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Altitudinal variation in the phenology of *Nothofagus pumilio* in Argentina

Variación altitudinal en la fenología de *Nothofagus pumilio* en Argentina

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ABSTRACT

Phenological changes of *Nothofagus pumilio* (Poepp et Endl. –Krasser–) were measured twice a month in natural forest located at elevations between 1,100 and 1,390 m, in the Nahuel Huapi National Park, Argentina. Leaf budding and foliage color change were measured using ranks, while seed and litterfall were estimated from traps in the soil. Size of leaves were also compared. Flowering was recorded qualitatively. The vegetative growth period began in September, ended in May, and was shortened with elevation due to the delayed leaf budding and the acceleration of leaf fall. Leaves were smaller at higher elevations. Flowering was simultaneous with leaf budding, and foliar color change showed no difference with altitude. Based on these data and on the characteristics of the mountain climate, it is suggested that temperature controls leaf budding and flowering and influences seed and leaf fall, while foliage color change is related to radiation.

Key words: Southern temperate forests, lenga, mountain climate, *Nothofagus*, seed dispersal, flowering.

RESUMEN

Se estudiaron quincenalmente los cambios fenológicos de *Nothofagus pumilio* (Poepp et Endl. –Krasser–) en bosques naturales entre los 1.100 y los 1.390 m en el Parque Nacional Nahuel Huapi, Argentina. El brote de hojas y el cambio de color del follaje se midieron empleando escalas mientras que las hojas y las semillas caídas se contaron de trampas colocadas en el suelo y se analizó también el tamaño foliar. La floración se registró cualitativamente. El período de actividad vegetativa comenzó en septiembre y se acortó con la altura debido al retraso en la brotación y la aceleración de la caída de hojas en mayo. El tamaño foliar presentó sus mínimos valores en las altitudes superiores. La floración fue simultánea con la brotación y el cambio de color del follaje no mostró diferencias con la altitud. En base a estos datos y a las características del clima de montaña, se sugiere que la temperatura controla la brotación y floración e influye sobre la caída de las hojas y semillas, mientras que el cambio de color del follaje está relacionado con la radiación.

Palabras claves: Bosques templados del sur, lenga, clima de montaña, *Nothofagus*, dispersión de semillas, floración.

INTRODUCTION

Temperate forest of South America form a narrow band which stretches along more than 2,000 km, between 34° and 55°S in Chile and Argentina (Dimitri 1972, Winograd, unpublished data) (Fig. 1). Monospecif forests of *Nothofagus pumilio* (Poep et Endl. –Krasser–) form the highest altitudinal belt throughout this region. Hence, this species must play a key role on the regulation of water flow (and sediment transport) of Andean rivers, which irrigate more than 780,000 km² in Patagonia, the austral portion of South America.

Despite an intensive destruction of Chilean forest in the past decades, *N. pumilio* still covers an area of more than 3 million ha in Chile and Argentina (Schmidt & Lara 1985, IFONA 1986), representing an important economic value for the region. Nevertheless, its use has been historically restricted to harvesting the best individuals in the forests, thus deteriorating the resource. Only in the last 10 years, sylvicultural techniques based on the criterion of sustained yield, have been implemented in the wetter range of this species distribution (Schmidt & Urzúa 1982). In this way, foresters can obtain 4 to 6 m³/ha of timber per year, also improving the quality of the wood and the rate of growth.

In the drier (northeastern) area, however, higher exploitation costs have not allowed

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the implementation of the correct management techniques. The problem of conservation of *N. pumilio* forests in this region is greater due the limited regeneration observed (Kalela 1942, Mutarelli & Orfila 1973, Rusch 1987[1]. Special attention must be payed therefore, to the management techniques adopted.

The objective of this work is to study the timing of phenological phases and their altitudinal variations in *N. pumilio*, and to determine the environmental factors that control each process.

In the mountain regions, where *N. pumilio* grows, climatic variations are complex and temperature data are sparse so plant phenology appears as a usefull predictor of the microclimatic differences to complement the meteorological data (Castonguay & Dubé 1985). No complete phenological study is known for this species. Krebs (1959) presented dates of initiation and ending of phenological phases for a population of *N. pumilio* planted ouside their natural range, while Donoso & Cabello (1978) determined flowering and fruit ripining times. In this study all the phenological phases were followed in natural populations at different altitudes.

MATERIALS AND METHODS

Study Area

The forests sampled are on the Diego de León Hill, in the "Manso Superior" river basin, Argentina (Fig. 1). An "Integrated Ecological Study" has been carried out in this 24,700 ha basin (Gallopin 1978), and thus a great deal of basic information is available. The area is included in the "Nahuel Huapi National Park" in the Río Negro province, and is located in the northeast of the Andean Patagonian Forest Region (Cabrera 1976). The basin has been modelated by glaciers which were active up to 11,000 years ago. Four glaciers are still active in the area surrounding Mt. Tronador, the highest peak, in the western limit of the basin. *N. pumilio* forests have developed mainly on Distrandepts and Criandepts, rich soils formed on recent volcanic ashes (presenting scarse clay minerals and little differences among the horizons).

Two agrometeorological stations ("Pampa Linda" and "Mascardi") operate in the area, the latest on the valley just below the forests sampled, at an elevation of 800 m. A snow pillows is also operating at 1,400 m near Tronador hill. Mean annual temperature in "Mascardi" is 7.3°C and that of coldest and warmest months are 1.5°C and 13.0°C respectively. Daylenght varies from more than 15 (summer) to nearly 9 hours (winter) (Fig. 2). Annual precipitation is 1,410 mm concentrated in autumn and winter (Fig. 3). In mountain regions, climatic variables present altitudinal variation. Air temperature falls with elevation in a roughly linear way up to 11 km above sea level. The vertical gradient of temperature is not constant and depends on the time of the day, the season and the site. Mean gradients of 0.5°C/100 m (Tranquillini 1964) and 0.65°C/100 m (Trewartha 1968) are commonly accepted. For the "Manso Superior" basin the gradients were calculated by Gallopin (1978) to be 0.37°C/100 m and 0.26°C/100 m for the warmest and the coldest months respectively.

A total number of 21 vegetation types have been identified in the Manso Superior watershed (Rodriguez *et al.* 1978). Forest and shrubland are the prevailing formations. The lower slopes are covered mainly by stands dominated by *Nothofagus antarctica*, *N. dombeyi* or *Austrocedrus chilensis*. Above 1,000 m, slopes are covered by *Nothofagus pumilio* forest (up to the timberline, at 1,500 m), and by *N. pumilio* scrub from 1,500 m to 1,800 m. In this way, this species occupies 44% of the area of the basin.

In the western portion of the basin, the presence of *Chusquea* sp. in the understorey is common, while in the eastern (and drier) portion *Drimys winteri*, *Leuceria* sp., *Acaena ovalifolia*, *Osmorhiza chilensis*, *Maytenus disticha* and *Berberis serrato-dentata* are the most common species.

Methods

To analyze the evolution of phenological processes two forest stands were sampled every

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[1] RUSCH V (1987) Estudio de la regeneración de los bosques de *Nothofagus pumilio* en la cuenca del Río Manso Superior. Informe interno, CONICET.

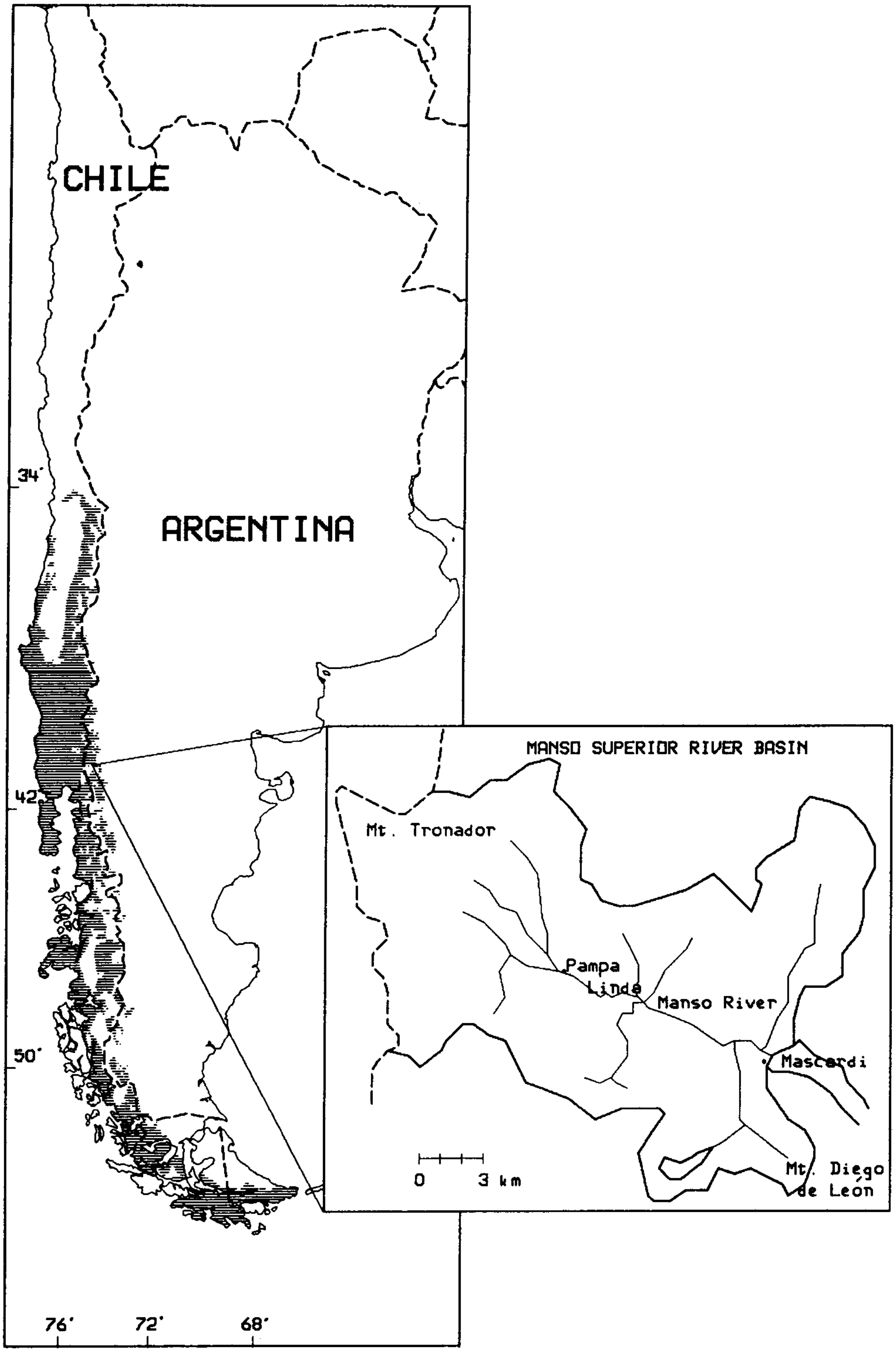

Fig. 1: Distribution of the Temperate Forest Region in South America (≡), (Winograd, unpublished data) and the "Manso Superior" River basin.

Distribución de la Región de los Bosques Templados en Sudamérica (≡), (Winograd, datos inéditos) y la Cuenca del Río "Manso Superior".

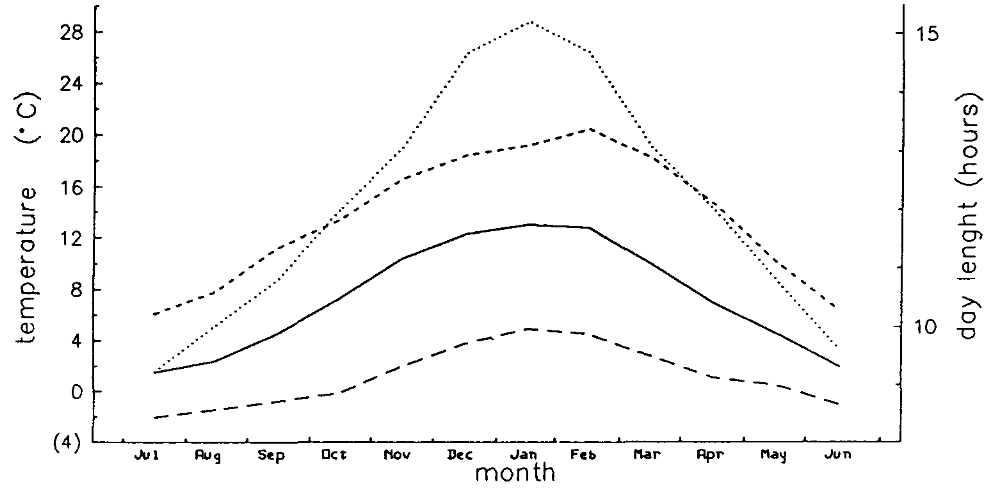

Fig. 2: Annual variation of temperatures and day lenght at Mascardi Station (—— monthly media,– – – – maximum media,– – minimum media and······ day lenght).

Variación anual de la temperatura y la longitud del día en la estación Mascardi (—— media mensual, – – – – media máxima,– – media mínima y······ duración del día).

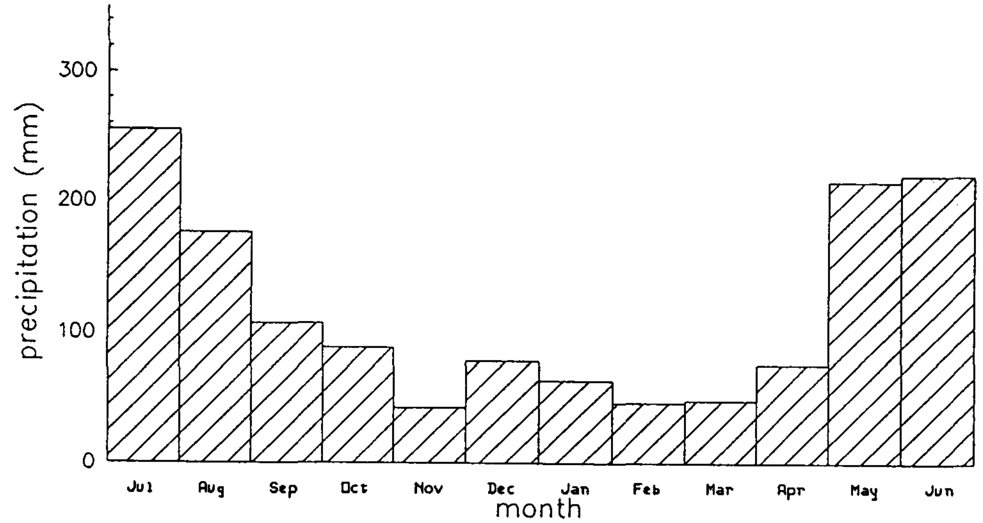

Fig. 3: Distribution of precipitation at Mascardi Station.

Distribución de la precipitación en la Estación Mascardi.

week or twice a month from August 1985 to May 1986, at an elevation of 1,225 m (stand 1, *S1*) and at 1,390 m (stand 2, *S2*). Their selection was based on their similar basal area (48.5 and 46.5 m²/ha), diametric structure, aspect (SW and SSW) and slope (56%).

To study in more detail the relationship between altitude and leaf budding, the bud stage was also recorded in September and October 1986, at 1,140, 1,185, 1,210, 1,225, 1,305, 1,330, 1,345 and 1,390 m. The maximum leaf size was analysed from fully formed leaves collected in April 1986, at 1,140, 1,185, 1,220, 1,225, 1,330, 1,390 and 1,410 m.

At *S1* and *S2*, the ten nearest crowns to a randomly selected point were monitored. Arbitrary ranks were constructed to describe the bud stage and foliage color change of the trees (Table 1). A similar method was used by Dierschke (in Müller-Dombois & Ellemberg 1974) for an herbaceous community. When

TABLE 1

Scales employed to measure (a) budding and (b) foliage color change in *Nothofagus pumilio*

Escalas empleadas en la medición de (a) brotación y (b) cambio de color del follaje en *Nothofagus pumilio*

State of buds(a) and leaf expansion	Rank	Proportion of the(b) tree with yellow or red leaves	Rank
Resting buds	0	0	0
Swollen buds	1	< 1%	1
Outbreak	2	1 - 5%	2
Expanding leaves	3	5.1 - 25%	3
Small leaves (<1.5 cm)	4	25.1 - 50%	4
Middle size leaves (1.5 - 3 cm)	5	50.1 - 75%	5
Fully-expanded leaves (> 3 cm)	6	> 75%	6

different stages were found within the same crown, those of the upper and lower halves were averaged. The median stage of the ten trees on each date represented the stages of the site. Measurement of bud stages at the eight altitudes in the following spring (1986) were made on 5 trees per site.

Initiation and ending of flowering period were registered at *S1* and *S2*. Flowering ended when the male peryginium fell.

Seed dispersal and leaf fall were quantified at *S1* and *S2* employing 20 cillindric collectors 10 cm diameter, half burried in the ground with a plastic mesh at its base (Schlichter 1982)[2].

Maximum leaf size was measured from leaves collected from the forest floor in autumn (n = 1,000 at each elevation). Each sample was randomly divided into groups of ten leaves and the lenght of the largest leaf was measured. The highest values (half of the sample) were employed to calculate the mean size of large leaves at that altitude. Lenght was considered a good predictor of area, because these variables are strongly correlated ($r = 0.89$ and $p < 0.01$) (Gómez & Gallopin 1987).

A randomization test was employed to analyze differences between sites in (a) the stages of the budding process and (b) foliage color. A Kruskall-Wallis test was employed to compare the pattern of seed fall, and Spearman correlation coefficient between budding and altitude was calculated. A Mann-Whitney "U" test was employed to compare leaf size at different altitudes. Non parametric statistical tests are based on Siegel (1956) and Day & Quinn (1989).

When data were quantitative and their variances were homogeneous parametric analysis were employed: the pattern of leaf fall was fitted to a curve by minimum squares and the confidence intervals of the slope of the curves were calculated.

RESULTS

In 1985, leaf budding started in mid September showing a "flushing" pattern (*sensu* Kikuzawa 1989). At higher elevation leaf budding was delayed about one week with respect to lower elevations (Fig. 4). Randomization tests showed significant differences between altitudes for each date until 18 February when the leaf expantion was no longer recorded. No changes were observed in mid January, when median values at 1,225 (*S1*) and 1,390 m (*S2*) coincided. Nevertheless all the individuals at *S1* reached the highest rank value for leaf expansion (leaves greater than 3 cm), whereas this did not happened at *S2* (Fig. 4). This suggests that larger leaves exist at lower altitudes. To explore this difference I studied the size of leaves at various altitudes.

Maximum leaf size showed and abrupt decrease above 1,350 m (Fig. 5). Results of Mann Whitney test indicate highly significant differences between the two higher forests (1,390 and 1,410 m) when compared with the others.

Results from spring 1986 showed a tight relationship between leaf size and elevation. Spearman's correlation coefficient (r_s) was 0.88 ($p < 0.01$) and the delay was 0.58 rank orders/100 m (Fig. 6).

Since climatic data are unavailable for higher altitudes, valley temperatures were related to the initiation of budding. Mean values for the 15 days following "swollen buds" stage were 4.7°C for *S1* (1,225 m) and 6.8°C for *S2* (1,390 m) in 1985, and 4.8°C (*S1*) and 5°C (*S2*) in 1986.

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[2] SCHLICHTER T (1982) Estudio ecológico de las poblaciones de lenga en el Parque y Reserva Nacional Lanín (Proyecto). Parques Nacionales.

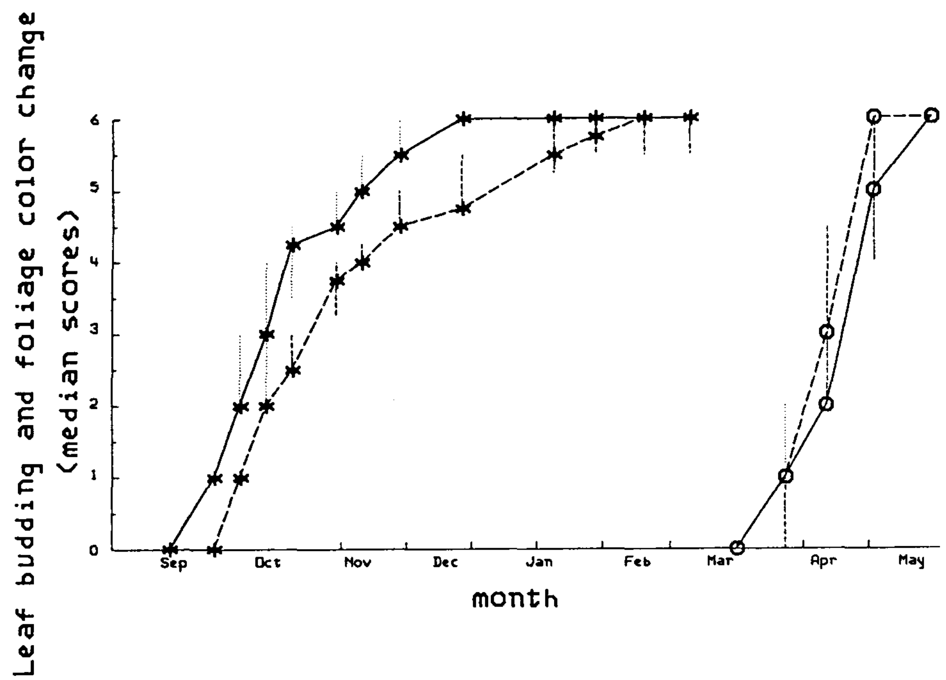

Fig. 4: Budding (*) and foliage color change(O) in *Nothofagus pumilio* forest at 1,225 m (*S1* —) and 1,390 (*S2* – – –) (Median values). Dispersion values represent the intervals between second and third quartile for *S1* (……) and *S2* (– – –). (See Table 1 for scores).

Brote (*) y cambio de color del follaje (O) de bosques de *Nothofagus pumilio* a 1.225 m s.n.m. (*S1* —) y 1,390 m s.n.m. (*S2*– – –) (valores medianos). Los valores de dispersión representan intervalos entre el 2º y 3er cuartil para *S1* (……) y *S2* (– – –). (Para los puntajes ver Tabla 1).

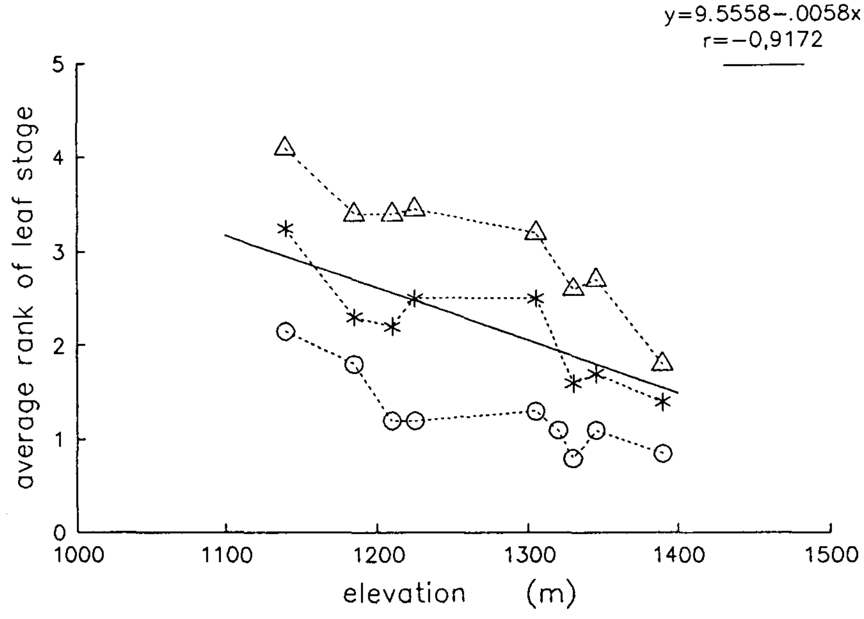

Fig. 5: Relationship between *Nothofagus pumilio* budding and elevation on three dates (1986 spring). The regression line ($p < 0.01$) was adjusted to 1 Oct. values. Measurement dates were: 26 Sep. 86 (O); 1 Oct. 86 (*) and 9 Oct. 86 (Δ).

Relación entre brotación de *Nothofagus pumilio* y altitud para tres fechas (primavera de 1986). La recta de regresión ($p < 0.01$) se ajustó a los valores del 1 Oct. Las fechas de medición fueron: 26 Sept. 86 (O); 1 Oct. 86 (*) y 9 Oct. 86 (Δ).

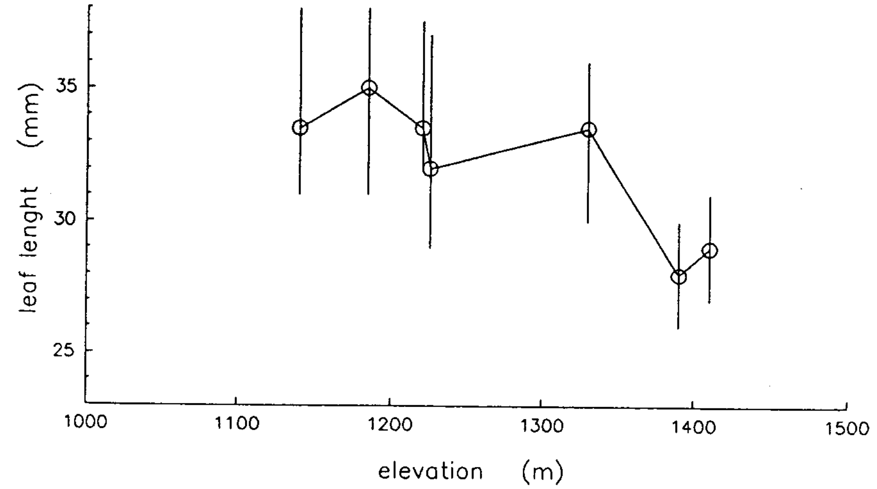

Fig. 6: Maximum foliar size related to elevation. Values with the same letter indicate no statistical differences ("U" test, $p < 0.001$) and $a \neq b$.

Tamaño foliar máximo relacionado a la altitud. La misma letra indica diferencias estadísticas no significativas (test "U", $p < 0,01$) y $a \neq b$.

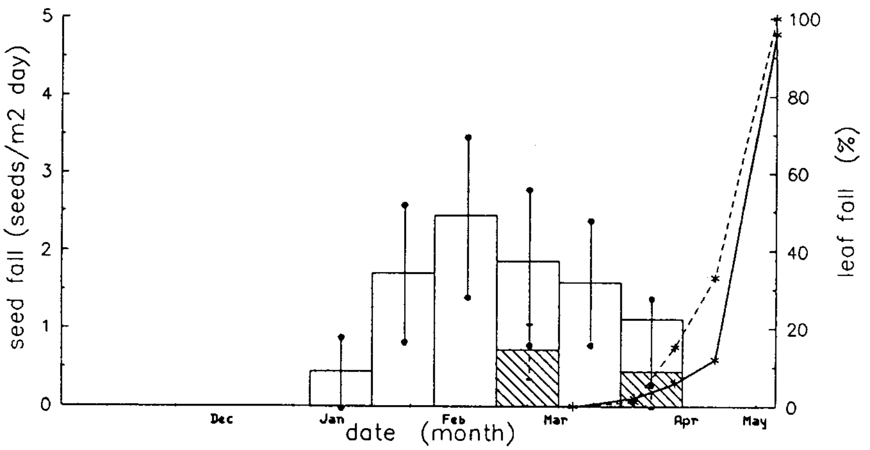

Fig. 7: Seed dispersion and leaf fall at two altitudes. Seed dispersion (bars) ▨ at 1,225 m and ☐ at 1,390 m. Vertical bars indicates standard deviation of the mean for fallen seeds values. Leaf fall ——— at 1,225 and at - - - - 1,390 m.

Dispersión de semillas y caída de hojas a dos altitudes. Dispersión de semillas (barras) ▨ a 1.225 m y a 1.390 m ☐. Las barras verticales indican desviación estándar de la media para los valores de semillas caídas. Caída de hojas ——— a 1.225 m y - - - - a 1.390 m.

Foliage color change (Fig. 4) began in early March and finished in May. Randomization test showed that the process was simultaneous at different altitudes. Falling of leaves began at the same time at 1,225 and 1,390 m, and was accelerated until complete defoliation (Fig. 7). The fitted curves had the following equations: $y1 = e^{-3,561 + 2,499 \text{ Ln } x}$ ($r = 0.946$, $p < 0.01$); and $y2 = e^{-5,107 + 3,048 \text{ Ln } x}$ ($r = 0.988$, $p < 0.01$); where y1 and y2 are "number of fallen leaves/m^2 day" at 1,225 (*S1*) and 1,390 m (*S2*) respectively, and x: "number of days since 5 March".

Flowering was synchronous with leaf formation presenting a delay with elevation. It began on September 30 at 1,225 m and on October 10 at 1,390 m, lasting for two weeks.

Seed fall began in January in both stands with a peak in February (Fig. 7). Though the mean number of seeds dispersed at 1,225 m was higher than at 1,390 m (134 seed/m^2 vs 19 seed/m^2, respectively), the heterogeneity due to the small quantity of seeds fallen, determined that no statistical difference was detected between the two forests (Kruskall-Wallis test).

Environmental variables during the 15 days prior to the onset of each phenophase were compared to a historical series of meteorological data of 20 years to determine if the year of study was representative of the general climate of the area (Table 2). The only value below normal was "minimum temperature" prior to seed dispersal. When the date of initiation of seed dispersal was compared with records of Kantolic (1985)[3] and personal observations it was determined that the process was clearly anticipated in 1986.

DISCUSSION

In temperate zones leaf development starts only after air and soil temperatures are higher than a threshold value following winter rest (Larcher & Bauer 1981). However, the genus *Fagus* is an exception as is photoperiodically controlled (Lechowicz 1984). The tight association between altitude and leaf formation shows that, in spite of its phylogenetic relationship, *N. pumilio* reacts to temperature as most of the temperature deciduous tree species.

Leaf emergence pattern in temperate trees are probably related to the trade off between potential production gains from early leafing and the danger of leaf damage or loss due to late frosts. Nevertheless, Lechowicz (1984) suggests that phylogenetic, historical or adaptative effects could modify leafing patterns. Late frosts are usual at the end of September and October, but no leaf damage was observed

TABLE 2

Climatic conditions on the 15 days prior to the begining of phenological processes and their relationship with normal values

Condiciones climáticas en los 15 días previos al inicio de los procesos fenológicos y su relación con los procesos normales

	Maximum Temperature (°C)	Minimum Temperature (°C)	Air Water Demand (mm/day) (a)	Wind speed (m/seq) (b)
Buding & Flowering (7-21/Sept.)				
x̄ ± SD (normal values)*	10.52 ± 3.75	–0.73 ± 3.69	0.73 ± 0.59	2.86 ± 2.59
extreme values for 1985 (1)	16.4	–7.2	1.4	7.3
probability of (1)	0.441	0.460	0.371	0.485
Seed fall (1-15/Jan)				
x̄ ± SD (normal values)*	20.34 ± 4.97	5.17 ± 3.42	3.02 ± 1.82	3.77 ± 2.8
extreme value for 1986 (1)	28.2	–2.0	4.7	6.7
probability of (1)	0.122	0.040**	0.264	0.235
Foliage color change & Leaf fall (1-15/Mar)				
x̄ ± SD (normal values)*	19.48 ± 4.97	3.76 ± 3.7	2.10 ± 0.92	2.92 ± 5.22
extreme values for 1986 (1)	23.1	–1.8	3.0	7.5
probability of (1)	0.308	0.129	0.29	0.273

* normal values from Mascardi station, 800 m above sea level; dates are for 1,225 m.
** $p < 0.05$, different from normal value
(a) from an evaporimeter tank placed at the meteorological station
(b) measured daily at 2 m high and 8.00 a.m.

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[3] KANTOLIC A (1985) Estructura y dinámica de un bosque de lenga (*Nothofagus pumilio*). Trabajo de intensificación. Facultad de Agronomía, Universidad de Buenos Aires.

in the two years study, suggesting that the timing of leafing in this species is well suited to its present environment. In his study of phenology of leaf emergence in forest trees, Lechowicz (1984) underlines the importance of the integrity of water-conducting tissues in relation to the moment of leaf emergence. Diffuse-porous species, such as *N. pumilio*, can potentially leaf out (and photosynthetize) early, as its xylem is seldom damaged. On the contrary, ring-porous species should have to rebuild their functional xylem in spring. The type of conducting system allows the individuals of *N. pumilio* to make efficient use of the brief warm period.

The shortening of the vegetative growth period with altitude is a well known phenomenon (Tranquillini 1964, Geiger 1971, Benecke & Havranek 1980). In *Nothofagus pumilio* forest this is expressed in the delay of the onset of budding and the acceleration of leaf fall.

Leaf life span can be related to a balance between costs and benefits. In this way, when the cost of maintaining a leaf through an unfavorable period exceeds its profits, the leaf should be discarded. Alternatively, a leaf should be disposed when the potential future income is less than the cost of losing it, measured in terms of the carbon and nutrient investment to produce a new leaf (Chapin *et al.* 1987, Chabot & Hicks 1982). Low temperatures at higher altitudes probably depress photosynthetic rates in such a way that they do not compensate the effect in the reduction of respiration.

Leaf abscission can be related to the effect of low temperatures on water stress, which is a common process in montane or high latitude woody species (Escudero & Arco 1987).

Kikuzawa (1989) mentions that an earlier expansion of leaves increases the net gain of carbon by extending the period of photosynthetic activity, but it has a negative effect by making leaves suffer aging and mortality for longer periods. As light intensity usually presents a unimodal pattern during the year, he suggests that plants should expand and shed leaves symmetrically with respect to the time of the peak. This actually happens in *N. pumilio* populations, as the maximum light intensity is supposed to occur in mid December.

In addition to the delayed leaf expansion, potential productivity decreases with altitude due to the smaller leaf size. Similar results were found by Benecke & Havranek (1980) in New Zealand where all growth parameters diminished with altitude.

The onset of flowering was synchronous at each altitude, reflecting a similar response to a uniform and unambiguous environmental cue (Rathcke & Lacey 1985). The photoperiod may be important in many species (Larcher & Bauer 1981). In moist tropical forests, meteorological factors (such as storms, droughts, or low cloudiness) cause little differences in day lenght (Wycherley 1973). In *N. pumilio*, as in most temperate woody species, flowering appears to be controlled by temperature. The duration of flowering was short; determining high floral density at the individual and community levels. This predictable and concentrated bloom is characteristics of seasonal environments (Rathcke & Lacey 1985). However, this concentrated bloom increases the risk of pollination or seed development failure, as environmental conditions during this period are critical.

As in many woody plants from temperate zones flowering in *N. pumilio* is simultaneous with leaf budding (Powell *et al.* 1986), hence, simple observation of the latest is advised when information is needed about flowering and seed production.

Fruiting times may be related to the timing of conditions that influence dispersal, but this is not the case in wind-dispersed *N. pumilio*. Wind speeds and frequencies are higher in spring and lower in autumn, when dispersal occcurs. The synchrony within the population is frequently considered a strategy to avoid predation through the satiation of predators. In *N. pumilio* high rates of consumption have been observed on the trees (pre-dispersal seed predation; Rusch 1987)[1]. It is also possible that the synchrony and timing of ripening and dispersal observed may be related to: (a) the brief period available for plant activity in cold montane habitats and (b) the micro-climate created by fallen leaves. The drop of leaves occur inmediatley after seed dispersal

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[1] RUSCH V (1987) Estudio de la regeneración de los bosques de *Nothofagus pumilio* en la cuenca del Río Manso Superior. Informe interno, CONICET.

protecting them from massive predation or downslope carriage on the ground, at the same time assuring moist conditions at the moment of germination in spring.

Environmental cues seldom stimulate the onset of fruit ripening but can influence the time of ripe fruit abscission. The anticipation of seed dispersal in the year of study coincided with temperatures lower than normal. Baker & French (1986) found that seedfall of *Arceuthobium* spp. occurred each time that temperature was lower than 0°C. In summer, *N. pumilio's* cambium is highly susceptible to low temperatures, suffering damage at –2°C (Alberdi *et al.* 1985). It is suggested that seed dispersal is initiated by low temperatures. Insect or parasitic attacks, which influence the timing of seed dispersal in other species (Nielsen 1977), were not observed in *N. pumilio.*

Foliage color changed quickly, and was altitudinally homogeneous. This supports the hypothesis of Walter (1973) for European deciduous forests, who suggests that this process is started by a photoperiodic stimulus.

Balátová-Tuláćková (1971) found that the phenological pattern of a species is not only influenced by climate and habitat factors, but also by the relationships with the rest of the species in the community. In this way, the development of a species can be delayed by the simultaneous development of other species with overlapping periods of activity. As *N. pumilio* generally forms monospecific stands, interspecific competition may not exist for adult individuals. Nevertheless this effect should be considered for other forests.

We conclude that, for *Nothofagus pumilio*, leaf budding, leaf size, flowering and leaf fall depend on temperature while foliage color change is related to daylenght. We suggest seed dispersal is triggered by low temperatures.

These results indicate that high altitude forests are in disadvantage in terms of productivity compared to lowland forests, but not necessarily in with respect to reproductive capacity. In the northeastern Patagonia summer water deficit may limit seedling survival, and hence high altitude forests would benefit from higher precipitation and less evapotranspiration. This may allow less seedling mortality compensating in part for the lower productivity.

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