Plant litter decomposition in a semiarid rangeland of Argentina: species and defoliation effects

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Abstract.   Plant litter decomposition is critical for terrestrial ecosystem productivity. *Poa ligularis* Nees ex Steud and *Nassella tenuis* (Phil.) Barkworth are native, desirable perennial grasses in central Argentina's rangelands. *Amelichloa ambigua* (Speg.) Arriaga & Barkworth is only consumed when a better forage is unavailable. Litter traps were used to collect aboveground litter during two years. In March 2012, six bags, each one containing either leaf blade (three bags, one per species) or root litter (three bags, one per species) of the three species were located below the canopy of each replicate plant of the studied species (hereafter referred to as 'location'). Blade litter bags were located on the soil surface, and root litter bags buried at 10 cm soil depth. This allowed evaluation of the effects of defoliation, the different species canopies and the microbial community activity around their roots on decomposition of above- and belowground litter. For each species, twenty plants were either defoliated twice (5 cm stubble height) or remained undefoliated during the growing season. Litter bags were collected after 2, 7, 13 and 24 months incubation. The study was repeated in 2013, with additional bags were placed for N content determination on leaf blade and root litters. Aboveground litter production was highest in *P. ligularis*; however, no differences were observed among species when the effect of plant size was eliminated. Aboveground litter of desirable species had higher N content and decomposed faster than that of *A. ambigua*. The opposite was recorded for root litter. Defoliation had no effect on litter decomposition, but location effects were detected after one year of incubation. Desirable perennial grasses promoted organic matter loss from litter, a key factor in increasing soil fertility in this semiarid ecosystem.

Additional keywords: desirable and undesirable grasses, leaf litter, nitrogen, perennial grasses.

Introduction

Plant litter (i.e. all plant organs and tissues that fall to the ground, as well as decomposing roots) is an important component in nutrient cycling and energy flow in terrestrial ecosystems (Bormann and Likens 1979). Litter amount depends on plant tissue characteristics, management of herbivory and plant consumption, and climatic and edaphic factors, which vary among sites and years (Aerts and Chapin 2000). Litter decomposition is critical for maintaining terrestrial ecosystem productivity (Bormann and Likens 1979) and is controlled by a combination of biotic and abiotic factors, such as soil microorganism activity, litter quality (i.e. C : N ratios, lignin concentrations), temperature, precipitation and ultraviolet radiation (Moretto *et al.* 2001; Austin and Vivanco 2006). Above- and belowground decomposition is often affected by different environmental parameters, with consequences for nutrient cycling. Herbaceous plant root decomposition can be faster (Seastedt *et al.* 1992) or slower (Biondini *et al.* 1998) than aboveground tissue decomposition. Root decomposition may differ between plants through morphological features such

as differences in cortical cells, specific area (Smith *et al.* 2014) or chemical composition.

Litter of a given species group decomposes faster in soil where these species are dominant, a concept referred to as 'advantage of the local' (Ayres *et al.* 2006). This is a consequence of specialisation of soil microbial communities in more efficiently decomposing litter to which they are often exposed. However, the litter chemical composition appears a better predictor of litter decomposition rate for any given species (Silver and Miya 2001). Cornwell *et al.* (2008) demonstrated a positive relationship between decomposition and leaf and litter N concentrations. Nitrogen might contribute to control of organic matter loss during the first phase of the decomposition process, whereas recalcitrant compounds, such as lignin or lignified carbohydrates, might be involved in controlling a second phase of that process (Berg 1986). Grass species desirable to livestock produce high quality litter (high N concentration, and a low C : N ratio and lignin concentration), have short-lived leaves and a faster decomposition rate (Distel and Bóo 1996; Campanella and Bertiller 2008; Poca *et al.* 2014). In contrast, grass species undesirable to livestock produce leaves with a longer-life span, and lower quality litter (low N concentrations, and high C : N ratio and lignin contents) (Saint Pierre *et al.* 2004).

Defoliation can be defined as tissue removal from a standing plant by either clipping, trampling or browsing causing an immediate change in plant height and canopy density in the community (Heady and Child 1994). It can affect plant microclimate through increased light penetration and soil surface temperature, and decreased soil water content (Busso *et al.* 2012). Moderate grazing intensities can increase net primary productivity and soil fertility in natural grasslands through increasing compensatory growth of grazed species, resource allocation and levels of radical exudation (Bardgett and Wardle 2003), which can favour microbial activity and mineralisation of soil nutrients (Wardle *et al.* 2004). Conversely, long-term overgrazing increases less desirable grasses in temperate, semiarid rangelands (Distel and Bóo 1996). These grasses have avoidance mechanisms against herbivores, which can delay litter decomposition, reducing nutrient mineralisation (Wardle *et al.* 2004).

Evaluation of the effects of different plant species on litter decomposition by microbial communities is critical when considering soil fertility in semiarid environments. Our hypotheses were that (1) aboveground litter production from undefoliated perennial grasses is greater in desirable than undesirable species; and (2) the above- and belowground litter decomposition from desirable species is faster than that of undesirable species; however, it varies according to defoliation, and location (i.e. litter of any studied species was decomposed below its own canopy or below that of the other two species). This study was performed with three perennial grass species: *Poa ligularis* Nees ex Steud and *Nassella tenuis* (Phil.) Barkworth, both desirable perennial grasses, and *Amelichloa ambigua* (Speg.) Arriaga & Barkworth, an undesirable perennial grass only consumed when more palatable forage is unavailable (Cano 1988). Both *P. ligularis* and *N. tenuis* produce high quality aboveground litter (Moretto and Distel 2003; Carrera *et al.* 2005). *Amelichloa ambigua* has a high fibrous content. These species initiate growth in March–April, vegetate in winter, flower by mid-October (*P. ligularis*) and November (*A. ambigua* and *N. tenuis*), fructify and disseminate

their seeds in late spring-early summer, becoming dormant during summer (Cano 1988; Ithurrart 2015).

The objectives of this study were to (1) compare aboveground litter production between three studied perennial grass species; and (2) evaluate the effects of defoliation and litter location on organic matter loss and N content from above- and belowground litters of the three grasses. Location was defined as whether the litter of any studied species was located below itself (i.e. plants of that species, or its source site), or below the canopy of each of the other two species.

Methods

Study area

The study was conducted within a 16-year-old exclosure (1.12 ha) to domestic herbivores in a temperate grassland of the Chacra Experimental Patagones, (40°39′S, 62°54′W; 40 m above sea level), in the south of Buenos Aires province, Argentina.

According to Thornthwaite, the climate is temperate semiarid. The rainfall gradient determines an ustic soil moisture regime with irregular distribution (Soil Survey Staff 2014). Mean annual temperature is 14.1°C and mean, annual precipitation 417 mm (1981–2010).

Data on air temperature, relative moisture, irradiance, precipitation and evapotranspiration were collected (January 2012 to April 2015) from an automatic weather station 1 km from the exclosure (Fig. 1).

The soil is a Typic Haplocalcid (Soil Survey Staff 2014). Table 1 shows the chemical and physical soil properties of the study site at 0–20 cm depth (Ambrosino 2017).

The plant community is characterised by an open shrubby stratum including herbaceous species of different quality for livestock production (Giorgetti *et al.* 1997). With moderate and continuous grazing, species composition changes occur, with both other desirable C$_3$ grasses and undesirable species recorded.

Aboveground litter production

The experimental design was completely randomised. In January 2012, 10 adult plants of each species were clipped to 5 cm height when plants were dormant post seed dispersal. Clipping removed senescent and dead shoots from the previous growing season, restricting any available green or pale yellow plant material to that produced during the 2012 growing season. Basal area and total tiller numbers on *P. ligularis* are higher than on *A. ambigua*, which are, in turn, higher than on *N. tenuis* (Ithurrart 2015), allowing plants with different tiller densities, photosynthetic surface areas and tissue turnover rates to be used. Aboveground monthly litter production was determined during the growing season (g plant^{-1} month^{-1}) after seed dispersal. Plants remain dormant thereafter until the initiation of the next growing season, about March of the next year. During the period plants remain dormant, so there is no litter production.

All plant residues within a radius of 0.2 m from the plant stem base were initially collected and discarded. Study plants were then surrounded by wire litter traps 0.8 m high, 0.4 m in diameter with 0.01 m screen mesh. Aboveground litter was collected monthly from April to the end of the growing season (early summer 2012). Total aboveground litter production, the sum of monthly litter within each trap, was expressed as
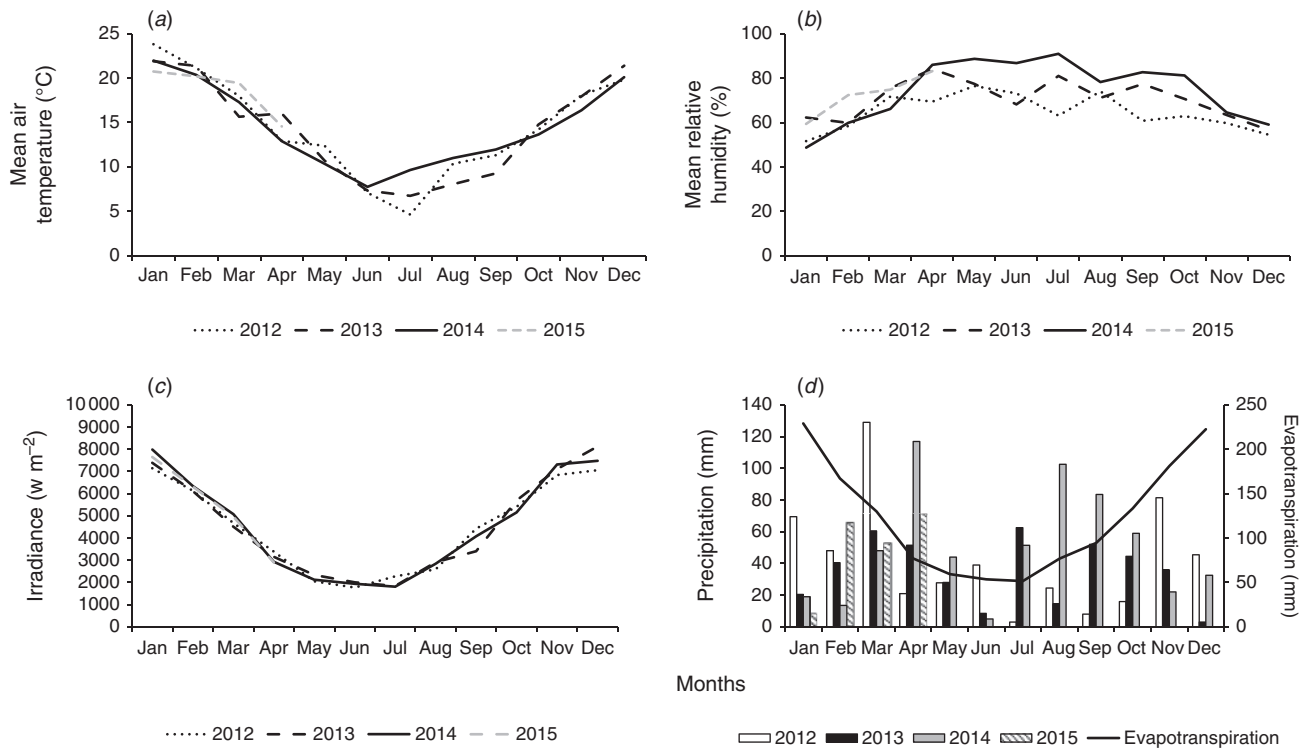
Fig. 1. Monthly climatic data at the Chacra Experimental of Patagones during the study (2012–2015): (*a*) mean air temperature (°C), (*b*) mean relative humidity (%), (*c*) mean irradiance (w m^{-2}), and (*d*) precipitation and evapotranspiration averaged over the study period (mm).

Table 1. Organic matter (SOM; g kg^{-1}), total N (STN; g kg^{-1}), extractable phosphorus (Pe; mg kg^{-1}), pH and soil texture (%) at the study site at 0–20 cm (mean ± s.e.; Ambrosino 2017)

SOM (g kg^{-1})	STN (g kg^{-1})	Pe (mg kg^{-1})	pH	Texture (%)		
				Sand	Silt	Clay
21.9 ± 0.3	1.2 ± 0.01	10 ± 0.1	8 ± 0.1	54.8 ± 12	22.3 ± 7.3	22.9 ± 7.9

g plant^{-1} year^{-1}. Plant circumference was also measured, allowing calculation of basal area and quantification of total aboveground litter production as g cm^{-2} year^{-1}.

The study was repeated during 2013 using procedures similar to those in 2012, but on different plants.

Decomposition and N content of aboveground (leaf blade) and belowground (root) litter

A substantial, but uncounted number of whole plants (a number more than sufficient to conduct the study) of each species were destructively harvested in November 2011. Soil blocks (20 × 20 × 20 cm) were obtained for each harvested plant. Fine roots and recently senesced leaf blades from standing tillers were collected from harvested plants. Roots were obtained after manually washing soil with tap water through a 35-mesh screen. Leaf blades and roots were allowed to dry to constant weight at ambient temperature. Plant parts were cut into 4-cm pieces and placed in gauze bags 10 × 10 cm (1 g of litter per bag); with 0.35 mm mesh. It was assumed that the mesh size used would prevent invertebrate entry into the bags.

In January 2012, when species were dormant, 40 plants of each species were cut to 5 cm height. This standardised conditions to only include shoot growth produced during the incubation period. In March 2012, six bags, each one containing either leaf blade (three bags, one per species) or root litter (three bags, one per species) were located below the canopy of each replicate plant (*n* = 5) of each of the studied species (hereafter referred to as 'location', Fig. 2*a*). Bags containing leaf blades were placed horizontally and fixed to the soil. Bags containing roots were treated similarly, but placed 10 cm below the soil surface (Fig. 2*a*). Five plants per species were used for each treatment and sampling date.

Half of the 40 previously selected plants of each species were defoliated to 5 cm during the growing season on 7 August and 14 September 2012; 18 July and 17 September 2013 and 18 July and 29 August 2014; the remaining plants were not defoliated (control). The aim was to simulate the grazing intensity and defoliation frequency common in the region surrounding the study exclousure, as well as mimic the common rotational grazing management (Giorgetti *et al.* 2006). Defoliation
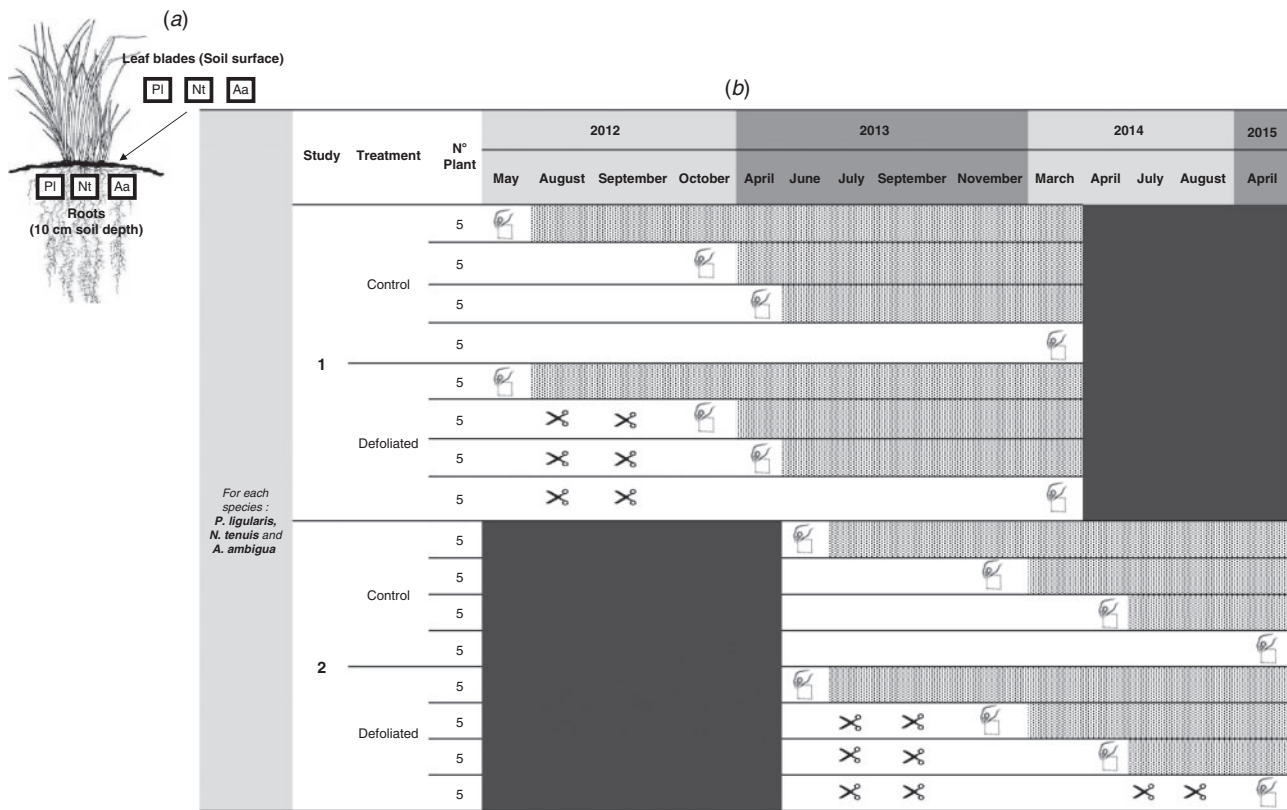
Fig. 2. (*a*) Litter bags placed beneath plants of the study species: *Poa ligularis* (Pl), *Nassella tenuis* (Nt) and *Amelichloa ambigua* (Aa). (*b*) Time schedule for the application of the defoliation treatments (✂) and sampling dates (🗒) from the studies of decomposition of aboveground (leaf blade) and belowground (root) litter in (1) 2012–2014 and (2) 2013–2015.

occurred at two developmental morphology stages, vegetative and immediately after differentiation of the apical meristem from vegetative to reproductive (Fig. 2*b*). Consequently, active growth meristems (intercalary, apical) remained on the plants after the defoliation, with the plant growth biological cycle unaffected in either case (Giorgetti *et al.* 2000).

Litter bags were collected on 4 sampling dates (i.e. after 2, 7, 13 and 24 months) (Fig. 2*b*). Organic matter loss (%) was obtained by subtracting the litter remaining at sampling from that initially placed.

The litter decomposition study was repeated during 2013–2015 (initiation date: April 2013; Fig. 2*b*). Financial constraints prevented determination of litter N content during 2012, and the use of only four rather than five replicates to make N determinations in 2013. Similarly to the evaluation of aboveground and root litter decomposition in 2012–2014 and 2013–2015 in the studied species, six additional litter bags were added per replicate plant below the same plant canopies (*n* = 4) used to conduct the litter decomposition study in 2013–2015. Total N was determined by the Kjeldahl method (Bremner 1996) on the aboveground and root litter samples. Nitrogen content was obtained after multiplying litter N concentrations by either the initial litter biomasses placed in each bag (i.e. mg of initial organic matter) or by the remnant, undecomposed litter biomasses collected at each sampling date (i.e. mg of remnant organic matter).

In both studies (aboveground litter production and litter decomposition), plant material was cleaned of residues, oven-dried at 60°C for 72 h, and weighed. Correction of plant material for inorganic contaminants in the samples (i.e. ash) was made after ignition in a muffle furnace at 550°C for 6 h (McNaughton *et al.* 1998).

Statistical analysis

Aboveground litter production

Data were transformed to ln $(x + 1)$ to fulfil assumptions of normality and homocedasticity (Sokal and Rohlf 1984). Litter production data during the growing season (g plant^{-1} month^{-1}) were analysed using a three-way analysis of variance (ANOVA), taking species, sampling periods and study years as factors. Because data corresponded to repeated-measures, linear mixed models with unstructured residual correlation and heterogeneous residual variances over time were used for analysis. Data corresponding to total aboveground litter production (sum of all litter collected at each sampling) were analysed using two-way ANOVA taking species and year as factors.

Decomposition and N content of aboveground (leaf blade) and belowground (root) litter

Since organic matter loss from above- and belowground litter was expressed as a percentage, these data were analysed

Table 2.   Monthly aboveground litter production (g plant^{-1} month^{-1}; mean ± s.e. of $n = 10$) during the growing season
Within each sampling date in 2012 and 2013, values followed by different letters indicate significant differences between species.
Significant differences were at $P < 0.05$

Year	Month	*Poa ligularis*	*Nassella tenuis*	*Amelichloa ambigua*
2012	April	0.38 ± 0.04 b	0.19 ± 0.03 a	0.58 ± 0.13 b
	May	0.19 ± 0.03 a	0.14 ± 0.02 a	0.17 ± 0.02 a
	July	0.23 ± 0.05 a	0.12 ± 0.01 a	0.22 ± 0.04 a
	August	0.19 ± 0.03 b	0.1 ± 0.02 a	0.08 ± 0.02 a
	September	0.17 ± 0.05 a	0.11 ± 0.01 a	0.15 ± 0.03 a
	October	0.43 ± 0.08 a	0.35 ± 0.06 a	0.35 ± 0.08 a
	November	0.58 ± 0.12 a	0.34 ± 0.07 a	0.35 ± 0.06 a
	December	0.53 ± 0.13 a	0.34 ± 0.08 a	0.33 ± 0.03 a
2013	Early May	0.83 ± 0.24 b	0.13 ± 0.03 a	0.48 ± 0.09 b
	Late May	0.53 ± 0.1 b	0.07 ± 0.02 a	0.39 ± 0.09 b
	July	0.83 ± 0.16 c	0.13 ± 0.01 a	0.44 ± 0.07 b
	August	0.59 ± 0.07 c	0.07 ± 0.02 a	0.35 ± 0.07 b
	September	0.80 ± 0.13 b	0.05 ± 0.01 a	0.67 ± 0.35 b
	October	1.31 ± 0.17 c	0.24 ± 0.05 a	0.49 ± 0.04 b
	November	0.69 ± 0.13 b	0.17 ± 0.03 a	0.62 ± 0.20 b
	December	2.03 ± 0.44 c	0.38 ± 0.07 a	1.01 ± 0.18 b

independently with multifactorial ANOVA using a split-plot design (main plot: study year (1 = 2012–2014 and 2 = 2013–2015), location, defoliation treatment and sampling date; subplot: species litter (blades or roots of each species, depending on the analysis)).

For each species' litter, organic matter loss rates (decomposition rates) were estimated for each location. Data were adjusted to a negative exponential regression model (Eqn 1) (Swift *et al.* 1979):

$$y = a * e^{-(t*k)} \qquad (1)$$

where y was the ash-free, remnant organic matter (g) at time t (months), a the material amount placed to decompose initially (1 g), and k was the rate of organic matter loss (i.e. decomposition rate) (g month^{-1}).

Estimated decomposition rates were compared using two-way ANOVA taking species litter and study year as factors.

N content data were transformed to $\sqrt{(x + 0.05)}$ to comply with normality and homocedasticity assumptions (Sokal and Rohlf 1984). N content of material initially placed in decomposition bags was analysed using a one-way ANOVA. N content in the remnant material was analysed with a multifactorial ANOVA using a split-plot experimental design (main plot: species, defoliation treatment, sampling date; subplot: plant part (blades or roots, depending on the analysis) of each species). Fisher l.s.d. tests (significance level of 5%) were conducted for mean comparisons whenever F-tests were significant ($P < 0.05$).

All statistical analyses were conducted with Infostat software (Di Rienzo *et al.* 2016).

Results

Aboveground litter production

Aboveground monthly litter production

The interactions between species, sampling dates and years were significant, so the treatments were analysed separately by year and by species.

Monthly litter production and statistical differences varied among species (Table 2). Litter production was initially highest (April 2012) in *P. ligularis* and *A. ambigua*, but by August had declined in *A. ambigua* relative to *P. ligularis*. For the remaining 2012 samplings, no significant differences between species were detected. In 2013, litter production was lowest in *N. tenuis*. *Amelichloa ambigua* values were intermediate to those of the desirable species on four occasions. On other sampling dates, litter production was highest in *P. ligularis* and *A. ambigua.*

During both years, *P. ligularis* had a significantly lower monthly plant litter production in May, July, August and September than at other samplings (Fig. 3*a*), and was significantly higher in 2013 than 2012 (except in April and November). *Nassella tenuis* showed a similar pattern to *P. ligularis* (Fig. 3*b*). However, litter production was higher in 2012 than 2013 in May, September and November.

Plant litter production in *A. ambigua* was highest late in both growing seasons, although differences were less evident than those in other species (Fig. 3*c*). *Amelichloa ambigua* litter production was significantly higher in 2013 than 2012 (Fig. 3*c*), except in April and in spring.

Total annual aboveground litter production

The analysis of total annual aboveground litter production when expressed as g plant^{-1} year^{-1} detected a significant interaction between the studied factors (i.e. species and year). In both years, total litter production was significantly higher in *P. ligularis* than in *N. tenuis* (Table 3), while values in *A. ambigua* were similar or less than *P. ligularis* in 2012 and 2013 respectively. Aboveground litter production in *P. ligularis* and *A. ambigua* was significantly higher in 2013 than 2012, while that of *N. tenuis* was the reverse.

However, when expressed as g cm^{-2} year^{-1}, total annual aboveground litter production was higher in 2013 than 2012, and no significant differences were detected between species (Table 3).
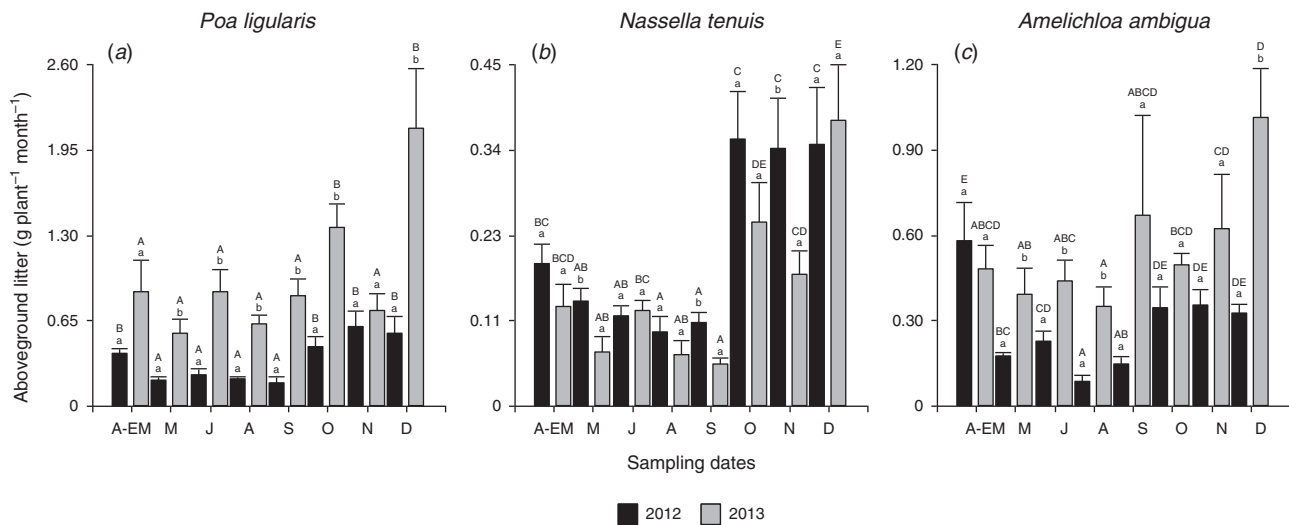
Fig. 3. Monthly aboveground litter production during the growing season (g plant^{-1} month^{-1}; mean ± s.e. of $n = 10$) of the study species. Above the histograms, different upper case letters indicate significant differences between sampling dates within any given year, and different lower case letters indicate significant differences between years within each sampling date. Sampling dates in the x axes: April 2012–early May 2013 (A-EM), May (M), July (J), August (A), September (S), October (O), November (N) and December (D). Significant differences were at $P < 0.05$. Note the differences in scale in the y-axes.

Table 3. Total annual aboveground litter production per plant (g plant^{-1} year^{-1}) and basal area unit (g cm^{-2} year^{-1}) (mean ± 1 S.E. of $n = 10$) of *Poa ligularis*, *Nassella tenuis* and *Amelichloa ambigua*

For each measurement, different upper case letters indicate significant differences between species within any given year, and different lower case letters indicate significant differences between years within each species. Significant differences were at $P < 0.05$

Year	Poa ligularis	Nassella tenuis	Amelichloa ambigua
	(g plant^{-1} year^{-1})		
2012	2.6916 ± 0.2817 B,a	1.6848 ± 0.1242 A,b	2.2306 ± 0.1488 B,a
2013	7.6296 ± 0.8472 C,b	1.2388 ± 0.1329 A,a	4.4144 ± 0.7722 B,b
	(g cm^{-2} year^{-1})		
2012	0.0237 ± 0.0025 A,a	0.0411 ± 0.0051 A,a	0.0246 ± 0.0027 A,a
2013	0.0548 ± 0.0120 A,b	0.0497 ± 0.0078 A,b	0.0493 ± 0.0074 A,b

Decomposition and N content of aboveground (leaf blade) and belowground (root) litter

Defoliation did not affect decomposition ($P > 0.05$) of neither above- or belowground tissues at any sampling. In both above- and belowground litter significant interaction occurred between leaf blades or roots on each species (depending on the analysis) and other factors (study year, sampling date and species).

Loss of organic matter from aboveground litter

Aboveground litter decomposition showed no location effect at the first two sampling dates. *Nassella tenuis* leaf blades showed a significantly higher percentage of organic matter loss than *P. ligularis*, which in turn lost more than *A. ambigua* regardless of location (Fig. 4a). After 13 months (i.e. April 2013), *N. tenuis* blades exhibited greater organic matter loss under the desirable species than under *A. ambigua* (Fig. 4a). *Poa ligularis* and *A. ambigua* blades did not differ in organic matter loss between locations, and no location effect was detected at final sampling. Highest organic matter loss percentages were recorded in blades of *N. tenuis*, and the lowest in *A. ambigua* blades.

Results of the first two samplings in 2013–2015 were similar to those in 2012–2014 (Fig. 4b). At the third sampling date, *N. tenuis* blades lost a higher organic matter percentage than in other species, and loss was the lowest in *A. ambigua* (Fig. 4b). When compared between locations, blades of *P. ligularis* lost significantly more organic matter beneath desirable than undesirable species. For *A. ambigua*, lowest values were recorded beneath plants of that species, but were similar to losses recorded beneath *P. ligularis* (Fig. 4b). At the last sampling date (after 24 months), there were no effects of location, and blades of *N. tenuis* showed the highest organic matter losses, followed by *P. ligularis* and then *A. ambigua* (Fig. 4b).

In both study years, desirable species recorded higher decomposition rates than *A. ambigua* (Table 4). All estimated rates were higher in 2013–2015 than 2012–2014.

Organic matter loss from belowground litter

At the first two samplings in 2012–2014, *A. ambigua* roots lost a significantly higher organic matter percentage than other
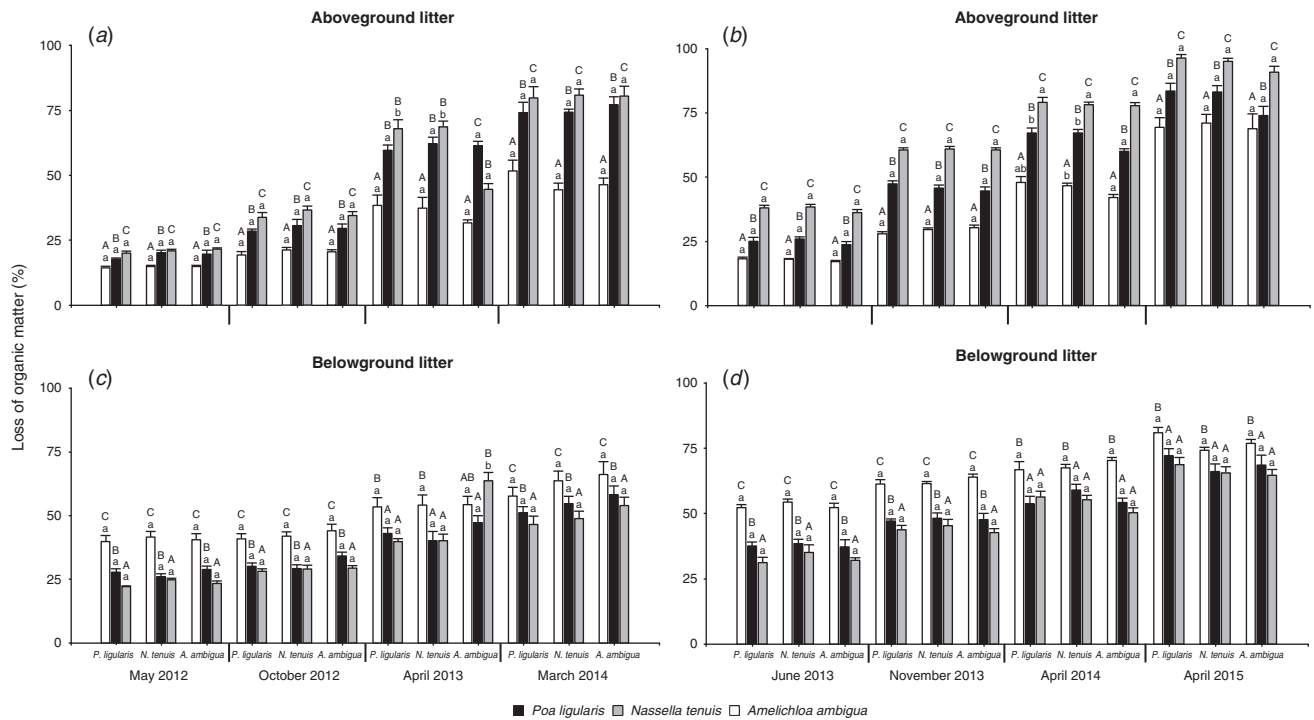
Fig. 4. Loss of organic matter (%; mean ± s.e. of *n* = 10) from (*a, b*) aboveground (leaf blade), and (*c, d*) belowground (root) litter placed beneath plants of the study species (location) at each sampling date of 2012–2014 (*a, c*) and 2013–2015 (*b, d*). For each sampling date, different upper case letters above histograms indicate significant differences between species litter within each location, and different lower case letters indicate significant differences between locations within each species litter. Significant differences were at *P* < 0.05.

Table 4. Rates of organic matter loss (i.e. decomposition rates) from above- and belowground litter (g month^{-1}; mean ± 1 S.E. of *n* = 3)

For each species litter, different either upper or lower case letters indicate significant differences between species or studies respectively. Significant differences were at *P* < 0.05

	Species	Rate of organic matter loss (g month^{-1})	
		2012–2014	2013–2015
Aboveground litter (leaf blades)	*Poa ligularis*	0.0629 ± 0.0013 B,a	0.0827 ± 00054 B,b
	Nassella tenuis	0.0700 ± 0.0059 B,a	0.1416 ± 0.0024 C,b
	Amelichloa ambigua	0.0304 ± 0.0014 A,a	0.0498 ± 0.0011 A,b
Belowground litter (roots)	*Poa ligularis*	0.0422 ± 0.0025 A,a	0.0706 ± 0.0010 A,b
	Nassella tenuis	0.0403 ± 0.0057 A,a	0.0632 ± 0.0025 A,b
	Amelichloa ambigua	0.0611 ± 0.0027 B,a	0.1319 ± 0.0046 B,b

species and loss was lowest in *N. tenuis* (Fig. 4*c*). After 13 months, *A. ambigua* litter had a higher percentage organic matter loss than the desirable species under the canopies of *P. ligularis* and *N. tenuis*; percentage losses under *A. ambigua* were intermediate to those of the desirable species, and root organic matter loss was highest in *N. tenuis*. At the last sampling, regardless of location, organic matter loss percentage in belowground litter of *A. ambigua* was highest, followed by *P. ligularis*, then *N. tenuis*.

From 2013 to 2015 there was no location effect for any of the four sampling dates. Belowground litter loss was highest in *A. ambigua* (Fig. 4*d*). Percentage organic matter loss in *P. ligularis* was higher than *N. tenuis* at the first two samplings.

In both studies, decomposition rates were highest in *A. ambigua* (Table 4). For all species, rates were higher in 2013–2015 than 2012–2014.

N content of above- and belowground litter

Total N content of the initial blade tissue differed among species. It was highest in *N. tenuis* (23.16 ± 0.80 mg of initial organic matter), followed by *P. ligularis* (16.96 ± 0.28 mg of initial organic matter) and then *A. ambigua* (7.90 ± 0.45 mg of initial organic matter). Conversely, root N contents were higher in *A. ambigua* (8.81 ± 0.19 mg of initial organic matter) than *N. tenuis* (7.73 ± 0.11 mg of initial organic matter) and *P. ligularis* (6.98 ± 0.20 mg of initial organic matter).
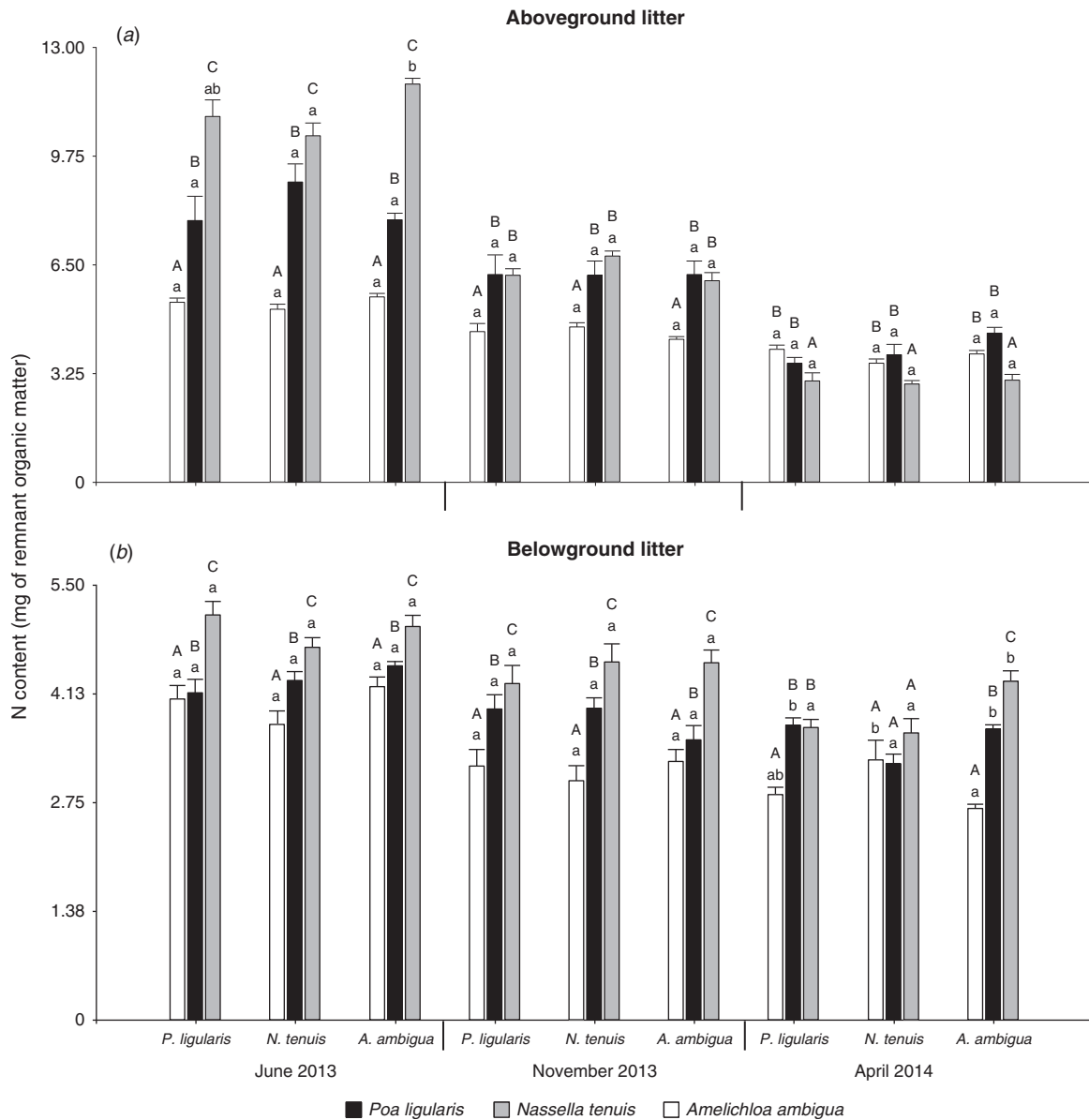
Fig. 5. Nitrogen content (mg of remnant organic matter; mean $\pm$ s.e. of $n = 8$) of the remnant material in 2013–2014 for (*a*) aboveground (leaf blade) and (*b*) belowground (root) litter placed beneath plants of the study species (location) at each sampling date. For each date, different upper case letters above histograms indicate significant differences between species litter within of each location, and different lower case letters indicate significant differences between locations within each species litter. Significant differences were at $P < 0.05$. Note the differences in scales in the *y*-axes.

There was no effect ($P > 0.05$) of defoliation at any sampling on the N content of remnant material. Thereafter, defoliation was not considered in the statistical analyses. In both analysis of above- and belowground litter significant interaction occurred between blades or roots of each species (depending on the analysis) and other factors (e.g. sampling date and species).

A location effect for aboveground litter was only detected at the first sampling for blades of *N. tenuis* which had lower N content material beneath its own species' canopy than below the canopy of *A. ambigua* (Fig. 5*a*). The highest N contents were in blades of *N. tenuis*, followed by *P. ligularis* and then

A. ambigua. At the second sampling date, the lowest values were recorded in *A. ambigua*, with *N. tenuis* and *P. ligularis* similar. At the end of the study, *A. ambigua* and *P. ligularis* blades had a similar N content, which was higher than that in *N. tenuis*.

At the first two samplings, belowground litter N content was significantly higher in *N. tenuis* and lower in *A. ambigua*, regardless of location (Fig. 5*b*). The species canopy effect was only detected at the last sampling. Root litter N content was similar in the desirable species but higher than that on *A. ambigua* underneath *P. ligularis*. Beneath *A. ambigua*, the

N content was highest in *N. tenuis* and *A. ambigua*. Belowground litter of *P. ligularis* recorded a lower N content underneath plants of *N. tenuis*. Root litter of *N. tenuis* had a lower N content beneath plants of desirable species. *Amelichloa ambigua* had a lower N content beneath itself, a value similar to that recorded when *A. ambigua* root litter was placed beneath *P. ligularis*.

Discussion

Aboveground litter production

Results did not support the hypothesis that aboveground litter production from undefoliated perennial grasses is greater in desirable than undesirable species. Regarding aboveground monthly litter production by plants during the growing season, differences between species were only detected in 2013. Litter production was always higher in *P. ligularis* than in *N. tenuis*, and in some cases, higher than in *A. ambigua*. Previous studies indicated a more advanced plant developmental morphology cycle (early spring flowering) in *P. ligularis*, an intermediate cycle in *N. tenuis* (mid-spring flowering), and a comparatively later cycle (late-spring flowering) in *A. ambigua* (Ithurrart 2015), which may explain the litter production of *P. ligularis*. Foliage appearance rates in grasses are lowest during flowering, a time when litter production is maximised (Langer 1972). Moreover, its greater basal area and biomass production could have resulted in greater aboveground senescing material in *P. ligularis* than *N. tenuis* (Ithurrart 2015).

In relation to litter production of each species, in cool season species, rates of leaf appearance appear higher than those of senescence at the vegetative stage, and plants remain mostly green during autumn and winter (Moore *et al.* 1991). This helps to explain the lower contribution of litter to the soil surface in these seasons than in spring on *P. ligularis* and *N. tenuis*. In *A. ambigua*, although litter production increased from September to November, differences in litter contribution were lower than in the other species in both years.

Nassella tenuis had the lowest total aboveground plant litter production in both years. This species has an inherently smaller basal area than *P. ligularis* (Ambrosino 2017). Larger plants allocate more carbon and nutrients to leaf formation (Ithurrart 2015). When the plant size effect was eliminated, and litter production analysed in terms of unit surface area, no differences were observed between species. Plants of *P. ligularis* and *A. ambigua* contributed more litter in 2013 than 2012 to the soil surface; the reverse of *N. tenuis*. In both years, precipitation (513 mm in 2012, and 422 mm in 2013) was above or similar to the long-term mean (1981–2012: 421 mm). However, the highest monthly rains were in March and November in 2012, and March, April, September and October in 2013 (Fig. 1). Rainfall distribution within each year might explain differences in litter contribution between both study years. Plant species responses to precipitation arise from the combination of their own morphogenetic traits and the temporal pattern of soil water dynamics (Golluscio and Sala 1993). Campanella and Bertiller (2010) demonstrated that after a rainfall, water recharge of the soil layers is facilitated in the rooting depth, and species such as *P. ligularis* can produce more biomass and litter than other perennial grass species. The positive response of *P. ligularis* to autumn and spring rains, and its more advanced developmental

morphology cycle, might explain its greatest total litter production in 2013.

Decomposition and N content of aboveground (leaf blades) and belowground (root) litter

Defoliation did not affect decomposition of above- or belowground litter on any species. It is likely that cutting all species equally could mask any effect of desirability versus undesirability in terms of litter production and litter decomposition. This result is in contrast to both the proposed hypothesis, and to studies where grazing increased radical exudation, favouring litter decomposition and nutrient mineralisation (Bardgett and Wardle 2003). The difference between these results and those of other studies might be that plants were clipped rather than grazed. The fact that clipping does not simulate grazing has been emphasised by Burritt (2015). Moderate, not excessive defoliation (i.e. clipping) treatments were applied to all three species. A grazed situation may differ from the clipping methodology used here. Undesirable grasses could potentially have larger canopies than desirable grasses, simply as a consequence of more limited consumption by livestock. Potentially, these larger, ungrazed canopies could produce greater amounts of litter, and have a different microclimate below them than grazed canopies. Conversely, Dam and Christensen (2015) found that the effects of defoliation on soil biota depend on the timing of defoliation. Early defoliation of *Deschampsia flexuosa* during the growing season had a negative effect on soil microbial biomass, while at the same site, a late season defoliation increased soil biota activity and biomass. They concluded that, based on soil biota responses, plants defoliated during active growth conserve resources, whereas defoliation after termination of growth results in release of resources.

Plant species alter the microbial communities around their roots to facilitate rapid litter decomposition (Wardle *et al.* 2002). It has been proposed that micro-organisms play a decisive role in litter decomposition in the most advanced stages, when labile substances are lost (Ayres *et al.* 2006). In general, the location effect proposed in hypothesis (2) was detected after one year from incubation on organic matter loss (i.e. blades of desirable species, and roots of *A. ambigua*) and litter N content (roots of the three species). These results agree in part with those of Moretto and Distel (2003), who found that aboveground litter decomposition of grass species of different palatability was determined by both plant quality and site characteristics, whereas root decomposition was determined only by its chemical quality. In the present study, the location effect was attributed to species' canopy differences affecting the microenvironment (aboveground soil surface temperatures and direct rainfall effects) within which aboveground litter decomposed. The effects of individual plant species on organic matter degradation by microorganisms, mostly on belowground litter, vary depending upon the release of carbon labile compounds from the live roots (Dam and Christensen 2015), and soil dryness because of plant water use (Jenkinson 1977).

In general, organic matter loss from aboveground litter was lowest in *A. ambigua* blades during both years. There is a direct relationship between leaf blade N content and its decomposition (Freschet *et al.* 2012). In this study, initial blade N content was

highest in *P. ligularis* and lowest in *A. ambigua*, although differences were less evident at the last sampling. The faster decomposition of the palatable species may have been associated with higher litter quality (Moretto and Distel 2003), mostly during the initial stages (Poca *et al.* 2014).

Higher belowground litter decomposition of *A. ambigua* could be attributed to its greater initial belowground N content (Smith *et al.* 2014). Also, Freschet *et al.* (2012) found other variables such as the organ dimensions could codetermine litter decomposition. *Amelichloa ambigua* roots have a larger diameter than those of *P. ligularis* (Ithurrart 2015). Larger diameter roots might contain larger storage root cells than finer roots, and may be more easily attacked by decomposers, mostly during the first months after the initiation of the decomposition process (Smith *et al.* 2014).

Estimated decomposition rates of above- and belowground litter were within the variation range reported for plant species of other arid and semiarid ecosystems (Silver and Miya 2001; Carrera *et al.* 2008). Differences found between studied species are related to the dynamics in organic matter loss and N content discussed above. There is a positive relationship between litter N content and the estimated *k* for litter decomposition (Wardle *et al.* 2004), that determined higher rates of decomposition in aboveground litter of desirable species, and belowground litter of *A. ambigua*. Organic matter loss was higher in 2013–2015 than 2012–2014. Also, the estimated *k* increased twice as much from one year to next for aboveground litter of *N. tenuis* and belowground litter of *A. ambigua*. This could be due to differences in total precipitation (2012–2014 = 898 mm; 2013–2015 = 1095 mm), and its annual distribution during the first phases of the decomposition process (higher values in July, September and October 2013 than in 2012; Fig. 1). Decomposition rates from above- and belowground litter have been shown to be strongly correlated with precipitation in arid and semiarid environments (Giese *et al.* 2009). Precipitation might facilitate rupture and lixiviation of aboveground litter (Swift *et al.* 1979), and increase both decomposer activity and biomass (Berg 1986).

Conclusions

Moderate and early defoliations (i.e. those which did not remove active meristems) did not affect decomposition of above- and belowground litter, probably because there were no changes in biomass accumulation, canopy light interception or soil microorganism activity associated with the studied species. The effect of 'location' was detected, in some cases, after one year of incubation. This effect would be a component to consider in advanced stages of decomposition, when the most labile compounds are lost.

Desirable perennial grass presence promoted organic matter loss from litter. This is a key factor in conservation of soil fertility and energy flow among trophic levels. Sustainable management practices that provide strict control of defoliation frequency and intensity and allow resting periods for seed dispersal and seedling establishment, are critical for persistence of desirable perennial grasses in the studied community.

Conflicts of interest

The authors declare no conflicts of interest.

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