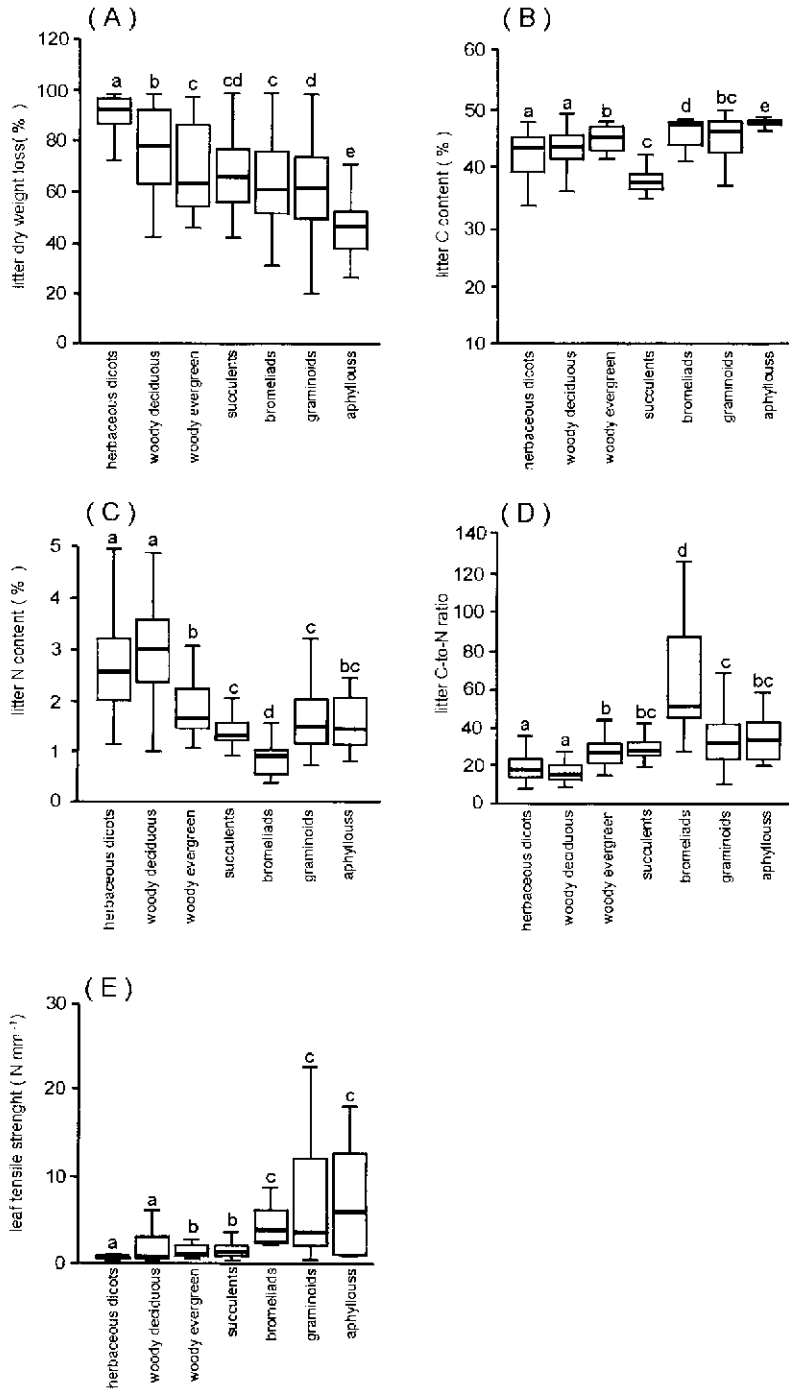
Figure 1. Decomposition rates (A), chemical quality (B, C, D), and physical quality (E) of different functional types of central Argentina. The box-plot shows the distribution of the values by the medians (central line), the quartiles 25 and 75% (box) and the ranges (whiskers). Different letters indicate 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 indicate 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 defenses 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
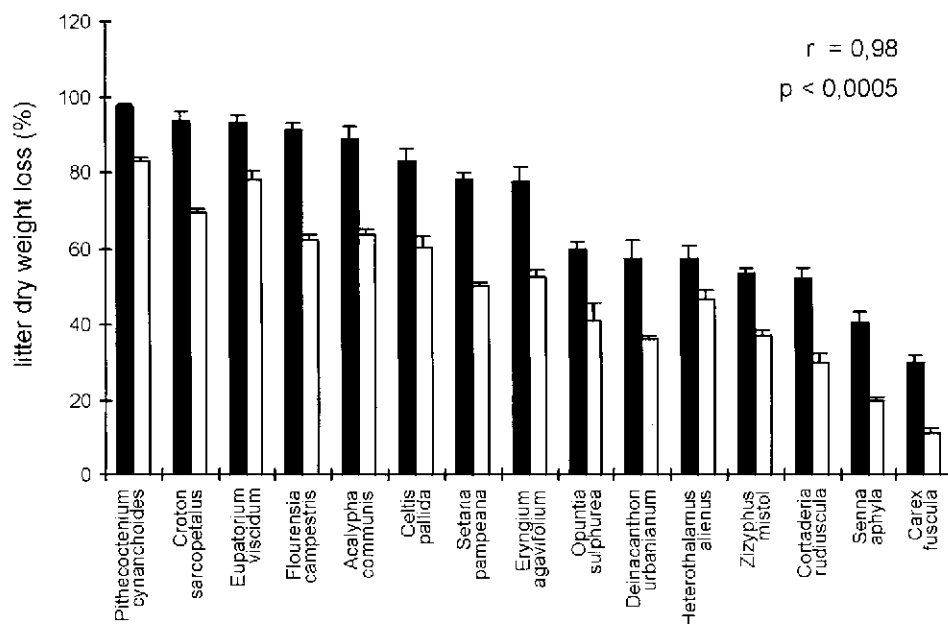
Figure 2. Decomposition rates for 15 Angiosperms from central Argentina, observed in Argentina (solid bars) and Britain (empty bars). Error bars indicate + SE.

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).

Acknowledgements

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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 steam succulents, FT5=bromeliads, FT6=graminoids, sedges and other narrow leafed monocots, FT7=aphyllous shrubs

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