

# Is N-resorption efficiency related to secondary compounds and leaf longevity in coexisting plant species of the arid Patagonian Monte, Argentina?

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**Abstract** Leaf longevity and nutrient resorption efficiency are important strategies to conserve plant nutrients. Theory suggests a negative relationship between them and also proposes that high concentration of phenolics in long-lived leaves may reduce nutrient resorption. In order to provide new evidence on these relationships, we explored whether N-resorption efficiency is related to leaf longevity, secondary compounds and other leaf traits in coexisting plant species of different life forms in the arid Patagonian Monte, Argentina. We assessed N-resorption efficiency, green leaf traits (leaf mass per area (LMA), leaf longevity and lignin, total soluble phenolics and N concentrations) and N concentration in senescent leaves of 12 species of different life forms (evergreen shrubs, deciduous shrubs and perennial grasses) with contrasting leaf traits. We found that leaf longevity was positively correlated to LMA and lignin, and negatively correlated to N concentration in green leaves. N concentrations both in green and senescent leaves were positively related. N-resorption efficiency was not associated with the concentration of secondary compounds (total soluble phenolics and lignin) but it was negatively related to LMA and leaf longevity and positively related to N concentration in green leaves. Furthermore, leaf traits overlapped among life forms highlighting that life forms are not a good indicator of the functional properties (at least in relation to nutrient conservation) of species. In conclusion, our findings indicated that differences in N-resorption efficiency among coexisting species were more related to N concentration in green leaves, leaf lifespan and LMA than to the presence of secondary compounds at least those assessed in our study (soluble phenolics and lignin). Accordingly, N-resorption efficiency seems to be modulated, at least in part, by the productivity–persistence trade-off.

**Key words:** green leaf, leaf mass per area, lignin concentration, N concentration, total soluble phenolics.

## INTRODUCTION

Leaf longevity and nutrient resorption efficiency are important strategies to conserve plant nutrients and to diminish the dependence of plants on nutrient uptake from the soil (Chapin 1980; Aerts 1990; Escudero *et al.* 1992; Carrera *et al.* 2000). Long leaf longevity is associated with a prolonged residence time of nutrients in leaves improving plant nutrient use efficiency (Chapin 1980; Chabot & Hicks 1982). Nutrient residence time also appears to be extended via nutrient resorption as by this process nutrients are withdrawn from leaves before abscission and redeployed in storage organs or new growth rather than lost with leaf fall (Chapin 1980; Noodén 2004).

Among nutrients, nitrogen is considered the most limiting for plant growth in arid environments (Skujins 1981). Nutrient concentration in green leaves (Chapin & Kedrowski 1983; Killingbeck & Costigan 1988),

water availability (del Arco *et al.* 1991; Pugnaire & Chapin 1992) and source–sink relationships (Chapin & Moilanen 1991; Nambiar & Fife 1991) are among the most cited controls over N-resorption. Theory suggests a negative relationship between these two main components of the mean N residence time, N-resorption efficiency and leaf longevity (Garnier & Aronson 1998; Eckstein *et al.* 1999) but direct evidence on this is still scarce. This negative relationship has been mostly supported by the fact that long leaf longevity requires substantial carbon allocation to structural (Chabot & Hicks 1982; Coley 1988; Wright *et al.* 2002; Silla & Escudero 2004) and to defensive compounds such as phenolics (Chapin 1989; Poorter & Villar 1997). Phenolic compounds may lead to precipitation of proteins before their hydrolysis, thus reducing nutrient resorption as highlighted by Chapin and Kedrowski (1983) and Aerts and Chapin (2000) among others. In order to provide new evidence on these relationships, we explored whether N-resorption efficiency is related to leaf longevity, secondary compounds and other leaf traits in coexisting plant species

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of different life forms (evergreen and deciduous shrubs and perennial grasses) with contrasting leaf traits in the arid Patagonian Monte, Argentina.

## MATERIALS AND METHODS

### Study area and selected species

The study was carried out at north-eastern Chubut Province (Argentina) in a floristically homogeneous area characteristic of the Patagonian Monte (Bisigato & Bertiller 1997). Mean annual precipitation is 238 mm and mean annual temperature is 13.4°C (14-year series). Precipitation events are highly variable within and between years and occur without a seasonal pattern or are slightly concentrated in the cold period (Barros & Rivero 1982). The characteristic vegetation is a shrubland of *Larrea divaricata* Cav. 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. Evergreen and deciduous shrubs are the dominant plant life forms in the upper canopy layer (1–2 m). The low canopy layer (<0.5 m) is formed by dwarf shrubs and perennial grasses (Bisigato & Bertiller 1997).

Within the study area (42°38'51"S, 65°23'03"W), samplings were taken at two sites of about 2 ha each with low impact of domestic grazers (sheep) and high floristic similarity. We selected 12 representative species of the three dominant life forms: *Chuquiraga avellanedae* Lorentz, *Chuquiraga erinacea* D. Don subsp. *hystrix* (Don) C. Ezcurra, *Larrea nitida* Cav. *L. divaricata* and *Atriplex lampa* Gill ex Moq (evergreen shrubs), *Prosopis alpataco* Phil., *Prosopis-trum globosum* Gillies ex Hook. et Arn., *Lycium chilense* Miers. ex Bertero and *Bougainvillea spinosa* (Cav.) Heimerl in Engler u. Prantl. (deciduous shrubs), *Nassella tenuis* (Phil.) Barkworth, *Jarava speciosa* (Trin. & Rupr.) Peñailillo and *Poa ligularis* Nees ex Steud (perennial grasses). We selected these species because they provided a gradient of leaf traits and were relatively abundant in the study site.

### Collection of green and senescent leaves

We collected fully expanded young to medium-aged green leaves (Reich *et al.* 1991; Bertiller *et al.* 2006) from the external canopy crown (sun leaves) of five randomly selected individuals of each species at each site in two consecutive years (2005–2006). At each year, leaves were collected from five different individuals. As leaf phenology is not synchronous among species (Bertiller *et al.* 1991; Campanella & Bertiller 2008), green leaves of *A. lampa*, *B. spinosa*, *C. avellanedae*, *C. erinacea* subsp. *hystrix*, *L. divaricata*, *L. nitida*, *P. alpataco* and *P. globosum* were harvested in November–December and those of *L. chilense*, *P. ligularis*, *J. speciosa* and *N. tenuis* were harvested in June–July.

Also, we collected recently senescent leaves (completely dry yellow without signs of deterioration, Carrera *et al.* 2000) from the canopy crown of five randomly selected individuals of each species at each site in two consecutive years (2005–

2006). Each year, leaves were collected from five different individuals. The plants from which we collected senescent leaves were not the same as those from which we had collected green leaves. This decision was taken because the collection of enough green leaf biomass for chemical analyses in small plants or plants with low leaf biomass could affect plant functioning, the N pool of the plant, and consequently the N concentration in senescent leaves. For all species, we collected senescent leaves monthly during the dry summer season (December–March) with the exception of *Chuquiraga* species, where senescent leaves were collected during winter (June–August). The collection period was chosen based on previous phenological studies (Campanella & Bertiller 2008). We took special care in perennial grasses to avoid sampling of old senescent leaves because they stay attached to the bunch for a long time after their senescence. Each year, we pooled the material collected of each individual during the whole senescence period because individual senescent leaf biomass collected on each date was inadequate to perform all chemical analyses.

### Assessment of leaf mass per area and leaf longevity

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 (1×1 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). For perennial grasses, leaf area only corresponded to the area of leaf blades. We calculated the mean value of LMA per individual.

In evergreen shrubs and perennial grasses, two to 14 new emerged leaves in six to 10 individuals of each species were monitored monthly until senescence to assess leaf longevity (from September 2004 to April 2007). 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). Furthermore, we calculated the mean value of longevity per individual. We did not calculate leaf longevity of *A. lampa* because of logistic problems in tagging small leaves. In deciduous shrubs, monthly observations of leaf phenology (from July 2004 to October 2005) were used instead of direct measurements on individual leaves.

### Chemical traits of green and senescent leaves

We analysed the N concentration in green and senescent leaves per individual (dried at 60°C for 48 h) by semi-micro Kjeldahl (Coombs *et al.* 1985). Also, we analysed the lignin concentration in green leaves by the Van Soest (1963) procedure and total soluble phenolics concentration by the

Folin-Ciocalteu method using 50% methanol as extract solution and tannic acid as standard (Waterman & Mole 1994). We did not perform chemical analyses of senescent leaves of *P. globosum* because there was not enough biomass. All concentrations were expressed on a dry mass basis. Wright *et al.* (2004) recommended this form of expression in a global study on leaf traits. N-resorption efficiency was calculated as the percentage of N reduction between green and senescent leaves in relation to green leaves. Using mass basis may underestimate nutrient resorption efficiency because of mass loss during senescence (Van Heerwaarden *et al.* 2003). Nevertheless, Kazakou *et al.* (2007) found that the ranking of species remained comparable when nutrient resorption efficiency was calculated with or without taking mass losses into account. We did not calculate N-resorption efficiency for *P. globosum* because we could not assess N concentration in senescent leaves. Because of inadequate biomass, we could not perform all the chemical analysis in all plants. Thus, the total number of replicates per species varied between six and 20.

### Statistical analysis

We evaluated the significance of the differences in leaf traits among species and life forms by ANOVA or Kruskal–Wallis test, depending on the distribution of the data. Multiple comparisons were performed by Tukey test. We did not include sites as a factor because we did not find significant differences between them for any variables. We did not address inter-annual variation in leaf traits but previous work in the area showed variations lower than 5% in leaf traits among years (Carrera *et al.* 2003; Bertiller *et al.* 2006). We used correlation analysis to evaluate relationships among leaf traits and regression analysis to describe relationships between N-resorption efficiency and leaf traits. For each relationship explored including N-resorption efficiency, we

performed two analyses with and without the only N<sub>2</sub>-fixing species, *P. alpataco*. As N-resorption efficiency and the N concentration in green leaves were partially correlated, we also assessed this relationship as suggested by Kobe *et al.* (2005) by fitting a power function between N concentration in senescent leaves (N-resorption proficiency *sensu* Killingbeck 1996) and N concentration in green leaves. The exponent (*B*) of the function determines the relationship as follows: *B* > 1 indicates decreasing N-resorption with increased N concentration in green leaves, *B* < 1 indicates increasing N-resorption with increasing N concentration in green leaves and *B* = 1 indicates that N concentration in green leaves has no effect on N-resorption efficiency (Kobe *et al.* 2005). Unless otherwise noted, the level of significance throughout the study was *P* < 0.05.

## RESULTS

### Leaf traits and N-resorption efficiency

Leaf longevity was higher in evergreen shrubs than in perennial grasses and deciduous shrubs ( $F_{2,8} = 10.45$ ,  $P = 0.006$ ; Table 1). The concentration of total soluble phenolics was lower in perennial grasses than in shrubs ( $H_2 = 6.27$ ,  $P < 0.03$ ,  $n = 12$ ). Lignin concentration and LMA did not differ among life forms ( $F_{2,9} = 0.73$ ,  $P = 0.51$ ;  $F_{2,9} = 2.45$ ,  $P < 0.14$ , respectively). Nitrogen in green leaves was higher in deciduous shrubs than in evergreen shrubs, whereas perennial grasses did not differ from both shrub life forms ( $F_{2,9} = 6.89$ ,  $P < 0.02$ ; Table 2). N concentration in senescent leaves and N-resorption efficiency did not differ among life forms ( $F_{2,8} = 2.79$ ,  $P = 0.12$ ;  $F_{2,8} = 0.93$ ,  $P = 0.43$ , respectively; Table 2).

**Table 1.** Mean  $\pm$  1 standard error of leaf longevity (days), LMA (g m<sup>-2</sup>), total soluble phenolics (%) and lignin (%) in green leaves of species (means are averages of sites and years) and life forms (means are averages of mean values of species)

	Leaf longevity (days)	LMA (g m <sup>-2</sup> )	Total soluble phenolics (%)	Lignin (%)
Evergreen shrubs	413 $\pm$ 69 <sup>B</sup> (4)	241 $\pm$ 57 <sup>A</sup> (5)	6.97 $\pm$ 3.46 <sup>B</sup> (5)	6.8 $\pm$ 1.1 <sup>A</sup> (5)
<i>Chusqueira avellaneda</i>	504 $\pm$ 24 <sup>f</sup> (7)	267 $\pm$ 12 <sup>c</sup> (20)	2.11 $\pm$ 0.06 <sup>cd</sup> (20)	10.4 $\pm$ 0.3 <sup>d</sup> (12)
<i>Chusqueira erinacea</i>	559 $\pm$ 31 <sup>f</sup> (8)	455 $\pm$ 14 <sup>f</sup> (20)	1.17 $\pm$ 0.04 <sup>b</sup> (20)	7.5 $\pm$ 0.5 <sup>d</sup> (12)
<i>Larrea nitida</i>	260 $\pm$ 31 <sup>de</sup> (8)	155 $\pm$ 3 <sup>d</sup> (20)	15.93 $\pm$ 0.35 <sup>f</sup> (20)	4.7 $\pm$ 0.2 <sup>c</sup> (12)
<i>Larrea divaricata</i>	336 $\pm$ 17 <sup>e</sup> (6)	170 $\pm$ 4 <sup>d</sup> (20)	14.93 $\pm$ 0.42 <sup>f</sup> (20)	4.2 $\pm$ 0.1 <sup>abc</sup> (12)
<i>Atriplex lampa</i>	–	160 $\pm$ 7 <sup>d</sup> (20)	0.71 $\pm$ 0.05 <sup>a</sup> (20)	7.3 $\pm$ 0.2 <sup>d</sup> (12)
Deciduous shrubs	144 $\pm$ 30 <sup>A</sup> (4)	105 $\pm$ 20 <sup>A</sup> (4)	2.80 $\pm$ 0.73 <sup>B</sup> (4)	4.9 $\pm$ 1.1 <sup>A</sup> (4)
<i>Prosopis alpataco</i>	214 <sup>d</sup> (10)	151 $\pm$ 8 <sup>de</sup> (20)	2.63 $\pm$ 0.14 <sup>df</sup> (20)	8.2 $\pm$ 0.4 <sup>d</sup> (12)
<i>Prosopidastrum globosum</i>	70 $\pm$ 4 <sup>a</sup> (10)	90 $\pm$ 4 <sup>b</sup> (19)	4.83 $\pm$ 0.19 <sup>ef</sup> (15)	3.2 $\pm$ 0.1 <sup>abc</sup> (6)
<i>Lycium chilense</i>	134 $\pm$ 5 <sup>b</sup> (10)	58 $\pm$ 4 <sup>a</sup> (20)	1.33 $\pm$ 0.06 <sup>bc</sup> (20)	4.4 $\pm$ 0.3 <sup>bc</sup> (12)
<i>Bougainvillea spinosa</i>	156 $\pm$ 5 <sup>bc</sup> (10)	123 $\pm$ 3 <sup>c</sup> (20)	2.41 $\pm$ 0.10 <sup>cd</sup> (20)	4.1 $\pm$ 0.3 <sup>abc</sup> (12)
Perennial grasses	144 $\pm$ 23 <sup>A</sup> (3)	143 $\pm$ 43 <sup>A</sup> (3)	0.63 $\pm$ 0.05 <sup>A</sup> (3)	4.8 $\pm$ 2.1 <sup>A</sup> (3)
<i>Nassella tenuis</i>	122 $\pm$ 13 <sup>b</sup> (10)	100 $\pm$ 3 <sup>b</sup> (20)	0.53 $\pm$ 0.01 <sup>a</sup> (20)	2.8 $\pm$ 0.3 <sup>ab</sup> (11)
<i>Jarava speciosa</i>	190 $\pm$ 13 <sup>cd</sup> (8)	229 $\pm$ 7 <sup>e</sup> (20)	0.70 $\pm$ 0.02 <sup>a</sup> (20)	9.0 $\pm$ 1.2 <sup>d</sup> (12)
<i>Poa ligularis</i>	121 $\pm$ 5 <sup>b</sup> (8)	99 $\pm$ 4 <sup>b</sup> (20)	0.65 $\pm$ 0.02 <sup>a</sup> (20)	2.7 $\pm$ 0.3 <sup>a</sup> (10)

Different capital letters indicate significant ( $P < 0.05$ ) differences among life forms within traits. Different lower-case letters indicate significant ( $P < 0.05$ ) differences among species within traits. Numbers of replicates are shown in parentheses. LMA, leaf mass per area.

**Table 2.** Mean  $\pm$  1 standard error of nitrogen (%) in green and senescent leaves and NRE (%) of species (means are averages of sites and years) and life forms (means are averages of mean values of species)

	N in green leaves (%)	N in senescent leaves (%)	NRE (%)
Evergreen shrubs	1.65 $\pm$ 0.19 <sup>A</sup> (5)	0.67 $\pm$ 0.08 <sup>A</sup> (5)	58.2 $\pm$ 2.1 <sup>A</sup> (5)
<i>Chuquiraga avellanedae</i>	1.27 $\pm$ 0.06 <sup>a</sup> (20)	0.44 $\pm$ 0.01 <sup>a</sup> (20)	64.0 $\pm$ 2.4 <sup>cd</sup> (20)
<i>Chuquiraga erinacea</i>	1.17 $\pm$ 0.04 <sup>a</sup> (20)	0.57 $\pm$ 0.02 <sup>bc</sup> (20)	50.7 $\pm$ 2.0 <sup>b</sup> (20)
<i>Larrea nitida</i>	2.21 $\pm$ 0.10 <sup>cd</sup> (20)	0.90 $\pm$ 0.03 <sup>ef</sup> (20)	58.0 $\pm$ 2.0 <sup>c</sup> (20)
<i>Larrea divaricata</i>	1.87 $\pm$ 0.07 <sup>bc</sup> (20)	0.75 $\pm$ 0.03 <sup>de</sup> (20)	58.7 $\pm$ 2.7 <sup>c</sup> (20)
<i>Atriplex lampa</i>	1.71 $\pm$ 0.08 <sup>b</sup> (20)	0.67 $\pm$ 0.03 <sup>cd</sup> (20)	59.5 $\pm$ 2.0 <sup>cd</sup> (20)
Deciduous shrubs	3.84 $\pm$ 0.62 <sup>B</sup> (4)	1.45 $\pm$ 0.54 <sup>A</sup> (3)	58.7 $\pm$ 14.5 <sup>A</sup> (3)
<i>Prosopis alata</i>	3.64 $\pm$ 0.07 <sup>c</sup> (20)	2.51 $\pm$ 0.07 <sup>g</sup> (20)	30.3 $\pm$ 2.8 <sup>a</sup> (20)
<i>Prosopidastrum globosum</i>	4.20 $\pm$ 0.15 <sup>f</sup> (20)	—	—
<i>Lycium chilense</i>	5.25 $\pm$ 0.09 <sup>g</sup> (20)	1.12 $\pm$ 0.04 <sup>fg</sup> (14)	78.2 $\pm$ 0.7 <sup>f</sup> (14)
<i>Bougainvillea spinosa</i>	2.25 $\pm$ 0.07 <sup>cd</sup> (20)	0.72 $\pm$ 0.02 <sup>de</sup> (14)	67.6 $\pm$ 1.5 <sup>c</sup> (14)
Perennial grasses	2.43 $\pm$ 0.51 <sup>AB</sup> (3)	0.67 $\pm$ 0.08 <sup>A</sup> (3)	70.8 $\pm$ 4.0 <sup>A</sup> (3)
<i>Nassella tenuis</i>	3.31 $\pm$ 0.06 <sup>c</sup> (20)	0.71 $\pm$ 0.04 <sup>d</sup> (20)	78.3 $\pm$ 1.3 <sup>f</sup> (20)
<i>Jarava speciosa</i>	1.53 $\pm$ 0.05 <sup>ab</sup> (20)	0.52 $\pm$ 0.03 <sup>ab</sup> (20)	64.8 $\pm$ 2.7 <sup>de</sup> (20)
<i>Poa ligularis</i>	2.44 $\pm$ 0.10 <sup>d</sup> (20)	0.77 $\pm$ 0.06 <sup>de</sup> (14)	69.4 $\pm$ 2.6 <sup>e</sup> (14)

Different capital letters indicate significant ( $P < 0.05$ ) differences among life forms within traits. Different lower-case letters indicate significant ( $P < 0.05$ ) differences among species within traits. Numbers of replicates are shown in parentheses. NRE, N-resorption efficiency.

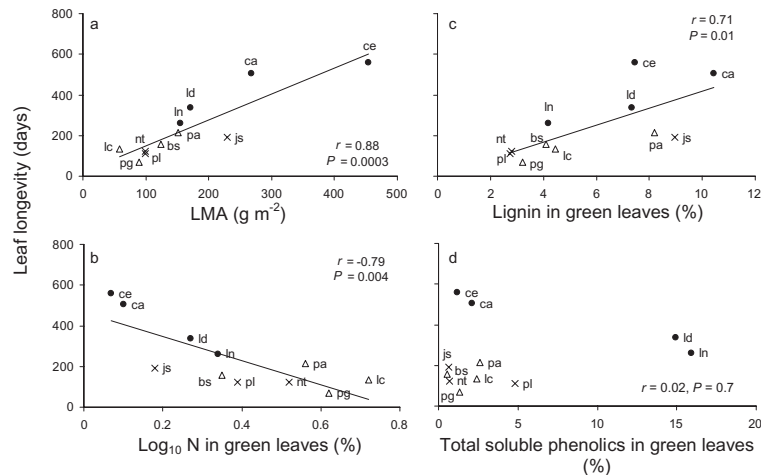
Leaf traits overlapped among species of different life forms. *P. globosum* (deciduous shrub) exhibited the shortest leaf longevity, whereas species of genus *Chuquiraga* (evergreen shrubs) had the longest leaf longevity ( $F_{10,84} = 92.01$ ,  $P < 0.0001$ ). The perennial grass, *J. speciosa* showed values of leaf longevity similar to those of other deciduous shrubs *P. alata* and *B. spinosa* and to the evergreen shrub *L. nitida* (Table 1). The evergreen shrub *C. erinacea* subsp. *hystrix* had the highest LMA followed by the evergreen shrub *C. avellanedae* and the perennial grass *J. speciosa* ( $F_{11,227} = 223.14$ ,  $P < 0.0001$ ). The deciduous shrub *L. chilense* showed the lowest LMA. The highest concentration of total soluble phenolics was assessed in evergreen shrubs of the genus *Larrea* with values four-fold to 10-fold higher than the rest of the species ( $H_{11} = 220.96$ ,  $P < 0.0001$ ;  $n = 235$ ). In contrast, perennial grasses and *A. lampa* (evergreen shrub) showed the lowest concentration of total soluble phenolics. Moreover, evergreen shrubs of the genus *Chuquiraga*, the deciduous shrub *P. alata* and the perennial grass *J. speciosa* presented the highest lignin concentration in green leaves ( $F_{11,123} = 29.07$ ,  $P < 0.0001$ ). The deciduous shrub *L. chilense* had the highest N concentration in green leaves and species of genus *Chuquiraga* (evergreen shrubs) and the perennial grass *J. speciosa* the lowest values of this trait ( $F_{11,228} = 231.96$ ,  $P < 0.0001$ ; Table 2). The N<sub>2</sub>-fixing deciduous shrub *P. alata* had the highest N concentration in senescent leaves, whereas *C. avellanedae* (evergreen shrub) and the perennial grass *J. speciosa* the lowest value ( $H_{10} = 150.09$ ,  $P < 0.0001$ ;  $n = 202$ ). *Prosopis alata* (N<sub>2</sub>-fixing deciduous shrub) had the lowest N-resorption efficiency, whereas *L. chilense*

(deciduous shrub) and *N. tenuis* (perennial grass) showed the highest N-resorption efficiency ( $F_{10,191} = 35.87$ ,  $P < 0.0001$ ; Table 2).

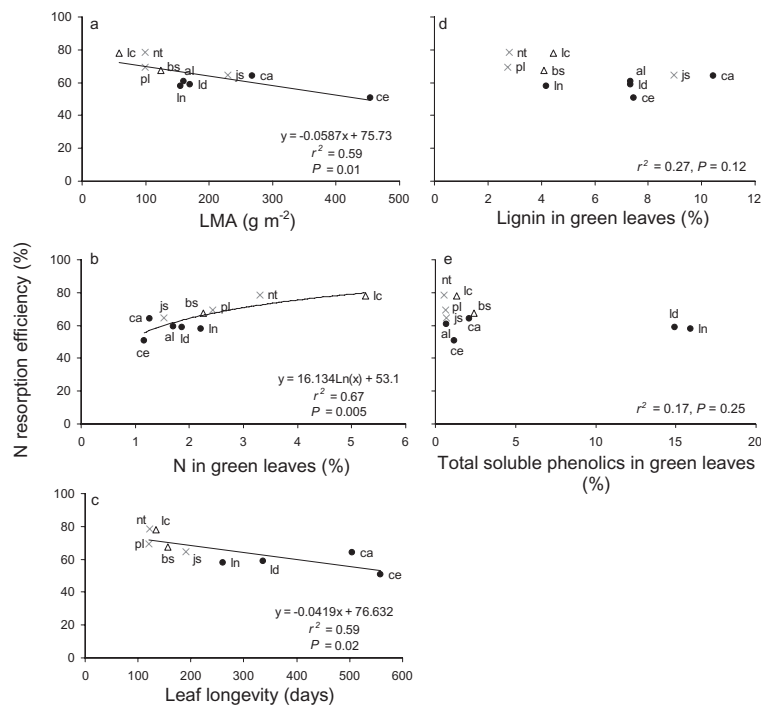
### Relationships among leaf traits and N-resorption efficiency

Leaf longevity was significantly correlated to LMA (positively), N (negatively) and lignin (positively) concentrations in green leaves (Fig. 1a–c, respectively). In contrast, leaf longevity was not correlated to total soluble phenolics concentration in green leaves (Fig. 1d).

N-resorption efficiency was not significantly related to leaf traits in any analyses including the N<sub>2</sub>-fixing species *P. alata*. N-resorption efficiency was related to LMA (negatively) and N concentration in green leaves (positively) when *P. alata* was excluded from the analyses (Fig. 2a,b, respectively). N-resorption efficiency was not related to total soluble phenolics and lignin concentrations in green leaves of non-N<sub>2</sub>-fixing species (Fig. 2d,e, respectively). Leaf longevity and N-resorption efficiency were negatively related in non-N<sub>2</sub>-fixing species (Fig. 2c). N concentration in senescent leaves (N-resorption proficiency) was significantly related to N concentration in green leaves and the exponent *B* of the fitted power function of this relationship was significantly lower than 1 indicating that N-resorption efficiency increased with increasing N concentration in green leaves ( $B = 0.5 \pm 0.11$ , Fig. 3). N concentration in senescent leaves was not related to N-resorption efficiency ( $r^2 = 0.18$ ,  $P = 0.21$ ) but was negatively related to LMA and lignin concen-



**Fig. 1.** Leaf longevity (days) of each studied species in relation to (a) leaf mass per area (LMA;  $\text{g m}^{-2}$ ), (b) logarithmic transformed N concentration (%), (c) lignin (%) and (d) total soluble phenolics (%) in green leaves (means are averages of sites and years) and Pearson correlation coefficients. Evergreen shrubs (filled circle): *Chuquiraga avellanadae* (c.), *Chuquiraga erinacea* subsp. *hystrix* (ce), *Larrea nitida* (ln), *Larrea divaricata* (ld) and *Atriplex lampa* (al). Deciduous shrubs (empty triangle): *Prosopis alpataco* (pa), *Prosopidastrum globosum* (pg), *Lycium chilense* (lc), *Bougainvillea spinosa* (bs). Perennial grasses (grey cross): *Nasella tenuis* (nt), *Jarava speciosa* (js) and *Poa ligularis* (pl).

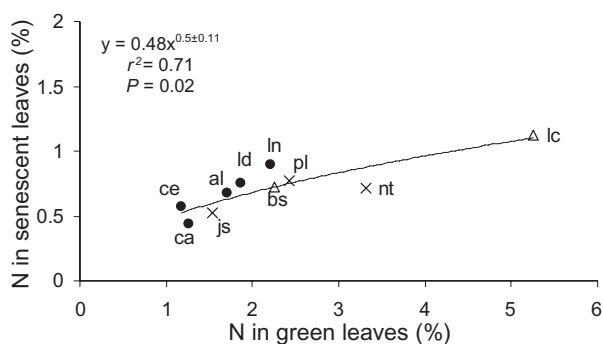


**Fig. 2.** N-resorption efficiency in relation to (a) leaf mass per area (LMA;  $\text{g m}^{-2}$ ), (b) N in green leaves (%), (c) leaf longevity (days), (d) lignin (%) and (e) total soluble phenolics of non- $\text{N}_2$ -fixing species (excluded *Prosopis alpataco*). Means are averages of site and years. Species symbols and acronyms as in Figure 1.

tration in green leaves ( $y = 4.3498x - 0.3634$ ,  $r^2 = 0.62$ ,  $P = 0.003$  and  $y = -0.0491x + 1.0111$ ,  $r^2 = 0.46$ ,  $P = 0.03$ , respectively). N concentration in senescent leaves was not related to total phenolics concentration in green leaves and leaf longevity ( $r^2 = 0.13$ ,  $P = 0.31$  and  $r^2 = 0.31$ ,  $P = 0.12$ , respectively).

## DISCUSSION

Coexisting species of different life forms showed a wide range of variation in leaf traits in the Patagonian Monte as reported in other ecosystems (Reich *et al.* 1999; Westoby *et al.* 2002). Most relationships among



**Fig. 3.** Relationship between N in senescent (N-resorption proficiency) and green leaves for non-N<sub>2</sub>-fixing species (excluded *Prosopis alpataco*) and equation of power function fitted with exponent  $B \pm 1$  standard error. Means are averages of site and years. Species symbols and acronyms as in Figure 1.

leaf traits of our studied species were consistent with those previously described (Chabot & Hicks 1982; Mooney & Gulmon 1982; Reich *et al.* 1992; Kazakou *et al.* 2006) and with global trends reported across ecosystems (Reich *et al.* 1997; Wright *et al.* 2004). Despite of the significant differences in mean values of traits among life forms, we found a large overlap in the variation ranges of life form leaf traits as highlighted by Wright *et al.* (2005). This was consistent with results reported in other studies across precipitation gradients in Patagonia (Bertiller *et al.* 2005, 2006) showing that species leaf traits may converge irrespective of life forms, phylogeny and biomes (Reich *et al.* 1997, 1999; Díaz *et al.* 2004; Wright *et al.* 2004). Accordingly, our findings denote that life form is not a good indicator of the functional properties (at least in relation to nutrient conservation) of species. Our data highlighted that species with short leaf longevity had low values of LMA and high values of N in green leaves and the reverse occurred with species with long leaf longevity. Accordingly, our studied species could be arranged along the 'leaf economics spectrum' suggested by Wright *et al.* (2004).

The range of N concentration in senescent leaves (N-resorption proficiency *sensu* Killingbeck 1996) found in our study (0.4–2.5%) fell into the range indicated by Killingbeck and Whitford (1996) for desert species all over the world (0.4–2.6%), corresponding the highest N concentration in senescent leaves to N<sub>2</sub>-fixing species in both studies. The average value of N-resorption efficiency (62%) found in the studied species was consistent with the values reported by Carrera *et al.* (2000, 2003, 2009) and was relatively high compared with N-resorption efficiency calculated on a dry mass basis reported in other ecosystems: 48% for plant species in the semi-arid region of northern China (Yuan *et al.* 2005a), 50.3% for plant species worldwide (Aerts 1996) and 46.9% for woody species

in a global survey (Yuan & Chen 2009). This highlighted the importance of N-resorption as a conservation strategy in coexisting non-N<sub>2</sub>-fixing species of dry-nutrient-poor Patagonian Monte ecosystems. Furthermore, our results suggest that N<sub>2</sub>-fixing species, such as the deciduous shrub *P. alpataco*, with the lowest N-resorption efficiency could be less dependent on plant N conservation strategies as N is mostly provided by the symbiotic interaction (Killingbeck 1996; Killingbeck & Whitford 2001).

Leaf longevity is other common strategy for N conservation in dry-nutrient-poor ecosystems of the world (Chapin 1980; Hemminga *et al.* 1999). Our findings showed that N-resorption efficiency in non-N<sub>2</sub>-fixing species was negatively related to leaf longevity suggesting that both components of the mean residence time of N could be interrelated processes as reported by Garnier and Aronson (1998) and Eckstein *et al.* (1999). However, other studies indicated that both processes of nutrient conservation are independent (Escudero *et al.* 1992; Kazakou *et al.* 2007). As found in our study, Wright and Westoby (2003) also reported that N-resorption efficiency declines with leaf lifespan in dry-nutrient-poor sites. This in turn could provide evidence of a trade-off between leaf longevity and N-resorption efficiency in non-N<sub>2</sub>-fixing species, at least at the leaf level, which could be in part modulated by a trade-off between traits that maximize productivity or persistence (Berendse & Aerts 1987; Reich *et al.* 1991, 1992; Reich 1993; Aerts & Chapin 2000; Wright *et al.* 2004). This trade-off is supported by the idea that it would be physically impossible to construct and maintain long-lived leaves with high net photosynthetic capacity (Reich *et al.* 1997, 1999).

In contrast to our expectation, we did not find a significant relationship between N-resorption efficiency and the concentration of secondary compounds (total soluble phenolics and lignin). Also, in terms of N-resorption proficiency, we found that the most proficient species were those with the highest lignin concentration. These findings contrast with evidence of studies reporting that large concentration of phenolic secondary compounds in long-lived leaves could cause the reduction of N-resorption through precipitation of proteins before their hydrolysis (Chapin & Kedrowski 1983; Aerts & Chapin 2000). However, our findings agreed with those reporting that N-resorption efficiency are modulated by N status in plants (Killingbeck & Costigan 1988; Dorrepaal *et al.* 2004; Yuan *et al.* 2005b). In this sense, our results highlighted that N-resorption efficiency calculated both as the percentage of N reduction between green and senescent leaves in relation to green leaves and by the relationship between N concentration in green and senescent leaves (Kobe *et al.* 2005) was positively correlated to N concentration in green leaves of non-N<sub>2</sub>-fixing species. This positive relationship could be partially explained by the

fact that N-rich species usually contain larger amounts of highly retranslocatable N than N-poor ones (Chapin & Kedrowski 1983; Lajtha 1987; Milla *et al.* 2005). In contrast, these latter with long-lived leaves and high LMA could have a higher fraction of less mobile N associated with structural proteins occluded in the cell wall matrix (Hikosaka 2004; Niinemets & Tamm 2005). Conversely, Kobe *et al.* (2005) found a negative relationship between N concentration in green leaves and N-resorption efficiency but this contradictory result may derive from the fact that the study of Kobe *et al.* (2005) compared species growing in a wide spectrum of habitats probably confounding phenotypic responses to environment and interspecific differences as interpreted by Kazakou *et al.* (2007). Finally, it should be noted that other factors that were not explored in our study could also affect N-resorption efficiency such as the presence of active nutrient sinks on plant (Nambiar & Fife 1991), soil moisture availability (del Arco *et al.* 1991; Pugnaire & Chapin 1992) and the relative cost of acquiring nutrient from soil or via resorption from older leaves (Wright & Westoby 2003).

In conclusion, our results showed that N-resorption efficiency in coexisting non-N<sub>2</sub>-fixing species from water-N poor ecosystems was negatively related to leaf longevity and positively related to N concentration in green leaves. These relationships could provide evidence of a trade-off between leaf longevity and N-resorption efficiency, at least at the leaf level, which could be probably modulated by a trade-off between traits that maximize productivity or persistence.

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