



Original article

Leafing patterns and leaf traits of four evergreen shrubs in the Patagonian Monte, Argentina

María Victoria Campanella^{a,*}, Mónica B. Bertiller^{a,b}

^a Centro Nacional Patagónico (CENPAT – CONICET), Boulevard Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

^b Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Chubut, Argentina

ARTICLE INFO

Article history:

Received 13 March 2009

Accepted 24 August 2009

Published online 15 September 2009

Keywords:

Anti-herbivore defenses

Defenses against water shortage

Leaf longevity

Duration of leafing

N concentration

Soluble phenolics

Variability in annual precipitation

ABSTRACT

We assessed leafing patterns (rate, timing, and duration of leafing) and leaf traits (leaf longevity, leaf mass per area and leaf-chemistry) in four co-occurring evergreen shrubs of the genus *Larrea* and *Chuquiraga* (each having two species) in the arid Patagonian Monte of Argentina. We asked whether species with leaves well-defended against water shortage (high LMA, leaf longevity, and lignin concentration, and low N concentration) have lower leaf production, duration of the leafing period, and inter-annual variation of leafing than species with the opposite traits. We observed two distinctive leafing patterns each related to one genus. *Chuquiraga* species produced new leaves concentrated in a massive short leafing event (5–48 days) while new leaves of *Larrea* species emerged gradually (128–258 days). Observed leafing patterns were consistent with simultaneous and successive leafing types previously described for woody plants. The peak of leaf production occurred earlier in *Chuquiraga* species (mid September) than in *Larrea* species (mid October–late November). Moreover, *Chuquiraga* species displayed leaves with the longest leaf lifespan, while leaves of *Larrea* species had the lowest LMA and the highest N and soluble phenolics concentrations. We also observed that only the leaf production of *Larrea* species increased in humid years. We concluded that co-occurring evergreen species in the Patagonian Monte displayed different leafing patterns, which were associated with some relevant leaf traits acting as plant defenses against water stress and herbivores. Differences in leafing patterns could provide evidence of ecological differentiation among coexisting species of the same life form.

© 2009 Elsevier Masson SAS. All rights reserved.

1. Introduction

Resource pulsing in arid ecosystems could provide axes of ecological differentiation among species facilitating their coexistence in these harsh environments (Chesson et al., 2004). Important adaptations for plant coexistence in arid ecosystems are those promoting the separation of water use in time (phenological asynchrony), the relative differences in the utilization of water in the upper soil, and differences in the readiness of plant responses to environmental triggers, among others (Reynolds et al., 2004).

The leafing pattern could be considered an important indicator of plant activity (Seghieri and Simier, 2002). The timing of leafing in perennial plants mostly depends on rainfall pulses and the time, length and intensity of the moist season (Chesson et al., 2004; Reynolds et al., 2004). In spite of this, some desert perennial plants could maintain vegetative activity throughout the year or during drought due to the utilization of external water sources stored in

different soil layers (Noy-Meir, 1973). This extended activity requires the construction of drought resistant aboveground tissues, which in turn may have high costs for plants (Crawley, 1998). However, in most plants, the benefits of having drought resistant tissues could outweigh the costs (Koricheva et al., 2004). In fact, drought resistant leaves have low turnover and long lifespan (Westoby et al., 2002). Leaf longevity is a plant trait of great ecological significance in arid ecosystems since it is related not only to plant functional responses to water shortage but also to a prolonged residence time of nutrients in leaves, thus improving both water and nutrient use efficiency in plants (Escudero et al., 1992; Aerts, 1996; Eckstein et al., 1999; Casper et al., 2001). In contrast, plant species with short-lived leaves, low LMA and high N concentration have greater potential for fast growth and eventually show higher plastic responses to variation in soil resources than those with long-lived leaves (Westoby et al., 2002).

Several studies described the variation in leaf traits or leafing patterns of a broad spectrum of species of different life forms growing in a wide range of environments (Castro-Díez et al., 1997; Nitta and Ohsawa, 1997; Williams et al., 1997; Reich et al., 1999; Broadhead et al., 2003; Wright et al., 2004; Bertiller et al., 2005;

* Corresponding author. Fax: +54 2965 451543.

E-mail address: campanella@cenpat.edu.ar (M.V. Campanella).

Sekhwela and Yates, 2007). Only few studies analyzed simultaneously leafing patterns and leaf traits (Williams-Linera, 2000; Sun et al., 2006) providing some evidence of relationships among leaf longevity, leaf area and leafing patterns in tree species. However, studies relating leafing patterns and leaf traits in desert species are very scarce. Addressing this topic could be important in providing possible evidence of ecological differentiation among coexisting species in harsh arid environments (Chesson et al., 2004).

In the arid Patagonian Monte, evergreen shrubs show a wide variation in leaf traits and phenological patterns (Bertiller et al., 1991; Carrera et al., 2000; Campanella and Bertiller, 2008), offering an interesting target plant group to test hypotheses about the relationships between leafing patterns and leaf traits among coexisting species of the same life form. In this paper, we assessed simultaneously the leafing pattern (rate, timing, and duration of leafing) in consecutive annual periods and leaf traits (leaf longevity, leaf mass per area and leaf-chemistry) of four coexisting dominant evergreen shrub species in the Patagonian Monte. We hypothesized that species with leaves well-defended against water shortage (high LMA, leaf longevity, and lignin concentration, and low N concentration) have lower leaf production, duration of the leafing period, and inter-annual variation of leafing than species with the opposite traits.

2. Materials and methods

2.1. Study site and evergreen shrub species

The study was undertaken in Estancia San Luis (42° 38' 51" S, 65° 23' 03" W) located in the northeastern of the Chubut Province (Argentina). The climate is arid with a mean annual precipitation of 258.14 mm and a mean annual temperature of 13.9 °C (8-year series). Precipitation events occur without a seasonal pattern or are slightly concentrated in the cold period with a high intra- and inter-annual variation (Barros and Rivero, 1982). We selected a floristic homogeneous area dominated by the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (Ares et al., 1990), characteristic of the Patagonian Monte (Bisigato and Bertiller, 1997). 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. Shrub clumps (1–2 m height) concentrate 60–80% of the total shrub cover and are dominated by *L. divaricata*, *Larrea nitida* Cav., *Chuquiraga avellanedae* Lorentz, *Chuquiraga erinacea* D. Don subsp. *hystrix* (Don) C. Ezcurra among other less abundant species (Bisigato and Bertiller, 1997). For this study, we selected the four dominant evergreen shrubs in the shrub clumps: *C. avellanedae*, *C. erinacea* subsp. *hystrix*, *L. divaricata*, and *L. nitida*. Daily precipitation events were registered at the study site with an automatic data recorder during the study period (21X Micrologger, Campbell Scientific). The study encompassed 3 consecutive yearly growth cycles from June to June (year 1: 2004–2005, year 2: 2005–2006, year 3: 2006–2007).

2.2. Leafing patterns

The appearance of new leaves on 1–2 terminal branches on 4–10 randomly selected individuals of each species was registered monthly. Then, we calculated the monthly cumulative number of new leaves per shoot of each plant at each year and fitted a sigmoid function to these data as follows:

$$CNL_{(x)} = a_0 / (1 + (e^{-(x-a_1)/a_2}))$$

where CNL is the cumulative number of new leaves per shoot at the month x , a_0 is the maximum cumulative number of new leaves per

shoot, a_1 is the date of the peak of leaf production, and a_2 is a constant that determines the curvature of the curve of cumulative number of new leaves per shoot and it is directly proportional to the duration of the leafing period (Fig. 1). We further computed the duration of the leafing period as the number of months between the beginning and the end (10 and 90%, respectively) of the leafing period as $4.4 \times a_2$ (Tateno et al., 2005).

2.3. Leaf traits

Leaf longevity was assessed by monitoring 4–14 new emerged leaves until senescence in 6–8 mature individuals of each species monthly. The date of emergence of each leaf was estimated as the mid-point time between the previous interval and the interval in which the new leaf was first observed. Similarly, the date of death of each leaf was estimated as the mid-point time between two successive observations of pre- and post leaf senescence. Leaf longevity was calculated as the number of days elapsed between the dates of leaf emergence and leaf death (Kikuzawa, 2003).

We collected fully expanded young to medium-aged green leaves (Reich et al., 1991; Bertiller et al., 2006) from the external canopy crown from 10 randomly selected plants in two consecutive years (2005–2006) for chemical analysis. We assessed N concentration by semi-micro Kjeldahl (Coombs et al., 1985), lignin concentration by the Van Soest (1963) procedure and soluble phenolics concentration by the Folin–Ciocalteu method using 50% methanol as extract solution and tannic acid as standard (Waterman and Mole, 1994). All concentrations were expressed on a dry mass basis. Leaf mass per area (LMA) of each species was obtained from Campanella and Bertiller (2008).

2.4. Statistical analysis

We used one-way ANOVA to evaluate (1) the significance of the differences in parameters of sigmoid functions (a_0 , a_1 and $4.4 \times a_2$) among species within each year, and among years within each species, and (2) the significance of the differences in leaf longevity, LMA, and N and lignin concentrations in green leaves among species. To perform these analyses, we used mean values of leaf longevity per individual as replicates. The significance of the differences in soluble phenolics concentration among species was evaluated by Kruskal–Wallis test. We used Tukey's test for multiple comparisons. Principal component analysis (PCA) was performed to explore associations between mean values of leafing parameters and leaf traits. We calculated the loading coefficients of each species with respect to the

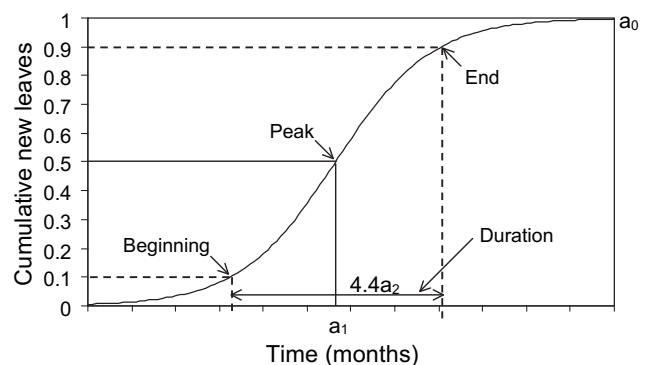


Fig. 1. Representation of the sigmoidal model used to estimate the cumulative number of new leaves per shoot during an annual period. $CNL_{(x)} = a_0 / (1 + (e^{-(x-a_1)/a_2}))$ where CNL is the cumulative number of new leaves per shoot at the month x , a_0 is the maximum cumulative number of new leaves per shoot, a_1 is the date of the peak of leaf production, and a_2 is a constant that determines the curvature of CNL and it is directly proportional to the duration of the leafing period ($4.4 \times a_2$ = number of months between the beginning and the end (10 and 90%, respectively) of leafing).

two first principal components of the correlation matrix of mean values of leaf and leafing traits. All statistical analyses were performed with the package SPSS 7.5 (Norusis, 1997).

3. Results

3.1. Precipitation

Precipitation differed among years (June–June) during the study period. Year 1 showed the lowest and year 3 the highest value of cumulated precipitation (Fig. 2). Monthly precipitation events were slightly concentrated in the cold period but we registered large precipitation events in July 2006 (winter), December 2005 (summer) and March 2007 (autumn).

3.2. Leafing patterns

3.2.1. Maximum cumulative number of new leaves per shoot (a_0)

Differences in the maximum cumulative number of new leaves per shoot (a_0) varied among species depending on the year. During the first year *C. erinacea* subsp. *hystrix* and *L. nitida* showed the highest and *L. divaricata* and *C. avellanadae* the smallest a_0 (Figs. 3 and 4a). In the second year *Chuquiraga* species showed the smallest and *L. nitida* the highest a_0 (*L. nitida* > *L. divaricata* > *C. avellanadae* = *C. erinacea* subsp. *hystrix*). In the third year, *L. nitida* presented the highest a_0 . *C. erinacea* subsp. *hystrix* presented its highest values of a_0 across years during the first year (the lowest cumulative precipitation) while in *Larrea* species the smallest a_0 occurred in the first year. In contrast, a_0 in *C. avellanadae* did not vary among years.

3.2.2. Date of the peak of leaf production (a_1)

The date of maximum leaf production rate was earlier in *Chuquiraga* species (mid September) than in *Larrea* species (mid October–late November) (Figs. 3 and 4b). The date of the peak of leaf production varied among years in *L. divaricata*, occurring earlier in year 1 (the lowest cumulative precipitation) than in the two others (Fig. 4b).

3.2.3. Duration of the leafing period ($4.4 \times a_2$)

Chuquiraga species showed the shortest duration of the leafing period (5–48 days) indicating that leaves appeared simultaneously in a massive single pulse. In contrast, new leaves of *Larrea* species emerged gradually during a longer time period of 128–258 days (Figs. 3 and 4c). In *Chuquiraga* species and *L. divaricata*, the duration of leafing was larger in year 3 (the largest cumulative precipitation) than in the other two years, while the duration of the leafing period did not vary among years in *L. nitida*.

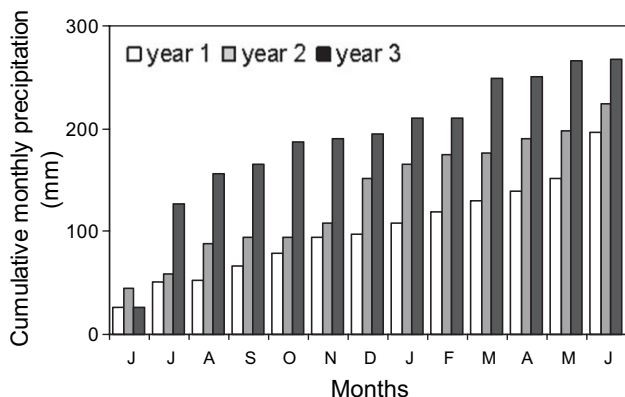


Fig. 2. Cumulative monthly precipitation at the three years during the study period (year 1: 2004–2005, year 2: 2005–2006, year 3: 2006–2007).

3.3. Leaf traits

Leaf longevity differed among species ($F_{3,25} = 26.46$, $p < 0.0001$) (Table 1). *C. avellanadae* and *C. erinacea* subsp. *hystrix* showed the largest leaf longevity since their leaves persisted on the plant during 16 and 18 months, respectively. On the other hand, leaves of *L. divaricata* and *L. nitida* lasted 11 and 8.5 months, respectively.

Nitrogen, lignin and soluble phenolics concentrations and LMA in green leaves differed among species ($F_{3,76} = 58.62$, $p < 0.0001$; $F_{3,44} = 78.97$, $p < 0.0001$; $H_3 = 67.30$, $p < 0.0001$; $F_{3,36} = 393.55$, $p < 0.0001$; respectively) (Table 1). *Chuquiraga* spp. presented the lowest N and soluble phenolics concentrations and the highest LMA and lignin concentration in green leaves.

3.4. Relationship between leafing patterns and leaf traits

The PCA axis 1 grouped at positive values leaf traits of *Larrea* species (high N and soluble phenolics concentration in green leaves) with high values of maximum cumulative number of new leaves (a_0), date of the peak of leaf production (a_1) and duration of the leafing period ($4.4 \times a_2$) (Fig. 5). In contrast, leaf traits of *Chuquiraga* species (long leaf lifespan, high LMA and high lignin concentration in green leaves) were grouped with low values of maximum, date, and duration of the leafing period at negative values of PCA axis 1. The PCA axis 2 further separated species of each genus, at negative values those with the highest lignin concentration in green leaves and at positive values species with the highest LMA.

4. Discussion

We observed two distinctive leafing patterns among coexisting evergreen shrub species consistent with those described for tree species by Kikuzawa (1983). *Chuquiraga* species produced new leaves concentrated in a massive short leafing event while new leaves of *Larrea* species emerged gradually during a longer period of time (simultaneous and successive leafing type, respectively *sensu* Kikuzawa, 1983). Both leafing patterns were associated with different leaf traits. The simultaneous leafing pattern was found in species with the longest leaf lifespan (*Chuquiraga* species), in accordance with results reported by Hikosaka (2005). In contrast, the successive leafing type was associated with low leaf lifespan and LMA and high N concentration. Species with the successive leafing type probably have the advantage of maintaining higher photosynthetic rates throughout the year by recruiting new leaves during longer periods than species with simultaneous leafing (Kikuzawa, 2003). Moreover, leaves with high LMA emerged earlier than those with low LMA in accordance with results reported by Sun et al. (2006). This seems to be advantageous for species with high leaf construction costs in arid ecosystems since the massive leafing early in the growing season could increase carbon gain when water is still not limiting to maintain high photosynthetic rates.

These results provide evidence of contrasting leafing patterns and leaf traits among coexisting species at a local scale, which are consistent with those occurring at regional scales (Castro-Díez et al., 1997; Nitta and Ohsawa, 1997; Williams et al., 1997; Reich et al., 1999; Broadhead et al., 2003; Wright et al., 2004; Bertiller et al., 2005; Sekhwela and Yates, 2007). Further, our findings could indicate some ecological differentiation among coexisting species of the same life form in harsh arid environments. This ecological differentiation could be associated with the ability of species to use soil water differentially in space and time, the readiness of species responses to water inputs, and species plasticity (Westoby et al., 2002; Chesson et al., 2004; Reynolds et al., 2004).

Water is an important resource influencing the beginning of sprouting and the duration of the growth period in many plant

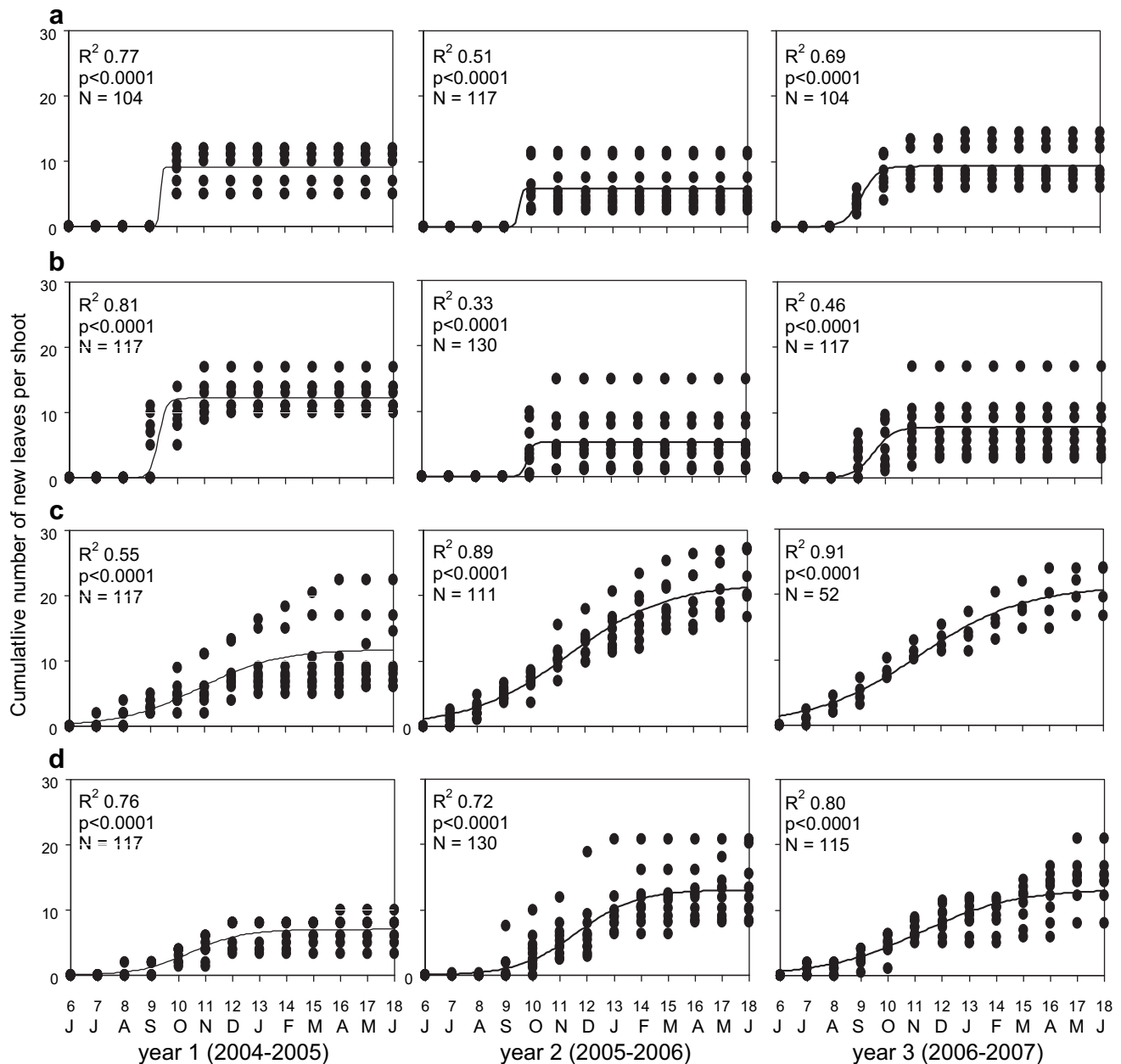


Fig. 3. Cumulated number of new leaves per shoot and plant (black dots) at monthly intervals and mean fitted sigmoid functions (line) at each year of a) *C. avellanadae*; b) *C. erinacea* subsp. *hystrix*; c) *L. nitida*, and d) *L. divaricata*.

species (Seghieri et al., 1995; Abd El-Ghani, 1997; De Bie et al., 1998; Ghazanfar, 1997; Haase et al., 1999; Shackleton, 1999; Pavón and Briones, 2001; Peñuelas et al., 2004; Otieno et al., 2005). In our study, the peak of leafing in all species (i.e. early spring in *Chuquiraga* species and late spring in *Larrea* species) occurred when water is available at intermediate depths (Coronato and Bertiller, 1997). But both groups of species showed large differences in leafing duration, which could also be sustained by differences in the rooting depth and root topology between them. *Larrea* species develop a very deep (more than 3 m) dimorphic root system with active fine roots in the upper soil layer (Bertiller et al., 1991; Rodríguez et al., 2007). This characteristic could, in turn, allow an extended leafing period by the rapid utilization of small precipitation events during summer in contrast to the non-dimorphic root system of *Chuquiraga* species with a root penetration ranging from

1.5 to 1.7 m (Bertiller et al., 1991). Our results on *Larrea* species are consistent with those reported for *Larrea tridentata* in the southern Chihuahuan Desert. This species also possesses a bimodal active root system allowing the use of different water sources at different times (Ogle et al., 2004).

Also, we found different species responses to inter-annual variation of precipitation. *Chuquiraga* species with long lasting leaves did not increase leaf production in humid years in contrast to *Larrea* species. This result is consistent with others obtained under experimental drought indicating lower leaf production in species with drought resistant traits (Ogaya and Peñuelas, 2006). Accordingly, our results reveal species/genus-specific responses in leafing patterns of evergreen shrubs probably related to different ability of species with different leaf traits and relative growth rates to respond to inter-annual variation in precipitation. We did not assess relative growth

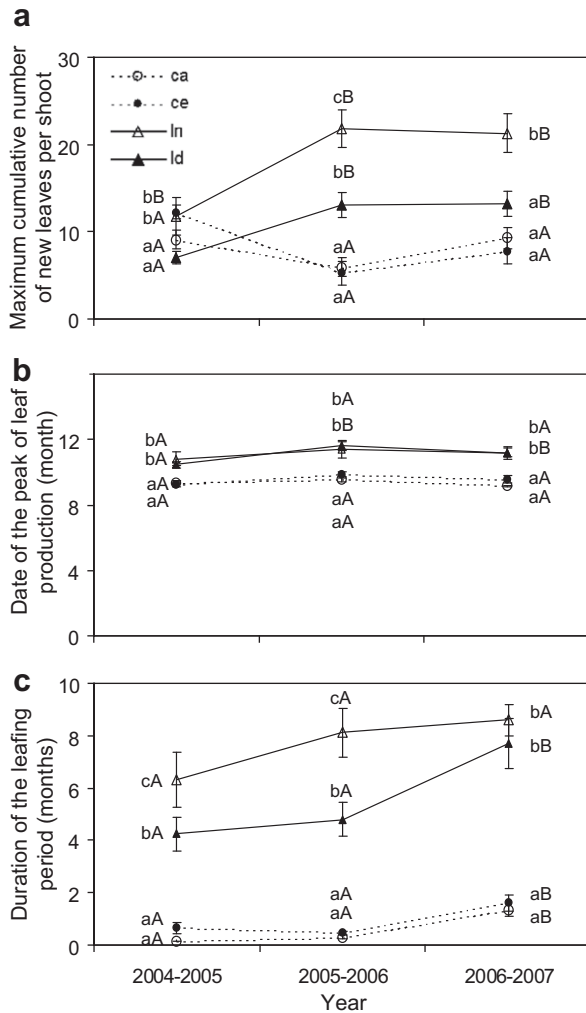


Fig. 4. Mean values \pm 1SE of parameters of the fitted sigmoid functions in Fig. 3. a) Maximum cumulative number of new leaves per shoot (a_0), b) Date of the peak of leaf production (a_1), months from 1 (January) to 12 (December), and c) Duration of the leafing period ($4.4 \times a_2$). Different capital letters indicate significant ($p < 0.05$) differences in the same parameter among years for each species. Different lowercase letters indicate significant ($p < 0.05$) differences in the same parameter among species for each year. ca = *C. avellanadae*, ce = *C. erinacea* subsp. *hystrix*, ln = *L. nitida* and ld = *L. divaricata*.

rates but there is evidence of a positive correlation between this trait and N concentration in green leaves (Poorter and Remkes, 1990; Reich et al., 1992, 1998). Accordingly, species with higher N concentration in green leaves and shorter leaf lifespan (*Larrea* species) probably have higher relative growth rate and consequently are more responsive to inter-annual variation in precipitation than species with low N concentration and high leaf longevity and LMA in green leaves such as *Chuquiraga* species (Aerts, 1995; Aerts and Chapin III, 2000).

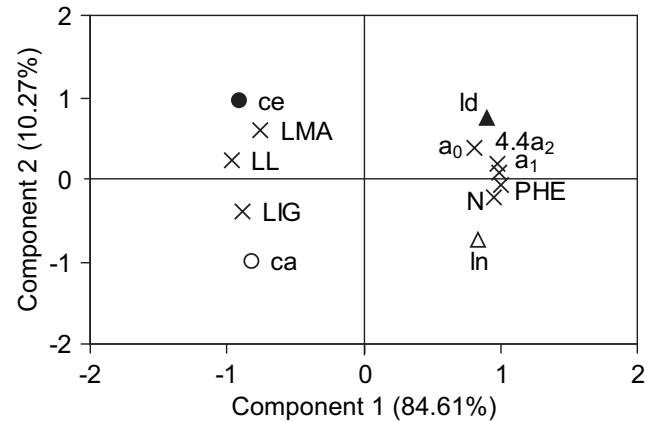


Fig. 5. Ordination of mean values of leaf attributes, parameters of the fitted sigmoid functions and species (loading coefficients) with respect to the two first principal components of the correlation matrix among leaf longevity (LL), leaf mass per area (LMA), N (N), lignin (LIG) and soluble phenolics (PHE) concentrations in green leaves, and fitted curve parameters (a_0 , a_1 , and $4.4 \times a_2$ as in Fig. 1). ca = *C. avellanadae*, ce = *C. erinacea* subsp. *hystrix*, ln = *L. nitida* and ld = *L. divaricata*.

Moreover, *Chuquiraga* species due to shorter leafing periods could be more affected by intra-annual changes in the precipitation regimen than *Larrea* species, a fact that should be further explored. However, both groups of species extended the duration of the leafing period in the most humid year. In addition, other environmental factors not explored in this study could influence the responses of species to annual precipitation such as antecedent conditions of soil water availability (Reynolds et al., 2004), non-gradual responses (Peñuelas et al., 2004) and precipitation thresholds (Schwinning et al., 2003).

Ecological differentiation among species could also be associated with the history of herbivory. There is some speculation on the large history of herbivory in Patagonian ecosystems (Lauenroth, 1998). The massive pattern of leaf production of *Chuquiraga* species in a very short time period when leaves of other more preferred species such as perennial grasses are still available (Bertiller et al., 1991; Campanella and Bertiller, 2008) could result from an adaptation to reduce herbivory on leaves of these species (Aide, 1988). In contrast, in *Larrea* species the high concentration of soluble phenolics in green leaves could be associated with an effective defense against herbivores (Hättenschwiler and Vitousek, 2000; Hyder et al., 2002) allowing the production of high amounts of new leaves during a long time period.

Studies on the ecology of canopy components such as those presented in our study are not only important in the context of species ecology but also in relation to the structure and functioning of arid ecosystems under climatic change. Our results suggest that coexisting evergreen shrub species could be differently vulnerable to shifts in the seasonality of precipitation induced by global change (Peñuelas and Filella, 2001; Gao and Reynolds, 2003; Jolly and Running, 2004). Accordingly, species-specific differences in responses to precipitation variation could affect the competitive ability of these species and their future distribution.

Table 1

Mean (\pm 1SE) leaf longevity and leaf attributes in green leaves of evergreen shrub species. Different lowercase letters indicate significant ($p < 0.05$) differences among species. *LMA values were obtained from Campanella and Bertiller (2008).

Evergreen shrubs	Leaf longevity		N concentration (%)	LMA* (g m^{-2})	Lignin concentration (%)	Soluble phenolics (%)
	No. individuals (no. leaves)	Mean leaf longevity (days)				
<i>C. avellanadae</i>	7 (68)	504.1 \pm 23.94 c	1.27 \pm 0.06 a	216.27 \pm 4.66 c	10.45 \pm 0.35 c	2.11 \pm 0.06 b
<i>C. erinacea</i> subsp. <i>hystrix</i>	8 (101)	558.6 \pm 31.38 c	1.17 \pm 0.04 a	411.50 \pm 7.36 d	7.47 \pm 0.48 b	1.17 \pm 0.04 a
<i>L. nitida</i>	8 (44)	260.4 \pm 30.86 a	2.21 \pm 0.10 c	148.2 \pm 3.90 a	4.71 \pm 0.23 a	15.93 \pm 0.35 c
<i>L. divaricata</i>	6 (29)	336.44 \pm 17.06 b	1.87 \pm 0.07 b	181.25 \pm 4.26 b	4.20 \pm 0.15 a	14.93 \pm 0.42 c

We concluded that co-occurring evergreen species in the Patagonian Monte display different leafing patterns, which were associated with some relevant leaf traits acting as plant defenses against water stress and herbivores. The association between leafing patterns and leaf traits found in our study at a local scale is consistent with that observed at a regional scale encompassing a wide range of ecosystem variation. Further, our results could provide evidence of ecological differentiation among coexisting species of the same life form to cope with spatial and temporal variability of soil water but also suggest that other environmental agents could be associated with ecological differentiation among species.

Acknowledgements

This research was supported by PICT 11131 and 20454 1201/OC-AR-1728/OC-AR, National Agency for Scientific and Technological Promotion. M.V. Campanella fellowship was supported by FONCYT and CONICET (National Research Council of Argentina). Recognition is also given to Mr Fermín Sarasa who allowed the access to the study area in Estancia “San Luis”. Authors are grateful to anonymous reviewers and Jacqui Shykoff for their useful comments.

References

- Abd El-Ghani, M., 1997. Phenology of ten common plant species in western Saudi Arabia. *J. Arid Environ.* 35, 673–683.
- Aerts, R., 1995. The advantages of being evergreen. *Trends Ecol. Evol.* 10, 402–407.
- Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.* 84, 597–608.
- Aerts, R., Chapin III, F.S., 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67.
- Aide, T.M., 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. *Nature* 336, 574–575.
- Ares, J.O., Beeskow, A.M., Bertiller, M.B., Rostagno, C.M., Irisarri, M.P., Anchorena, J., Defossé, G.E., Merino, C.A., 1990. Structural and dynamic characteristics of overgrazed land of northern Patagonia, Argentina. In: Breymeyer, A. (Ed.), *Managed Grasslands*. Elsevier, The Netherlands, pp. 149–175.
- Barros, V., Rivero, M., 1982. Mapas de probabilidad de precipitación de la Provincia del Chubut. Monografía 54. Centro Nacional Patagónico, Puerto Madryn, Chubut, Argentina.
- Bertiller, M.B., Beeskow, A.M., Coronato, F., 1991. Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). *J. Arid Environ.* 21, 1–11.
- Bertiller, M.B., Sain, C.L., Carrera, A.L., Vargas, D.N., 2005. Patterns of nitrogen and phosphorus conservation in dominant perennial grasses and shrubs across an aridity gradient in Patagonian. *J. Arid Environ.* 62, 209–223.
- Bertiller, M.B., Mazzarino, M.J., Carrera, A.L., Diehl, P., Satti, P., Gobbi, M., Sain, C.L., 2006. Leaf strategies and soil N across a regional humidity gradient in Patagonia. *Oecologia* 148, 612–624.
- Bisigato, A.J., Bertiller, M.B., 1997. Grazing effects on patchy dry land vegetation in northern Patagonia. *J. Arid Environ.* 36, 639–653.
- Broadhead, J.S., Ong, C.K., Black, C.R., 2003. Tree phenology and water availability in semi-arid agroforestry systems. *For. Ecol. Manag.* 180, 61–73.
- Campanella, M.V., Bertiller, M.B., 2008. Plant phenology, leaf traits, and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina. *J. Veg. Sci.* 19, 75–85.
- Carrera, A.L., Sain, C.L., Bertiller, M.B., 2000. Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant Soil* 224, 185–193.
- Casper, B.B., Forseth, I.N., Kempenich, H., Seltzer, S., Xavier, K., 2001. Drought prolongs leaf life span in the herbaceous desert perennial *Cryptantha flava*. *Funct. Ecol.* 15, 740–747.
- Castro-Díez, P., Villar-Salvador, P., Pérez-Rontomé, C., Maestro-Martínez, M., Montserrat-Martí, G., 1997. Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. *Trees* 11, 127–134.
- Chesson, P., Gebauer, R., Schwinning, R., Huntly, N., Wiegand, K., Ernest, M., Sher, A., Novoplansky, A., Weltzin, J., 2004. Resources pulses, species interactions, and diversity maintenance in arid and semi-arid ecosystems. *Oecologia* 141, 236–253.
- Coombs, J., Hind, G., Leegood, R.C., Tieszen, L., Vonshak, A., 1985. Analytical techniques. In: Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M.O. (Eds.), *Techniques in Bioproductivity and Photosynthesis*. Pergamon Press, Oxford, pp. 219–228.
- Coronato, F.R., Bertiller, M.B., 1997. Climatic controls of soil moisture in an arid steppe of northern Patagonia (Argentina). *Arid Soil Res. Rehab.* 11, 277–288.
- Crawley, M.J., 1998. Life history and environments. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell Science, Oxford, pp. 73–131.
- De Bie, S., Ketner, P., Paase, M., Geertling, C., 1998. Woody plant phenology in the West Africa savanna. *J. Biogeogr.* 25, 883–900.
- Eckstein, R.L., Karlsson, P.S., Weih, M., 1999. Leaf lifespan and nutrient resorption as determinants of plant nutrient conservation in temperate-temperate regions. *New Phytol.* 143, 177–189.
- Escudero, A., del Arco, J.M., Sanz, L.C., Ayala, J., 1992. Effects of leaf longevity and retranslocation efficiency on the retention time of nutrients. *Oecologia* 90, 80–87.
- Gao, Q., Reynolds, J.F., 2003. Historical shrub-grass transitions in the northern Chihuahuan Desert: modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. *Glob. Change Biol.* 9, 1475–1493.
- Ghazanfar, S.A., 1997. The phenology of desert plants: a 3 year study in a gravel desert wadi in northern Oman. *J. Arid Environ.* 35, 407–417.
- Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1999. Environmental control of canopy dynamics and photosynthetic rate in the evergreen tussock grass *Stipa tenacissima*. *Plant Ecol.* 145, 327–339.
- Hättenschwiler, S., Vitousek, P.M., 2000. The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends Ecol. Evol.* 15, 238–243.
- Hikosaka, K., 2005. Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover. *Ann. Bot.* 95, 521–533.
- Hyder, P.W., Fredrickson, E.L., Estell, R.E., Tellez, M., Gibbens, R.P., 2002. Distribution and concentration of total phenolics, condensed tannins, and nordihydroguaiaretic acid (NDGA) in creosotebush (*Larrea tridentata*). *Biochem. Syst. Ecol.* 30, 905–912.
- Jolly, W.M., Running, S.W., 2004. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari. *Glob. Change Biol.* 10, 303–308.
- Kikuzawa, K., 1983. Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees. *Can. J. Bot.* 61, 2133–2139.
- Kikuzawa, K., 2003. Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. *Funct. Ecol.* 17, 29–38.
- Koricheva, J., Nykänen, H., Gianoli, E., 2004. Meta-analysis of trade-offs among plant antiherbivore defenses: are plants jacks-of-all-trades, masters of all? *Am. Nat.* 163, E64–E75.
- Lauenroth, W.K., 1998. Guanacos, spiny shrubs and the evolutionary history of grazing in the Patagonian steppe. *Ecol. Aust.* 8, 211–215.
- Nitta, I., Ohsawa, M., 1997. Leaf dynamics and shoot phenology of eleven warm-temperate evergreen broad-leaved trees near their northern limit in central Japan. *Plant Ecol.* 130, 71–88.
- Norusis, M.J., 1997. SPSS Advanced Statistic 7.5. SPSS, Chicago.
- Noy Meir, I., 1973. Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* 4, 25–52.
- Ogaya, R., Peñuelas, J., 2006. Contrasting foliar responses to rain exclusion in *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plant* 50, 373–382.
- Ogle, K., Wolpert, R.L., Reynolds, J.F., 2004. Reconstructing plant root area and water uptake profiles. *Ecology* 85, 1967–1978.
- Otieno, D.C., Schmidt, M.W.T., Kinyamario, J.I., Tenhunen, J., 2005. Responses of *Acacia tortilis* and *Acacia xanthophloea* to seasonal changes in soil water availability in the savanna region of Kenya. *J. Arid Environ.* 62, 377–400.
- Pavón, N.P., Briones, O., 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. *J. Arid Environ.* 49, 265–277.
- Peñuelas, J., Filella, I., 2001. Responses to a warming world. *Science* 294, 793–795.
- Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytol.* 161, 837–846.
- Poorter, H., Remkes, C., 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* 83, 553–559.
- Reich, P.B., Uhl, C., Walters, M.B., Ellsworth, D.S., 1991. Leaf lifespan as a determinant of leaf structure and function among 23 tree species in Amazonian forest communities. *Oecologia* 86, 16–24.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62, 365–392.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D., Buschena, C., 1998. Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct. Ecol.* 12, 327–338.
- Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80, 1955–1969.
- Reynolds, J.F., Kemp, P.R., Ogle, K., Fernández, R.J., 2004. Modifying the pulse-reserve paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141, 194–210.
- Rodríguez, M.V., Bertiller, M.B., Bisigato, A., 2007. Are fine roots of both shrubs and perennial grasses able to occupy the upper soil layer? A case study in the arid Patagonian Monte with non-seasonal precipitation. *Plant Soil* 300, 281–288.
- Schwinning, S., Starr, B., Ehleringer, J.R., 2003. Dominant cold desert plants do not partition warm season precipitation by event size. *Oecologia* 136, 252–260.
- Seghier, J., Floret, C., Pontanier, R., 1995. Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. *J. Trop. Ecol.* 11, 237–254.
- Seghier, J., Simier, M., 2002. Variations in phenology of a residual invasive shrub species in Sahelian fallow savannas, south-west Niger. *J. Trop. Ecol.* 18, 897–912.
- Sekhwela, M.B.M., Yates, D.J., 2007. A phenological study of dominant acacia tree species in areas with different rainfall regimes in the Kalahari of Botswana. *J. Arid Environ.* 70, 1–17.
- Shackleton, C.M., 1999. Rainfall and topo-edaphic influences on woody community phenology in South African savannas. *Glob. Ecol. Biogeogr.* 8, 125–136.
- Sun, S., Jin, D., Li, R., 2006. Leaf emergence in relation to leaf traits in temperate woody species in East-Chinese *Quercus fabri* forests. *Acta Oecol.* 30, 212–222.

- Tateno, R., Aikawa, T., Takeda, H., 2005. Leaf-fall phenology along a topography-mediated environmental gradient in a cool-temperate deciduous broad-leaved forest in Japan. *J. For. Res.* 10, 269–274.
- Van Soest, P.J., 1963. Use of detergents in the analysis of fibrous feeds. II A rapid method for the determination of fiber and lignin. *J. Assoc. Off. Anal. Chem.* 46, 830–835.
- Waterman, P.G., Mole, S., 1994. Extraction and chemical quantification. In: Lawton, G.F., Likens, G.E. (Eds.), *Methods in Ecology, Analysis of Phenolics Plant Metabolites*. Blackwell Scientific Publications, Oxford, pp. 66–103.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159.
- Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A., Eamus, D., 1997. Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* 78, 2542–2558.
- Williams-Linera, G., 2000. Leaf demography and leaf traits of temperate-deciduous and tropical evergreen-broadleaved trees in a Mexican montane cloud forest. *Plant Ecol.* 149, 233–244.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü, Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.L., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.