Plant Soil
DOI 10.1007/s11104-016-2864-7

REGULAR ARTICLE

Combined effects of litter features, UV radiation, and soil water on litter decomposition in denuded areas of the arid Patagonian Monte

Tomás Bosco · Mónica Beatriz Bertiller · Analía Lorena Carrera

Received: 26 August 2015 / Accepted: 15 March 2016
© Springer International Publishing Switzerland 2016

Abstract
Aims We evaluated the combined effects of litter type, UV radiation, and soil water on litter decomposition processes in denuded areas of the arid Patagonian Monte.
Methods We conducted a manipulative experiment with litterbags with litter dominated by evergreen shrubs (ES), and litter dominated by perennial grasses and evergreen shrubs (PG) placed on undisturbed upper soil blocks from denuded areas. We subjected soil blocks with litterbags to near ambient and attenuated UV radiation levels, and low and high soil water levels. We evaluated litter mass loss and changes in N, soluble phenolic and lignin contents during 420 days.
Results PG litter decomposed faster than ES litter, and UV radiation and soil water enhanced decomposition of both litter types. PG litter immobilized N while ES litter released N. During decomposition, soluble phenolic content decreased while lignin content did not vary in both litter types.
Conclusions Our results highlighted that abiotic and biotic controls differed between mass loss and N release/immobilization. We found additive effects of the studied factors on mass loss while litter chemistry controlled microbial N release or immobilization from decaying litter. Further studies should explore the effects of these factors on species or functional groups shifts in microorganism communities.

Keywords C/N ratio · Litter chemistry · Photo-degradation · N · Lignin · Soluble phenolics

Responsible Editor: Per Ambus.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-016-2864-7) contains supplementary material, which is available to authorized users.

T. Bosco (✉) · M. B. Bertiller · A. L. Carrera
Instituto Patagónico para el Estudio de los Ecosistemas Continentales (IPEEC), CENPAT-CONICET, Boulevard Brown 2915, 9120 Puerto Madryn, Chubut, Argentina
e-mail: bosco@cenpat-conicet.gob.ar

M. B. Bertiller
e-mail: monika@cenpat-conicet.gob.ar

A. L. Carrera
e-mail: unanalia@cenpat-conicet.gob.ar

M. B. Bertiller · A. L. Carrera
Facultad de Ciencias Naturales – UNPSJB, Boulevard Brown 3000, 9120 Puerto Madryn, Chubut, Argentina

Introduction

Litter (quantity and chemistry), climate, soil properties, and microbial communities exert a strong control on nutrient cycling in most terrestrial ecosystems (Meentemeyer 1978; Aerts 1997; Carrera et al. 2005; Arriaga and Maya 2007). The litter accumulated on the soil acts as an input-output system for nutrient dynamics. Nutrients mineralized during decomposition processes may be immobilized in the microbial biomass associated with litter or released to the soil (Gartner and Cardon 2004; Arriaga and Maya 2007). Models based on litter chemistry (e.g. N concentration, C:N or

Published online: 24 March 2016

lignin:N) and climatic variables (e.g. precipitation and temperature) adequately describe litter decomposition and N mineralization-immobilization dynamics in most mesic ecosystems (Meentmeyer 1978; Brandt et al. 2007; Parton et al. 2007; Adair et al. 2008). However, these models usually underestimate litter decomposition rates and N release in arid and semiarid ecosystems exposed to high doses of ultraviolet (UV) radiation (Meentmeyer 1978; Whitford et al. 1981; Parton et al. 2007; Adair et al. 2008; Gallo et al. 2009; Brandt et al. 2010).

Mesic ecosystems are characterized by a high proportion of the soil surface covered by plant canopies (Fiala et al. 2006), large accumulation of litter on the soil surface, and high soil water availability promoting microbial decomposition processes underneath plant canopies (Couteaux et al. 1995; Aerts 1997; Gholz et al. 2000; Collins et al. 2008; Zhang et al. 2008). On the other hand, arid and semiarid ecosystems are characterized by a low and patchy plant cover and erratic water pulses (Ludwig and Tongway 1996). Patchy vegetation induces spatial heterogeneity in soil resources (fertility islands) and spatial microclimatic variation (Whitford 2002). In general, the areas in the vicinity or beneath plant patches have higher input and retention of organic matter and nutrients, lower exposure to UV radiation, and lower temperature and evaporative demand than the inter-patch denuded areas (i.e. areas of bare soil or with scattered vegetation) (Bertiller et al. 2002; Callaway 2007; Prieto et al. 2011). Also microorganism abundance is considerably higher under plant canopies than in denuded areas and the activity of their populations is positively associated with soil water availability (Austin et al. 2004; Arriaga and Maya 2007; Prieto et al. 2011). Moreover, part of the litter is exposed to solar radiation promoting litter decomposition by photo-degradation both underneath open plant canopies and in denuded areas (Rozema et al. 1997; Pancotto et al. 2003; Austin and Vivanco 2006; Gallo et al. 2006, 2009; Day et al. 2007; Brandt et al. 2007, 2010; Adair et al. 2008; Vanderbilt et al. 2008; Smith et al. 2010). In addition, Austin and Vivanco (2006) indicated that photo-degradation may dominate over microbial decay in dry environments with high radiation levels. Litter decomposition via photo-degradation was mainly attributed to the degradation of compounds absorbing in the UV radiation range (280–400 nm) such as phenolic compounds (including lignin), cellulose and hemicellulose (Moorhead and Reynolds 1989; Rozema et al. 1997; Brandt et al. 2007). Some studies suggested that lignin is the primary carbon fraction that is photodegraded, so litter with high content of lignin could be more susceptible to photo-degradation than that with low lignin content (Moorhead and Reynolds 1989; Rozema et al. 1997; Day et al. 2007; Parton et al. 2007; Gallo et al. 2009; Austin and Ballare 2010). However, these studies were not unequivocal in finding that lignin is the primary fraction of plant litter degraded by photo-degradation in arid and semiarid ecosystems (Lin and King 2014; Baker and Allison 2015), and suggested that other structural and non-structural C compounds of the lignocellulose matrix (i.e. cellulose and hemicellulose, other phenolics) may be firstly photo-degraded (Gehrke et al. 1995; Rozema et al. 1997). In addition, exposure to solar radiation can also potentially affect litter decomposition by altering the microbial community composition and by selecting microbial populations tolerating high doses of UV radiation (Duguay and Klironomos 2000; Moody et al. 2001; Pancotto et al. 2003).

Disturbances such as grazing, fire or mechanical removal of vegetation in arid and semiarid ecosystems may lead to a significant increase in the size of denuded areas, to structural changes in plant patches (e.g. reduced size and number of plant patches; diminished plant patch cover), and to the lost and replacement of plant species (Ares et al. 1990; Milchunas and Lauenroth 1993; Tongway and Ludwig 1996; Bisigato and Bertiller 1997; Rostagno et al. 2006; Carrera et al. 2009; Boyd and Svejcar 2011). Particularly, long-term grazing disturbance leads directly or indirectly to a reduction in the percentage of plant cover, shifts in plant species composition, and a decrease in the relative abundance of perennial grasses increasing the dominance of shrubs with high concentration of secondary compounds (Schlesinger et al. 1996; Bardgett et al. 1998; Carrera et al. 2008; Bertiller and Ares 2011). Thus, litter from areas disturbed by grazing may have low concentration of labile C due to the high contents of lignin and soluble phenols and may be more recalcitrant to microbial degradation than that of undisturbed areas. Additionally denuded areas induced by grazing are characterized by lower levels of soil organic matter and nutrients, harsher micro-environmental conditions (higher evaporative demand, water losses, and exposure to UV radiation) and higher incidence of wind and water erosion (by precipitation and run-off) than vegetated patches (Ares et al. 1990; Tongway and Ludwig 1996). Under these circumstances, litter is more exposed to photo-degradation and microbial activity may be limited by reduced soil moisture and increased exposure to UV radiation (Pancotto et al. 2003; Marcos et al. 2015). Additionally, grazing disturbance may affect soil bacteria communities, soil enzymes, and the rates of microbial activity thus affecting organic matter decomposition, and C and N dynamics in soil (Austin et al. 2004; Olivera et al. 2014; Marcos et al. 2015).

Several studies described the effects of individual factors such as UV radiation, water availability and litter chemistry on litter decomposition processes in arid ecosystems but there is scarce knowledge about the effect of UV radiation exposure combined with soil water levels on decomposition of litter mixtures with different proportions of secondary compounds. This knowledge is relevant to assess the effects of changes induced by long term grazing disturbance on soil C and N balances in arid ecosystems (Gallo et al. 2006; Vargas et al. 2006; Brandt et al. 2007; Carrera et al. 2008; Carrera and Bertiller 2013; Larreguy et al. 2014). This study explores the combined effects of UV radiation, soil water content, and litter mixtures with different proportions of shrubby components on litter decomposition. This issue has been scarcely explored since most previous studies were concentrated on litter decomposition of single species (Pancotto et al. 2003; Gallo et al. 2006, 2009; Arriaga and Maya 2007; Brandt et al. 2010). We hypothesized that in litter mixtures with low concentration of phenolic compounds, soil water controlling microbial activity (biotic control) has larger effect than UV radiation on mass loss and N release during decomposition processes; while in litter mixtures with high concentration of phenolic compounds, UV radiation (abiotic control) is a main factor controlling decomposition processes (Fig. 1).

Materials and methods

Study area

The study area is located in the southern portion of the Monte Phytogeographical Province (Patagonian Monte), Argentina. The average annual temperature is 13.4 °C, the mean annual precipitation is 235.9 mm and the average annual speed of wind (prevailing from west-southwest) is 4.6 m sec^{-1} (Centro Nacional Patagónico 2009). Soils are a complex of Typic Haplocalcids and Typic Petrocalcids (del Valle 1998; Soil Survey Staff 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa spp.* (León et al. 1998). Plant canopy covers less than 40 % of the soil and presents a random patchy structure formed by shrubs and/or perennial grasses bunches within a matrix of bare soil (Bisigato and Bertiller 1997). Within the study area we selected six representative sites of at least 3 ha each (minimal area *sensu* Mueller-Dombois and Ellenberg 1974) with large denuded areas (> 2 m without vegetation cover or with scattered herbaceous plants) induced by grazing or fire disturbances (detailed site location in Bosco et al. 2015).

Sampling and manipulative experiment

We selected 12 plant patches dominated by evergreen shrubs and 12 plant patches dominated by both perennial grasses and evergreen shrubs in each site. Patches were selected by walking 10 steps at random directions from a randomly selected point. We collected the litter accumulated on the soil surface and up to 2 cm underneath each patch canopy within a plot (30 × 40 cm) during the period June/August 2012. The litter collected was cleaned of attached soil particles with a brush, pooled into one sample per patch type, homogenized by mixing, and dried at 45 °C for 48 h. The litter from evergreen shrub patches (ES) mostly consisted of a mixture of leaves and fine woody stems from evergreen shrub species, predominantly *Larrea divaricata*. The litter from perennial grass and evergreen shrub patches (PG) consisted of a mixture dominated by leaves of perennial grasses (*Nassella tenuis*) accompanied by leaves of different species of evergreen shrubs. We also selected 8 denuded areas (> 2 m in diameter) per site following the same procedure used for plant patches. From each denuded area, we extracted one block of the upper soil (30 cm × 40 cm × 14 cm deep) without altering its structure, burying a sharp metal frame with a hammer, digging around it, introducing a metal plate underneath the soil block and pulling it out in one piece. Then, we collected the sub-superficial soil (30 cm × 40 cm × 14–28 cm deep) corresponding to each block with a shovel. Blocks of the surface soil and the sampled sub-superficial soil from each denuded area were placed in individual waterproof wooden boxes (30 cm × 40 cm × 28 cm deep) reconstructing the soil stratigraphy (microcosm, Fig. 2a). After this, the surface litter was carefully removed from each microcosm.

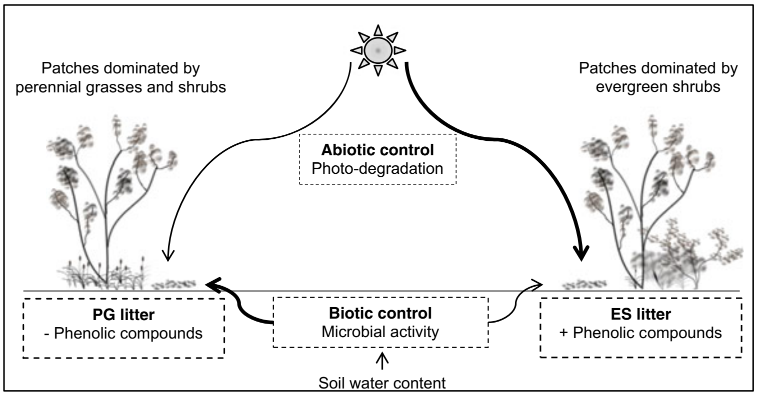

Fig. 1 Conceptual framework for decomposition of two contrasting litter mixtures. The relative incidence of biotic and abiotic controls on litter decomposition and N release from litter depends on litter chemistry. Photo-degradation would prevail in decaying processes of litter mixtures with high concentration of phenolic compounds (litter mixtures dominated by evergreen shrubs (ES)), while microbial activity, constrained by soil water content, would be a main control on decaying processes of litter with low concentration of phenolic compounds (litter mixtures with perennial grasses and shrubs (PG)). Thicker arrows indicate the prevalent control (biotic or abiotic) on litter decomposition and N release from litter

From January 2013 to March 2014 a manipulative experiment was conducted in the experimental area of the Centro Nacional Patagónico (CENPAT) (42° 47′ 10.4″S, 65° 00′28.2″W, 5 m a.s.l.) with disturbed natural vegetation characteristic of the Patagonian Monte. This area is characterized by large denuded areas generated by anthropic disturbance through the patchy removal of vegetation. In this experimental area, we selected six large (> 2 m in diameter) denuded areas (without vegetation), each of which received the 8 microcosms from a single collection site arranged in two sets of 4 microcosms. The surface of each microcosm was divided into 48 cells of 5 cm × 5 cm each. With these microcosms we performed a factorial experiment to evaluate the simultaneous effect of litter type (two levels), UV radiation (two levels) and soil water (two levels) on decomposition rates.

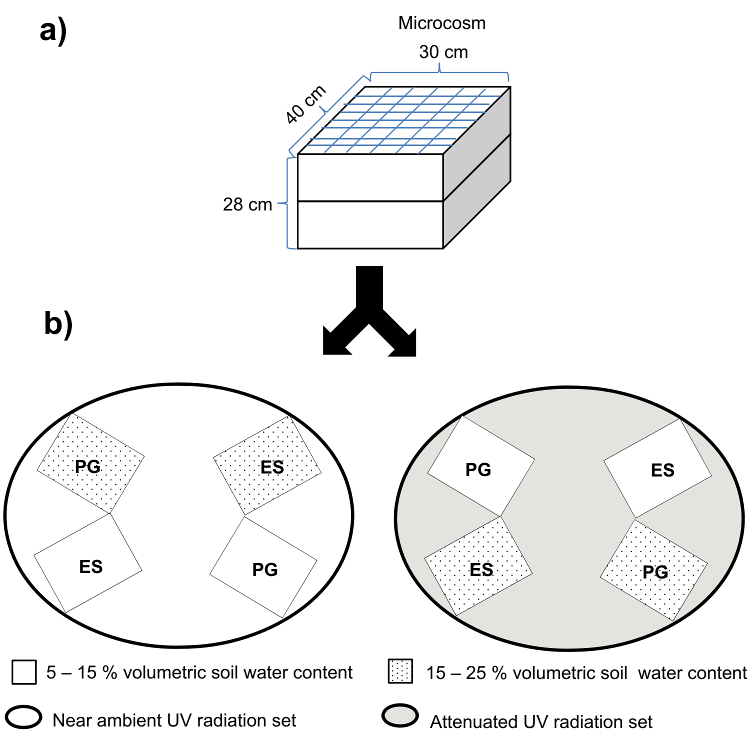

Fig. 2 **a** Scheme of a microcosm and **b** its arrangement of each set in the experimental site. PG: litter from perennial grass and evergreen shrub patches; and ES: litter from evergreen shrub patches

Litter, UV and water levels

We constructed 1104 litterbags (5 × 5 cm) with approximately 1 g of each litter type (552 with ES litter and 552 with PG litter), allowing a homogeneous incidence of the radiation on the litter confined in the litterbag. This amount of litter corresponds to mean values of litter mass accumulated on the soil in sites with low disturbance signs that are representative of the study area (Carrera and Bertiller 2010). The upper side of litterbags was constructed with a 2 mm nylon mesh that avoided litter losses by wind. This mesh size blocked approximately 7 %, 13 % and 10 % of the photosynthetically active radiation (PAR), UVB and UVA incident radiation, respectively. The bottom of the litterbag was constructed with a 0.3 mm nylon mesh preventing that small litter fragments passed through the mesh to the soil.

Each set of 4 microcosms was assigned to one litter type and we randomly placed 23 litterbags of the corresponding litter type at each microcosm. Each litterbag was fixed to the soil surface with 4 stainless metal pins (3 cm long). Finally, we added 1 g of unconfined litter of the corresponding litter type on the soil surface in the rest of the cells (25 empty cells, without litterbags) remaining as buffer zones.

We manipulated the UV radiation received by litterbags on microcosms using UV-blocking and UV-passing screens. Two microcosms per set were covered with a Mylar-D polyester filter (Dupont) blocking 55 % and 85 % of the incident UVA and UVB radiation (280–400 nm) respectively and 15 % of PAR (reduced UV radiation: UV-). The other two microcosms of each set were covered with an Aclar fluorocarbon plastic filter (Allied chemical) which transmitted approximately 85 % of the incident UVA, UVB and PAR (near ambient UV radiation: UV+). Both filter types were supported by a structure of PVC and wood with a slope of 1 % for preventing water accumulation after rainfall events and placed 40–45 cm above the soil surface of the microcosms (Mylar and Aclar, respectively). These filters did not allow rainwater to reach the soil surface of the microcosms. Spectral properties of both filters were monitored twice a month in cloudless days at the same hour (13:30 h) with a radiometer SKYE SpectroSense 2. Filters were continuously monitored and periodically cleaned or replaced to avoid changes in their spectral properties. Temperature under Aclar fluorocarbon plastic filter and Mylar filters was monitored with iButton Thermochron sensors model 1921G (Maxim Integrated Products Incorporated, Sunnyvale, CA, U.S.A.). We did not find significant differences in temperature between filters across the study period ($p > 0.05$).

One microcosm of each litter type and UV radiation level was subjected to a high (range 15 to 25 %) soil volumetric water content (W+) and the other microcosm was subjected to a low (range 5 to 15 %) soil volumetric water content (W-) (Fig. 2b). These levels of volumetric soil water content corresponded to the mean values of soil moisture assessed in the study area in fall-winter wet season) and spring-summer (dry season), respectively (Coronato and Bertiller, 1997). Water levels of soil microcosms were controlled every 2 or 4 days depending on the season with an IMKO TDR probe. The microcosm surface was homogeneously watered with tap water when needed using a manual sprinkler. The duration of the experiment was 420 days.

Mass loss and chemical analysis

To evaluate litter mass loss, we randomly collected one litterbag per treatment (combination of litter type, UV radiation level, and soil water level) and denuded area at 68, 133, 229, 321 and 420 days from the beginning of the experiment. After removal, litterbags were cleaned from visible soil particles, oven dried at 45 °C for 48 h, and weighed to assess the remaining mass. After that, an aliquot of the remaining mass of each litterbag was ashed at 550 °C to correct the mass remaining at each litterbag for residual attached soil particles. We expressed the remaining mass at each litterbag on an ash-free dry mass basis.

We assessed the chemical composition in three subsamples of each litter type (ES and PG) before the beginning of the experiment (Table 1) and in four randomly selected litterbags per combination of litter type, UV radiation level, and soil water level after 133, 229, 321 and 420 days from the beginning of the experiment. We measured the concentration of soluble phenolics by the Folin-Ciocalteu method using tannic acid as standard (Waterman and Mole 1994), lignin by the acid-detergent digestion technique (van Soest 1963), C concentration by dry digestion at 550 °C (Schlesinger and Hasey 1981), and total N by semi-micro Kjeldahl (Coombs et al. 1985). All chemical analyses were expressed per unit of free-ash dry mass.

Table 1 Mean ± 1 standard error (n = 3) of the initial concentration of C, N, soluble phenolics, lignin and C/N, soluble phenolics/N and lignin/N ratios in perennial grass and evergreen shrub dominated (PG) and evergreen shrub dominated litter types (ES)

Litter type	C (mg g^{-1})	N (mg g^{-1})	Soluble phenolics (mg g^{-1})	Lignin (mg g^{-1})	C/N	Soluble phenolics/N	Lignin/N
PG	445.70 ± 4.53 a	9.13 ± 0.21 b	5.13 ± 0.39 b	113.29 ± 14.43 b	48.91 ± 1.65 a	0.56 ± 0.06 a	12.49 ± 1.86 a
ES	380.63 ± 3.79 b	24.54 ± 0.60 a	11.79 ± 0.79 a	198.80 ± 11.48 a	15.53 ± 0.40 b	0.48 ± 0.04 a	8.11 ± 0.48 a

Different lowercase letters indicate significant differences between litter types

Statistical analyses

We used a paired t-test to compare initial chemistry (C, soluble phenolics, lignin, N, and C/N, lignin/N and soluble phenolics/N ratios) between litter types. To assess mass loss rates (k) of litter dry mass during the 420 days of the experiment at each microcosm we fitted a simple negative exponential model (Swift et al. 1979) as follows:

$$y = 100{*}e^{-(t{*}k)}$$

where y is the percent of litter dry mass remaining in litterbags at time t (month) and k is the mass loss rate. We performed a three-way ANOVA to test the differences in the dry mass loss rate (k) among treatments and contents of lignin, soluble phenolics and N for each collection date. In these models, we included litter type, UV radiation and soil water as fixed factors and tested all fixed factor interactions. Tukey's test was used for multiple comparisons among treatments. For evaluating relationships between the N content and the remaining ash-free dry mass in litterbags across the study period, we fitted linear and non-linear models. We also evaluated relationships between the relative N content (% of initial N) and the remaining ash-free dry mass by fitting linear and non-linear models constraining the function to the "y" value equal to 0 when litter mass is 0 and equal to 100 when litter mass is 100 % according to Parton et al. (2007). Fitted models were compared using the Akaike's information criterion (AIC), considering the best model that with the lowest AIC value. ANOVA assumptions were tested before analyses. Unless otherwise noted, the level of significance throughout this study was $p \leq 0.05$. All statistical analyses were performed with OriginLab Pro (OriginLab, Northampton, MA) and SPSS (Norusis 1997).

Results

Decomposition rate and mass loss

After 420 days of incubation, PG litter lost between 24 % and 34 % of initial mass and ES litter lost between 10 % and 33 % of the initial mass depending on the combined effects of soil water and UV radiation levels (Fig. 3a). We found significant effects of litter type, soil water content and UV radiation on the remaining dry mass. PG litter lost more mass than ES litter. Mass loss was higher at high soil water content (W+) than at low soil water content (W-), and under near ambient UV radiation (UV+) than that at reduced UV radiation (UV-) ($p < 0.05$, data not shown). There were no three-way or two-way interactions between litter type, soil water content and UV radiation levels affecting remaining litter mass.

Mass loss rate (k) for the 420 day period differed among treatments. All the exponential curves fitted to mass loss values were significant (p < 0.05) at each microcosm, with r^2 values ranging from 0.42 to 0.99 with an average value of 0.83. We found significant effects of litter type, soil water content and UV radiation on k-rates. PG litter showed higher mass loss rate than ES litter ($F_{1,47}$ = 14.53, p < 0.01). High soil water content (W+) was associated with the highest mass loss rates ($F_{1,47}$ = 6.39, p = 0.02), and k-rates were higher under UV+ than at UV- ($F_{1,47}$ = 5.92, p = 0.02). There were no three-way or two way interactions between litter type, soil water and UV radiation levels affecting k-rates (Fig. 3b).

N, lignin and soluble phenolic contents

There were no two or three-way significant effects of interactions among factors on lignin, soluble phenolics and N content fraction (% of initial) at any collection date. However, litter type, UV radiation and soil water content differentially affected these compound fractions

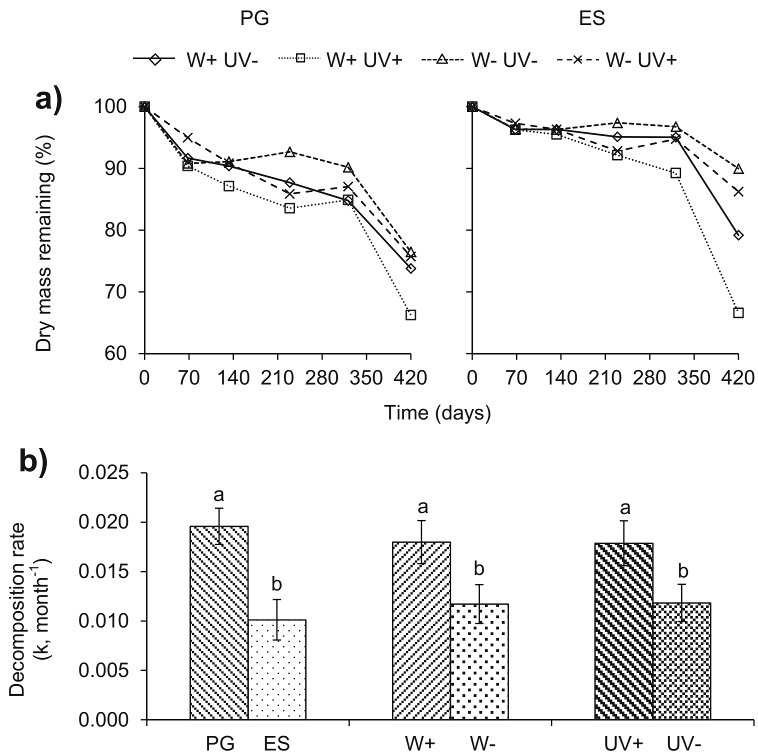

Fig. 3 **a** Mean values of the percentage of ash-free dry mass remaining in litterbags as a function of time (day) of litter from perennial grass and evergreen shrub patches (PG) and litter from evergreen shrub patches (ES) under the combination of UV radiation level (UV+: ambient UV radiation, and UV-: reduced UV radiation), and soil water content levels (W+: high soil water volumetric content, and W-: low soil water volumetric content) (SE bars were excluded from the graph). **b** Mean values ±1SE of decomposition rates (k, month^{-1}) by the factors litter type (PG and ES), UV radiation level (UV+ and UV-), and soil water levels (W+ and W-). Different letters indicate significant differences ($p < 0.05$) within factors

at each collection date. Lignin content was only affected by litter type after 420 days of incubation. At this date, the relative lignin content in PG litter (98 %) was higher than in ES litter (87 %). Neither soil water content nor UV radiation affected lignin contents at any collection date (Table 2). Soluble phenolics were affected by soil water content at all collection dates and by UV radiation after 229, 321 and 420 days of incubation. High soil water content (W+) promoted the loss of soluble phenolic content ranging from 40 % to 66 % approximately across the study period while low soil water content (W-) led to decreases in soluble phenolic content between 17 % and 50 % of the initial values. The relative soluble phenolic content decreased under ambient UV radiation (UV+) compared to reduced UV radiation (UV-) at three incubation dates (Table 2). In general, we found N immobilization (increased N content) in PG litter across the incubation period. In contrast, N content tended to decrease in ES litter across the study period. Overall, we found a significant effect of litter type at all incubation date and of soil water content at the first and the last dates with values of N content in litter higher at high (W+) than at low soil water content (W-). UV radiation did not affect litter N content at any date of the study period (Table 2).

The relationship between N content and litter mass remaining did not differ between UV radiation and soil water content levels but was different between litter types. A second grade polynomial model was the best fit for all treatments combinations (lowest AIC). PG litter immobilized N whilst ES litter released N over the entire incubation period independently of treatment combinations (Fig. 4). The same trends were found in relationships between the relative N content (% of initial) and mass remaining of both litter types (Supplementary material).

Discussion

Contrary to our hypothesis, our results indicated that mass loss and N release/immobilization were differentially affected by soil water and UV radiation. In general, mass loss was controlled by the additive effect of soil water, litter chemistry and UV radiation while litter chemistry was the single factor controlling microbial N release and immobilization processes from decaying litter. Litter mixtures containing perennial grasses decayed faster than that containing predominance of shrub components at all treatments.

Table 2 Results of the three-way ANOVA for the effects of litter type, soil water and UV radiation levels at any date collection on lignin, soluble phenolic and N contents in litter. Two and three-way interactions were not significant

	Days of incubation	Litter type		Soil water content		UV radiation level	
		PG	ES	W+	W-	UV+	UV-
Relative lignin content (% of initial)	133	97 ± 3	93 ± 3	93 ± 3	98 ± 3	93 ± 4	97 ± 2
	229	93 ± 3	94 ± 3	91 ± 3	95 ± 3	96 ± 3	91 ± 2
	321	106 ± 4	99 ± 4	100 ± 4	105 ± 5	105 ± 4	100 ± 4
	420	**98 ± 3**	**87 ± 4**	88 ± 4	97 ± 3	95 ± 4	91 ± 3
Relative soluble phenolic content (% of initial)	133	70 ± 6	73 ± 8	**60 ± 6**	**83 ± 8**	67 ± 8	76 ± 7
	229	68 ± 3	65 ± 6	**60 ± 3**	**73 ± 5**	**57 ± 3**	**77 ± 5**
	321	75 ± 3	67 ± 4	**63 ± 2**	**79 ± 4**	**67 ± 3**	**75 ± 4**
	420	44 ± 2	40 ± 3	**34 ± 2**	**50 ± 2**	**38 ± 3**	**46 ± 3**
Relative N content (% of initial)	133	**105 ± 4**	**91 ± 2**	**93 ± 4**	**103 ± 3**	98 ± 4	98 ± 3
	229	**117 ± 3**	**92 ± 4**	100 ± 4	108 ± 5	104 ± 4	104 ± 6
	321	**110 ± 4**	**86 ± 3**	97 ± 5	99 ± 4	100 ± 4	96 ± 5
	420	**102 ± 3**	**82 ± 4**	**87 ± 4**	**98 ± 4**	94 ± 5	91 ± 4

Bold values indicate significant effects ($p < 0.05$)

Faster decomposition rates in litter containing perennial grasses could be due to lower contents of secondary compounds than in the litter dominated by evergreen shrubs. This is in agreement with other studies reporting that labile C sources in litter may accelerate mass loss (Moorhead and Sinsabaugh 2006; Gallo et al. 2009; Carrera and Bertiller 2013). Secondary compounds such as soluble phenolics and lignin may reduce litter decomposition by either toxic effects on microorganisms or by retarding microbial breakdown of organic matter (Aerts and Chapin 2000; Kraus et al. 2003; Carrera and Bertiller 2013). In contrast to our hypothesis (Fig. 1), exposure to UV radiation promoted similar mass loss in both litter types. This could indicate that photo-

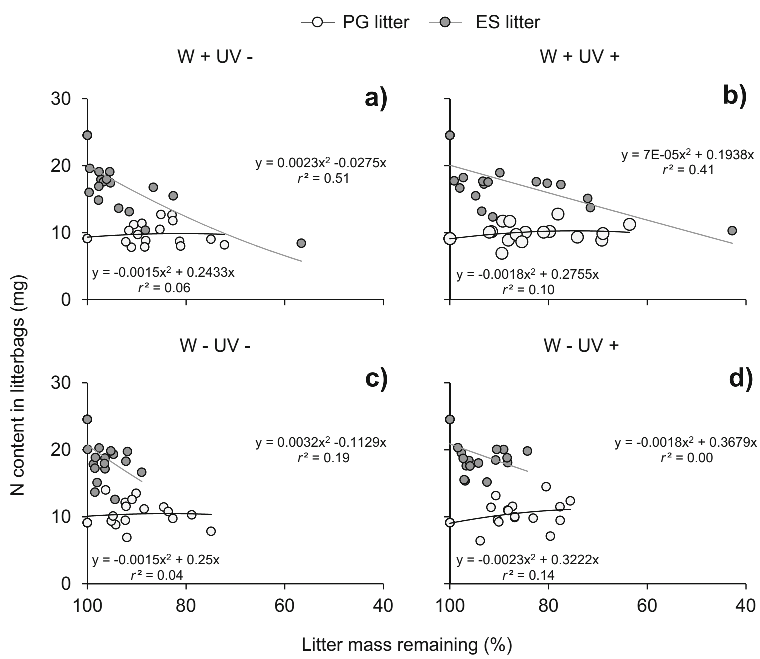

Fig. 4 Relationship between litter mass remaining (%) and N content in litterbags (mg) with litter from perennial grass and evergreen shrub patches (PG) and litter from evergreen shrub patches (ES) under the combination of **a** high soil water volumetric content (W+) and reduced UV radiation (UV-), **b** W+ and ambient UV radiation (UV+), **c** low soil water volumetric content (W-) and UV- and **d** W- and UV+

degradation was not directly related to litter chemistry (lignin or soluble phenolic concentration). Even more, after 321 days, lignin content tended to increase in PG litter. Similar results in other studies were attributed to a buildup of "lignin-like" microbial products such as partially humified compounds (Couteaux et al. 1995; Brandt et al. 2010; Lin and King 2014). Further, the exposure to UV radiation reduced soluble phenolic content in both litter types. This is in agreement with some studies reporting no effects of UV radiation on the lignin fraction in decomposing litter in arid and semiarid ecosystems (Brandt et al. 2007, 2009; Lin and King 2014; Baker and Allison 2015) and may indicate that photolysis could affect other structural and non-structural C compounds (i.e. cellulose and hemicellulose, other phenolics) (Gehrke et al. 1995; Rozema et al. 1997; Day et al. 2007; Brandt et al. 2007, 2010; King et al. 2012; Lin and King 2014). Finally, in contrast to our hypothesis (Fig. 1) high soil water content promoted mass loss to a similar extent in both litter types, indicating that water availability might be influencing decomposition rates of litter types through its effects on the activity of decomposers communities, probably having confounding effects with UV radiation (Berg 1986; Liu et al. 2006; Brandt et al. 2007). On the other hand, UV radiation might be a main control of decomposition when soil water availability is scarce (Brandt et al. 2007). Moreover, our results could also indicate that soluble phenolics may be rapidly lixiviated from litter (Chomel et al. 2014).

Inorganic nitrogen dynamics (i.e. release or immobilization) differed between both litter types. In this sense, differences in the C/N ratios between PG and ES litters (48.91 vs 15.53 in PG and ES, respectively) could indicate N and C constraints for decomposer-microbial activity in PG and ES litter, respectively. Decomposers tend to grow following relatively rigid stoichiometric requirements and C and N are typically processed together in order to achieve balanced growth conditions (Cleveland and Liptzin 2007; Manzoni et al. 2010). In our study, the main constraints could be the low initial labile C fraction in ES and the low initial N content in PG litter. On the other hand, solar UV radiation did not affect the relationship between mass loss and litter N dynamics in PG litter as it immobilized N in the early stages of mass loss, indicating that microbial activity was the main driver of decomposition. In contrast, ES litter N dynamics was decoupled from mass loss probably indicating that abiotic processes may prevail over microbial mineralization (Brandt et al. 2007, 2010; Parton et al. 2007). In general, net N mineralization occurs when the C/N ratio falls below the critical 20:1 ratio (Lambers et al. 2008). Accordingly, litter dominated by perennial grasses and evergreen shrubs (PG litter: C/N> 20) exhibited increases in N, while that dominated by evergreen shrubs (ES litter: C/N< 20) released N. This is particularly important in relation to soil fertility since N immobilized in the microbial biomass constitutes an important mechanism of N conservation in a labile form (Mazzarino et al. 1998; Wardle 2002; Parton et al. 2007; Carrera and Bertiller 2013).

We concluded that the three factors analyzed were important controls of decomposition processes in denuded soil areas of the Patagonia Monte. These factors differentially controlled mass loss and N dynamic processes, but did not interact with one other. Soil water content, UV radiation, and litter chemistry had additive effects on mass loss while litter chemistry controlled microbial N release and immobilization from decaying litters. Litter mixtures dominated by shrubs released N during decomposition indicating that this litter may exert an immediate effect on soil N availability. However, this litter type could have lower impact on soil fertility in the long term in comparison with litter mixtures dominated by perennial grasses since N released could be rapidly lost by leaching in denuded areas. Alternatively, litter mixtures with perennial grass components could have a stronger effect on soil fertility than that dominated by evergreen shrubs since N retained in the microbial biomass constitutes a labile form to conserve N avoiding eventual inorganic N leaching in denuded areas. Further studies should explore the direct or indirect effects of these factors on species or functional groups shifts in microorganism communities related to C and N cycling.

Acknowledgments We would like to thank MJ Mazzarino for her helpful comments and manuscript revision. This work was supported by the National Agency for Scientific, Technological Promotion (PICTs 1349, 1368) and the National Research Council of Argentina (PIPs 112-200801-01664 and 112-201301-00449-CONICET). T. Bosco fellowship is supported by CONICET. Samples processing and chemical analyses were performed in the Laboratorio de Ecología de Pastizales (LAEPA-IPEEC). Recognition is also given to Fundación Patagonia Natural who allowed access to the study area in Refugio de Vida Silvestre La Esperanza, and HM Carrera who allowed access to the study area in Estancia La Elvira. We also thank three anonymous reviewers for their helpful comments on an earlier version of this manuscript.

References

Adair EC, Parton WJ, Del Grosso SJ, Silver WI, Harmon ME, Hall SA, Burke IC, Hart SC (2008) Simple three-pool model accurately describes patterns of long term litter decomposition in diverse climates. Glob Change Biol 14:2636–2660

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

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Ares JO, Beeskow AM, Bertiller MB, Rostagno CM, Irisarri M, Anchorena J, Defossé G, Merino C (1990) Structural and dynamic characteristics of overgrazed lands of Northern Patagonia, Argentina. In: Breymeyer A (ed) Managed grasslands. Elsevier Sci Amsterdam, The Netherlands, pp. 149–175

Arriaga L, Maya Y (2007) Spatial variability in decomposition rates in a desert shrub of Northwestern Mexico. Plant Ecol 189:213–225

Austin AT, Ballare CL (2010) Dual role of lignin in plant litter decomposition in terrestrial systems. Proc Natl Acad Scis USA 107:4618–4622

Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nat 442: 555–558

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta D, Schaeffer SM (2004) Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–235

Baker NR, Allison SD (2015) Ultraviolet photodegradation facilitates microbial litter decomposition in a Mediterranean climate. Ecol 96:1994–2003

Bardgett RD, Wardle DA, GW Y (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. Soil Biol Biochem 30(14):1867–1878

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

Bertiller MB, Ares JO (2011) Does sheep selectivity along grazing path negatively affects biological crusts and soil seed bank in arid shrublands? A case study in the Patagonian Monte, Argentina. J Environ Manag 92:2091–2096

Bertiller MB, Ares JO, Bisigato AJ (2002) Multiscale indicators of land degradation in the Patagonian Monte, Argentina. Environ Manag 5:704–715

Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in Northern Patagonia. J Arid Environ 36: 639–653

Bosco T, Bertiller MB, Carrera AL (2015) Micro-environmental conditions affect grass and shrub seedling emergence in denuded areas of the arid Patagonian Monte, Argentina. Flora 210:66–71

Boyd CS, Svejcar TJ (2011) The influence of plant removal on succession in Wyoming big sagebrush. J Arid Environ 75: 734–741

Brandt LA, King JY, Milchunas DG (2007) Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Glob Change Biol 13:2193–2205

Brandt LA, Bohnet C, King JY (2009) Photochemically induced carbon dioxide production as a mechanism for carbon loss from plant litter in arid ecosystems. J Geophys Res 114: 2156–2202

Brandt LA, King JY, Hobbie SE, Milchunas DG, Sinsabaugh RL (2010) The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. Ecosyst 13:765–781

Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, The Netherlands

Carrera AL, Bertiller MB (2010) Relationships among plant litter, fine roots and soil organic-C and N across an aridity gradient in Northern Patagonia, Argentina. Eco Sci 17:276–286

Carrera AL, Bertiller MB (2013) Combined effects of leaf litter and soil microsite on decomposition process in arid rangelands. J Environ Manag 114:505–511

Carrera AL, Vargas DN, Campanella MV, Bertiller MB, Sain CL, Mazzarino MJ (2005) Soil nitrogen in relation to quality and decomposability of plant litter in the Patagonian Monte, Argentina. Plant Ecol 181:139–151

Carrera AL, Bertiller MB, Larreguy C (2008) Leaf litterfall, fine-root production, and decomposition in shrublands with different canopy structure in the Patagonian Monte, Argentina. Plant Soil 311:39–50

Carrera AL, Mazzarino MJ, Bertiller MB, del Valle HF, Carretero EM (2009) Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina. J Arid Environ 73:192–201

Centro Nacional Patagónico. 2009. Unidad de Investigación de Oceanografía y Meteorología http://www.cenpat.edu.ar

Chomel M, Fernandez C, Bousquet-Melou A, Gers C, Monnier Y, Santonja M, Gauquelin T, Gros R, Lecareux L, Baldy V (2014) Secondary metabolites of *Pinus halepensis* alter decomposer organisms and litter decomposition during afforestation of abandoned agricultural zones. J Ecol 102:411–424

Cleveland CC, Liptzin D (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochem 85:235–252

Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, Stursova M, Zeglin LH (2008) Pulse dynamics and microbial processes in aridland ecosystems. J Ecol 96:413–420

Coombs J, Hind G, Leegood RC, Tieszen L, Vonshsk A (1985) Analytical techniques. In: Coombs J, Hall DO, Long S P, Scurlock JM (eds) Techniques in bioproductivity and photosynthesis. Pergamon Press, Oxford, pp. 219–228

Couteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Tree 10:63–66

Day TA, Zhang ET, Ruhland CT (2007) Exposure to solar UV-B radiation accelerates mass and lignin loss of *Larrea tridentata* litter in the Sonoran Desert. Plant Ecol 193:185–194

del Valle HF (1998) Patagonian soils: a regional synthesis. Ecol Austral 8:103–123

Duguay KJ, Klironomos JN (2000) Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi. Appl Soil Ecol 14:157–164

Fiala ACS, Garman SL, Gray AN (2006) Comparison of five canopy cover estimation techniques in the western oregon cascades. Forest Ecol Manag 232:188–197

Gallo M, Sinsabaugh RL, Cabaniss SE (2006) The role of ultraviolet radiation in litter decomposition in arid ecosystems. Appl Soil Ecol 34:82–91

Gallo ME, Porras-Alfaro A, Odenbach KJ, Sinsabaugh RL (2009) Photoacceleration of plant litter decomposition in an arid environment. Soil Biol Biochem 41:1433–1441

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246

Gehrke C, Johanson U, Callaghan TV, Chadwick D, Robinson CH (1995) The impact of enhanced ultraviolet-B radiation on litter quality and decomposition processes in *Vaccinium* leaves from the Subarctic. Oikos 72:213–222

Gholz HL, Wedin DA, Smitherman SM, Harnon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environ: toward a glob model of decomposition. Glob Change Biol 6:751–765

King JY, Brandt LA, Adair EC (2012) Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. Biogeochem 111:57–81

Kraus TEC, Dahlgren RA, Zasoski RJ (2003) Tannins in nutrient dynamics of forest ecosystems–a review. Plant Soil 256:41–66

Lambers H, Chapin FS III, Pons T (2008) Plant physiological ecology, 2nd edn. Springer Verlag, NY

Larreguy C, Carrera AL, Bertiller MB (2014) Effects of long-term grazing disturbance on the belowground storage of organic carbon in the Patagonian Monte, Argentina. J Env Manag 134:47–55

León RJC, Bran D, Collantes M, Paruelo JM, Soriano A (1998) Grandes unidades de vegetación de la Patagonia extra andina. Ecol Austral 8:125–145

Lin Y, King JY (2014) Effects of UV exposure and litter position on decomposition in a California grassland. Ecosyst 17:158–168

Liu P, Huanga J, Han X, Suna OJ, Zhou Z (2006) Differential responses of litter decomposition to increased soil nutrients and water between two contrasting grassland plant species of inner Mongolia, China. Appl Soil Ecol 34:266–275

Ludwig JA, Tongway DJ (1996) Rehabilitation of semiarid landscapes in Australia II. restoring vegetation patches. Restor Ecol 4:398–406

Manzoni S, Trofymow JA, Jackson RB, Porporato A (2010) Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. Ecol Monogr 80:89–106

Marcos MS, Bertiller MB, Saraví Cisneros H, Olivera NL (2015) Incremento de la abundancia de bacterias oxidadoras de amoníaco de suelos del Monte Patagónico en respuesta a la humedad del suelo y a la calidad del mantillo vegetal. III CAMAyA, Ciudad Autónoma de Buenos Aires.

Mazzarino MJ, Bertiller MB, Sain CL, Satti P, Coronato F (1998) Soil nitrogen dynamics in Northeastern Patagonia steppe under different precipitation regimes. Plant Soil 202:125–131

Meentemeyer V (1978) Microclimate and lignin controls of litter decomposition rates. Ecol 59:465–472

Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a glob range of environ. Ecol Monogr 63:327–366

Moody SA, Paul ND, Björn LO, Callaghan TV, Lee JA, Manetas Y, Rozema J, Gwynn-Jones D, Johanson U, Kyparissis A, Oudejans AMC (2001) The direct effects of UV-B radiation on *Betula pubescens* litter decomposing at four European field sites. Plant Ecol 154:29–36

Moorhead DL, Reynolds JF (1989) Mechanisms of surface litter mass loss in the Northern Chihuahuan desert: a reinterpretation. J Arid Environ 16:157–163

Moorhead DL, Sinsabaugh RL (2006) A theoretical model of litter decay and microbial interaction. Ecol Monogr 76:151–174

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. John Wiley and Sons, New York

Norusis MJ (1997) Advanced statistics. SPSS Inc., Chicago

Olivera NL, Prieto LH, Carrera AL, Saraví Cisneros H, Bertiller MB (2014) Do soil enzymes respond to long-term grazing in an arid ecosystem? Plant Soil 378:35–48

Pancotto VA, Sala OE, Cabello M, Lopez NI, Robson TM, Ballaré CL, Caldwell MM, Scopel AL (2003) Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community. Glob Change Biol 9:1465–1474

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, Fasth B (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315:361–364

Prieto LH, Bertiller MB, Carrera AL, Olivera NL (2011) Soil enzyme and microbial activities in a grazing ecosystem of Patagonian Monte, Argentina. Geoderma 162:281–287

Rostagno CM, Defossé G, del Valle HF (2006) Post fire vegetation dynamics in three rangelands of Northeastern Patagonia, Argentina. Rangel Ecol Manag 59:163–170

Rozema J, Tosserams M, Nelissen HJM, van Heerwaarden L, Broekman RA, Flierman N (1997) Stratospheric ozone reduction and ecosystem processes: enhanced UV-B radiation affects chemical quality and decomposition of leaves of the dune grassland species *Calamagrostis epigeios*. Plant Ecol 128:285–297

Schlesinger WH, Hasey MM (1981) Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecol 62:62–774

Schlesinger WH, Raikes JA, Hartley AE, Cross F (1996) On the spatial patterns of soil nutrients in desert ecosystems. Ecol 77:364–374

Smith WK, Gao W, Steltzer H, Wallenstein MD, Tree R (2010) Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. Glob Change Biol 16:484–495

Soil Survey Staff (1998) Keys to soil taxonomy. USDA, Washington, DC

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Blackwell, Cambridge, Mass

Tongway DJ, Ludwig JA (1996) Rehabilitation of semiarid landscapes in Australia I restoring productive soil patches. Restor Ecol 4:388–397

van Soest PJ (1963) Use of detergents in the analysis of fibrous feeds. II A rapid method for the determination of fiber and lignin. J Assoc Off Anal Chem 46:829–835

Vanderbilt KL, White CS, Hopkins O, Craig J (2008) Aboveground decomposition in arid environ: results of a long-term study in Central New Mexico. J Arid Environ 72: 696–709

Vargas DN, Bertiller MB, Ares JO, Carrera AL, Sain CL (2006) Soil C and N dynamics induced by leaf-litter decomposition of shrubs and perennial grasses of the Patagonian Monte. Soil Biol Biochem 38:2401–2410

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, New Jersey

Waterman PG, Mole S (1994) Analysis of plant phenolic metabolites. Blackwell Scientific Publications, NY

Whitford WG (2002) Desertification. In: Whitford WG (ed) Ecology of Desert Systems. Academic Press. San Diego, USA, pp. 275–304

Whitford WG, Meentemeyer V, Seastedt TR, Cromack K Jr, Crossley DA Jr, Santos P, Todd RL, Waide JB (1981) Exceptions to the AET model: deserts and clear-cut forest. Ecol 62:275–277

Zhang D, Hui D, Luo Y, Zhou G (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J Plant Ecol 2:85–93