

Structural and functional changes in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina

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Abstract. Structural (density, height, basal area, above-ground tree biomass, leaf area index) and functional (leaf phenology, growth rate, fine litter fall, leaf decomposition) traits were quantified in four mature forests of *Nothofagus pumilio* (lenga) along an altitudinal sequence in Tierra del Fuego, Argentina. Three erect forest stands at 220, 440 and 540 m and a krummholz stand at 640 m a.s.l. were selected. Along the altitudinal sequence, stem density increased while DBH, height, biomass, leaf-size and growth period, mean growth rate and decay rate decreased. Dead stems increased and basal area and fine-litter fall decreased with an increase in elevation among erect forests, but these trends inverted at krummholz. We suggest that krummholz is not only a morphological response to the adverse climate but is also a life form with functional advantages.

Keywords: Cold temperate forest; Growth rate; Krummholz; Leaf decay; Leaf phenology; Litter fall; Timberline.

Nomenclature: Moore (1983).

Introduction

The forests of Tierra del Fuego are composed of broadleaved species of *Nothofagus* (southern beeches). *N. antarctica*, 'ñire' and *N. pumilio*, 'lenga' form deciduous forests. *N. betuloides*, 'guindo' forms evergreen forests. However, *N. pumilio* and *N. betuloides* do grow together in some mid-altitude forests. Usually, deciduous forests grow under wider annual climatic variation than evergreen forests (Frangi & Richter 1994). *N. pumilio* forests occur at cooler sites and on better-drained soils than those preferred by *N. betuloides* (Gutiérrez et al. 1991; Frangi & Richter 1994; Veblen et al. 1996).

N. pumilio forests dominate on the mountains of the Andean Cordillera, forming a low-temperature treeline at higher elevations and a wet treeline with bogs on the valley floors. They grow at different temperatures than mid-latitude, northern hemisphere forests. The mean of the warmest month is below the normally accepted threshold of 10 °C (Williams 1961; Tranquillini 1979).

Extrapolation to the timberline indicates southern Andean warmest month mean temperatures from around 7 °C in northern localities to only 5.7 °C near Ushuaia compared with 10 °C in New Zealand (P. Wardle 1998). Deciduous *Nothofagus* from the Andes are more cold-resistant than evergreen *Nothofagus* from New Zealand timberlines (P. Wardle 1998). Seasonal temperature differences are small and thawing can occur during winter (Puigdefábregas et al. 1988). Precipitation is of low intensity and high frequency, is evenly distributed throughout the year and shows a decreasing gradient from SW to NE.

On Isla Grande, *N. pumilio* forest extends from near Lake Fagnano in the north to the Beagle Channel islands in the south, and from the seashore to ca. 600-700 m a.s.l. on the slopes of the Andes. Krummholz can reach 750 m a.s.l. at sheltered sites (Tuhkanen et al. 1990). The term krummholz is applied here in a wide sense, to all genetically or environmentally determined stunted and dwarf trees at the timberline (Norton & Schönenberger 1984). *N. pumilio* stands are not homogenous from the sea coast to the altitudinal timberline, and striking changes in growth forms and stand structure occur (Fig. 1). At the highest altitudes the most common krummholz growth forms are similar to the decurrent and prostrate types described by Norton & Schönenberger (1984). In some areas, between the erect forests and the more stunted trees, some individual trees exhibit an intermediate morphology known as 'buttsweep'. The upper *N. pumilio* limit in the Valle de Andorra is abrupt and level, interrupted only by avalanches and landslides. The area is covered mainly by erect forests but a krummholz strip 20 - 30 m wide forms a closed, stunted, timberline.

This study develops the hypothesis that changes in growth form, forest structure and physiognomy are an adaptation to increasing elevation (Mattheck 1991), with low temperatures and stresses such as snow accumulation being especially important at the timberline. Increasing altitude reduces the growth period, affects reproductive success and diminishes the rate of ecological processes. The objective was to quantify structural

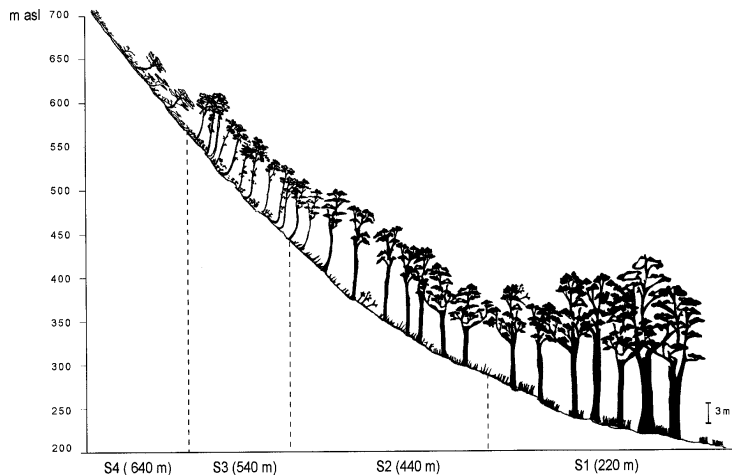


Fig. 1. Profile of *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego.

(density, height, basal area, above-ground biomass, fine litter mass) and functional (leaf phenology, growth rates, fine litter fall, leaf decomposition) traits in four mature *N. pumilio* forests along an altitudinal sequence and relate them to climatic conditions (temperature and precipitation).

Methods

Study area

The study was carried out in the Valle de Andorra (54° 49' S, 68° 42' W) on Isla Grande, Tierra del Fuego, South America. Three mature erect forest stands with southern aspects in an altitudinal sequence at 220 m (S1), 440 m (S2), 540 m (S3) and a krummholz stand at 640 m a.s.l. (S4), with slopes of 17, 30, 60 and 73%, respectively, were selected for structure and function, with the exception of phenology and determination. Phenological observations were recorded in the nearby Valle El Martial at sites of similar slope, aspect and elevation.

At sea level mean annual temperature is 5–6 °C, the absolute minimum is ca. –14 °C; frosts occur in all months. The elevational air temperature gradient (lapse rate) is 0.55 °C/100 m on average and ranges between 0.43 and 0.70 (Anon. 1989). Precipitation increases with increasing elevation from ca. 550 mm near Ushuaia (southern Isla Grande) to 1190 mm at 535 m a.s.l. at the upper El Martial skilift station (54° 45' S - 68° 19' W) (Anon. 1989).

Soils tend to be well-drained with an udic (humid) soil moisture regime (Frederiksen 1988). They are leached, acidic brown soils with a moder type humus layer. On mid and lower slopes soils are developed in sandy till, at times overlain by tephra. Under krummholz, frost-weathering produces accumulations of rock debris ranging from coarse sand to large fragments (Tuhkanen et al. 1990); there are also soils characterized by a thin organic horizon overlying rock fragments and solid rock (Frederiksen 1988).

Temperature and precipitation

Soil temperature at 10 cm depth was measured between 11 am and 3 pm on dates when phenology was recorded. For each site, air temperatures were calculated by applying the regressions of Puigdefábregas et al. (1988) to the Ushuaia weather station (14 m a.s.l.) temperature data and atmospheric sounding records. Temperature data were used to define seasons, according to Puigdefábregas et al. (1988).

Precipitation data from long-term records for Ushuaia and 4-yr records from Valle de Andorra (160 m a.s.l.) and El Martial glacier (535 m a.s.l.) (Anon. 1989) were used to estimate the precipitation gradient. The annual percentage of precipitation falling as snow was estimated from the mean temperature of each site and the regression ($y = 92.4 - 10.03x$, $r^2 = 0.93$) between monthly mean temperatures and the snow percentage at Ushuaia.

Stand structure

Seedlings (<0.5 m tall) were counted in 10–60 random plots (0.25 m²) in each stand. Living and dead saplings (>0.5 m tall and <5 cm DBH) were recorded in 8–10 random plots (9 m²) in each stand. Living and dead trees (>5 cm DBH) were counted in five krummholz (10 m²) and 10 erect (100 m²) forest plots. Diameter at breast height (erect trees) and at stem base (krummholz) and heights of all individual stems were measured. In stands S1 to S3 tree density was equivalent to stem density; at S4 density refers to stems emerging from buried trunks and branches.

Biomass and litter standing crop

Above-ground tree biomass was determined by dimension analysis (Whittaker & Marks 1975). At S4, 18 stems were harvested after measuring length and basal diameter at the soil surface. At S3, eight trees were harvested. The weight of trees >26 cm DBH from S1 and S2 was estimated from the equations obtained by

Richter & Frangi (1992) for trees of similar size and shape from low altitude stands. 21 trees with DBH < 26 cm were harvested. All trees were separated into stem, branches and leaves and were weighed fresh in the field. Sub-samples were weighed fresh, oven-dried at 70 °C and the ratio used to estimate dry weights of complete samples. Dry weights of plant fractions were used for regression analysis (Table 1). Stand biomass was obtained by applying the equations to data from trees measured in the plots. Cross sections cut at breast height at each site were used to measure the sapwood area of sampled trees.

Moss and herb biomass and litter standing crop were estimated by harvesting 10 random plots of 25 cm × 25 cm (S4) or 50 cm × 50 cm plots (other sites). The material was oven-dried and weighed.

Leaf size, leaf area index and specific leaf area

A composite sample of leaves from harvested trees at each site was taken to the laboratory and a subsample of ca. 300 leaves per site measured for individual leaf size with a LI-COR 3100 area meter. Specific leaf areas (SLA) were calculated from the dry weights and leaf area of subsamples. Leaf area index (LAI) was obtained from leaf biomass and SLA. The ratio of leaf area to sapwood area (aridity index, Waring & Schlesinger 1985) was also calculated.

Leaf phenology

In September 1995, before seasonal growth had commenced, 10 canopy trees in each forest site and four individual 'spots' at the krummholz site were selected and tagged for weekly leaf phenology observation (Table 2).

Table 1. Parameters for the regression of tree biomass components (y = dry mass, kg). Relative errors for linear and logarithmic regressions (Whittaker & Marks 1975) are indicated. All were significant at $P < 0.01$. DBH in cm, H = height (m), DSB = diameter at stem base (cm).

Equation form: (1) $\ln y = a + b \ln x$, (2) $y = a + b x$.

Compartment	a	b	r^2	x	Error	equation
S1 and S2 < 26 cm DBH						
Leaves	-6.62	0.88	0.90	DBH*H	1.63	(1)
Branches < 1 cm	-4.76	0.75	0.94	DBH*H	1.58	(1)
Branches 1-5 cm	-4.82	0.88	0.92	DBH*H	1.10	(1)
Branches 5-10 cm	-5.19	2.48	0.89	DBH	1.06	(1)
Stems	-3.54	0.94	0.97	DBH*H	1.01	(1)
S3						
Leaves	-0.56	0.10	0.88	DBH	0.27	(2)
Branches < 1 cm	-0.90	0.202	0.90	DBH	0.21	(2)
Branches 1-5 cm	1.30	0.002	0.94	DBH*H	0.20	(2)
Branches 5-10 cm	0.46	0.005	0.83	DBH*H	0.13	(2)
Stems	0.62	0.021	0.99	DBH*H	0.06	(2)
S4						
Leaves	-7.59	2.99	0.81	DSB	1.57	(1)
Branches < 1 cm	-4.94	1.91	0.70	DSB	1.59	(1)
Branches 1-5 cm	-7.28	1.14	0.72	DSB	0.59	(2)
Stems	-4.80	0.61	0.72	DSB	0.51	(2)

Table 2. Criteria for leaf phenological states of *Nothofagus pumilio*.

Phenological state	Criteria
Bud swelling	3- to 4-fold size increase and a change of shape and bud colour, compared to dormant buds
Initiation of bud break	Buds start to open with one or two non-expanded prefoliated leaves visible
Bud break	All buds with one or two non-expanded leaves
Bud break-leaving buds	Lower buds with expanded leaves and upper with non-expanded leaves
Full leaf	Leaves fully expanded
Initiation of reddish	< 50 % with red leaves
50 % reddish	> 50 % but < 100 % with red leaves
100 % reddish	All leaves were fully red
Abscised 1	50 % of leaves abscised
Abscised 2	100 % of leaves abscised

Fine-litter fall

Fine-litter fall was collected in 20 rectangular, 0.5 m² (S1, S2 and S3) and 0.1 m² (S4) plastic mesh traps. The material was collected at the end of one leaf-fall period and sorted into leaves, fruits, branches < 1 cm diameter, *Misodendron* spp. (hemiparasite) and miscellaneous. The material was oven-dried. Mean litter fall fractions from each site were compared using one-way analysis of variance (ANOVA) and Duncan's multiple range test.

Leaf decomposition

The litter bag method was used (Bocock et al. 1960). Approximately 10 g of freshly fallen leaves from each stand were placed into a 20 cm × 10 cm plastic bags with 1-cm² mesh (80 per plot). 10 bags from each stand were collected after 1 and 2 yr. Low decay rates reported by Richter & Frangi (1992) allowed collection of the bags at yearly intervals. Leaf subsamples were oven-dried at 70 °C, mean dry mass remaining at each interval was expressed as percent of initial weight and adjusted to an exponential model (Olson 1963) by regression analysis to calculate k , the decomposition constant.

Tree age, growth rate and biomass increment

Increment cores from all DBH size classes were obtained to determine age and mean annual radial growth increments. The cores were collected at breast height and were processed following standard procedures (Stokes & Smiley 1968). Ring widths were measured with a Velmex UniSlide traversing table connected to a Metronics Quick-Check QC-1000 digital counter (accurate to ± 0.01 mm). Crossdating was verified by means of computer program COFECHA (Holmes 1983), which examines ring measurement series for possible errors in dating or measurement. For cores that missed the pith, the number of rings to the centre was estimated following the procedure of Duncan (1989). The numbers of tree-ring cores used in the final analysis were 28 (S1), 27 (S2), 25 (S3) and 17 (S4).

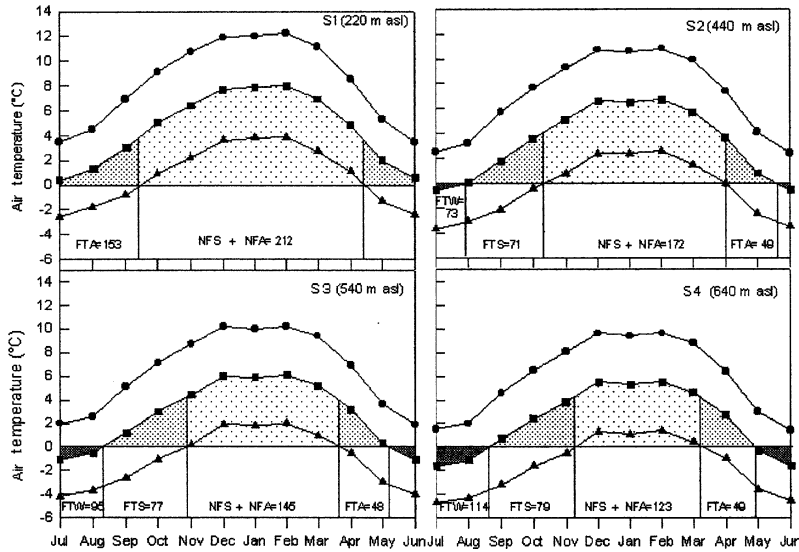


Fig. 2. Thermal seasonality (air temperatures) at the study sites. FTS = freeze-thaw spring, FTA = freeze-thaw autumn, FTW = freeze-thaw winter, NFS = non-freeze spring, NFA = non-freeze autumn. See explanation in the text. ● = Maximum mean; ■ = Mean; ▲ = Minimum mean.

Biomass increment was estimated by applying wood biomass equations, derived from each plot, to the basal area increment. Current annual biomass growth at stand level was estimated by stand-table projection (Husch et al. 1982). Results for this study were based on biomass production for the period 1989-1993.

Results

Growth period, precipitation and soil temperatures

The period without frozen soils extends from September to April at low elevations. This period reduces with decreasing altitude, ranging from 212 to 123 days/yr (Fig. 2).

Precipitation increases with increasing elevation, at a mean rate of ca. 120 mm/100 m. Mean precipitation at S1 was estimated as 660 to 720 mm. Total annual precipitation and percentage falling as snow roughly doubles between the lower and upper erect forest. At Ushuaia the snow percentage was 33% versus ca. 68-70% at S4. Precipitation measured at an altitude equivalent to S3 was nearly 1200 mm, of which around 820 mm should be snow; the gradients indicate that higher figures apply to the krummholz belt.

Soil temperatures ranged from -2° to 6.5°C , with temperature values and range decreasing with increasing elevation (Fig. 3). Daytime soil temperatures included sub-zero values, at least during the first half of spring. This indicates that soils can freeze during this season and that at S4 soils are likely to be frozen for one month longer than at S1. From mid-spring to early-summer soil temperatures at S3 and S4 were similar. S4 had temperatures below 0°C during March, in April all sites had temperatures above zero.

Stand structure

Seedling density increased from S1 to S3, but there were no seedlings at S4 (Table 3). Sapling density showed high variation, which was 1-2 orders of magnitude greater at S2 than at the other sites. Stand 1 had the lowest density. At S4 'saplings' were rooted branches emerging from buried trunks and main branches. Dead saplings decreased exponentially with increasing altitude and were absent at S4. The ratio live/dead saplings was very low at S1, but above 87% at the other sites. Stem density increased from S1 to S4, except for dead stems which were absent from S4. The ratio live/dead stems decreased from S1 to S3, whereas at S4 all stems were alive. Basal area reduced from the lower to the upper erect forests, but increased in the krummholz. Mean DBH and height diminished exponentially with elevation. Butts and stems at S1 and S2 were straight. At S3 the majority of trees were buttswept. Butt and stem cuts showed that trees are

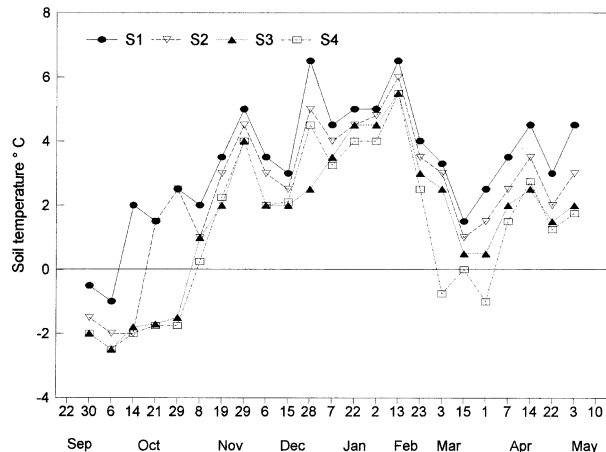


Fig. 3. Soil temperatures recorded at the study sites.

Table 3. Forest characteristics in four mature forests of *Nothofagus pumilio* along an altitudinal gradient in Tierra del Fuego. Mean \pm standard error; # = stem density.

Stand	Seedlings/ha	Saplings/ha				Trees/ha		Basal area (m ² /ha)	DBH (cm)	Height (m)	Age (yr)
		Live		Dead		Live	Dead				
1	23200 \pm 7000	222 \pm 141	1607 \pm 972	360 \pm 40	20 \pm 13	80	53	26	180		
2	616000 \pm 72100	28100 \pm 10220	900 \pm 458	780 \pm 113	150 \pm 40	67	33	18	158		
3	305000 \pm 45800	694 \pm 390	88 \pm 37	2125 \pm 144	1088 \pm 137	39	15	8	128		
4	0	1200 \pm 180	0	7520 \pm 1670#	0	56	10	2	137		

pulled into an upright position by growth of tension wood. Tree age decreased from lower to upper forest sites (S1 to S3), then increased at S4 although only by 9 yr.

Total above-ground tree biomass diminished dramatically from the lower forest to the krummholz (Table 4). Percentage of leaf biomass to total above-ground biomass was 0.9, 1.9, 2.0 and 10% for S1 to S4, respectively. Ground mosses were more important than herbs except at S1 and increased with altitude in the erect forests, being remarkably abundant at 540 m a.s.l. (S3) with more than 354 g/m². This decreased by 50% in the krummholz. Herbs were scarce, with biomass values below 20 g/m² at all sites (Table 4). Shrubs were unimportant or absent in all sites. LAI was similar at all stands. The predominant leaf-size class diminished with increasing elevation from 3.5 cm² (S1), 2.5 cm² (S2 and S3) to 1.5 cm² (S4) (Fig. 4). SLA was greater in the erect forests than the krummholz; but among those sites least at lowest elevation. The aridity index (leaf area/sapwood area) decreased along the sequence, changing abruptly between S2 and S3 (Table 4).

Fine litter mass decreased with elevation in erect forests but increased in the krummholz (Table 4).

Temperature and leaf phenology

Bud swelling in *N. pumilio* occurred over a period of 15 to 30 days and started at a mean air temperature of 2.4 to 3.5°C and a mean minimum of -1.7 to -0.4°C, during the freeze-thaw spring period (FTS). Leaf expansion began with a mean temperature of 4.7 to 5.7°C at the beginning of the non-freeze spring and non-freeze autumn (NFS+NFA) period. Both began at lower temperatures at higher altitudes. The period with expanded leaves corresponded reasonably with the NFS+NFA period with soil and minimum mean air temperature both above 0°C (Figs. 2 and 3). Autumnal leaf colour change coincided with mean air temperature decreasing to 5.8 - 5°C and mean minimum to 1.9 - 0.8°C. Leaf-fall began at the autumn freeze-thaw period (FTA) with mean air temperatures between 0.4 and 2.7°C and a mean minimum of -0.7 to -3°C. Leaf colour change and fall began at lower mean and mean minimum temperatures as elevation increased.

The onset of bud swelling and foliar expansion are

later at higher elevations, the lag-time over the gradient being from 22 to 40 days. Autumnal colour change began earlier at higher altitudes, whereas leaf-fall was more or less simultaneous over the gradient (Fig. 5). As a result the vegetative period decreased with altitude. Leaves are retained into the dormant season in the krummholz.

Growth rate, wood increment and fine-litter fall

Radial growth decreased from the low altitude forests to the krummholz. Wood increment was noticeably higher at S1 and S2 (Table 4).

The total fall diminished with elevation among erect forests (Table 5). Values at S1 and S4 were similar and significantly different from the other sites. Leaves were the main component, ranging from 83% (S1) to 69% (S4). Fruit fall was greatest at S2 and S3.

Leaf decomposition

The *k* values decreased with altitude being 0.79, 0.59, 0.46 and 0.40/yr for S1, S2, S3 and S4, respectively. The half-life doubled from the lowest to the highest sites (0.88 to 1.73 yr).

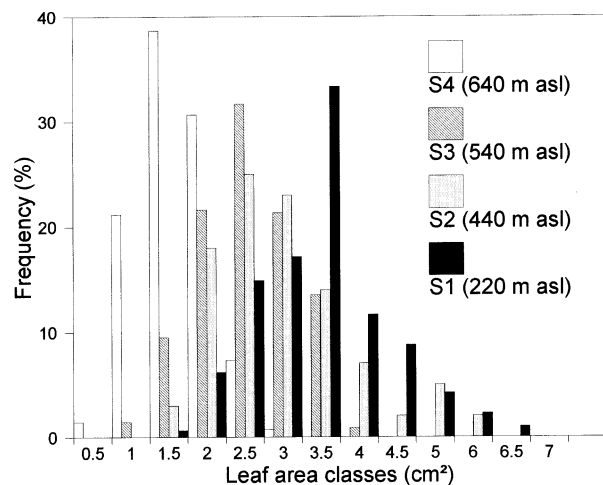


Fig. 4. Leaf size frequency in four *Nothofagus pumilio* stands along an altitudinal gradient in Tierra del Fuego.

Table 4. Tree fractions (mg/ha), mosses, herbs and fine litter biomass (mg/ha \pm standard error), leaf area index (LAI), specific leaf area (SLA, cm²/g), mean radial growth rate (mm/yr \pm S.D.), wood biomass increment (mg ha⁻¹ yr⁻¹) and aridity index in four mature *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego.

	S1	S2	S3	S4
Leaves	4.2	4.1	2.1	2.9
Branches < 1 cm	14.2	11.0	4.7	3.3
Branches 1 - 10cm	78.4	58.8	18.9	18.5
Stems	395.7	276.0	106.8	5.6
Total	492.5	349.8	132.5	30.4
Mosses	0.12 \pm 0.04	1.47 \pm 0.41	3.54 \pm 0.86	1.67 \pm 0.64
Herbs	0.17 \pm 0.04	0.01 \pm 0.001	0.19 \pm 0.08	0.12 \pm 0.03
Fine litter mass	10.1 \pm 1.1	7.0 \pm 0.7	2.9 \pm 0.8	6.6 \pm 1.3
LAI	2.9	2.9	3.1	3.3
SLA	132.2	145.2	146.1	112.3
Radial growth rate	1.69 \pm 0.80	1.31 \pm 0.62	0.72 \pm 0.36	0.67 \pm 0.40
Wood biomass incr.	7.90	6.78	0.88	2.2
Aridity index	0.23	0.21	0.11	0.09

Discussion

Various studies show that forest variables change along altitudinal gradients but comparisons are difficult because: (1) elevation provides a complex gradient where ecological factors vary in different spatial patterns; (2) plants respond to different combinations of ecological factors; (3) the lengths of altitudinal gradients analysed range from less than 200 to 3000m; (4) the forest sequences involved may or may not include a krummholz belt.

Two patterns were observed in structural and functional variables of *N. pumilio* forests in relation to elevation. One group of variables (stem density, dead saplings, DBH, height, biomass, leaf-size, oldest tree age, leaf phenology, growth rate, litter decay) showed increasing or diminishing trends through the whole altitudinal forest sequence. The other group of variables differed between erect forests and krummholz (seedling density, dead stems, live/dead stems ratio, basal area, litter fall).

Martínez Pastur et al. (1994) found no significant differences in basal area of old-growth erect *N. pumilio* forests between 1000 and 1300 m a.s.l. in continental Argentina. In New Zealand, the basal area of *Nothofagus solandri* var. *cliffortioides* increased from 40.9 to 51.8 m²/ha along an elevation gradient of 800 to > 2000 m

Table 5. Fine litterfall (g/m², mean \pm standard error) in four *Nothofagus pumilio* mature forest along an altitudinal gradient in Tierra del Fuego. Within a column, means followed by the same letter are not significantly different at $P < 0.05$ (using ANOVA and Duncan's multiple range test).

Stand	Leaves	Fine wood	Fruits	<i>Misodendron</i> spp.	Miscellaneous	Total
S1	297.13 \pm 9.66 a	43.27 \pm 6.57 a	0.17 \pm 0.08 a	2.45 \pm 0.82 a	15.61 \pm 2.20 a	358.45 \pm 18.12 a
S2	193.28 \pm 15.12 b	51.07 \pm 5.17 a	4.13 \pm 1.93 b	4.72 \pm 0.52 b	23.16 \pm 2.17 b	276.37 \pm 20.30 b
S3	220.53 \pm 15.17 b	33.82 \pm 2.38 a	3.80 \pm 0.34 c		11.89 \pm 1.19 a	270.04 \pm 17.76 b
S4	230.04 \pm 28.57 ab	53.82 \pm 6.30 a	0.58 \pm 0.19 d		51.31 \pm 5.0 c	335.74 \pm 30.09 ab

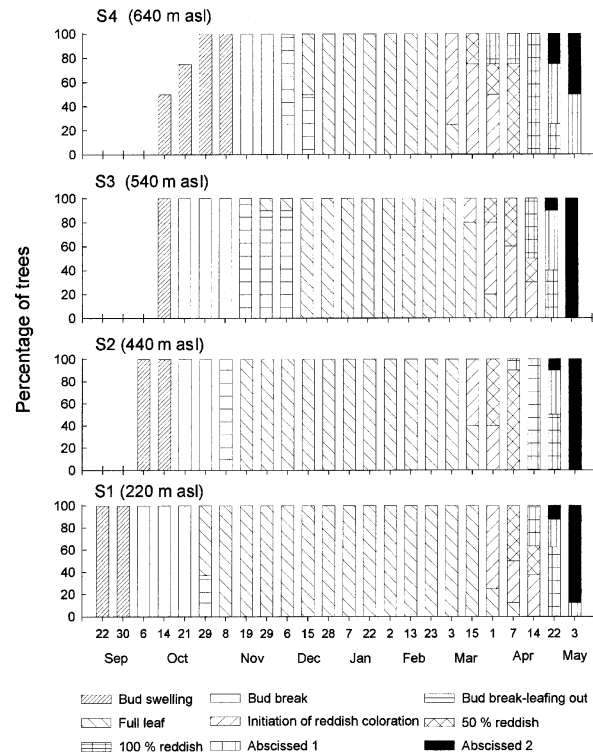


Fig. 5. Leaf phenology in four *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego.

a.s.l. (J.A. Wardle 1984). The latter trend is opposite to that observed here, suggesting that the influence of site factors on basal area is variable.

Total above-ground biomass decreased strongly with altitude. However, in the krummholz an important fraction not measured during the biomass harvest was below-ground large branches and trunks. The aboveground stems were branches emerging from these buried organs which had rooted when partially buried or were in firm contact with the soil surface. A total standing crop recovery would probably show different biomass partitioning and total.

The LAI values along the sequence agree with others reported from the same types of forest (Gutiérrez et al. 1991) suggesting that *N. pumilio* forests have reached maximal photosynthetic potential to local light availability. Nevertheless, smaller leaf size and lower SLA

values of the krummholz suggest desiccating conditions during daytime, owing to higher temperatures near soil and rock surfaces. The aridity index values indicate that more sapwood is needed to supply water and nutrients per unit leaf area in the krummholz than at lower altitudes. In the erect forests there is a reduction in leaf size with increasing elevation coinciding with decreasing temperature and increasing precipitation, whereas SLA does not change significantly. The sharp decrease in SLA in the krummholz compared to nearby erect forest suggests differences in leaf microclimate that are important for water balance.

Nothofagus species exhibit pronounced periodicity and intersite differences in seed production (Miller & Hurst 1957; Veblen et al. 1996). Prolific *N. pumilio* seed production occurred in the area studied in the summers of 83/84, 88/89 and 95/96 (Aloggia pers. comm.). Our seed production data corresponded to a non-mast year. The erect forests produced most fruit, the greatest abundance of seedlings, and the greatest sapling recruitment at the intermediate elevation site. The lower density of seedlings and saplings at S3 compared to S2 indicates difficult recruitment of genets in the higher erect forests. Severe limitations to reproduction in the krummholz result from a decrease in fruit production and the absence of seedling and seed-originated saplings. For other *Nothofagus* species, it is known that seed viability increases during mast years (Burschel et al. 1976; Allen & Platt 1990), which should increase the opportunity for seedling recruitment. However, Martínez Pastur et al. (1997) demonstrated that krummholz *N. pumilio* seeds were smaller and failed to germinate in lab assays, and that in the field seedlings are very scarce. The limitation for tree growth with increasing elevation has been attributed to the inability of trees to complete summer growth with subsequent death because of winter desiccation and frost damage (Tranquillini 1979). This is particularly important at the seedling stage (P. Wardle 1971).

Leaf phenology

Shorter growth periods at higher altitudes is well documented (Tranquillini 1964; Rusch 1993). For tree species, the end of the dormant period in spring is largely controlled by temperature, although precipitation could also be important (Ahlgren 1967).

Bud swelling is a phenophase characterized by translocation of stored carbohydrates to growing organs and a negative carbon balance (McLaughlin & McConathy 1979). It starts when daytime soil temperatures are below zero and soil water is unavailable because of freezing. Bud swelling, foliar expansion and leaf colour change began at lower temperatures at higher elevations, suggesting an ecotypic adaptation or acclimation allowing individuals

to make more effective use of the shorter, colder growing season. In addition, in krummholz, daytime temperatures close to the ground are warmer than at the canopy of erect trees and this also favours growth (P. Wardle 1971). Foliar expansion begins in the spring and colour change in the autumn when minimum temperatures of -3°C can occur at sea level. This suggests that foliar frost resistance lies within the range of -2.5 to -3°C reported by Alberdi et al. (1985) for continental *N. pumilio*.

Delay of foliar expansion should delay growth of shoots and branches. Benecke & Havranek (1980) demonstrated that initiation and amount of growth are closely temperature (energy) dependent. In spring, the delay in onset of growth with increasing altitude was ca. 5 to 9 days/100 m for both bud swelling and foliar expansion initiation. These gradients may be compared with the 4.4 to 7 days/100 m found for New Zealand beeches between 729 and 1219 m altitude (J.A. Wardle 1984) and 4 days/100 m for *N. pumilio* forests in continental Argentina (Rusch 1993).

Despite diffuse-porous xylem species being less susceptible to cold damage than ring-porous species (Lechowicz 1984), temperatures should also be above those that cause frost damage during the period when leaves are expanded and photosynthetically active.

The one-month earlier start of autumnal leaf coloration at higher elevations suggests the influence of low temperatures. This is in contrast to the observations of Rusch (1993) for the same species in the continental Andes, who argued that simultaneous leaf colour change observed over a 160 m elevational difference indicates photoperiodic control.

The onset of leaf coloration observed during March indicates that retranslocation and reduction of photosynthesis begin when there is a noticeable decrease of solar energy.

Leaf-fall began at lower mean and mean minimum temperatures in the krummholz, suggesting that frosts towards the end of the short NFS + NFA period are harsher at the timberline. These early frosts have led to some leaf retention by interrupting abscission and also caused leaf fall to start. Consequently, several phenophases coexist in stunted trees.

Growth rate and wood increment

Three points appear most important: (1) mean annual increments near sea level compared with other *N. pumilio* forests, (2) growth rate and (3) wood biomass change with elevation. With respect to the first point, published data for *N. pumilio* growth on the island are scarce. Schmidt & Urzúa (1982) reported a mean radial increment of 0.87 mm/yr for *N. pumilio* in Chilean low altitude unmanaged forests. In Tierra del Fuego, a mean radial increment of 0.96 mm/yr was measured for an old-growth *N. pumilio*

forest at 80 m a.s.l. (Barrera unpubl.) and 1.34 mm/yr at 260 m a.s.l. (Gutiérrez 1990), both on north-facing slopes. These values are 50 to 80% of the annual radial increment of the comparable forest site in this study. All these growth rates were measured in old-growth stands, so variation indicates differences related to site conditions. Concerning the second point, Herbert (1973) reported that the growth rate of *N. menziesii* in New Zealand decreases with increasing elevation. In contrast, J.A. Wardle (1970) reported little variation in diameter growth of *N. solandri* at different altitudes within a *Nothofagus solandri* association, but quite large differences between associations. Norton (1984) observed that shoot and radial growth in *N. solandri* started later at higher elevations in New Zealand and related this to low temperatures. The decrease in growth rate with altitude observed in *N. pumilio* suggests similar controls. Wood biomass increment in erect forest diminishes with increasing elevation but the krummholz showed more than twice the wood increment of the nearest erect forest. Evidently the change in life form increases the efficiency of the species under harsher conditions.

Fine-litter fall

Fine-litter fall values were similar to those measured in cold temperate forests at similar latitudes, mainly in the northern hemisphere (Bray & Gorham 1964). Richter & Frangi (1992) reported 370 g/m² for an old-growth *N. pumilio* forest at 80 m a.s.l. in Tierra del Fuego, similar to that estimated for our lower site. Total litter production (leaves + twigs) for mountain and subalpine forests in New Zealand reported by J.A. Wardle (1984) ranged from 255 to 466 g/m², with a clear cut relationship with altitude. For *N. solandri* var. *cliffortioides* forests, the highest litter production rates were 150–200 m below the timberline, and a pronounced reduction occurred both towards timberline and lower downslope. Conversely, *N. menziesii* had the lowest production near the timberline which increased downslope, but this sequence excluded krummholz. Our data for the erect forests agree with those for *N. menziesii*, in that the litter fall decreases with increasing altitude, but increases between the upper erect forest and the krummholz, although not significantly. This increased leaf production in the krummholz is perhaps explained by a higher LAI and the stimulus of higher temperatures.

Leaf decomposition

Decrease in decomposition rate with increasing elevation appears to be related to lower temperatures. Changes in biological attributes such as SLA and nitrogen concentration of *N. pumilio* leaves (highest in krummholz; Frangi,

unpubl.) might also influence decay. Decay rates are in the range expected for deciduous species in cold temperate climates (Gosz et al. 1973; Lousier & Parkinson 1976). The *k* value at 220 m a.s.l. represents faster decay than that estimated in another trial on the island on a N-facing slope (Richter & Frangi 1992). Aspect can significantly affect decay rates; pole-facing slopes have the highest rates as they are moister because less net radiation reaches the ground, facilitating fungal and micro-arthropod activity (Mudrick et al. 1994).

Structural changes along the altitudinal gradient

Tree stem density increases and mean diameter and height decrease with increasing elevation. In erect forest this is because trees are smaller due to less favourable growing conditions. In the krummholz there is also an architectural change. In the erect forests the density represents individual trees, though at 540 m a.s.l. we observed root grafts between trees. Root connections were also reported for *Cryptomeria japonica* at the upper segment of its elevational distribution in the Northern Japanese Alps (Taira et al. 1997). In the krummholz, density values include partially buried branches that emerge from the buried trunks of a smaller number of individuals. Vegetative multiplication was not seen at lower elevations, whereas adventitious rooting and consequent vegetative multiplication prevailed in the krummholz. Veblen et al. (1996) also mentioned that tipping (i.e. the production of vertical leader branches from the lying stem) is the dominant mode of regeneration following blowdown near the timberline. Intrapopulation genetic homogeneity due to layering has been demonstrated for *Cryptomeria japonica* (Taira et al. 1997). In that species greater genetic homogeneity over patches helps to explain the patchy phenological response. Stunting and adventitious rooting of branches cause an increase in photosynthetic and absorptive organs compared to erect trees, by increasing the capacity for water and nutrient absorption and reducing transport distances. Compared to nearby erect forest, buds and developed leaves of dwarf trees benefit from warmer daytime temperatures close to the ground (Gates 1962; P. Wardle 1971), this may increase leaf production rates during the short growing season. The small leaf-size and physiological indices indicate further adaptive traits to cope with harsh daily cycles of microclimate during the growing season. The greater wood biomass increment indicates the efficiency of the krummholz at the timberline. Partial retention of leaves during the early part of the resting season in krummholz suggest that early frosts interrupt the process of leaf abscission. Leaf retention was also observed in some trees at S2 and S3 (but not those marked for this study) indicating that early frosts also occur at lower elevations, but less frequently.

The N. pumilio cold-timberline

Stevens & Fox (1991) reviewed the causes of tree line formation and stressed the difficulties of testing treeline hypotheses. For *N. pumilio*, the upper timberline can be related to the seasonal cycle of freezing resistance. In Chile, *N. pumilio* foliar buds survive temperatures below -18°C (Alberdi et al. 1985). The absolute minimum winter temperature recorded at Ushuaia (1914-1960) was -19.6°C (cf. Tukhanen et al. 1990), but this value is questionable or at least very infrequent. More reliable data for the 1950-1990 period indicate values between -15°C to -13.9°C (Schwerdtfeger 1976; Anon. 1989). Accordingly, winter absolute minima can be estimated as -18.2 to -17.1°C at the timberline, i.e. values similar to bud resistance temperatures.

For *N. pumilio*, we advance hypotheses related to reduction in height, biomass allocation, change in growth form and the importance of vegetative multiplication toward the upper cold timberline. All these structural traits reach specific values and significance at the timberline, as do phenologic behaviour and ecosystem functioning. Although it is not known whether the dwarf forms have a genetic basis, trees show morphological responses that minimize external loading through accumulation and impact of snow and rock debris. At the upper erect forest site, there is butt sweep, but growth of tension wood brings trunks to an upright position, as in other angiosperm trees (Mattheck 1991). In multi-stemmed krummholz branches respond to environmental damage by development of new s-bended knees at the basis of leaders and intertwining stems that are nearly parallel to the soil surface. We suggest that the krummholz *N. pumilio* is an architecture shaped by low temperatures, the increasing importance of snow and rock accumulation and other disturbances that may injure buds and stems, but also cause the plants to improve survival through greater production.

Concluding remarks

The *Nothofagus pumilio* forests in Tierra del Fuego change along an elevational gradient where decreasing temperatures (with small annual variation) and increasing precipitation (and proportion falling as snow) are related to latitude and degree of oceanic influence. Low temperatures affect water availability, growth period, occurrence of early frosts, mechanical impact of snow and biological functions such as foliar phenology, radial growth and decomposition rates. At the individual level *N. pumilio* shows characteristic trends in morphology (e.g. leaf size, SLA, tree height), architecture (growth form), physiology (temperature at which bud swells and

leaf expansion is initiated) and reproductive and multiplicative traits. At the stand level, mature *N. pumilio* forest shows reduction of basal area, biomass, net primary productivity (wood increment + fine litter), leaf decomposition and an increase in stem density and LAI with increase of elevation. The growth, fine litter-fall and decomposition rates are within those reported for forests at comparable latitudes to Tierra del Fuego.

Acknowledgements. The authors gratefully acknowledge the comments and suggestions of P. Wardle on earlier versions of the manuscript. We also thank J.B. Wilson and two anonymous referees for their helpful suggestions. This study was carried out with a grant from the Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (PID 3627/92). The Centro Austral de Investigaciones Científicas (CADIC) provided local logistical support.

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Received 30 November 1998;

Revision received 16 July 1999;

Accepted 16 July 1999.

Coordinating Editor: J.B. Wilson