

Plant phenology, leaf traits and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina

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Abstract

Question: Do coexisting plant life forms differ in overall phenology, leaf traits and patterns of leaf litterfall?

Location: Patagonian Monte, Chubut Province, Argentina.

Methods: We assessed phenology, traits of green and senesced leaves and the pattern of leaf litterfall in 12 species of coexisting life forms (perennial grasses, deciduous shrubs, evergreen shrubs).

Results: We did not identify differences in phenology, leaf traits and patterns of leaf litterfall among life forms but these attributes contrasted among species. Independent of the life form, the maintenance of green leaves or vegetative growth during the dry season was mostly associated with leaves with high leaf mass per area (LMA) and high concentration of secondary compounds. Low LMA species produced low litterfall mass with low concentration of secondary compounds, and high N concentration. High LMA species produced the largest mass of leaf litterfall. Accordingly, species were distributed along two main dimensions of ecological variation, the dimension secondary compounds in leaves - length and timing of the vegetative growth period (SC - VGP) and the dimension leaf mass per area - leaf litterfall mass (LMA - LLM).

Conclusions: Phenology, leaf traits and leaf litterfall varied among species and overlapped among life forms. The two dimensions of ecological variation among species (SC - VGP, LMA - LLM) represent distinct combinations of plant traits or strategies related to resource acquisition and drought tolerance which are reflected in the patterns of leaf litterfall.

Keywords: Deciduous shrub; Evergreen shrub; Leaf litter mass; Leaf mass per area; Lignin; Nitrogen total; Perennial grass; Phenolics total.

Abbreviations: LAI = Leaf area index; LLM = Leaf litterfall mass; LMA = Leaf mass per area; SC - VGP = (Dimension secondary compounds in leaves) - (Length and timing of the vegetative growth period).

Nomenclature: Correa (1971, 1978, 1984, 1988, 1999).

Introduction

Leaf litterfall is a major pathway for nutrient return to the soil and the maintenance of soil fertility in most terrestrial ecosystems (Lambers et al. 1998). Leaf litter chemistry and the amount and timing of leaf litterfall are main controls of the temporal rates of leaf litter decomposition, nutrient mineralization and nutrient cycling (Vitousek 1984; Lambers et al. 1998). Plant life forms or species may differ in leaf litter chemistry and in the quantity and timing of leaf litterfall depending on their intrinsic characteristics, particularly those related to carbon fixation and nutrient conservation strategies (Lambers et al. 1998; Kikuzawa 2004; Carrera et al. 2005).

Slow growing plants, characteristic of water and N-stressed ecosystems, tend to produce dense and well defended, long-lived leaves with high concentrations of secondary compounds, low N-concentration and low photosynthetic rates (Coley 1988; Poorter & Remkes 1990; Reich et al. 1992, 1997). High production costs of dense leaves are often compensated by long leaf life span, allowing an extended activity period with a more prolonged use of N in the plant (Aerts 1996; Westoby et al. 2002; Wright et al. 2002; Escudero & Mediavilla 2003; Kikuzawa 2004). Mechanical and chemical structures acting as defences against herbivores and water shortage may also protect leaf litter from the attack of soil organisms delaying its decay, affecting the nutrient cycling and other related ecosystems processes (Takeda et al. 1987; Cornelissen & Thompson 1997).

Plant species or life forms are important controllers of ecosystem functioning, particularly of those processes linking plants with soils (Hobbie 1992; van Breemen 1993; Díaz & Cabido 1997; Grime et al. 1997; Tilman et al. 1997; Wardle et al. 1998; Cornelissen et al. 1999). Phenological studies provide information regarding the linking between plant processes (i.e. growth, senescence of plant tissues or organs) and the biotic and abiotic environment (Shackleton 1999). Plants vary widely in their phenological behaviour according to morphological traits related to resource acquisition and conservation (Bertiller et al. 1991; Castro-Díez et al. 2003; Diaz et

al. 2004). In arid ecosystems, high diversity in plant structure and function, among coexisting species, related to adaptations for the efficient use of resources in space and time, contributes to reducing plant competition (Chesson et al. 2004).

Several studies reported contrasting leaf traits and leaf litterfall patterns among plant species or life forms from different ecosystems (Reich et al. 1992; Kikuzawa & Ackerly 1999; Eckstein et al. 1999; Kikuzawa 2004) but few of them addressed these differences among coexisting species or life forms in arid ecosystems. We assessed plant phenology, leaf traits and the mass and timing of litterfall in coexisting species of the life forms characteristic of arid ecosystems: perennial grasses, deciduous shrubs and evergreen shrubs. We hypothesized that coexisting life forms differ in overall phenology, leaf traits and patterns of leaf litterfall. We expected smaller and less seasonal leaf litterfall events in evergreen shrubs than in perennial grasses due to the building of leaves with high amount of secondary compounds. Deciduous shrubs would display intermediate patterns.

Material and Methods

Study area

The study was undertaken in the northeastern part of the Chubut Province (Argentina) in a floristically homogeneous area characteristic of the Patagonian Monte (Bisigato & Bertiller 1997). The climate is arid with a mean annual precipitation of 258 mm, mostly concentrated in the cold period, and a mean annual temperature of 13.9 °C (8-year series). The characteristic vegetation is a shrubland of *Larrea divaricata* and *Stipa* spp. (Ares et al. 1990). Plant canopy 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 (Bisigato & Bertiller 1997). Evergreen and deciduous shrubs are the dominant plant life forms in the upper canopy layer (1.0 m - 2.0 m). Evergreen shrubs are more abundant than deciduous shrubs, occupying between 60% and 80% of the total shrub cover (Bisigato & Bertiller 1997). Species of both life forms are randomly mixed in the community. Within the study area, the sampling was carried out at two sites (site 1: 42°39' S 65°23' W and site 2: 42°41' S 65°22' W, 115 m a.s.l.) of ca. 2 ha each with low impact of domestic grazers (sheep) and high floristic similarity.

Climatic measurements

During the period July 2004 - September 2005, we registered the monthly maximum and minimum air temperature at 25 cm above the soil surface at both study sites, and the daily precipitation with an automatic data recorder (21X Micrologger, Campbell Scientific) at one study site.

Study species

We selected 12 representative species of the three dominant life forms: *Atriplex lampa*, *Chuquiraga avelanadae*, *Chuquiraga hystrix*, *Larrea divaricata*, *Larrea nitida*, (evergreen shrubs), *Bougainvillea spinosa*, *Lycium chilense*, *Prosopis alpataco*, *Prosopidastrum globosum* (deciduous shrubs), *Poa ligularis*, *Stipa tenuis*, *Stipa speciosa* (perennial grasses).

Dominant deciduous shrubs are *L. chilense*, *P. alpataco*, *P. globosum* and *B. spinosa*. The low canopy layer (<0.50 m) is formed by dwarf shrubs and perennial grasses. Dominant perennial grasses are *S. tenuis*, *S. speciosa*, *S. humilis* and *P. ligularis* (Bisigato & Bertiller 1997).

Phenological observations

We randomly selected five modal individuals of each species at each site and registered the phenological evolution of each individual at monthly intervals from August 2004 to September 2005. Based on Bertiller et al. (1991), we defined five phenological phases:

- (1) vegetative inactivity: no visible vegetative growth but leaves and/or shoots may remain green;
- (2) vegetative growth: visible growth of shoots or tillers with expanding leaves;
- (3) flowering: buds or flowers visible;
- (4) fruiting: green or mature fruits;
- (5) leaf senescence: standing senesced leaves produced during the current growing period.

At each sampling date, we registered all simultaneous phenological phases occurring at the same individual.

Plant height, canopy area and cover

At the same time, we measured height, canopy area and cover of individuals selected for phenological observations. The height was measured from the base of the plant to the tallest part of the canopy. The canopy area was estimated by the crown diameter method (Mueller-Dombois & Ellenberg 1974). The canopy cover was visually estimated (Bisigato & Bertiller 1997).

Collection of green leaves, assessment of leaf mass per area and leaf area index

We collected fully expanded, young to medium aged green leaves (Reich et al. 1991; Bertiller et al. 2006) from the external canopy crown (sunny and partially sunny leaves) of five randomly selected individuals of each species at each site, different from those selected for phenological observations. Since phenology is not synchronic among species (Bertiller et al. 1991), green leaves of *A. lampa*, *B. spinosa*, *C. avellaneda*, *C. hystrix*, *L. divaricata*, *L. nitida*, *P. alpataco* and *P. globosum* were harvested in November-December 2004 and those of *L. chilense*, *P. ligularis*, *S. speciosa* and *S. tenuis* were harvested in June-July 2005. We assessed the leaf mass per area (LMA) in five randomly selected leaves per individual by measuring the leaf area and the leaf dry mass of green leaves. To measure leaf area, we placed each green leaf on a transparent squared grid paper (1 mm × 1 mm), and counted the number of squares intercepted by each leaf. Subsequently, green leaves were oven dried at 60 °C for 48 h, and weighed to assess leaf dry mass (Bertiller et al. 2005, 2006).

Leaf area index (LAI) was assessed in five randomly selected plants of each species on the same dates as for LMA sampling following the protocol in Jonckheere et al. (2004). For shrubs, we counted the number of branches per sampled plant and harvested a modal branch of each individual of each species. For perennial grasses, we collected the whole bunch. We hand separated all the leaves of each branch or bunch, measured the dry weight (dried at 60 °C for 48 h) and calculated the total leaf mass per individual. We estimated the LAI of each individual using the total leaf mass per individual, the mean values of area and mass of individual leaves assessed for LMA calculations and the value of canopy area.

Leaf litterfall

The leaf litterfall was assessed for the same individuals selected for phenological observations, from August 2004 to September 2005 in evergreen and deciduous shrubs and from September 2004 to September 2005 in perennial grasses. To collect leaf litterfall of evergreen and deciduous shrubs, we hung 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 height of the canopy of each individual. The number of the litter traps depended on the canopy diameter. 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). Leaf litterfall was removed monthly from each litter trap, oven-dried at 60 °C for 48 h and weighed.

Collection of senesced leaves and chemical traits of green and senesced leaves

We collected standing, recently senesced leaves from the canopy crown of five randomly selected individuals of each species (different from those selected for phenological observations), from January 2005 to August 2005. Senesced leaves of all collection dates were pooled by individual.

Green and senesced leaves per individual (dried at 60 °C for 48 h) were analysed for N-concentration by semi-micro Kjeldahl (Coombs et al. 1985); lignin by the Van Soest (1963) procedure and total phenolic concentration by the Folin-Ciocalteu method using 50% methanol as extract solution and tannic acid as standard (Waterman & Mole 1994). When the mass of senesced leaves was scarce, we pooled the material of two or more individuals of the same species and site in order to obtain enough mass for the chemical analysis. The collected mass of leaves of *P. globosum* was not enough to perform all chemical analyses.

Statistical analysis

We used ANOVA or the Kruskal Wallis test (depending on the distribution of the data) to evaluate the significance of the differences between maximum and minimum monthly leaf litterfall events for each species and the significance of the differences in annual leaf litterfall, traits of green and senesced leaves and plant traits among species and life forms (Norusis 1997). We did not include sites as a factor since for these variables we did not find significant differences between them. Tukey's test was used for multiple comparisons (Norusis 1997). In those cases in which we used ANOVA, we previously tested assumptions for this analysis. We included mean values of LMA per individual as replicates in statistical analysis. The level of significance throughout this study was $P < 0.05$. We analysed the relationship among the annual leaf litterfall, duration of the vegetative period (months), LMA and chemistry of green and senescent leaves by principal components analysis (PCA). For species ordination according to these traits, we calculated the loading coefficients of each species with respect to the two first principal components (Norusis 1997). We excluded *P. globosum* from the analysis since lignin concentration in green leaves and chemistry of senesced leaves data of this species were not available.

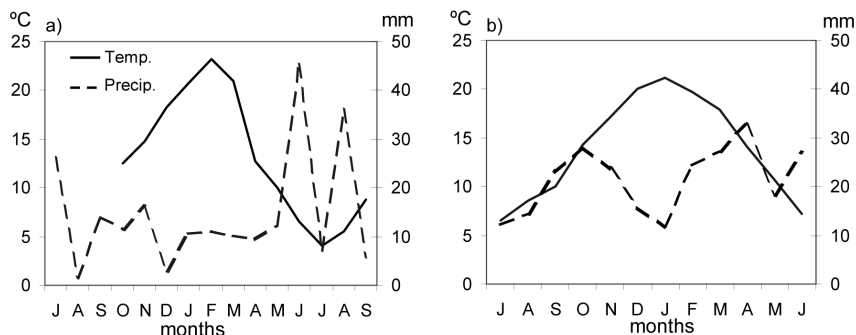


Fig. 1. Seasonal dynamics of mean monthly temperature and monthly precipitation at the study site (a) during the period July 2004-September 2005, (b) means for the 8-year series (1994-2001).

Results

Climatic measurements

During the study period total precipitation was 250 mm (July 2004 - September 2005). The largest precipitation events were concentrated in winter, associated with the lowest temperatures. Maximum mean temperature was in February, and minimum mean temperature was in July. These trends were similar to those observed in the 8-year series (Fig. 1).

Leaf area index

C. avellanadae showed the highest values of LAI and canopy cover and *P. globosum* displayed the lowest LAI with the highest canopy cover. *L. divaricata*, *B. spinosa* (the tallest shrubs) and *P. apataco* (the shrub with the largest canopy area) showed low LAI. *L. chilense* was the lowest shrub with high LAI. Perennial grasses were the smallest species; among these, *S. speciosa* was the largest (Table 1).

Phenological observations

Evergreen shrubs

Evergreen shrubs displayed a similar phenological evolution at both study sites. *C. avellanadae* (Fig. 2a) and *C. hystrix* (Fig. 2b) developed vegetative growth (VG) from late winter to summer. All individuals flowered from mid spring to mid summer and fruited from mid summer to autumn. Vegetative inactivity (VI) occurred from autumn to late winter. Leaf senescence occurred throughout the year with a maximum in autumn in *C. avellanadae* and in winter in *C. hystrix*. *L. nitida*, *L. divaricata* and *A. lampa* developed vegetative growth during the whole year (Fig. 2c, d, e; respectively) with a maximum in autumn-winter in the *Larrea* spp. In the three species, flowering occurred in spring and fruiting started in late spring lasting up to summer in *A. lampa* and up to early autumn in *Larrea* spp. Leaf senescence occurred throughout the year with a maximum in spring-summer.

Table 1. Plant height, canopy area, canopy cover and leaf area index (LAI) of species of each life form (mean values \pm 1 SE). Different uppercase letters indicate significant ($P < 0.05$) differences among life forms. Different lowercase letters indicate significant ($P < 0.05$) differences among species.

Species by life form	Plant height (cm)	Canopy area (dm ²)	Canopy cover (%)	LAI
Evergreen shrubs	B	A	A	A
<i>Chuquiraga avellanadae</i>	66.2 \pm 4.86 b	111.07 \pm 24.86 d	65.5 \pm 6.77 f	1.05 \pm 0.14 c
<i>Chuquiraga hystrix</i>	96.7 \pm 3.61 cd	114.85 \pm 13.64 d	35.5 \pm 1.57 cd	0.30 \pm 0.06 ab
<i>Larrea nitida</i>	121.5 \pm 9.17 d	139.72 \pm 24.27 de	16.2 \pm 2.36 a	0.18 \pm 0.04 a
<i>Larrea divaricata</i>	186.8 \pm 8.92 e	451 \pm 71.46 f	27.5 \pm 3.67 abc	0.22 \pm 0.06 ab
<i>Atriplex lampa</i>	66.25 \pm 4.69 b	105.22 \pm 18.16 d	38 \pm 6.42 cd	0.65 \pm 0.29 abc
Deciduous shrubs	B	A	A	A
<i>Prosopis alataco</i>	82.7 \pm 6.34 bc	364.91 \pm 54.53 ef	49.5 \pm 4.68 de	0.31 \pm 0.07 ab
<i>Prosopidastrum globosum</i>	54.7 \pm 5.7 b	144.1 \pm 54.53 d	61.5 \pm 4.95 ef	0.09 \pm 0.02 a
<i>Lycium chilense</i>	77.2 \pm 4.59 bc	47.96 \pm 10.89 c	20.5 \pm 3.9 ab	0.84 \pm 0.25 bc
<i>Bougainvillea spinosa</i>	117.6 \pm 11.18 d	206.03 \pm 51.37 d	36 \pm 3.23 cd	0.38 \pm 0.25 ab
Perennial grasses	A	A	A	A
<i>Stipa tenuis</i>	19 \pm 2.28 a	1.06 \pm 0.25 ab	32.5 \pm 5.18 cd	0.38 \pm 0.08 ab
<i>Stipa speciosa</i>	17.9 \pm 1.25 a	1.73 \pm 0.26 b	45 \pm 5.63 bc	0.26 \pm 0.02 ab
<i>Poa ligularis</i>	7.4 \pm 1.15 a	0.48 \pm 0.08 a	34.4 \pm 9.13 cd	0.31 \pm 0.05 ab

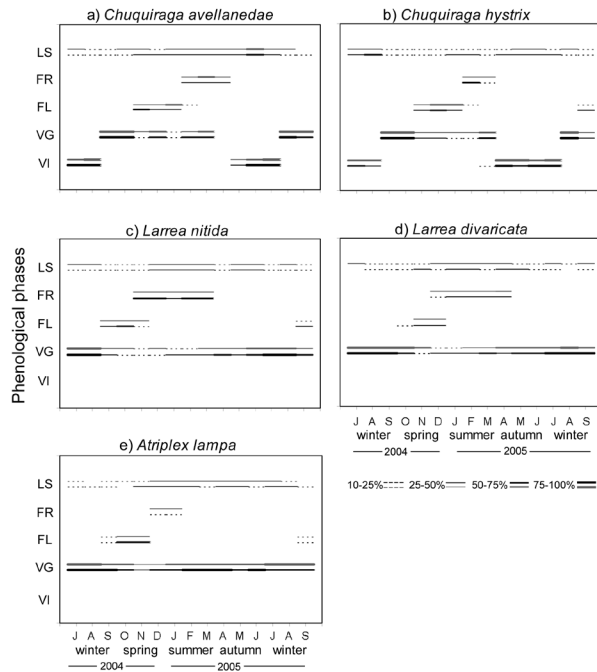


Fig. 2. Phenological evolution of species of evergreen shrubs at each site (site 1: grey lines and site 2: black lines) during the study period. The thickness of the lines indicates the percentage of plants at each phase. Phenological phases: LS = leaf senescence, FR = fruiting, FL = flowering, VG = vegetative growth, VI = vegetative inactivity.

Deciduous shrubs

P. alpataco (Fig. 3a) exhibited vegetative growth from spring to autumn, flowering occurred in spring and fruiting from late spring to summer. *P. globosum* (Fig. 3b) showed vegetative growth from mid spring to early summer, flowered in spring-early summer and fruited in the period from late summer to early autumn. Leaf senescence in *P. alpataco* started in early summer lasting up to autumn. In *P. globosum*, leaf senescence was concentrated in a short period during summer and was one month delayed at site 2. Both species concentrated vegetative inactivity during the cold period. *L. chilense* (Fig. 3c) developed vegetative growth from autumn to late spring. This phase began three months earlier in one of the sites. Flowering occurred in late winter-early spring and fruiting arose only in one site in late spring. Leaf senescence occurred in spring-summer reaching a maximum in late spring-early summer. The species displayed vegetative inactivity during summer-autumn. *B. spinosa* (Fig. 3d) developed vegetative growth from mid winter to early summer and did not exhibit reproductive growth during the study period. Leaf senescence occurred in late spring-summer with a maximum in mid-late summer. The species displayed a period of inactivity during summer-autumn.

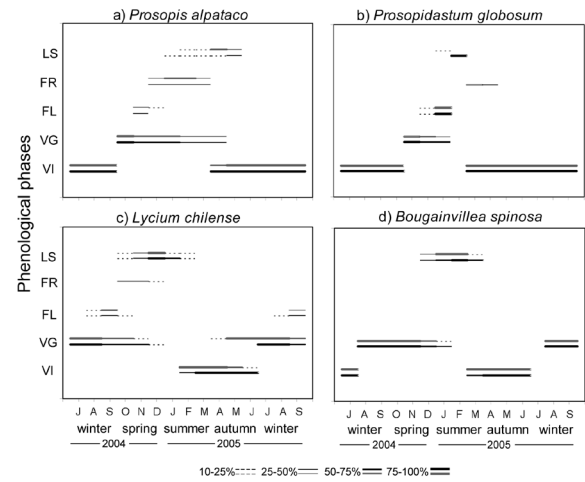


Fig. 3. Phenological evolution of species of deciduous shrubs at each site (site 1: grey lines and site 2: black lines) during the study period. The thickness of the lines indicates the percentage of plants at each phase. Abbreviations as Fig. 2.

Perennial grasses

Perennial grasses displayed similar phenological evolution at both study sites. The three species showed vegetative growth from autumn to spring-early summer. *Stipa tenuis* (Fig. 4a) and *S. speciosa* (Fig. 4b) flowered in mid spring and fruited from late spring to early summer. *Poa ligularis* (Fig. 4c) flowered in early spring and fruited in late spring. *Stipa speciosa* was the only perennial grass species maintaining green leaves during throughout the year with a maximum in summer. Most

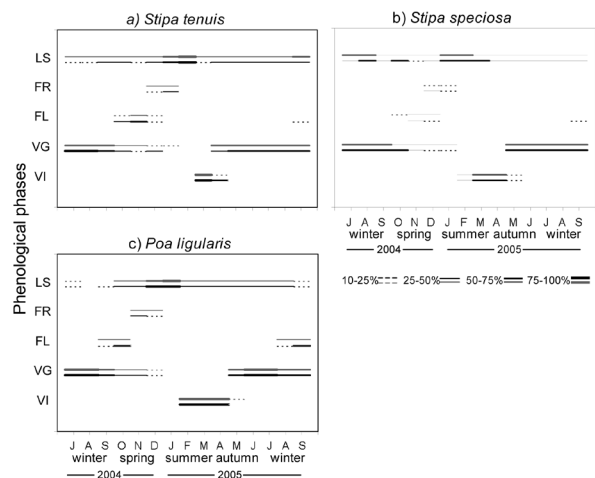


Fig. 4. Phenological evolution of species of perennial grasses at each site (site 1: grey lines and site 2: black lines) during the study period. The thickness of the lines indicates the percentage of plants at each phase. Abbreviations as in Fig. 2.

Table 2. Leaf mass per area (LMA), leaf area (mm²) and chemistry of green leaves (mean values \pm 1 SE) of species of each life form. Different uppercase letters indicate significant ($P < 0.05$) differences among life forms. Different lowercase letters indicate significant ($P < 0.05$) differences among species. nd: no data.

Species by life form	LMA (g.m ⁻²)	Leaf area (mm ²)	N concentration (%)	Total phenolics concentration (%)	Lignin concentration (%)
Evergreen shrubs	A	A	A	A	A
<i>Chuquiraga avellanadae</i>	216.27 \pm 4.66 fg	61.89 \pm 4.32 d	1.50 \pm 0.06 ab	2.01 \pm 0.09 bcd	11.21 \pm 0.51 c
<i>Chuquiraga hystrix</i>	411.50 \pm 7.36 h	21.89 \pm 0.87 b	1.10 \pm 0.05 a	1.08 \pm 0.05 ab	9.67 \pm 0.56 bc
<i>Larrea nitida</i>	148.20 \pm 3.90 cd	20.36 \pm 1.24 b	2.47 \pm 0.09 c	16.03 \pm 0.44 g	7.15 \pm 0.46 ab
<i>Larrea divaricata</i>	181.25 \pm 4.26 de	29.54 \pm 1.74 b	1.77 \pm 0.06 b	14.45 \pm 0.57 f	6.19 \pm 0.59 ab
<i>Atriplex lampa</i>	197.49 \pm 8.41 ef	12.67 \pm 0.56 a	1.32 \pm 0.07 a	1.29 \pm 0.14 abc	9.43 \pm 0.65 bc
Deciduous shrubs	A	A	B	A	A
<i>Prosopis alata</i>	166.44 \pm 15.12cde	18.04 \pm 1.79 b	3.65 \pm 0.08 d	2.62 \pm 0.16 d	12.52 \pm 0.53 c
<i>Prosopidastrum globosum</i>	87.33 \pm 4.77 a	3.69 \pm 0.75 a	3.71 \pm 0.08 d	5.47 \pm 0.28 e	nd
<i>Lycium chilense</i>	98.36 \pm 4.73 a	4.02 \pm 0.32 a	5.20 \pm 0.17 e	1.50 \pm 0.08 abcd	4.19 \pm 0.28 a
<i>Bougainvillea spinosa</i>	144.32 \pm 3.98 bc	5.17 \pm 0.34 a	2.42 \pm 0.06 c	2.35 \pm 0.08 cd	6.35 \pm 0.44 ab
Perennial grasses	A	A	AB	A	A
<i>Stipa tenuis</i>	113.15 \pm 3.41 ab	27.27 \pm 1.95 b	3.51 \pm 0.08 d	0.55 \pm 0.02 a	3.62 \pm 0.54 a
<i>Stipa speciosa</i>	237.94 \pm 9.16 g	98.41 \pm 8.87 e	1.44 \pm 0.04 ab	0.68 \pm 0.03 a	9.57 \pm 1.00 bc
<i>Poa ligularis</i>	143.99 \pm 6.72 bc	41.19 \pm 6.77 c	2.24 \pm 0.11 c	0.66 \pm 0.03 a	3.70 \pm 0.32 a

of the leaves senesced during the study period remained attached to the bunch.

Traits of green leaves

Leaf mass per area (LMA) and leaf area varied significantly among species ($F_{11,120} = 146.8$, $p < 0.0001$, $F_{11,120} = 58.48$, $p < 0.0001$, respectively) but did not show differences among life forms (Table 2). Two deciduous shrubs (*P. globosum* and *L. chilense*) showed the lowest LMA and the lowest leaf area and one evergreen shrub (*C. hystrix*) the largest LMA. Among grasses, *S. speciosa* showed the largest LMA and the largest leaf area. The leaf area was significantly positively correlated to LMA ($r = 0.58$, $P = 0.049$, $n = 6$, power function). The concentration of N varied significantly among life forms

($F_{2,12} = 6.29$, $p = 0.0198$) and species ($F_{11,120} = 188.72$, $p < 0.0001$). Evergreen shrubs showed the lowest values and deciduous shrubs the highest ones. Concentrations of total phenolics and lignin varied significantly among species ($F_{11,120} = 545.9$, $p < 0.0001$; $\chi^2 = 51.79$, $p < 0.0001$, respectively) but did not show differences among life forms. *Larrea* spp. showed the highest values of total phenolics and perennial grasses the lowest ones. The highest lignin concentrations were found in the evergreen shrub *C. avellanadae* while the lowest values of this trait were showed by the deciduous shrub *L. chilense* and the perennial grasses *S. tenuis* and *P. ligularis*.

Table 3. Chemistry of senesced leaves (mean values \pm 1 SE) of species of each life form. Different uppercase letters indicate significant ($P < 0.05$) differences among life forms. Different lowercase letters indicate significant ($P < 0.05$) differences among species.

Species by life form	N concentration (%)	Total phenolics concentration (%)	Lignin concentration (%)
Evergreen shrubs	A	A	A
<i>Chuquiraga avellanadae</i>	0.40 \pm 0.01 a	3.05 \pm 0.09 bc	12.52 \pm 0.09 c
<i>Chuquiraga hystrix</i>	0.57 \pm 0.03 abc	1.89 \pm 0.09 ab	7.29 \pm 0.86 b
<i>Larrea nitida</i>	0.97 \pm 0.05 d	14.67 \pm 0.82 e	7.52 \pm 0.79 b
<i>Larrea divaricata</i>	0.72 \pm 0.03 bc	12.79 \pm 0.28 d	5.65 \pm 0.74 ab
<i>Atriplex lampa</i>	0.67 \pm 0.03 bc	1.68 \pm 0.08 ab	7.83 \pm 0.42 bc
Deciduous shrubs	A	A	A
<i>Prosopis alata</i>	2.26 \pm 0.07 e	3.72 \pm 0.36 c	10.09 \pm 0.5 bc
<i>Lycium chilense</i>	1.06 \pm 0.02 d	2.32	3.94
<i>Bougainvillea spinosa</i>	0.75 \pm 0.03 c	2.72 \pm 0.49 bc	4.55 \pm 0.83 ab
Perennial grasses	A	A	A
<i>Stipa tenuis</i>	0.75 \pm 0.03 c	0.50 \pm 0.02 a	2.80 \pm 0.48 a
<i>Stipa speciosa</i>	0.53 \pm 0.02 ab	0.88 \pm 0.03 a	9.57 \pm 2.18 bc
<i>Poa ligularis</i>	0.98 \pm 0.08 d	0.72 \pm 0.06 a	4.31

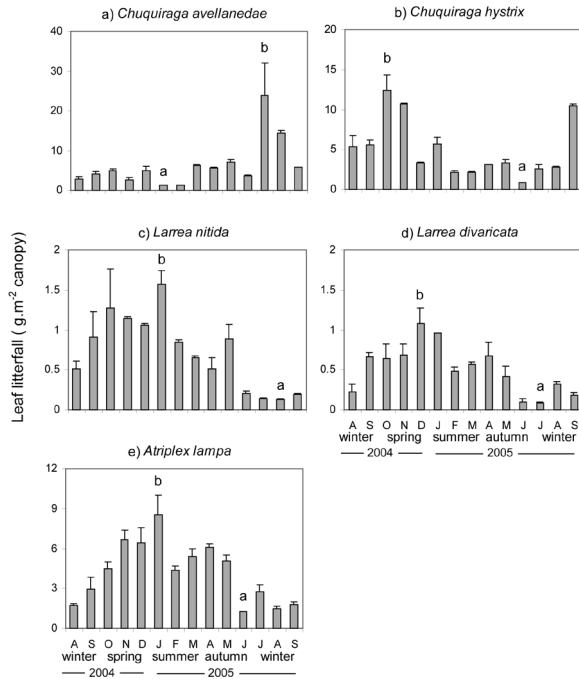


Fig. 5. Monthly leaf litterfall ($\text{g}\cdot\text{m}^{-2}$ canopy) in evergreen shrubs. Mean values \pm 1 SE. Different lowercase letters indicate significant differences ($P < 0.05$) between months with the maximum and the minimum events.

Traits of senesced leaves

Traits of senesced leaves varied among species ($F_{10,92} = 172.47, p < 0.0001$; $F_{9,82} = 226.99, p < 0.0001$; $\chi^2 = 29.84, p = 0.0009$; for N concentration, total phenolics and lignin concentration, respectively) but did not differ among life forms (Table 3). We found the lowest N concentration in senesced leaves of the evergreen shrub *C.*

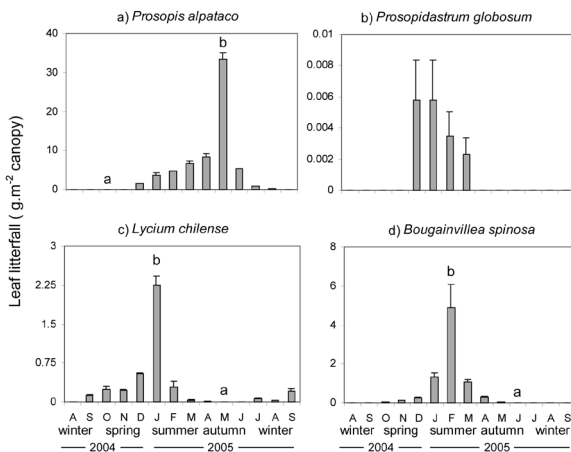


Fig. 6. Monthly leaf litterfall ($\text{g}\cdot\text{m}^{-2}$ canopy) in deciduous shrubs. Mean values \pm 1 SE. Different lowercase letters indicate significant differences ($P \leq 0.05$) between months with the maximum and the minimum events.

avellanedae and the highest value in those of *P. alpacato*. *Larrea* spp. showed the highest values of total phenolics and perennial grasses the lowest ones. The highest concentration of lignin in senesced leaves was shown by the evergreen shrub *C. avellanedae*. The perennial grass *Stipa speciosa*, the deciduous shrub *P. alpacato* and the evergreen shrubs *C. hystrix*, and *A. lampa* also showed a high lignin concentration in senesced leaves that did not significantly differ from that of *C. avellanedae*. Senesced leaves of all species strongly reduced the N-concentration ($F_{1,212} = 274.005, p < 0.0001$) while they maintained similar concentrations of lignin and total phenolics relative to green leaves.

Mass and timing of leaf litterfall

The mass of annual leaf litterfall (September 2004 - August 2005) varied significantly among species ($\chi^2 = 96.38, p < 0.0001$) showing a large overlap among life forms ($F_{2,12} = 1.326, p = 0.313$). Two deciduous shrubs, *P. globosum* and *L. chilense*, produced the lowest mass of annual leaf litterfall while the perennial grass *S. speciosa* and the evergreen shrub *C. avellanedae* yielded the highest values (Table 4).

Species differed in the timing of leaf litterfall events across the year but all of them showed a seasonal pattern. We did not identify a pattern associated with each life form except for deciduous shrubs. Evergreen shrubs showed gradual leaf shedding with leaf litterfall events occurring throughout the year (Fig. 5) but the timing of maximum/minimum events varied among species (winter/summer in *C. avellanedae*; spring/autumn in *C. hystrix*; spring-summer/winter in *L. divaricata* and *L.*

Table 4. Mass of annual (September 2004 to August 2005) leaf litterfall (mean values \pm 1 SE) of species of each life form. Different capital letters indicate significant ($P \leq 0.05$) differences among life forms. Different lowercase letters indicate significant ($P < 0.05$) differences among species.

Species by life form	Annual leaf litterfall ($\text{g}\cdot\text{m}^{-2}$ canopy \cdot year $^{-1}$)
Evergreen shrubs	
<i>Chuquiraga avellanedae</i>	79.88 \pm 13.58 d
<i>Chuquiraga hystrix</i>	54.64 \pm 5.53 cd
<i>Larrea nitida</i>	9.33 \pm 2.89 ab
<i>Larrea divaricata</i>	6.67 \pm 1.43 ab
<i>Atriplex lampa</i>	55.48 \pm 10.39 cd
Deciduous shrubs	
<i>Prosopis alpacato</i>	64.58 \pm 9.47 cd
<i>Prosopidastrum globosum</i>	0.017 \pm 0.012 a
<i>Lycium chilense</i>	3.81 \pm 1.17 a
<i>Bougainvillea spinosa</i>	7.99 \pm 1.55 ab
Perennial grasses	
<i>Stipa tenuis</i>	46.13 \pm 5.06 cd
<i>Stipa speciosa</i>	110.53 \pm 26.68 d
<i>Poa ligularis</i>	28.03 \pm 6.43 bc

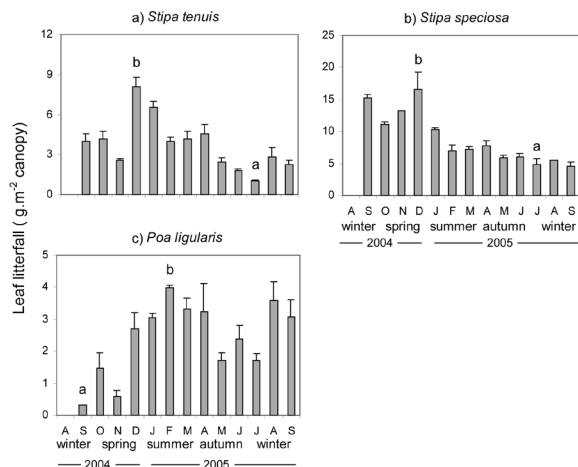


Fig. 7. Monthly leaf litterfall ($\text{g}\cdot\text{m}^{-2}$ canopy) in perennial grasses. Mean values \pm 1 SE. Different lowercase letters indicate significant differences ($P < 0.05$) between months with the maximum and the minimum events.

nitida and summer/autumn in *A. lampa*). All deciduous shrub species showed a massive seasonal pulse of litterfall in summer-autumn (Fig. 6). Perennial grasses had leaf litterfall events throughout the year. The maximum/minimum events occurred in spring/winter in *S. speciosa*, in spring-summer/winter in *S. tenuis* and in *S. speciosa* and in summer/winter in *P. ligularis*, respectively (Fig. 7). In all perennial grasses, most leaves senesced in the current year remained attached to bunch and leaf litterfall consisted of a small proportion of recently senesced leaves and a large proportion of leaves senesced in the previous years.

Relationship among the annual mass of leaf litterfall, the length of the vegetative growth period and leaf traits

The LMA of green leaves and lignin concentrations in green and senesced leaves were the leaf traits most related to the annual mass of leaf litterfall. Three evergreen shrub species (*A. lampa*, *C. avellanadae* and *C. hystrix*), one deciduous shrub species (*P. alpataco*) and one perennial grass species (*S. speciosa*) had the highest values of these leaf traits, and the highest values of annual mass of litterfall (Fig. 8). Among the rest of the species we distinguished two other groups. One of them was formed by two perennial grass species (*P. ligularis*, *S. tenuis*) and two deciduous shrub species (*L. chilense*, *B. spinosa*) characterized by low lignin and phenolics concentrations leaves, low/intermediate values of LMA in green leaves and low/intermediate annual mass of leaf litterfall. Among these species, the deciduous shrub *L. chilense* displayed the lowest values of these traits. The

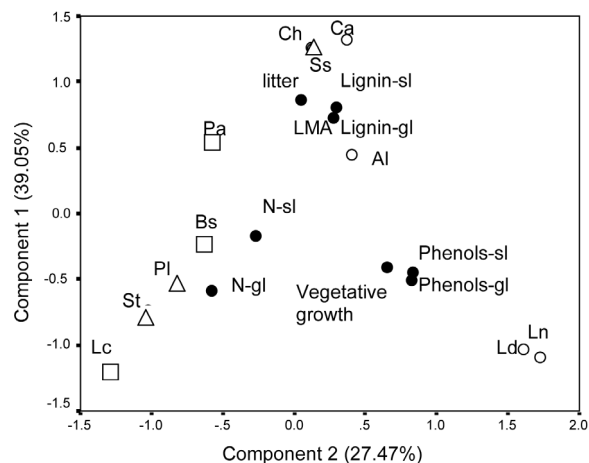


Fig. 8. Ordination of plant attributes and species (loading coefficients) with respect to the two first principal components of the correlation matrix among annual leaf-litter production, duration of the period of vegetative growth (months), LMA, and chemistry of green and senesced leaves (gl, and sl, respectively) of species (filled circles). ○ = Evergreen shrubs (Ca: *C. avellanadae*, Ch: *C. hystrix*, Ln: *L. nitida*, Ld: *L. divaricata* and Al: *A. lampa*); □ = deciduous shrubs (Pa: *P. alpataco*, Pg: *P. globosum*, Lc: *L. chilense* and Bs: *B. spinosa*); △, perennial grasses (St: *S. tenuis*, Ss: *S. speciosa* and Pl: *P. ligularis*).

other group included *Larrea* spp. with low lignin concentration and high phenolics concentration in leaves, intermediate values of LMA of green leaves and low annual mass of leaf litterfall. Furthermore, phenolics concentration in leaves was strongly related with the duration of the vegetative period.

Discussion

We hypothesized that coexisting life forms in the Patagonian Monte differ in overall phenology, leaf traits and patterns of leaf litterfall. We found that these plant attributes varied among species but overlapped among life forms (evergreen shrubs, deciduous shrubs and perennial grasses). Species were distributed along two main dimensions of ecological variation, the dimension secondary compounds in leaves - length and timing of the vegetative growth period (SC - VGP) and the dimension leaf mass per area - leaf litterfall mass (LMA - LLM).

The SC - VGP dimension indicated the production of drought resistant leaves in plants with short or long vegetative growth period which extends over the dry season (Cunningham et al. 1999; Wright & Cannon 2001). This axis of ecological variation is also related to other plant traits such as rooting depth (Sala et al. 1989; Bertiller et al. 1991; Meinzer et al. 1999). In the study

area, the entire soil profile is wet in winter-spring while at the beginning of the summer, water is only available at deep soil layers (Coronato & Bertiller 1997). Accordingly, some deep rooted shrubs (the evergreens: *Larrea* spp., *A. lampa*, *Chiquiraga* spp. and the deciduous *P. alpataco*) with drought resistant leaves (high LMA; high lignin or phenolics concentrations) showed vegetative activity during the dry season. In contrast, species with shallow root systems and/or non-drought resistant leaves (low LMA and low concentration of lignin or phenolics) concentrated phenological activity in the wet winter-spring period (the deciduous shrubs: *L. chilense*, *P. globosum*, *B. spinosa* and the perennial grasses: *S. tenuis*, *P. ligularis*). In these species, phenological inactivity during drought was associated with massive leaf senescence. An intermediate case was the shallow rooted *S. speciosa* maintaining green leaves with high LMA and high lignin concentration during the inactive growth period in the dry season. Similar findings were reported by Golluscio & Sala (1993) for Patagonian forbs. They found that differences in plant traits (morphology, phenology, physiology) among species of this life form reflected the hierarchical structure of the temporal pattern of soil water dynamics. Our results are also consistent with the high diversity in functional and adaptive strategies among perennial species (Aerts 1996) coexisting in unpredictable, water limited ecosystems (Zunzunegui et al. 2005, Golluscio et al. 2005).

The LMA – LLM dimension indicated that species with the largest LMA and lignin concentration in leaves produced the largest mass of leaf litterfall. This was not in accordance with our expectations of small leaf litterfall mass in species with high amounts of secondary compounds in leaves and observations indicating that leaf lifespan in high LMA Patagonian species lasts more than one year (Bertiller et al. 1991; Carrera et al. 2000; Bertiller et al. 2006). High LMA species with high concentrations of secondary compounds in leaves usually have long leaf lifespan thus compensating for the high costs of production of drought/herbivore resistant leaves (Crawley 1998; Westoby et al. 2002). An alternative explanation for our findings could be related to plant traits other than leaf lifespan such as plant architecture, height or LAI. In the case of the deciduous *P. globosum*, low litterfall mass could be the result of a very low LAI and small leaves with very low LMA probably associated with the occurrence of photosynthetic stems. In *L. chilense*, despite the large LAI, low leaf litterfall mass may be primarily attributed to small leaves with low LMA. In contrast, high leaf litterfall mass in *C. avellanadae* may be the consequence of high LAI, high canopy cover and large leaves with high LMA. However, as expected for evergreens, *Larrea* species produced very low leaf litterfall mass probably due to large leaf lifespan but also

to low LAI and canopy cover.

Furthermore, both the mass and chemistry of leaf litterfall are relevant in relation to decomposition and nutrient cycling (Lambers et al. 1998). We found that drought tolerant species produced large or low mass of leaf litterfall with high concentration of secondary metabolites (lignin or phenolics) that could decelerate litter decomposition and nutrient cycling (Carrera et al. 2005; Vargas et al. 2006). Also, species producing low amounts of N-rich litterfall could control the rates of nutrient cycling through limiting the mass of decomposable substrate. Accordingly, species varying along the above described two main dimensions of ecological variation showed contrasting mechanisms to control decomposition and nutrient cycling and probably to reduce nutrient losses in water/nutrient poor habitats (Bertiller et al. 2006).

We concluded that the two dimensions of ecological variation (SC – VGP, LMA – LLM) among species represent distinct combinations of plant traits or strategies related to resource acquisition and drought tolerance which are reflected in the patterns of leaf litterfall and in the eventual plant controls on nutrient losses, nutrient release from leaf litter and nutrient cycling.

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