Leaf phenology and its associated traits in the wintergreen species
Aristotelia chilensis (Mol.) Stuntz (Elaeocarpaceae)

Fenología foliar y sus caracteres asociados en la especie invierno-verde *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae)

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ABSTRACT

The post-summer leaf demography of the wintergreen species *Aristotelia chilensis* growing near San Carlos de Bariloche, Argentina, is described. Its specific leaf mass (SLM, g m^{-2}) is compared to that of the deciduous and evergreen species of the Andean-Patagonian forests and to that of other communities abroad. The pattern of leaf emergence is intermediate, with leaf flush in spring (basal cohort, BC), followed by successive unfolding of the remaining leaves (distal cohort, DC) during summer. The senescence of the BC occurs mainly in autumn, with a loss of 11-31 % of its SLM. The DC falls synchronously in mid-spring and the SLM loss in winter is 10-13 %. The SLM of *A. chilensis* (103.6 ± 6.2 g m^{-2}) is intermediate when compared to the general mean values of deciduous (73.7 ± 15.9 g m^{-2}) and evergreen species (154.8 ± 45.8 g m^{-2}). The SLM of deciduous and evergreen species of three different forests near San Carlos de Bariloche varied significantly at the end of the growing season while that of *A. chilensis* showed more constant values. The periodicity of leaf production and senescence in *A. chilensis* allows the maintenance of one leaf cohort throughout the year, covering the carbon demand for flowering and leaf production in spring. This differentiates the deciduous from the wintergreen species, despite their similar mean leaf life span values, while the evergreen species have a longer leaf turnover. Considering the conditions for growth in each studied forest, the leaf life span was not the only factor determining the SLM value. This variable would also depend on multiple stresses that may act during the ontogenesis and evolution of the leaves in each phenological group.

Key words: deciduousness, leaf life span, specific leaf mass, temperate forest, wintergreen species.

RESUMEN

Se describe la demografía foliar después del verano de la especie invierno-verde *Aristotelia chilensis*, creciendo cerca de la ciudad de San Carlos de Bariloche, Argentina. Se compara su peso específico foliar (SLM, g m^{-2}) con los valores de especies deciduas y siempreverdes de los bosques andino-patagónicos y de comunidades de otras regiones. El patrón de emergencia foliar es intermedio, con un pulso de hojas en primavera (cohorte basal, BC) seguido por la emergencia en forma sucesiva de las restantes hojas (cohorte distal, DC) durante el verano. La senescencia de BC ocurre principalmente en el otoño, con una pérdida de 11-31 % de su SLM. La DC cae sincrónicamente a mediados de primavera y su pérdida de SLM en el invierno es de 10-13 %. El SLM de *A. chilensis* (103.6 ± 6,2 g m^{-2}) es intermedio cuando se compara con los valores medios generales de especies deciduas (73,7 ± 15,9 g m^{-2}) y siempreverdes (154,8 ± 45,8 g m^{-2}). El SLM de las especies deciduas y siempreverdes pertenecientes a tres diferentes bosques cercanos a San Carlos de Bariloche varió significativamente al final de la estación de crecimiento, mientras que *A. chilensis* mostró valores más constantes. La periodicidad en la producción y senescencia de las hojas en *A. chilensis* permite el mantenimiento de una cohorte foliar a través del año, cubriendo la demanda de carbono para la floración y la producción de hojas en primavera. Esto distingue a las especies invierno-verdes de las deciduas a pesar de sus similares tiempos promedio de vida de la hoja, mientras que las especies siempreverdes tienen un ciclo de reemplazo foliar más largo. Tomando en consideración las condiciones de crecimiento en cada uno de los bosques estudiados, el tiempo de vida de la hoja no fue el único factor que determinó el valor de SLM de las especies. Esta variable también dependería de múltiples estreses, que pueden actuar durante la ontogénesis y la evolución de la hoja en cada grupo fenológico.

Palabras clave: deciduidad, tiempo de vida de la hoja, peso específico foliar, bosques templados, especies invierno-verdes.

INTRODUCTION

The phenology of wintergreen leaves (sensu Bell & Bliss 1977) comprises a distinct phenological group between deciduous and evergreen species, since wintergreen leaves survive only one winter after their growth in the preceding growing season. It is, nevertheless, possible to detect some variations in the wintergreen phenology. The wintergreen species *Tipularia discolor* (Orchidaceae) produces only one leaf at the end of summer. This leaf survives the winter, becoming senescent after its brief activity in spring (Whigham 1989). In other species, a cohort of leaves (*Rhododendron lapponicum*, Jonasson 1989) or fronds (*Polystichum acrostichoides*, Minoletti & Boerner 1993) expands in spring and survives until the following spring, when a new foliar cohort emerges. The leaves of *Daphne kamtschatica* var. *jezoensis* that develop in the autumn survive the winter, together with other spring leaves, undergoing abscission in early summer (Kikuzawa 1984). Thus, the leaves of the wintergreen species may have a similar leaf life span as that of the deciduous species (6 months, Chabot & Hicks 1982, Mooney & Gulmon 1982). In their comparison of different phenological groups, Chabot & Hicks (1982) pointed out that wintergreen phenology can be considered a brief evergreen strategy.

In spite of some variations in wintergreen phenology, the principal function of winter leaf retention is to keep the balance of carbon as positive as possible (Jonasson 1995), increasing or intensifying the period of autotrophy. *Rhododendron lapponicum* has old leaves during early spring, when temperature and light are suitable for photosynthesis and the new leaf cohort is budding (Jonasson 1995). The leaves that persist during winter in wintergreen herbs, which grow in deciduous forests, can use the maximum available incident radiation in early spring, when the tree canopies are devoid of leaves (Tissue et al. 1995, Landhäusser et al. 1997). The leaves of *Polystichum acrostichoides* may be photosynthetically active at moderate temperatures in winter and autumn (Minoletti & Boener 1993).

The available literature reports studies on only 12 wintergreen species. These studies include ferns (*Polystichum acrostichoides* and *Dryopteris intermedia*, Minoletti & Boener 1993, Buskirk & Edwards 1995, Nooden & Wagner 1997) and herbaceous species in deciduous temperate forests in the Northern Hemisphere: *Asarum europaeum*, *Cornus canadensis*, *Gentiana zollingeri*, *Cremastra appendiculata*, *Botrychium multifidum*

var *robustus*, and *Helleborus vesicarius* (Kriebitzsch 1992, Uemura 1993, Werner & Ebel 1994, Tissue et al. 1995, Landhäusser et al. 1997). There are also three studies on prostrate shrubs: *Daphne kamtschatica* var. *jezoensis* from deciduous forests (Kikuzawa 1984), *Ledum palustre* from bogs (Jonasson 1989), and *Rhododendron lapponicum* from the northern tundra (Karlsson 1994, Jonasson 1995). The topics assessed in these studies were growth and reproduction (Snow & Whigham 1989, Whigham 1989, Karlsson 1994), photosynthetic activity (Kriebitzsch 1992, Minoletti & Boener 1993, Tissue et al. 1995, Landhäusser et al. 1997, Nooden & Wagner 1997), changes in nutrient concentrations between seasons (Jonasson 1989, Whigham 1989, Minoletti & Boener 1993, Karlsson 1994, Jonasson 1995), and leaf phenology (Kikuzawa 1984, Jonasson 1989). On the other hand, only the wintergreen species *Aristotelia chilensis* was studied in the Southern Hemisphere. The topics assessed were the photosynthetic activity of the old leaves (Prado & Damascos in press) and the importance of these leaves to shoot growth (Damascos & Prado 2001) in *Aristotelia chilensis*.

Deciduous and evergreen species differ in regard to leaf traits such as specific leaf mass (SLM), nitrogen concentration, and photosynthetic capacity based on area and mass (Chabot & Hicks 1982, Mooney & Gulmon 1982, Reich et al. 1991, 1992, Prado & Moraes 1997). Therefore, the wintergreen species may have foliar characteristics that differ from those of deciduous and/or evergreen species and some leaf traits may change according to microclimatic conditions (Gratani 1995).

No comparative studies have so far been made between the leaf traits of wintergreen species, including the leaf life span, and evergreen and deciduous species. In addition, the literature contains only two published values of SLM for wintergreen species (*Rhododendron lapponicum* and *Ledum palustre*, Jonasson 1989, 1995, Karlsson 1994) and no studies are available concerning SLM vis-à-vis natural resources.

The wintergreen species *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae), which can reach a height of up to 2 m, is a native shrub of Argentina's Andean-Patagonian forests. In forests where rainfall is low (i.e., *Austrocedrus chilensis* forest) *A. chilensis* has higher relative plant frequency, foliar area, and branch growth under canopies (Damascos 1998). The wintergreen leaves expand in spring. These leaves survive the winter, quickly becoming senescent the following

spring, immediately after full development of the newly budding leaves.

The purpose of this article is to describe the phenology of *A. chilensis* and the interdependency between sources (expanded new leaf cohorts and old leaf cohorts) and sinks (flowers and expanding leaves) during the annual carbon balance. The second goal is to compare the SLM of *A. chilensis* with that of other wintergreen, evergreen and deciduous species in order to demonstrate that SLM values are determined mainly by the duration, intensity and interaction of stresses in all phenological groups.

MATERIAL AND METHODS

Study sites

The phenology of *A. chilensis* was studied in an open area in a cypress forest, *Austrocedrus chilensis* (Don) Florin et Boutleje (Cupressaceae), at 750 m above sea level on the Cerro Otto mountain, near the city of San Carlos de Bariloche (41° 04' S, 71° 08' W), province of Rio Negro, Argentina.

The specific leaf mass (SLM) was determined in plants from open areas in the three main forests near San Carlos de Bariloche: (1) a humid coihüe forest, *Nothofagus dombeyi* (Mirb.) Oerst., Fagaceae, in the region of Llao-llao, 690 m of altitude, with an average annual rainfall of 2,000-2,200 mm (Barros et al. 1983); (2) a cypress forest, *Austrocedrus chilensis*, located at 750 m on the Cerro Otto mountain, 30 km from the Llao-llao region, and with an average annual rainfall of 1,400-1,500 mm (Barros et al. 1983); and (3) a lenga forest, *Nothofagus pumilio* (P.et E.) Krasser, Fagaceae, also on the Cerro Otto mountain, at the same latitude and with similar rainfall values, but at 1,100 m. The *Austrocedrus chilensis* forest is on northern slopes that receive higher solar radiation being, therefore, drier than the other forests (Damascos 1998). The cypress forest is also poorer in nutrients than the coihüe and lenga forests (Buamscha et al. 1998, Mazarino et al. 1999).

The rainfall in the three forests occurs in autumn and winter months, while the annual mean temperature (measured near Cerro Otto mountain) ranges from 10-12 °C .

Studied species

The SLM was determined in the nine most abundant woody shrubs (Damascos 1996). These are: the wintergreen species *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae); the evergreen species *Baccharis rhomboidalis* Remy (Compositae), *Berberis serrato-dentata* Lechler (Berberidaceae), *Lomatia hirsuta* (Lam.) Diels ex Mac (Proteaceae), *Nothofagus dombeyi* (Mirb.) Oerst. (Fagaceae), *Schinus patagonicus* (Phil.) Johnst. (Anacardiaceae), *Luma apiculata* (DC) Burret (Myrtaceae); and the deciduous species *Myoschilos oblonga* R. et P. (Santalaceae) and *Ribes magellanicum* Poir. (Saxifragaceae).

Leaf phenology

The leaf mortality was determined at the end of summer in five *A. chilensis* plants randomly selected. The totally expanded leaves were marked in March, 1998. These leaves comprised both leaf cohorts attached to the plants. One cohort was named the basal cohort (BC) and the another the distal cohort (DC). A set of 300 leaves attached to the proximal portion of the branches (BC, developed in the spring of 1997) and a set of 600 leaves on the distal portion of the branches (DC, developed in the summer of 1997-1998) were marked on five plants. Because the study began at the end of summer, the period of leaf emergence was estimated from phenological observations carried out in 1997 and 1998. Therefore, the date of BC unfolding was estimated to be October 15, 1997 and the DC emergence was estimated to be February 15, 1998. In order to identify both cohorts during the measurements, two to four leaves were marked at the base and at the apex of the branches.

The leaf life span was determined until all the marked leaves fell, and the presence of the leaves was evaluated every 15-30 days from March to November 1998. The measurements were taken in autumn and winter because of the extensive leaf mortality during this period and because events during this season define the wintergreen phenology.

Leaf size, leaf biomass and specific leaf mass

The length of both new and old leaves of *A. chilensis* was measured (November 20, 1998) to compare their sizes immediately prior to abscission of the old leaves. On the same day, 10 plants were randomly selected and one branch was detached from each plant. The old and new leaves were separated and dried at 60 °C until they reached a constant weight. The leaf area of the branches was estimated using the total dry weight and the specific leaf mass (SLM, g m^{-2}).

After summer, the SLM was measured to assess its seasonal variation in different cohorts of *A. chilensis*. At the end of March 1998, five plants growing under full solar radiation were randomly selected. Two groups of 50 leaves were collected from each plant. One sample of 50 leaves was named old autumn leaves (OAL, green leaves), which remained on the branches after the plant was shaken. Another sample of 50 leaves was named senescent autumn leaves (SAL, yellow leaves), which became detached after the plant was shaken. In November 1998, 50 old spring leaves (OSL), which persisted during the winter, and 50 new spring leaves (NSL), which developed between October and November 1998, were collected from five *A. chilensis* plants.

The leaves of the wintergreen *A. chilensis*, deciduous and evergreen species from three different forests were sampled in order to compare their SLM values. The leaves were collected simultaneously at the end of the growing season (mid-March 1998), avoiding variations during leaf expansion (Jurik 1986, Chapin & Van Cleve 1991). Fifty expanded leaves free of infection or damage were collected from the apical part of the branches of five plants in each species.

The SLM was determined using one foliar disc per detached leaf. The disks were taken from the region between the leaf's edge and the midrib and dried at 60 °C until they reached a constant weight. The dry weight and the area of the foliar discs were used to calculate the SLM (g m^{-2}). Worldwide bibliographical data on SLM values of deciduous, evergreen and wintergreen species in the growing season were compiled in order to discuss the results obtained here.

Data analysis

The leaf life span of *A. chilensis*, BC and DC leaf cohorts were estimated on a daily basis, considering the dates of foliar unfolding. The difference between the two medians was compared with a median test (Zar 1999). Leaf demography in *A. chilensis* was evaluated based on survival (1), leaf abscission at each observation time (2), and leaf mortality (3), according to the equations proposed by Silverstown (1982):

$lx = Nx_t/No$ (1)
$dx = Nx_t - Nx_{t+1}$ (2)
$qx = dx/Nx_t$ (3)

where lx are the survivors of each cohort at time t, No is the number of leaves at t_o (BC = 300 and DC = 600 leaves), Nx_t is the number of leaves at

t time (observations every 15-30 days after summer), dx is the number of abscised leaves between time t and t +1, and qx corresponds to leaf mortality.

The SLM values for the OAL and OSL and the maximum leaf length between OSL and NSL were compared using the Student t test (Zar 1999). The dependent data were compared with the Student t test for paired samples (Zar 1999), i.e., the SLM of OAL and SAL from the same plant, the total area of OSL and NSL and the total dry weight of OSL and NSL per branch.

The average SLM values for the species of each forest with different deciduousness were compared by one-way ANOVA (Zar 1999) using five plants per species. The two-way ANOVA with two fixed factors (species and forests, n = 5 plants per species in each forest) was applied in order to assess the variation of SLM among common species (*Aristotelia chilensis, Ribes magellanicum* and *Schinus patagonicus*) in three different forests (cypress, coihüe and lenga). The Student-Newman-Keuls multiple comparison procedure was used as a posteriori test (Zar 1999).

RESULTS

Phenology of Aristotelia chilensis

Aristotelia chilensis leaves showed a combined pattern of leaf emergence (Fig. 1). One flush of five to eight pairs of leaves (data not shown) that form the basal cohort (BC) unfolded in spring (end of September). During summer the leaf emergence was sequential and made up the second foliar cohort (distal cohort, DC, Fig. 1). The flower buds opened in mid-October (Fig. 1) and the expansion of BC occurred between the end of October and during November. Both foliar cohorts fell with different intensity in autumn and in the following spring (end of November, Fig. 1 and 2) after the expansion of the new leaf cohort. Fruits ripened at the beginning of December (Fig. 1).

The spring foliar unfolding contributed with a photosynthetic area equivalent to that of the old leaves remaining on each shoot, but its biomass was only half that of those leaves (Table 1). When old leaves started to become senescent (end of November), the length of new leaves was similar to that of the old leaves, but with a lower SLM value (Table 1).

At the end of the summer, the survival curves (lx) of leaves that had emerged during the previous spring (BC) and of the summer leaves (DC) differed from each other (Fig. 2). The BC leaves
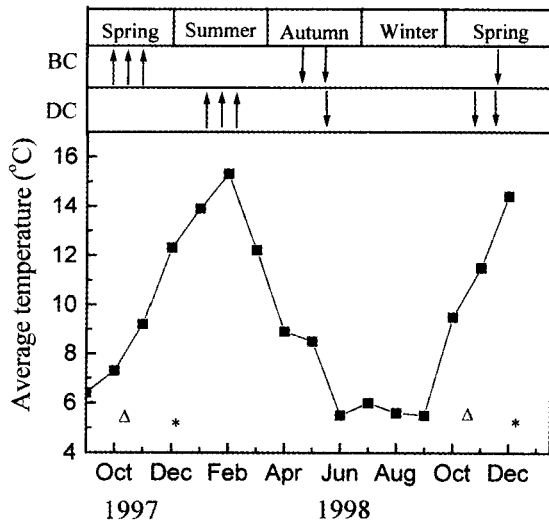
Fig. 1: Monthly average of air temperature and phenological events in *Aristotelia chilensis* during 1997-1998. BC = basal cohort; DC = distal cohort; ↑ = leaf emergence; ↓ = shedding of leaves. The number of arrows indicates the intensity of leaf emergence or fall for each foliar cohort in different seasons. The beginning of the flowering (Δ) and fructification (*) are indicated at the base of the graph.

Valores promedio mensuales de temperatura ambiente y eventos fenológicos de *Aristotelia chilensis* durante 1997-1998. BC = cohorte basal; DB = cohorte distal, ↑ = emergencia foliar, ↓ = caída de las hojas. El número de flechas indica la intensidad en la emergencia o en la caida de hojas para cada cohorte foliar en las diferentes estaciones. El comienzo de la floración (Δ) y de la fructificación (*) es indicado en la base del gráfico.
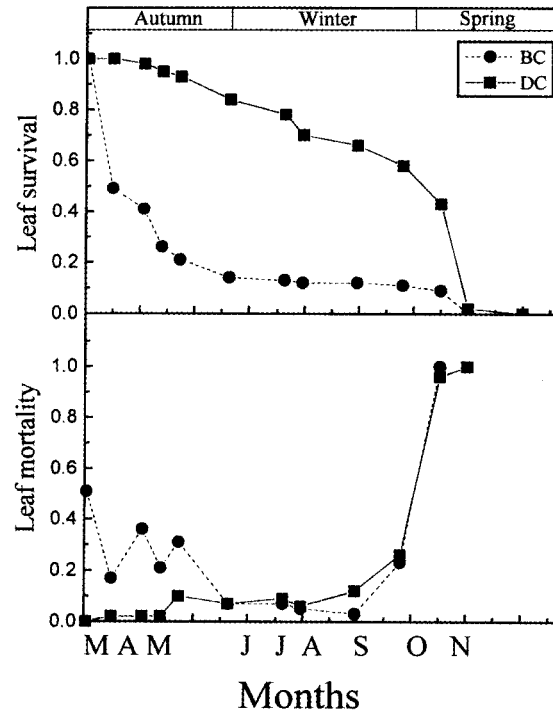

Fig. 2: Survival and mortality between March and November 1998 for both foliar cohorts of *Aristotelia chilensis*. BC = basal cohort (leaves formed in November 1997, n = 300 leaves marked on five plants); DC = distal cohort (leaves emerged between January and March 1998, n = 600 leaves marked on five plants).

Sobrevivencia y mortalidad entre marzo y noviembre de 1998 de las dos cohortes foliares de *Aristotelia chilensis*. CB = cohorte basal (hojas formadas en noviembre de 1997, n = 300 hojas marcadas en cinco plantas); CD = cohorte distal (hojas emergidas entre enero y marzo de 1998, n = 600 hojas marcadas en cinco plantas).

TABLE 1

General foliar features of *A. chilensis* in spring. Mean values ± standard deviation of length (cm), specific leaf mass (g m⁻²), total photosynthetic area (cm²) and total dry biomass (g) of the old and new leaves per shoot. Different letters indicate significant differences (P < 0.05) between foliar cohorts using the Student t test (leaf length and specific leaf mass) or the paired Student t-test (total leaf area and total leaf dry biomass per shoot). n corresponds to the sample size

Algunas características foliares de *A. chilensis* en primavera. Valores promedio ± desviación estándar de la longitud de las hojas (cm), peso específico foliar (g m⁻²), área fotosintética total (cm²) y peso seco foliar total (g) de hojas viejas y nuevas por rama. Distintas letras indican diferencias significativas (P < 0,05) entre cohortes foliares comparadas mediante la prueba t de Student (longitud de la hoja y peso específico foliar) o usando la prueba t de Student para muestras pareadas (área foliar total y peso foliar total por rama). n corresponde al tamaño de muestra

Variable	Old leaves	New leaves
Mean length of leaf (n = 150 leaves)	7.3 ± 1.5 a	7.1 ± 0.8 a
Specific leaf mass (n = 5 plants)	93.5 ± 16.5 a	61.8 ± 7.3 b
Photosynthetic area per shoot (n = 10 shoots)	722.1 ± 342.2 a	571.8 ± 311.9 a
Dry leaf biomass per shoot (n = 10 shoots)	6.1 ± 3.0 a	3.2 ± 1.8 b

senesced in autumn, with a small percentage of survivors (< 10 %), but 43 % of the DC leaves remained attached to the plant until the following spring (Fig. 2). The maximum DC leaf mortality occurred only in spring, when all the remaining leaves fell synchronically (end of November, Fig. 2).

The leaf life span of each foliar cohort is shown in Fig. 3. The median leaf life span for both foliar cohorts (BC = 176 days and DC = 223 days) was similar. It should be noted that the unfolding of the two foliar cohorts was estimated from phenological observations in 1997 and 1998, with the BC values having an error of ± 15 days, while the error for DC was ± 30 days. The leaves that fell in autumn (SAL) had lower SLM values (85.97 ± 17.77 g m^{-2}) than the leaves that remained attached to the plant during autumn (OAL, SLM = 108.16 ± 9.97 g m^{-2}). The old spring leaves (OSL) lost 10 to 13 % of their mass (Table 1) during autumn and winter (no significant decrease).

Specific leaf mass of species with different leaf phenology

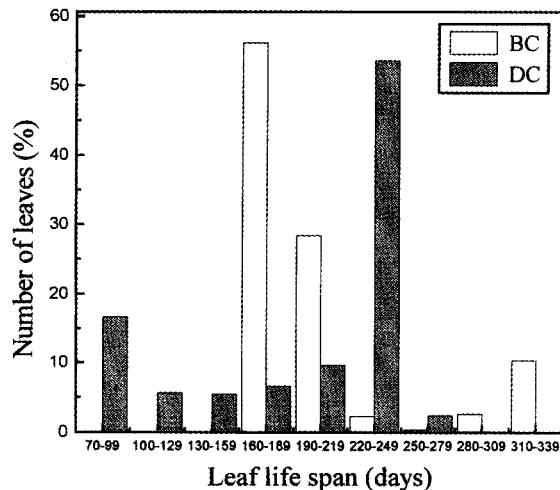Table 2 shows the mean SLM values for the deciduous, evergreen and wintergreen species in

the *Austrocedrus chilensis, Nothofagus dombeyi* and *Nothofagus pumilio* forests in San Carlos de Bariloche. Significant differences were found for the SLM values in species with different foliar phenology in each forest (Table 3). The deciduous species had the lowest SLM values, the evergreen species had the highest SLM values and the wintergreen species had intermediate SLM values (Table 2). The same pattern was observed for woody species from other regions (Table 4).

The SLM of the three species with different phenological characteristics (*Aristotelia chilensis, Ribes magellanicum* and *Schinus patagonicus*) present in the three studied forests is shown in Fig. 4. The two way ANOVA test indicated significant differences among the species and forests (Table 3). The SLM values for *R. magellanicum* and *S. patagonicus* were forest-
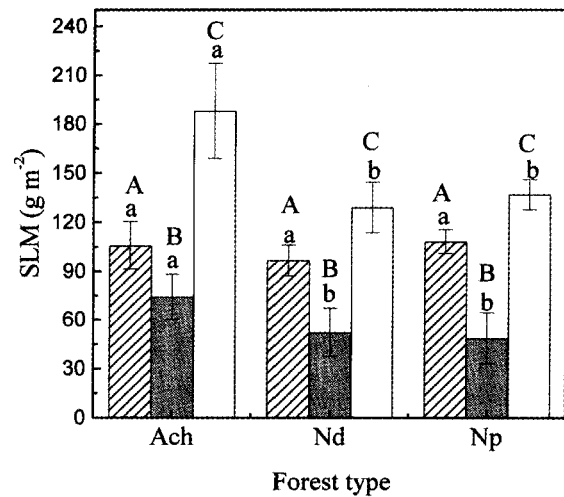

Fig. 3: Percentage of leaves in different age classes for both foliar cohorts. BC = basal cohort (leaves formed in November 1997, n = 300 leaves marked on five plants); DC = distal cohort (leaves emerged between January and March 1998, n = 600 leaves marked on five plants).

Porcentaje de hojas en diferentes clases de edad para las dos cohortes foliares. CB = cohorte basal (hojas formadas en noviembre de 1997, n = 300 hojas marcadas en cinco plantas); CD = cohorte distal (hojas emergidas entre enero y marzo de 1998, n = 600 hojas marcadas en cinco plantas).

Fig. 4: Mean specific leaf mass (SLM) ± standard deviation of three species present in the forests of *Austrocedrus chilensis* (Ach), *Nothofagus dombeyi* (Nd) and *Nothofagus pumilio* (Np). Deciduous species, *Ribes magellanicum* ▓; evergreen species, *Schinus patagonicus* ☐; and wintergreen species, *Aristotelia chilensis* ◹. Different capital letters above bars in the same forest indicate significant differences among species. Different low case letters above bars indicate significant differences for the same species among forests.

Peso específico foliar (SLM) promedio ± desviación estándar de tres especies presentes en los bosques de *Austrocedrus chilensis* (Ach), *Nothofagus dombeyi* (Nd) y *Nothofagus pumilio* (Np). Especie decidua, *Ribes magellanicum* ▓; especie siempreverde, *Schinus patagonicus* ☐; y especie invierno-verde, *Aristotelia chilensis* ◹. Diferentes letras mayúsculas sobre las barras indican diferencias significativas entre especies en el mismo bosque. Diferentes letras minúsculas sobre las barras indican diferencias significativas para la misma especie entre bosques.

TABLE 2

Mean specific leaf mass (SLM) ± standard deviation of the dominant species in *Austrocedrus chilensis* (Ach), *Nothofagus dombeyi* (Nd) and *Nothofagus pumilio* (Np) forests. Different letters indicate significant differences (ANOVA, $P < 0.05$) among species in the same forest. Sample size corresponds to 5 plants of each species in each forest

Peso específico foliar (SLM) promedio ± desviación estándar de las especies dominantes en los bosques de *Austrocedrus chilensis* (Ach), *Nothofagus dombeyi* (Nd) y *Nothofagus pumilio* (Np). Letras diferentes indican diferencias significativas (ANOVA, $P < 0,05$) entre especies dentro de cada bosque. El tamaño de muestra corresponde a 5 plantas por especie en cada bosque

Forest	Species	Phenological group	SLM (g m^{-2})
Ach	*Aristotelia chilensis*	Wintergreen	105.8 ± 14.5 a
	Myoschilos oblonga	Deciduous	50.4 ± 9.5 b
	Ribes magellanicum	Deciduous	74.2 ± 14.0 b
	Lomatia hirsuta	Evergreen	196.5 ± 17.2 c
	Baccharis rhomboidalis	Evergreen	136.2 ± 5.7 c
	Schinus patagonicus	Evergreen	188.0 ± 29.1 c
Nd	*Aristotelia chilensis*	Wintergreen	96.6 ± 9.4 a
	Ribes magellanicum	Deciduous	52.4 ± 14.8 b
	Luma apiculata	Evergreen	129.1 ± 15.4 c
	Nothofagus dombeyi	Evergreen	140.6 ± 0.4 c
	Schinus patagonicus	Evergreen	129.1 ± 15.4 c
Np	*Aristotelia chilensis*	Wintergreen	108.3 ± 7.4 a
	Ribes magellanicum	Deciduous	48.8 ± 15.7 b
	Berberis serrato-dentata	Evergreen	167.0 ± 10.9 c
	Schinus patagonicus	Evergreen	136.9 ± 9.2 c
	Average	Deciduous	54.4 ± 5.7
		Evergreen	156.0 ± 26.9

dependent (species x forest: $P < 0.05$), and were higher for both species in the *Austrocedrus chilensis* forest (Fig. 4). The *A. chilensis* SLM value was intermediate and different from the other two species in the same forest, but it did not vary among forests (Fig. 4).

DISCUSSION

Aristotelia chilensis showed no apparent lag between the flush of new leaves in spring and the successive expansion of other leaves during the growing season, indicating that a combined foliar unfolding occurred (sensu Kikuzawa 1984). Therefore, the initial carbon demand for new leaves growing after winter was probably covered by the photosynthetic activity of old leaves (Prado & Damascos in press) and possibly by some material from heterotrophic tissues. Flowering occurred in spring, concurrently with leaf production, imposing additional demands of carbon and nutrients (Bazzaz et al. 1987, Snow & Whingham 1989). This demand was assumed to be met by the old leaves before abscission and by the new leaves upon their total expansion. Old

leaves played the role of a carbon source throughout their photosynthetic activity before abscising after winter (Prado & Damascos in press), and defoliated *A. chilensis* plants in autumn showed a lower branch growth during the following spring compared to the control plants (Damascos & Prado 2001). The fall of old leaves in autumn (particularly the old basal cohort) was accompanied by a great reduction of foliar mass, whose maximum value (31 %) was higher than the species from the temperate forests studied by Chapin & Van Cleve (1991). This indicated that an important mass translocation from old leaves may have occurred to cover the demand for the growth of new leaves and flowers in early spring.

Old leaves of *A. chilensis* were photosynthetically active after winter (Prado & Damascos in press), but became yellow and abscise in just one week, highlighting the strong endogenous coordination of its senescence. Furthermore, the senescence of old leaves of *A. chilensis* in early spring was faster than that of deciduous species growing in the same forests in early winter. It would be unsuitable for *A. chilensis* to maintain old and new leaves cohorts simultaneously, on account of to the greater

TABLE 3

One-way and two way-analysis of variance of the SLM mean values. Effect of the species factor into each studied forest (one-way ANOVA). Interaction between species and forest factors (two way ANOVA). (df = degrees of freedom; MS = mean square; F = Fisher's statistic; P = associated value of probability)

Análisis de varianza de una y dos vías de los valores medios de SLM. Efecto del factor especie en cada bosque estudiado (ANOVA de una vía). Interacción entre los factores especie y bosque (ANOVA de dos vías). (df = grados de libertad; MS = cuadrado medio; F = estadístico de Fisher; P = valor de probabilidad asociado)

| | One-way ANOVA[1] Forest | | | | | | | | | | | | Two-way ANOVA[2] | | | |
| | Austrocedrus chilensis | | | | Nothofagus Dombeyi | | | | Nothofagus pumilio | | | | | | | |
Source of variation	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Species (S)	5	17728.7	63.6	<0.0001	4	6451.6	41.2	<0.0001	3	10403.4	27.7	<0.0001	2	32352.6	133.37	<0.0001
Forest (F)	-	-			-	-			-	-			2	3838.0	15.82	<0.0001
F x S	-	-			-	-			-	-			4	1210.4	4.99	0.0026
Error	24	278.5			20	156.5			16	375.5			36	242.6		

[1]Among species present in each forest (mean SLM values shown on Table 2)
[2]Among three common species growing in all three studied forests (mean SLM values shown on Fig. 4)

demand for defense compounds for the new foliar cohort (Bazzaz et al. 1987) in addition to greater leaf predation during the growing season in temperate climates (Mooney & Gulmon 1982).

The average leaf life span of A. chilensis (6.5 months) was found to be similar to that of other wintergreen species, such as Daphne kamtschaca var. jezoensis (6 months, Kikuzawa 1984) or to the general values for deciduous species (6 months, Chabot & Hicks 1982, Mooney & Gulmon 1982). However, wintergreen species always support at least one foliar cohort during the year while deciduous species do not. Thus, wintergreen species are potentially autotrophic throughout the year and their foliar construction at the beginning of the growing season does not depend exclusively on the material stored in heterotrophic parts, as is the case in deciduous species. This would be beneficial for wintergreen species growing under canopies, which are able to make use of direct solar radiation during winter (Minoletti & Boener 1993) or at the beginning of the growing season, when the tree strata in deciduous forests shows lower values of leaf area (Tissue et al. 1995, Landhäusser et al. 1997). If a species has constraints that prevent translocation from heterotrophic tissues or lacks large organs to store assimilated material, then the wintergreen phenology would be a clear adaptation, since it keeps the canopy ready to assimilate carbon to cover the plant's requirements all the time during the year. On the other hand, the life span of A. chilensis leaves is shorter than that of evergreen species, and A. chilensis does not keep its leaves through several winters. This latter characteristic reduces the cost of defense and maintenance for each cohort holding at least one leaf cohort ready for work, as in evergreen species.

Although the mean leaf life span of A. chilensis and deciduous species are similar, their SLM differ. The average SLM of A. chilensis is close to that determined by Karlsson (1994) and Jonasson (1995) for a woody wintergreen species, Rhododendron lapponicum, but it is greater than that of the deciduous species growing in the same forest near San Carlos de Bariloche. This difference suggests that the SLM is determined by factors others than the leaf life span.

Leaves of Aristotelia chilensis overcome the thermal and water stresses during winter as well as those related to herbivores, excessive radiation and water stress during the growing season. These stresses may promote leaf scleromorphism: a more compact mesophyll, thicker cell walls and an abundant cutin layer. Such leaf traits may increase the SLM (Jurik 1986), providing protection against low temperatures (thermal isolation), abrasion

TABLE 4

Mean values and ranges of the specific leaf mass (SLM, g m^{-2}) ± standard deviation in species of the three phenological groups from different communities. All the data were obtained under field conditions during the growing season, except those from Lange et al. (1982), who obtained SLM values in potted adult plants under controlled conditions similar to field conditions. n = species number

Valores promedio y rangos de peso específico foliar (SLM, g m^{-2}) ± desviación estándar en especies de los tres grupos fenológicos en diferentes comunidades. Todos los datos fueron obtenidos en condiciones de campo durante la estación de crecimiento, con excepción de aquellos provenientes de Lange et al. (1982), quien obtuvo los valores de SLM en plantas adultas plantadas bajo condiciones controladas similares a las de campo. El número de especies (n) se indica entre paréntesis

Community	Phenological group			Reference
	Deciduous	Evergreen	Wintergreen	
Temperate forest	73.1 ± 16.2 28 - 112 (n = 58)	147 ± 21.6 123 - 196 (n = 12)	104 (n = 1)	Jurik (1986), Koike (1988), Harrington et al. (1989), Miyazawa et al. (1998), Damascos et al. (unpublished results), this study
Mediterranean climate	46 (n = 1)	159.8 ± 53.6 90 - 318 (n = 29)	-	Lange et al. (1982), Field & Mooney (1983), Field et al. (1983), Mooney et al. (1983), Gratani (1995), Abril & Hanano (1998)
Bog	77.6 ± 13.5 52 - 97 (n = 17)	148.0 ± 42.7 113 - 236 (n = 8)	120.7 (n = 1)	Small (1972) Jonasson (1989)
Tundra			115.0 (n = 1)	Karlsson (1994), Jonasson (1995)
Total	73.7 ± 15.9 28 -112 (n = 76)	154.8 ± 45.8 90 - 318 (n = 49)	113.5 ± 8.5 104 - 120 (n = 3)	

(caused by snow), and loss of water (thicker cutin layer) during winter.

The leaves of deciduous species avoid the stressful conditions caused by winter or dry seasons. In contrast, the leaves of evergreen species are exposed to a variety of stresses during several winters and growing seasons. This is a stressful situation that reinforces the above mentioned leaf traits, causing usually the highest SLM values in evergreen species. However, deviations can be detected in each phenological leaf group, depending on the environmental growth conditions and the phenotypic plasticity of each species (Gratani 1995). In this study, the most adverse condition for growth was found in the *Austrocedrus chilensis* forest, which is drier (Damascos 1998) and has poorer soil than the other two forests studied (Mazarino et al. 1999). In this forest, the deciduous (*Ribes magellanicum*) and the evergreen species (*Schinus patagonicus*)

showed higher SLM values than they did in the two other forests.

However, one question still remains unanswered, i.e., why no differences were found in the SLM values of *A. chilensis* among the studied forests near San Carlos de Bariloche ? This may be in consequence of the wintergreen phenology. The leaves of *A. chilensis* live through a single winter, which is a stressful period. Some differences of resources availability among studied forests are relatively less significant in determining the SLM, even during leaf ontogenesis in the growing season. Thus, the expanded leaves of *A. chilensis* were found to be more sclerophyllous reducing the risk of leaf injury during winter, and showing higher SLM values than the deciduous species in the three forests studied or in comparison to the mean values of the deciduous species in communities of other countries.

If the winter months are important in determining the SLM values of *A. chilensis* why does the same not apply to the evergreen species growing in identical forests near San Carlos de Bariloche? Evergreen species maintain the same leaf for several winters. During the ontogenesis of this type of leaf, a great deal of material accumulates to build up a hard sclerophyllous leaf that is capable of surviving at least two winters (usually more). First, the structural carbon demand to ensure the survival of leaves during winters is covered, which leads to higher SLM than in other phenological groups. This processes is relatively more costly and the efficiency is essential for the annual plant and leaf carbon balance. Thus, in order to operate with higher SLM levels for several years, it is convenient for the evergreen species to modify their SLM according to the resources available in each forest. This enables them to make better use of the available carbon to grow and maintain their foliar cohorts, without risking the survival of their leaves. The resources saved over several years by this way of acting in evergreen species may be transferred to parallel processes (defense, growth or reproduction) during the plant's life cycle, as indicated by Bazzaz et al. (1987). This may occur even during leaf ontogenesis, when efficiency is crucial, since the available resources are used to cover both the maintenance and the growth of the leaf.

It is evident, from all the phenological groups studied here, that leaf phenology and leaf life span estimated on a daily basis simply serve as clues for the identification of leaf traits (e.g., possible range of SLM values). It is highly important to assess the stress conditions in which a leaf cycle occurs, the interdependency between leaf growth and defense, and the efficient use of available resources in order to understand the ecophysiological meaning of the SLM values.

LITERATURE CITED

ABRIL M & R HANANO (1998) Ecophysiological responses of three evergreen woody Mediterranean species to water stress. Acta Oecologica 19: 377-387.

BARROS V, V CORDON, C MOYANO, R MENDEZ, J FORGUERA & O PIZZIO (1983) Cartas de precipitación de la zona oeste de las provincias de Río Negro y Neuquén. Primera contribución. Universidad Nacional del Comahue, Consejo Nacional de Investigaciones Científicas y Técnicas. 35 pp.

BAZZAZ FA, NR CHIARELLO, PD COLEY & LF PITELKA (1987) Allocating resources to reproduction and defense. BioScience 37: 58-67.

BELL KL & LD BLISS (1977) Overwinter phenology of plants in a polar semidesert. Arctic 30: 118-121.

BUAMSCHA MG, M GOBBI, MJ MAZARINO & F LAOS (1998) Indicators of nitrogen conservation in *Austrocedrus chilensis* forest along a moisture gradient in Argentina. Forest Ecology and Management 112: 253-261.

BUSKIRK J & J EDWARDS (1995) Contribution of wintergreen leaves to early spring growth in the wood fern *Dryopteris intermedia*. American Fern Journal 85: 54-57.

CHABOT BF & DJ HICKS (1982) The ecology of leaf life spans. Annual Review of Ecology and Systematics 13: 229-259.

CHAPIN III FS & K VAN CLEVE (1991) Approaches to studying nutrient uptake, use and loss in plants. In: Pearcy RW, J Ehleringer, HA Mooney & PW Rundel (eds) Plant physiological ecology. Fields methods and instrumentation: 185-207. Chapman and Hall, New York, New York.

DAMASCOS MA (1996) Análisis morfológico-estructural en comunidades de la patagonia austral. Tesis Doctoral, Universidad Nacional de La Plata, La Plata, Argentina. 160 pp.

DAMASCOS MA (1998) Tendencias morfológicas de las plantas de los claros y áreas sombreadas del bosque de *Austrocedrus chilensis*, Argentina. Ecología Austral 8: 13-22.

DAMASCOS MA & CHBA PRADO (2001) Defoliación en la especie invierno-verde *Aristotelia chilensis* y sus efectos sobre el crescimiento inicial de hojas y ramas. Bosque 22: 45-50.

FIELD C & HC MOONEY (1983) Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. Oecologia 56: 348-355.

FIELD C, MERINO J & HC MOONEY (1983) Compromises between water use efficiency and nitrogen use efficiency in five species of California evergreens. Oecologia 60: 384-389.

GRATANI L (1995) Structural and ecophysiological plasticity of some evergreen species of the Mediterranean maquis in response to climate. Photosynthetica 31: 335-343.

HARRINGTON RA, BJ BROWN & PB REICH (1989) Ecophysiology of exotic and native shrubs in southern Wisconsin. I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia 80: 356-367.

JONASSON S (1989) Implications of leaf longevity, leaf nutrient reabsorption and traslocation for the resource economy of five evergreen species. Oikos 56: 121-131.

JONASSON S (1995) Resource allocation in relation to leaf retention time of the wintergreen *Rhododendron lapponicum.* Ecology 76: 475-485.

JURIK TW (1986) Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. American Journal of Botany 73: 1083-1092.

KARLSSON PS (1994) The significance of internal nutrient cycling in branches for growth and reproduction of *Rhododendron lapponicum.* Oikos 70: 191-200.

KIKUZAWA K (1984) Leaf survival of woody plants in deciduous broad-leaved forest. 2. Small trees and shrubs. Canadian Journal of Botany 62: 2551-2556.

KOIKE T (1988) Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Plant Species Biology 3: 77-87.

KRIEBITZSCH WU (1992) CO_2 and H_2O gas-exchange of understory plants in a submontane beech forest on limestone. 1. Seasonal-changes of the photosynthetic response to light. Flora 186: 67-85.

LANDHÄUSSER SM, KJ STADT & VJ LIEFFERS (1997) Photosynthetic strategies of summergreen and evergreen understory herbs of the boreal mixed wood forest. Oecologia 112: 173-178.

LANGE OL, JD TENHUNEM & M BRAUN (1982) Midday stomatal closure in Mediterranean type sclerophylls under simulated habitat conditions in an environmental chamber. I. Comparison of the behaviour of various European Mediterranean species. Flora 172: 563-579.

MAZARINO MJ, MB BERTILLER, T SCHLICHTER & M GOBBI (1999) Nutrient cycling in Patagonian ecosystems. Ecología Austral 8: 167-181.

MINOLETTI ML & REJ BOERNER (1993) Seasonal photosynthesis, nitrogen and phosphorus dynamics, and resorption in the wintergreen fern *Polystichum acrostichoides* (Michx) Schott. Bulletin of the Torrey Botanical Club 120: 397-404.

MIYAZAWA S, S SATOMI & Y TERASHIMA (1998) Slow leaf development of evergreen broad-leaved tree species in Japanese warm temperate forest. Annals of Botany 82: 859-869.

MOONEY HA & SL GULMON (1982) Constraints on leaf structure and function in reference to herbivory. BioScience 32: 198-206.

MOONEY HA, C FIELD, SL GULMON, P RUNDEL & FJ KRUGER (1983) Photosynthetic characteristic of South African sclerophylls. Oecologia 58: 398-401.

NOODEN LD & WAGNER WH (1997) Photosynthetic capacity and leaf reorientation in two wintergreen ferns, *Polystichum acrostichoides* and *Dryopteris intermedia.* American Fern Journal 87: 143-149.

PRADO CHBA & MA DAMASCOS (2001) Gas exchange and leaf specific mass of different foliar cohorts of the wintergreen shrub *Aristotelia chilensis* (Mol.) Stuntz (Elaeocarpaceae) fifteen days before the flowering and the fall of the old cohort. Brazilian Archives of Biology and Technology (in press).

PRADO CHBA & JAPV MORAES (1997) Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field conditions. Photosynthetica 33: 103-112.

REICH PB, C UHL, MB WALTERS & DS ELLSWORTH (1991) Leaf life span as a determinant of leaf structure and function among 23 Amazonian tree species. Oecologia 86: 16-24.

REICH PB, MB WALTERS & DS ELLSWORTH (1992) Leaf life span in relation to leaf, plant and stand characteristics among diverse ecosystems. Ecological Monographs 62: 365-392.

SILVERTOWN JW (1982) Introduction to plant population ecology. Logman, London, United Kingdom. 208 pp.

SMALL E (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Canadian Journal of Botany 50: 2227-2233.

SNOW AA & DF WHIGHAM (1989) Cost of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology 70: 1286-1293.

TISSUE DT, JB SKILLMAN, EP MCDONALD & BR STRAIN (1995) Photosynthesis and carbon allocation in *Tipularia discolor* (Orchidaceae), a wintergreen understory herb. American Journal of Botany 82: 1249-1256.

UEMURA S (1993) Patterns of leaf phenology in forest understory. Canadian Journal of Botany 72: 409-414.

WERNER K & F EBEL (1994) Life-history of the genus *Helleborus* L (Ranunculaceae). Flora 189: 97-130.

WHIGHAM DF (1989) The effects of experimental defoliation on the growth and reproduction of a woodland orchid, *Tipularia discolor.* Canadian Journal of Botany 68: 1812-1816.

ZAR JH (1999) Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey. 663 pp.