

Leaf litterfall patterns of perennial plant species in the arid Patagonian Monte, Argentina

María Victoria Campanella ·
Mónica Beatriz Bertiller

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Abstract The objective of this study was to investigate the variation in leaf litterfall patterns of desert plant species in relation to the intra- and interannual variation of precipitation. We collected the leaf litterfall of 12 representative species of the dominant life forms in the arid Patagonian Monte (evergreen shrubs, deciduous shrubs, and perennial grasses) at monthly intervals during three consecutive years. All shrub species showed a marked seasonality in the pattern of leaf litterfall, but the date of the peak of leaf litterfall differed among them. The peak of leaf litterfall in three deciduous and three evergreen shrubs occurred in summer months while in one deciduous shrub and in two other evergreen shrubs the peak of leaf litterfall was in autumn and winter, respectively. In contrast, the leaf litterfall of perennial grasses occurred through the year without a seasonal pattern. In most shrub species, increasing annual precipitation was related to increasing leaf litterfall and the peak of leaf litterfall was positively related to precipitation events occurred some months before, during winter. Moreover, the magnitude of responses

in terms of variation in leaf litterfall in relation to interannual variation of precipitation was not the same for all species. Evergreen shrubs showed lower responses than deciduous species. These differences in leaf litterfall patterns were consistent with differences in leaf traits. In conclusion, we found new evidence of species-specific responses of leaf litterfall patterns to precipitation, suggesting that other factors than precipitation may control leaf litterfall in desert plants.

Keywords Evergreen shrubs · Deciduous shrubs · Perennial grasses · Intra- and interannual variation of precipitation · Leaf traits

Introduction

Leaf litterfall is a major control of nutrient cycling and the maintenance of soil fertility in terrestrial ecosystems (Facelli and Pickett 1991). The amount of leaf litter income to soil depends on leaf traits of species conforming plant communities, climatic conditions and edaphic factors, varying between sites and years (Bray and Gorham 1964; Maya and Arriaga 1996; Martínez-Yrízar et al. 1999; Bussotti et al. 2003). Leaf litterfall is usually seasonal (Lambers et al. 2000), and the largest rate occurs during the dry season in most arid woodlands (Martínez-Yrízar et al.

M. V. Campanella (✉) · M. B. Bertiller
Centro Nacional Patagónico (CENPAT—CONICET),
Boulevard Brown 2915, 9120 Puerto Madryn, Chubut,
Argentina
e-mail: campanella@cenpat.edu.ar

M. B. Bertiller
Universidad Nacional de la Patagonia San Juan Bosco,
Puerto Madryn, Chubut, Argentina

1999; Descheemaeker et al. 2006). The high rate of leaf litterfall during the dry season was interpreted as a way to evade water stress through reducing leaf area (Grace 1998) and the involved mechanisms could depend on complex interactions linking soil moisture, temperature and species phenology (Martínez-Carretero and Dalmasso 1992).

Many studies performed in different ecosystems found increasing litter production in years with above-average precipitation (Strojan et al. 1979; Münster-Swendsen 1984; Bo Pedersen and Bille-Hansen 1999; Pavón et al. 2005). However, few of them addressed the effect of the intra- and interannual variation of precipitation on the functioning of individual species and how this could influence not only the total annual leaf litter production but also the relative contribution of species with different leaf litter quality to the annual leaf litterfall. For example, a study in the Mojave Desert found that total leaf litter production and the relative contribution of litter with low C:N ratio were greater in a wet than in a dry year (Weatherly et al. 2003). These results provided evidence of the eventual effect of intra- and interannual variation in precipitation on the relative contribution of species to leaf litterfall in desert ecosystems, a fact that should be further explored.

Considering that leaf litterfall is the principal aboveground return of C and N to the soil in nutrient-poor ecosystems (Vitousek 1984) and high yearly variation of precipitation is a distinctive feature of most desert ecosystems (Noy Meir 1973), long-term research on leaf litterfall dynamics in deserts could be relevant to understand ecosystem functioning under these changing nutrient poor environments (Stohlgren 1995; Martínez-Yrízar et al. 1999). The objective of this study was to investigate the variation in leaf litterfall patterns of dominant desert species in relation to the intra- and interannual variation of precipitation.

Materials and methods

Study area and selected species

The study was conducted at Estancia San Luis ($42^{\circ}38'51''$ S, $65^{\circ}23'03''$ W), a floristic homogeneous area characteristic of the Patagonian Monte located in the northeastern part of the Chubut Province

(Argentina) (Bisigato and Bertiller 1997). The climate is arid with a mean annual temperature of 13.4°C and a mean annual precipitation of 237.67 mm (14-year series). The Patagonian Monte comprises the southern portion of the Monte Phytogeographical Province limiting with the Patagonian Phytogeographic Province. Precipitation events mostly occur without a defined seasonal pattern (Cabrera 1976) with a high intra- and interannual variation (Barros and Rivero 1982). However, depending on the year rains could be slightly concentrated in the cold period (Patagonian regime), in the warm period (Monte regime) or in both periods (Cabrera 1976; Coronato and Bertiller 1997; Mazzarino et al. 1998). The characteristic vegetation is a shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (Ares et al. 1990). Vegetation covers between 20% and 40% of the soil and presents a random patchy structure formed by clumps of shrubs and perennial grasses on a matrix of bare soil or sparse vegetation. Evergreen and deciduous shrubs are the dominant plant life forms in the upper canopy layer (1–2 m) and perennial grasses and dwarf shrubs form the low canopy layer (<0.5 m). We selected 12 representative species of three dominant life forms. Evergreen shrubs: *Chuquiraga avellaneda* Lorentz, *Chuquiraga erinacea* D. Don subsp. *hystrix* (Don) C. Ezcurra, *Larrea divaricata* Cav., *Larrea nitida* Cav. and *Atriplex lampa* Gill ex Moq. Deciduous shrubs: *Prosopis alpataco* Phil., *Prosopidastrum globosum* Gillies ex Hook. et Arn., *Lycium chilense* Miers. ex Bertero, and *Bougainvillea spinosa* (Cav.) Heimerl in Engler u. Prantl. Perennial grasses: *Nasella tenuis* (Phil.) Barkworth, *Jarava speciosa* (Trin. & Rupr.) Peñailillo and *Poa ligularis* Nees ex Steud. These species show different phenological strategies. The deciduous shrubs *L. chilense*, *P. globosum*, *B. spinosa*, and the perennial grasses *N. tenuis*, *P. ligularis*, *J. speciosa* concentrate vegetative activity in the wet winter–spring period. In contrast, the period of phenological activity in the evergreen shrubs *Larrea* spp., *A. lampa*, *Chuquiraga* spp., and the deciduous shrub *P. alpataco*, with deep-rooted systems and drought-resistant leaves, includes the dry summer season (Bertiller et al. 1991; Campagna and Bertiller 2008).

Samplings were carried out at two sites (separated by 5 km from each other) of about 2 ha each with low impact of domestic grazers (sheep) and high floristic similarity.

Climatic measurements

We registered the monthly maximum and minimum air temperature at 25 cm above the soil surface at both study sites during October 2004–August 2007, using mercury thermometers. The daily precipitation was recorded with an automatic data recorder ($21 \times$ Micrologger, Campbell Scientific) at one site during January 2004–August 2007.

Leaf litterfall

The leaf litterfall of five individuals per species and site was collected at periods ranging from 22 to 37 days during three consecutive 12-month collection periods (September 2004–August 2007). Values of leaf litterfall of the first collection period were obtained from Campanella and Bertiller (2008). To collect leaf litterfall of evergreen and deciduous shrubs, we hanged two to four conical litter-traps (10.5 cm diameter of the circular collecting-surface, 30 cm depth, 0.3 mm mesh) at the mid-canopy of each individual. The number of the litter-traps was proportional to the canopy diameter of each individual. In the case of perennial grasses, we enclosed each individual within a cylindrical litter-trap (30 cm diameter, 30 cm height, 2 mm mesh at the 5 cm basal height, and 2 cm mesh above). The harvested leaf litter was oven-dried at 60°C for 48 h and weighed. The leaf litterfall produced by m^2 of canopy at monthly periods of 30 days ($LLP_{[30]}$) was calculated as follows: $LLP_{[30]_i} = LLP_i * 30/IC_i$ where LLP_i = leaf litter production collected at the date t expressed by m^2 and IC_i = interval in days between the date of litter collection t and the previous date of collection $t - 1$, i = month interval. Moreover, we calculated the total annual leaf litterfall of each species as the sum of monthly leaf litterfall in the three collection periods: September 2004–August 2005 (year 1), September 2005–August 2006 (year 2), September 2006–August 2007 (year 3). We referred annual values of leaf litterfall of each species to the annual precipitation occurred in the previous January–December period (i.e., January–December 2004, 2005, 2006). This allowed including the previous whole winter precipitation period, which is a relevant control of primary production in Patagonian ecosystems (Jobbág and Sala 2000).

Statistical analysis

We assessed the significance of the differences in the monthly leaf litter fall among species by ANOVA of repeated measures. In this analysis, we included species as a fixed factor and month and year (collection period) as repeated measures within each species. To evaluate the differences in annual (September–August) leaf litter within species, we performed ANOVA of repeated measures, including species as a fixed factor and year as a repeated measure within species. We did not include sites as a factor because we did not find significant differences between them for these variables. The delay between monthly precipitation and monthly leaf litterfall for each species was analyzed using cross correlation.

Results

Climatic measurements

The largest precipitation event of the whole period occurred in July 2006. Also, we registered large events in December 2005 (summer) and in March 2007 (autumn) (Fig. 1). Annual precipitation increased during the study period. The lowest precipitation (185.39 mm) was recorded in year 2004. In the years 2005 and 2006, precipitation was 204.99 and 241.53 mm, respectively. The monthly mean temperature for the entire period was 13.84°C. The monthly maximum temperature varied between 19 and 45.5°C while monthly minimum temperature ranged between –15.5 and 3°C.

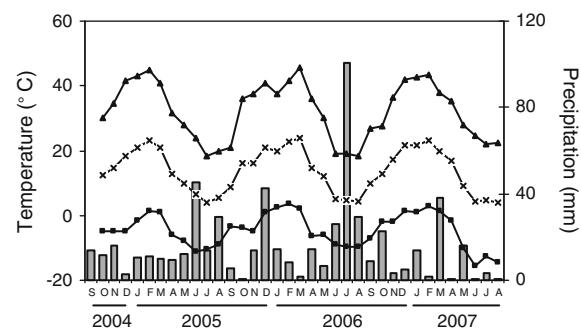


Fig. 1 Monthly maximum (dark line with triangles), mean (gray line with crosses), and minimum (dark line with squares) air temperature and monthly precipitation (gray bars) during the study period

Interannual litterfall variation in relation to precipitation

Interannual variation in leaf litterfall was not the same for all species (species \times year interaction $F_{22,192} = 7.11$; $P < 0.0001$) (Table 1). Among evergreen shrubs, annual leaf litterfall increased in *L. nitida*, *L. divaricata*, and *A. lampa* and diminished in *C. erinacea* subsp. *hystrix* with increasing precipitation during the study period (Fig. 1). In contrast, the annual leaf litterfall of *C. avellanedae* did not differ among years. Moreover, except for *P. alpataco*, annual leaf litter production of deciduous shrubs increased with increasing precipitation during the study period. In the case of perennial grasses, only *N. tenuis* showed differences in leaf litterfall among years, presenting the largest annual leaf litter production after the driest year (2004). The magnitude of the changes in leaf litter production among years depended on the life form. These changes were lower in evergreen shrubs (*L. nitida*, *L. divaricata*, *A. lampa*, and *C. erinacea* subsp. *hystrix*) and perennial grasses (*Nasella tenuis*) than in deciduous shrubs (*P. globosum*, *L. chilense*, and *B. spinosa*) (Table 1).

Intraannual litterfall variation in relation to precipitation

Intraannual patterns of leaf litterfall varied among species depending on the year (species \times month \times year interaction $F_{242,2376} = 5.19$; $P < 0.0001$). In evergreen shrubs leaf litterfall occurred through the year but with species peaking at different months (Fig. 2). In *C. avellanedae* and *C. erinacea* subsp. *hystrix*, the main peak of leaf litterfall occurred in winter and winter–early spring, respectively. In the former species, the peak of leaf litterfall was recorded in the same month (July) in the 3 years and in the second species the peak occurred at different months in the 3 years. A second peak in both species was produced in January 2006 (summer). In contrast, *A. lampa* and *Larrea* spp. produced the largest amount of leaf litterfall during summer (December–March).

In deciduous shrubs, leaf litterfall occurred during summer and/or autumn (Fig. 3). The peak of leaf litterfall in *P. alpataco* was recorded in autumn and occurred in the same month (May) throughout the study period. In the case of *P. globosum*, the leaf litterfall peak occurred in autumn but at different

Table 1 Mean \pm 1 SE of annual (period September–August) leaf litterfall production (g m^{-2} canopy year $^{-1}$) for the species belonging to each life form in the three study years and percent of significant differences between year 1 and 3

	Annual leaf litterfall (g m^{-2} canopy year $^{-1}$)			Relative significant differences between year 1 and 3 (%)
	Year 1	Year 2	Year 3	
Evergreen shrubs				
<i>Chuquiraga avellanedae</i>	79.88 \pm 13.58	115.49 \pm 13.75	80.46 \pm 12.38	–
<i>Chuquiraga erinacea</i> subsp. <i>hystrix</i>	54.64 \pm 5.53	40.13 \pm 5.47	22.97 \pm 5.12**	–57.8
<i>Larrea nitida</i>	9.33 \pm 2.82	12.81 \pm 2.99	17.55 \pm 3.13*	88.1
<i>Larrea divaricata</i>	6.67 \pm 1.43	8.31 \pm 1.52	12.67 \pm 2.59**	89.9
<i>Atriplex lampa</i>	55.48 \pm 10.39	55.57 \pm 11.77	83.02 \pm 15.63*	48.6
Deciduous shrubs				
<i>Prosopis alpataco</i>	64.58 \pm 9.47	59.77 \pm 8.51	74.34 \pm 9.49	–
<i>Prosopidastrum globosum</i>	0.017 \pm 0.012	0.97 \pm 0.41	6.76 \pm 0.90***	39664.7
<i>Lycium chilense</i>	3.81 \pm 1.17	23.56 \pm 3.82	36.09 \pm 4.93***	847.2
<i>Bougainvillea spinosa</i>	7.99 \pm 1.55	39.88 \pm 4.22	57.04 \pm 6.79***	613.9
Perennial grasses				
<i>Nasella tenuis</i>	46.13 \pm 5.06	25.03 \pm 2.85	34.04 \pm 3.79**	–26.2
<i>Jarava speciosa</i>	110.53 \pm 26.68	63.27 \pm 16.36	72.06 \pm 20.49	–
<i>Poa ligularis</i>	28.03 \pm 6.43	39.17 \pm 7.57	44.98 \pm 4.36	–

Asterisks indicate significant differences among years in each species (* $P < 0.01$; ** $P < 0.001$; *** $P < 0.0001$)

Fig. 2 Mean \pm 1 SE of monthly leaf litterfall (g m^{-2} canopy month $^{-1}$) from evergreen shrubs during the study period. Gray bars corresponded to year 1 (Sep2004–Aug2005), black bars corresponded to year 2 (Sep2005–Aug2006) and white bars to year 3 (Sep2006–Aug2007). s = spring, su = summer, a = autumn, w = winter

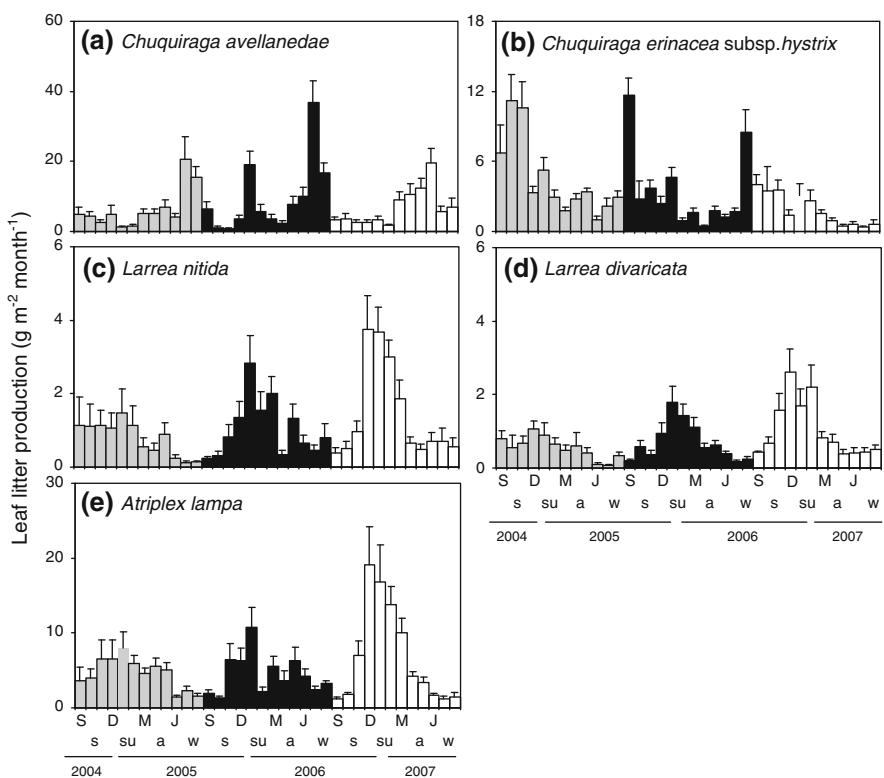
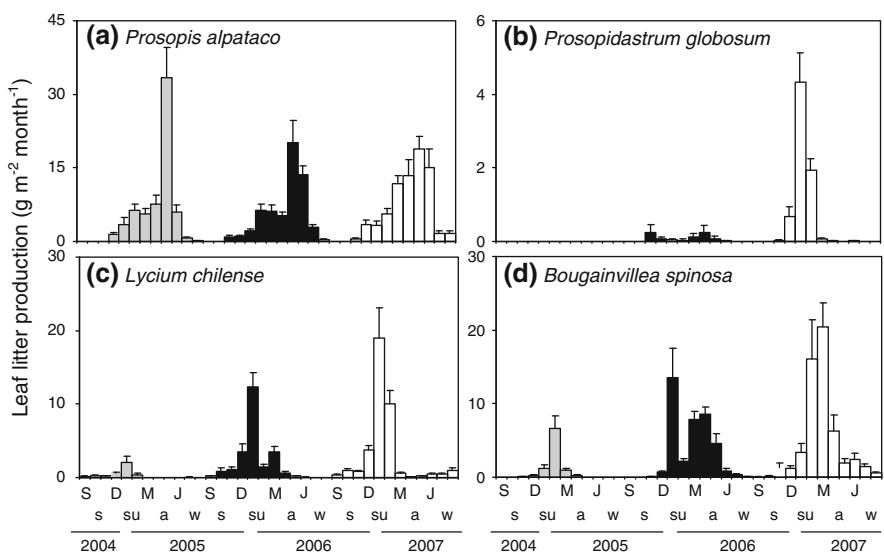


Fig. 3 Mean \pm 1 SE of monthly leaf litterfall (g m^{-2} canopy month $^{-1}$) from deciduous shrubs during the study period. Symbols, colors, and acronyms as in Fig. 2



months at the 3 years. The main peak of leaf litterfall in *L. chilense* was recorded in summer and at the same month (January) during the whole study period. However, a second peak was registered in autumn at March 2006. The peak of leaf litterfall in *B. spinosa*

occurred at mid-late summer at different months in the 3 years. Also, this species showed a second peak in March–April 2006 (year 2). These results indicated that some species extended the leaf litterfall period, delayed the peak of litterfall and/or produced a

Fig. 4 Mean \pm 1 SE of monthly leaf litterfall (g m^{-2} canopy month $^{-1}$) from perennial grasses during the study period. Symbols, colors, and acronyms as in Fig. 2

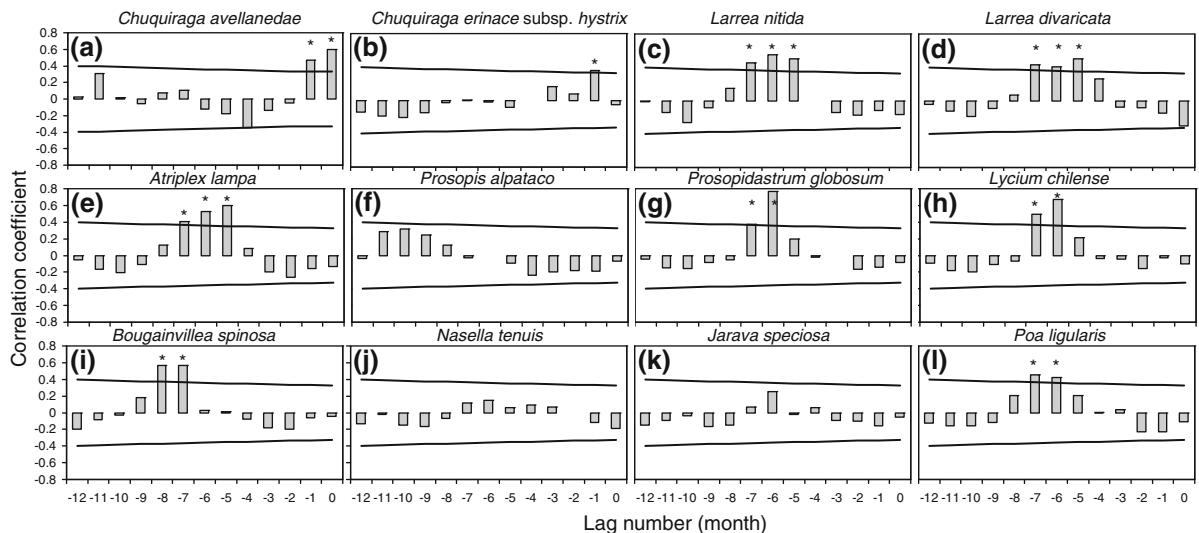
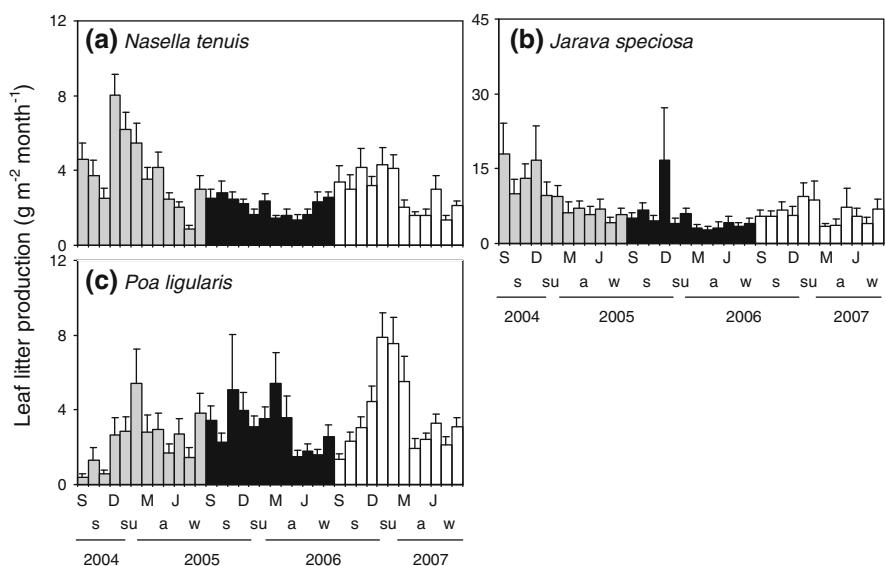


Fig. 5 Cross correlation between leaf litterfall and precipitation. Asterisks indicate significant correlations at $P < 0.05$. Lines indicate confidence intervals for cross correlations (bars) at $P < 0.05$

second peak of leaf litterfall in the wettest year. The leaf litterfall of perennial grasses occurred through the year without a seasonal pattern (Fig. 4).

The different intraannual patterns of monthly leaf litterfall were differently associated with monthly precipitation. Leaf litterfall of *Chuquiraga* species peaked at the same month or one month latter than the peak of monthly precipitation in winter. In contrast, the highest peak of leaf litterfall of *Larrea* species, *A. lampas*, *P. globosum*, *L. chilense*, *B. spinosa*, and *P. ligularis* occurred between 5 and

8 months, depending on species, after the largest precipitation events. In the other species (*P. alpataco*, *N. tenuis*, and *J. speciosa*), the peak of monthly leaf litterfall was not related to precipitation events (Fig. 5).

Discussion

Our findings showed that the inter- and intraannual patterns of leaf litterfall in most species varied with

precipitation in accordance to other studies carried out both in forests (Münster-Swendsen 1984; Bo Pedersen and Bille-Hansen 1999) and deserts (Strojan et al. 1979; Maya and Arriaga 1996; Sala et al. 1988; Lauenroth and Sala 1992; Alvarez et al. 2009). These studies argued that mean annual precipitation accounts for most of the net primary aboveground production variability and consequently for the interannual variability in leaf litter production. In our study area, large precipitation events during winter along with low temperatures facilitate the water recharge of soil layers in the rooting depth of most species (Coronato and Bertiller 1997; Bisigato and López Laphitz 2009). Accordingly, we found that in most species increasing annual precipitation was related to increasing leaf litterfall and the peak of leaf litterfall was positively related to precipitation events occurred some months before, during winter. Moreover, the largest event of monthly leaf litterfall occurred some months delayed with respect to the vegetative growth of most species (Campanella and Bertiller 2008). These findings provide evidence of some dependence of litterfall production on the amount of rainfall and nutrient use during the plant growth period (Pavón et al. 2005; Milla et al. 2005). Increasing annual precipitation was not only associated with higher, but also with latter peaking of leaf litterfall suggesting an extended plant growth period in wet than in dry years. This is consistent with studies reporting that the duration of leafing depends on the availability of water (Ghazanfar 1997; De Bie et al. 1998; Seghieri and Galle 1999). In contrast, leaf litterfall of *Chuquiraga* species either did not respond (*C. avellaneda*) or decreased (*C. erinacea* subsp. *hystrix*) with increasing precipitation. This finding is related to other obtained for these species in the same area showing no responses of leaf production to increasing precipitation (Campanella and Bertiller 2009). This indicates that responses to precipitation may be species-specific providing some evidence of different mechanisms controlling leaf litterfall (Myers et al. 1998), an issue scarcely studied in desert plant species.

Our results also showed that the magnitude of responses, in terms of leaf litterfall, to interannual variation of precipitation were not the same for all species. Evergreen shrubs showed relative lower responses than deciduous species. These differences could be related to leaf traits. It is well known that

species with mesophytic traits (i.e., high-growth rate, specific leaf area, and N concentration in green leaves and short leaf longevity; Chabot and Hicks 1982; Coley 1988; Aerts and Chapin 2000; Westoby et al. 2002) may have more responsiveness to changes in precipitation (Aerts and Chapin 2000; Aerts 1995) than species with the opposite (xerophytic) traits. In our study case, species with more mesophytic traits (deciduous shrubs) (Campanella and Bertiller 2008; Campanella 2009) presented a larger increment of leaf litterfall with increasing precipitation than species with more xerophytic traits (evergreen shrubs). Similarly, a study in the northern Mojave Desert found that litter species composition changed with precipitation variation, the proportion of litter with low C:N ratio increased in a wet year, and decreased in a dry year (Weatherly et al. 2003). The seasonal patterns of leaf litterfall were also consistent with species-specific responses to precipitation indicating that these responses could be associated with differences in traits and production of vegetative structures among species. Some studies reported higher impacts of precipitation on leaf production and growth in less drought tolerant species (Maya and Arriaga 1996; Olivares and Squeo 1999; Peñuelas et al. 2002; Ogaya and Peñuelas 2006).

Moreover, despite of the marked seasonality in the pattern of leaf litterfall of all shrub species, the date of the peak of leaf litterfall differed among species. Three deciduous species (*P. globosum*, *L. chilense*, and *B. spinosa*) concentrated the largest leaf litterfall events in summer months, probably due to the presence in these species of nondrought-resistant leaves (low leaf mass per unit area, and concentration of secondary metabolites such as lignin or phenolics) (Campanella and Bertiller 2008). In contrast, *P. alpataco* having drought-resistant leaves [high leaf mass per unit area and lignin concentration, and a deep root system (Campanella and Bertiller 2008)] showed the peak of leaf litterfall in autumn. On the other hand, evergreen shrubs (*L. nitida*, *L. divaricata*, and *A. lampa*) also concentrated leaf litterfall in summer months but showed also small events during the other seasons. In these species, leaf fall in the dry season is consistent with the reduction of the total leaf area as a way to evade water stress (Grace 1998). In this sense, Orshan (1954) highlighted the major role of reducing leaf area during summer in controlling plant water balance in desert plants. This pattern

was also similar to that found in evergreen shrub species of the *Larrea divaricata* community in Mendoza, Argentina (Martinez-Carretero and Dalmasso 1992). Nevertheless, *Chuquiraga* species having drought-resistant leaves (high leaf mass per unit area and lignin concentration), presented the peak of leaf litterfall in winter months, a fact that could remark the existence of controls other than drought on leaf litterfall. Probably, large precipitation events in winter could provoke the mechanical shedding of senesced leaves. A recent study in the Central Monte Desert stood out the role of rainfall as a turnover control of plant parts (Alvarez et al. 2009). Lastly, perennial grasses did not show a clear seasonal leaf litterfall pattern probably due to leaves remained attached to the bunch for long periods (Soriano 1956).

In conclusion, our results showed that water availability played a major role in leaf litterfall patterns of most desert species. However, we found new evidence of species-specific responses of leaf litterfall patterns to precipitation, suggesting that other factors may also control leaf litterfall. Among these factors leaf traits could account for an important part of the variation in leaf litterfall patterns. Considering that differences in litter quality of species in the Patagonian Monte are related to litter decomposability (Carrera et al. 2005; Vargas et al. 2006), our results suggest that intra- and interannual changes in the production of leaf litter among species caused by year-to-year differences in precipitation could significantly alter litter composition, decomposition rates, and nutrient availability in subsequent years. Moreover, arid ecosystems are expected to be one of the ecosystems most vulnerable to global change (Smith et al. 2000). It was predicted that southern South America would mostly undergo a decline in total precipitation as a consequence of a decrease in the number of precipitation events (Núñez et al. 2009). In this context, our results suggest that lower total precipitation may reduce growth and litter production in most plant species and increase the relative contribution of drought-resistant species producing recalcitrant litter, thus decelerating nutrient cycling and accelerating desertification processes.

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