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Nutrient cycling in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego, Argentina

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Abstract

Nothofagus pumilio (lenga) forests form monocultures from sea level to timberline in Tierra de Fuego, Argentina. Past studies suggested that the life form change from erect forest to krummholz had advantages to forest function. Aboveground net primary productivity (NPP) and organic matter production per unit leaf area and growing season day were higher in krummholz than in adjacent short erect forests at lower elevation. We compared tall erect, short erect, and krummholz lenga stands in terms of the concentration, accumulation, fluxes, turnover, and use-efficiency of nutrients (N, P, K, Ca, and Mg) along an elevation gradient (220–640 m) in Tierra del Fuego (Valle de Andorra, 54°9'S, 68°2'W). With few exceptions, patterns of decreasing values of nutrient concentration, nutrient stock, nutrient flux, and nutrient turnover reversed at the krummholz, which had higher values of these parameters than an adjacent short erect forest at lower elevation. Nutrient cycles accelerated at the krummholz but nutrient use-efficiency of organic matter production and nutrient return to the forest floor decreased. Several functional attributes of krummholz support the notion that this life form has functional advantages at timberline. For example: (1) a shift towards fast turnover compartments for nutrient storage; (2) a switch from high storage of nutrients in stemwood biomass to nutrient storage in branch biomass; (3) faster rates of internal nutrient transfer (recycling and retention); (4) greater dependence on biotic recycling of nutrients; (5) morphological characteristics associated with leaf size, leaf duration, number of leaves, and leaf area to sapwood area ratio. Nutrient cycling attributes measured in Tierra del Fuego span values reported for forests across temperate and boreal latitudes, with krummholz and tall erect forests representing either the low or the high values. Lenga krummholz is different from coniferous krummholz in North America's tundra in that lenga appears to be a nutrient-rich forest that acts as a nutrient sink, while coniferous krummholz scavenge for nutrients on tundra soils and reduce their nutrient pools. © 2005 Elsevier B.V. All rights reserved.

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1. Introduction

Nothofagus pumilio (Popp. et Endl.) Krasser (lenga) is the most important native timber species from the south Patagonia of Chile and Argentina (Martínez Pastur et al., 2000). The growth of monospecific stands of lenga along an elevation gradient in Tierra del Fuego, Argentina, offers an opportunity to study forest functioning under extreme environmental conditions while keeping species composition constant. Lenga, a deciduous broad leaf species, grows to a height of 26 m and accumulates up to 490 Mg/ha of aboveground biomass at 220 m elevation (Barrera et al., 2000). However, stands at 640 m elevation accumulate a biomass of only 30 Mg/ha and trees form a krummholz (sensu Norton and Schönenberger, 1984) less than 2 m tall. Barrera et al. (2000) found that the elevation trends of several structural and functional attributes of lenga forests reversed at the krummholz (Table 1), and suggested that krummholz is not only a morphological response to adverse climate, but its also a life form with functional advantages. Körner (1999) suggested that the prostrate krummholz crown architecture might result in a more favorable microenvironment than the vertical growth form found at tree line.

We used data in Barrera et al. (2000) to illustrate the change in annual aboveground net primary productivity (NPP, Fig. 1 top) and show that compared to erect forests, krummholz had a higher efficiency in the productivity per unit leaf area and

per day of growing season (Fig. 1 bottom). Thus, in spite of adverse conditions at higher elevations (low air and soil temperature, frozen soil for long time periods, and high wind velocities), the formation of krummholz results in greater productivity and performance by its photosynthetic apparatus than is realized with a short erect tree habit. Little is known if nutrient limitations play a role in the position of tree line and there are few data available about the nutrient status of trees growing at the krummholz. For example, Barrick and Schoettle (1996) showed that foliar nutrient concentrations at tree line were similar to those found in lower-elevation forests, and only slightly higher than those in the krummholz while Richardson et al. (2001) and Richardson (2004) reported no changes in foliar chemistry in coniferous species along elevational gradients. These findings raise questions about the nutrient cycling characteristics of krummholz.

We approached the issue comparatively by analyzing ecosystem- and tree-level nutrient cycling rates in tall erect, short erect, and krummholz forest stands. We addressed three questions: What magnitudes of nutrient flux, storage, and turnover are associated with these high latitude forests in South America, and how do they change along the elevation gradient? What is the influence of life form (erect tree or krummholz) on nutrient cycling and nutrient-use efficiency? How do nutrient cycling dynamics at Tierra del Fuego compare with those of forests at other latitudinal regions of the world?

Table 1

Structural and functional characteristics of *Nothofagus pumilio* forest stands along an elevation gradient in Tierra del Fuego, Argentina (Barrera et al., 2000)

Characteristic	Stand and elevation (m) above mean sea level			
	S1 at 220	S2 at 440	S3 at 540	S4 at 640
Live trees (ha)	360	780	2125	7520
Basal area (m ² /ha)	80	67	39	56
Predominant leaf area (cm ²)	3.5	2.5	2.5	1.5
Leaf area Index	2.9	2.9	3.1	3.3
Aboveground biomass (Mg/ha)	493	350	133	30
Leaf biomass (Mg/ha)	4.2	4.1	2.1	2.9
Annual litterfall (Mg/ha)	3.6	2.8	2.7	3.4
Annual leaf fall (Mg/ha)	2.97	1.93	2.20	2.30
Annual radial tree growth (mm)	1.69	1.31	0.72	0.67
Wood biomass increment (Mg ha ⁻¹ y ⁻¹)	7.9	6.8	0.9	2.2

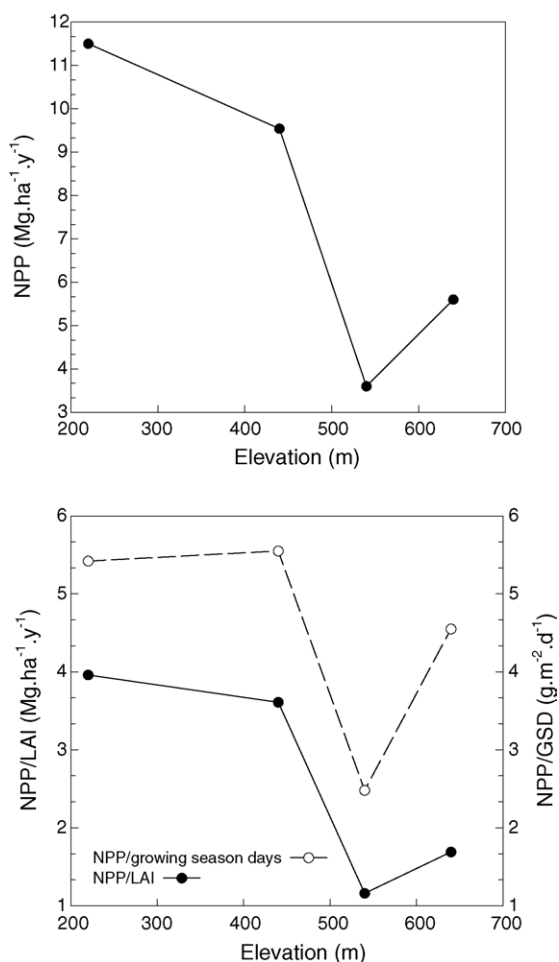


Fig. 1. Net primary productivity of *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego expressed on an area basis (top) and per unit leaf area and growing season day (bottom). Table 1 contains original data.

2. Materials and methods

2.1. Study area

We studied mature forest stands in the Valle de Andorra (54°9'S, 68°2'W) near the city of Ushuaia (Barrera et al., 2000). Study sites were located at 220 m asl (S1), 540 m asl (S3) and 640 m asl (S4) corresponding, respectively, to a tall erect forest, short erect forest, and krummholz. We excluded S2 from the study.

Soils of the Andean slopes covered by lenga forests have been described as Cryumbrepts (Umbrepts, Inceptisols) and Cryohumods (Humods, Spodosols) (Godagnone and Irisarri, 1990), or as Spodic clayish soils (Colmet Daage et al., 1991). Upslope soils are characterized by a thin organic horizon overlying rock fragments while the mid- and downslope soils are developed on sandy moraines (Frederiksen, 1988). Upslope soils are more leached with lower base saturation than downslope soils (Frederiksen, 1988). Soils are not deep (B or B/C horizons commonly at 40–60 cm depth), with frequent high retention of phosphorus and water in lower horizons. The parent material is till, composed of lutites containing mainly chlorite and illite, and tephra (Frederiksen, 1988).

2.2. Methods

The study took place between 1993 and 1996. Barrera et al. (2000) contains detailed methods and results for aboveground organic matter dynamics of these sites. All plots were located at random at each site. The area and number of plots (lower number in the krummholz) varied with the type of vegetation. For vegetation: 10–60, 0.25 m² plots for seedlings (<0.5 m tall); 8–10, 9 m² plots for living and dead saplings (>0.5 m tall, <5 cm dbh); 5, 10 m² plots for living and dead trees in krummholz; 10, 100 m² plots for living and dead trees in erect forests. Forty-seven trees were harvested and dissected into stems, branches, and leaves. Three hundred leaves were sub sampled, and measured individually for area and weight. Litterfall was based on 20 randomly located 0.5 m² traps in each erect forest, and 20 randomly located 0.1 m² traps in krummholz. Standing litter crop was harvested from 10 randomly located 0.25 m × 0.5 m plots in krummholz and 10 randomly located 0.5 m × 0.5 m plots in erect forests. Leaf decomposition was measured at each site with 20 randomly located 20 cm × 10 cm plastic bags with 1 cm² mesh and 10 g of material inside. Ten bags were collected from each site annually for 2 y.

We used the samples from the study of Barrera et al. (2000) for nutrient (N, P, K, Ca, and Mg) analyses and converted organic matter storage and fluxes to nutrient storage and fluxes by multiplying nutrient concentrations by the mass of the corresponding compartment or flux. We supplemented the sampling of Barrera

et al. with determinations of soil chemistry. On February 1996, we collected three 0–10 cm depth samples at each site and combined them into one composite sample for chemical analysis. We also collected cylindrical vertical soil samples (354 cm³) at the same depth for bulk density determination. Soil nutrient content to 10 cm was estimated by multiplying soil nutrient concentration by the bulk density and depth.

Sub samples of aboveground plant compartments (leaves, branches, bark, stemwood, herbaceous plants, mosses, etc.), litterfall, forest floor litter, and soil were transported to the laboratory for chemical analyses. We used litter decomposition samples to estimate nutrient mineralization or immobilization. We measured nutrient concentrations of recently fallen senescent leaves before placing them in decomposition bags and after 1 y of field-incubation. With those data and a 2-year study of decomposition from Barrera et al. (2000), we estimate instantaneous decomposition rate (k) and net annual mineralization or immobilization rate of elements in leaf litter. We estimated total annual decomposition or mineralization of macronutrients in litter by multiplying the respective rates per total stock in litter. The litter layer was rarely thicker than 2–3 cm. However, we sampled litter near its lowest standing crop at mid-summer.

All biomass samples were oven dried at 70 °C, ground in a Wiley mill, and prepared for chemical analyses. Plant material was digested with concentrated HNO₃ and 30% H₂O₂ (Luh Huang and Schulte, 1985). The plant concentration of P, K, Ca, and Mg and available and exchangeable elements in soil samples were determined with a plasma emission spectrometer (Beckman Spectra Span V). Total carbon and nitrogen concentrations in soil and plant parts were determined with the dry combustion method (LECO Corporation 1993) using a LECO CNS-2000. Incineration of sub samples in a microwave oven gave us plant ash content.

Soil samples were air-dried prior to chemical analysis. Soil available Ca and Mg was extracted with 1N KCl employing a vacuum mechanical extractor Centurion-Model 24. Soil exchangeable P and K concentrations were determined with the Olsen EDTA (NH₄NaHCO₃) method (Hunter, 1982). Soil pH was determined in a 1:1 (soil:KCl 1N) using an Orion Ionalyzer Model 901 with combination probe.

The precision of chemical analyses was obtained by running samples of known chemical composition every 40 determinations. Control plant material consisted of pine, peach, and citrus leaves from the USA National Institute of Standard Technology.

Leaf retranslocation was estimated as the difference in elemental concentration between fully expanded mature leaves and freshly fallen senescent leaves. We applied this calculation to all macronutrients because the elemental loss due to leaching during the color change and abscission period was negligible. For example, the reduction in leaf nutrient mass attributed to leaching during senescence was nil for N, <1% for P and Mg, and <2% for K (Frangi unpublished data).

Nutrient fluxes at plot level (uptake, requirement, and recycling) were calculated according to the procedure in Cole and Rapp (1981). Uptake = annual element increment in aboveground biomass + annual element return in litterfall, leaching, and stemflow. Requirement = annual elemental increment in bole- and branchwood biomass + annual element return in litterfall. Recycling = requirement – uptake. As we did not measure leaf leaching and stemflow in our sites, we used nutrient data from throughfall and stemflow measurements minus nutrients in precipitation from a nearby lenga stand (Frangi, unpublished data) to approximate the contribution of these fluxes to nutrient return. Retention was the annual nutrient accumulation in woody tissue. Turnover times, and nutrient-use efficiency and circulation indexes were those of Chapin (1980), Gray (1983), and Cuevas and Medina (1998). Aboveground NPP was the sum of annual biomass increment and annual litterfall.

We estimated four nutrient-use efficiency indices: (1) The weighted nutrient concentration of aboveground and forest floor biomass (total nutrient storage/total biomass), which measures nutrient storage per unit biomass in the aboveground and forest floor compartments. (2) The production of aboveground biomass per unit nutrient uptake. This index measures the efficiency of nutrient use in relation to aboveground biomass productivity. (3) Within-stand nutrient-use efficiency was calculated as the ratio of fine litterfall to nutrients in fine litterfall (Vitousek, 1982). (4) The ratio of nutrient turnover rate to biomass turnover rate (Gray, 1983). This is the ratio nutrient return/total aboveground nutrient stock to NPP/total

aboveground biomass. Values >1.0 indicate a faster turnover of nutrients per turnover of biomass.

We compared the concentrations of elements in all materials in the study with ANOVA (Tukey test for samples with unequal n). We used specific contrast codes in the ANOVA to compare the linear effect of elevation and the two erect forest tree sites with the krummholz. Significance was based on $P < 0.05$.

3. Results

3.1. Magnitude and pattern of nutrient cycling

We summarized our stand-level results with a simple nutrient balance diagram composed of four nutrient storages and six fluxes (Fig. 2).¹ The total nutrient stock of stands (sum of four storages in Fig. 2 for each nutrient) decreased with elevation for K, Ca, and Mg. Nitrogen and P stocks decreased with elevation among erect forests but increased at krummholz. The total N stock was higher at krummholz than in erect forests.

Only the wood compartment exhibited a consistent pattern of decreasing nutrient stock with elevation for all nutrients (Fig. 2). The same was true for Ca and Mg stocks in soil. With two exceptions (K and Mg), all other compartments and nutrients had a pattern of decreasing stock between tall and short erect forest but increasing stock at krummholz. For N and P, the amount stored in litter and soil was higher in krummholz than in erect forests.

Wood and soil compartments stored most of the nutrients in the three stands (Fig. 2). Soil to 10 cm depth usually contained the highest fraction of nutrient stocks with the exception of P and K at tall erect forest. The percentage of nutrients in soils relative to soil plus total biomass followed the same pattern—N: 85, 94, and 98; P: 36, 48, and 75; K: 17, 48, and 60; Ca: 74, 81 and 80; Mg: 54, 67, and 72, respectively for tall erect, short erect, and krummholz forests. In some cases, wood and soil had similar stocks of a particular nutrient, i.e., P and K at short erect forest. The percentage of macronutrients stored in leaves, relative to total aboveground element mass, increased with

elevation as follows—N: 13, 24, and 67; P: 12, 15, and 29; K: 7, 8, and 26; Ca: 7, 9, and 23; Mg: 6, 9, and 19 (respectively) for tall erect, short erect, and krummholz forests.

With one exception, rates of nutrient uptake, requirement, and retention decreased from tall erect to short erect forest but increased at krummholz (Fig. 2). The exception was N retention rate, which decreased with elevation. The uptake of N and P by krummholz was higher than that of erect forests, and retention of P in krummholz was similar to that of tall erect forest.

Rates of N recycling decreased in erect forests with elevation but increased in the krummholz (Fig. 2). Recycling of P, K, and Mg declined with elevation. Calcium is not recycled, although we estimated a higher rate of Ca requirement than uptake in krummholz, which resulted in an estimate of recycling. Some of this difference may be due to leaching and stemflow, which we estimated but did not measure. Nitrogen and P return in krummholz was higher than that of any stand. The pattern of nutrient uptake, requirement, and retention was the same for all nutrients except the retention of N. These rates decreased with elevation in erect forests and increased in the krummholz. Nitrogen decreased throughout the whole elevation range.

3.2. Nutrient concentrations

Nutrient concentrations within a stand decreased from leaves, to branches, to stems (data not shown). The lowest nutrient concentrations were in heartwood, with the notable exception in krummholz. Branch bark and stem bark had similar nutrient concentrations. Nutrient concentrations in sapwood tended to be low, particularly Ca and Mg. Most of the nutrient concentrations were significantly different along the elevation and between the erect forests and the krummholz (Table 2). The concentration of N in leaves and branches <1 cm diameter increased from the erect forests to the krummholz, while it decreased in the others compartments. Concentrations of most elements were highest at the krummholz. The weighed ash concentration (ash mass divided by total tree biomass) was similar in both erect forests but three-fold higher at krummholz: 0.56, 0.61, and 1.81%, respectively, along the elevation gradient.

¹ Nutrient concentration data by parameter and site are available through the senior author.

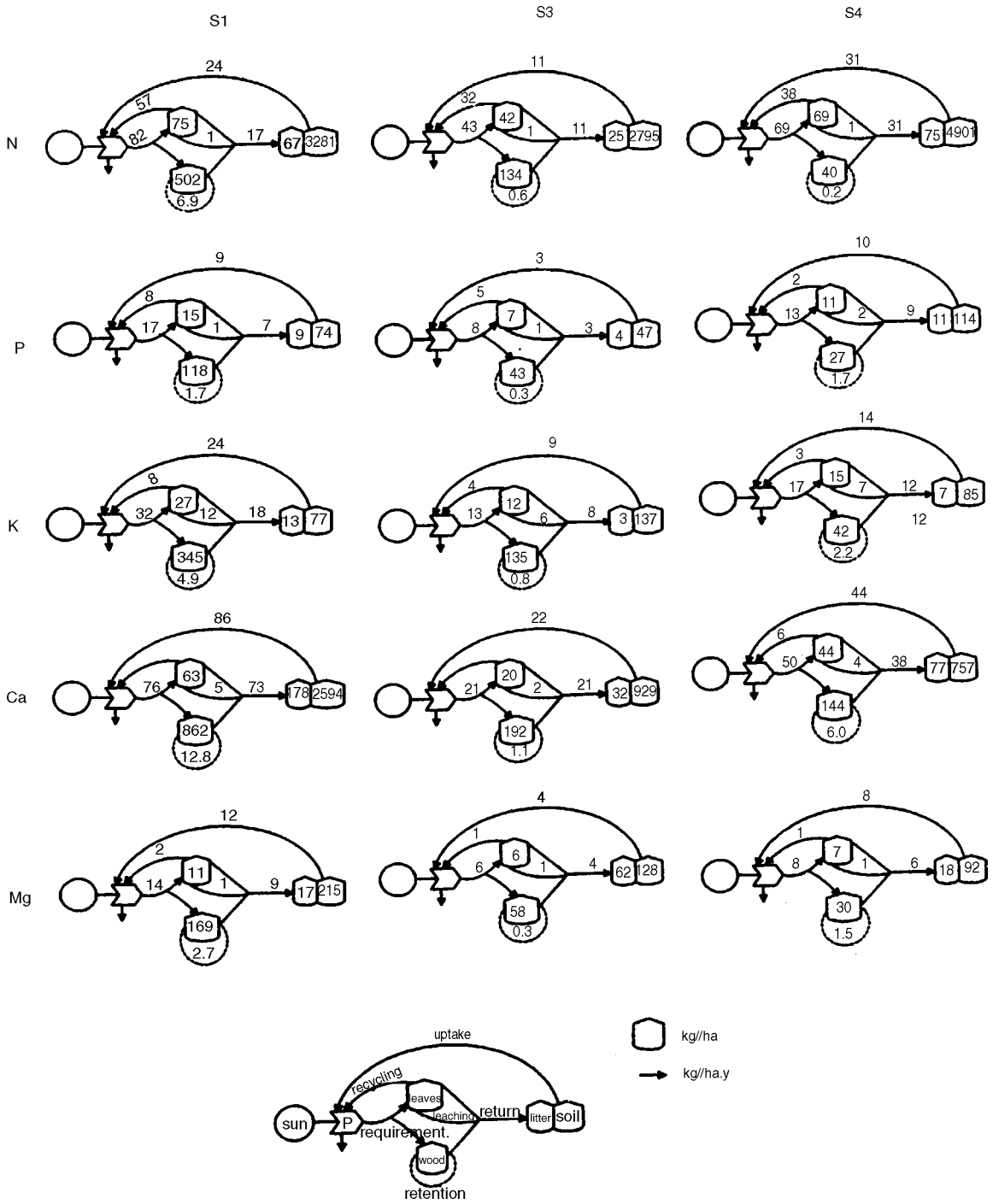


Fig. 2. Nutrient stocks and fluxes for *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego. Tall erect, short erect, and krummholz forests correspond to S1, S3, and S4, respectively. The return flux includes litterfall and tree fall.

Table 2

P-values from statistical analysis of nutrient concentration of various plant parts for the elevation gradient and a comparison of erect forest (EF) with krummholz (K)

	N	P	K	Ca	Mg
Leaves					
Elevation	< 0.001	0.69	0.054	0.83	0.04
EF vs. K	< 0.001	0.47	0.08	< 0.001	0.03
Branches <1 cm					
Elevation	< 0.001	< 0.001	< 0.001	< 0.001	0.02
EF vs. K	0.04	< 0.001	< 0.001	< 0.001	< 0.001
Branches 1–5 cm complete					
Elevation	< 0.001	< 0.001	0.98	0.05	< 0.001
EF vs. K	< 0.001	< 0.001	0.29	< 0.001	< 0.001
Branches 1–5 cm bark					
Elevation	0.04	0.69	0.46	< 0.001	0.05
EF vs. K	0.002	0.08	0.99	0.006	0.14
Branches 5–10 cm complete					
Elevation	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
EF vs. K	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Branches 5–10 cm bark					
Elevation	0.13	0.07	0.90	< 0.001	0.29
EF vs. K	0.43	0.15	0.95	0.01	0.30
Stem complete					
Elevation	0.01	< 0.001	< 0.001	< 0.001	< 0.001
EF vs. K	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Stem heartwood					
Elevation	0.07	< 0.001	< 0.001	< 0.001	< 0.001
EF vs. K	0.35	< 0.001	< 0.001	0.02	< 0.001
Stem sapwood					
Elevation	0.48	< 0.001	0.09	0.24	0.06
EF vs. K	0.24	< 0.001	0.04	0.10	0.14
Stem bark					
Elevation	0.01	< 0.001	< 0.001	< 0.001	< 0.001
EF vs. K	0.004	< 0.001	< 0.001	< 0.001	< 0.001
Mosses					
Elevation	0.004	0.03	0.87	0.31	0.18
EF vs. K	0.05	0.20	0.94	0.49	0.11
Herbs					
Elevation	0.01	0.53	0.22	< 0.001	< 0.001
EF vs. K	0.30	0.03	0.08	< 0.001	< 0.001

Significant *P*-values (<0.05) are shown in bold.

The concentrations of soil C, N, and P at krummholz (25.0, 12, and 0.28 mg/g, respectively) was the highest among the three study sites, while soil pH was the lowest (4.8, 4.3, and 3.9 for tall erect, short erect, and krummholz, respectively). Calcium, Mg, and ECEC concentrations were higher in the tall erect

forest (5.2, 0.42 mg/g, and 35 meq/100 g, respectively) while K concentration was similar in all three forests (0.15, 0.22, and 0.20 for tall erect, short erect, and krummholz, respectively).

3.3. Leaf decomposition

3.3.1. Nutrient concentrations

Nutrient concentrations changed as mature leaves senesced, fell, and decomposed as part of the litter layer (Fig. 3). The concentrations were significantly higher in mature leaves but were not significantly different in the other stages of decomposition and litter. Ash content was higher in litter than in the other compartments and lowest in leaf litter. Concentrations of Ca and Mg throughout the leaf decomposition process were different from those in other elements (Fig. 3). Mature leaves had lower Ca concentration than senesced leaves in erect forests but not in krummholz. Calcium concentrations were lower in short erect and krummholz forests than in tall erect forest. Concentrations of Mg in leaf litter increased with elevation.

3.3.2. Decomposition, mineralization, and immobilization rates

Leaf decomposition rate decreased steadily with elevation, as did the mineralization of Ca and Mg (Fig. 4). The mineralization of N was much slower than that of leaf decomposition and decreased with elevation in erect forests. At krummholz, N mineralization increased sharply to rates similar to those of leaf decomposition. Phosphorus and K mineralization increased sharply at krummholz.

4. Discussion

4.1. Nutrient cycling along the elevation gradient

Many aspects of the nutrient cycling characteristics of lenga forests were in agreement with the observed declining structural and physiognomic changes of stands along the elevation gradient (Figs. 2 and 4; Tables 1–3). However, many aspects of nutrient cycling did not conform to expectations based on the declining structural complexity of stands (e.g., tree height and stand biomass) with increased elevation.

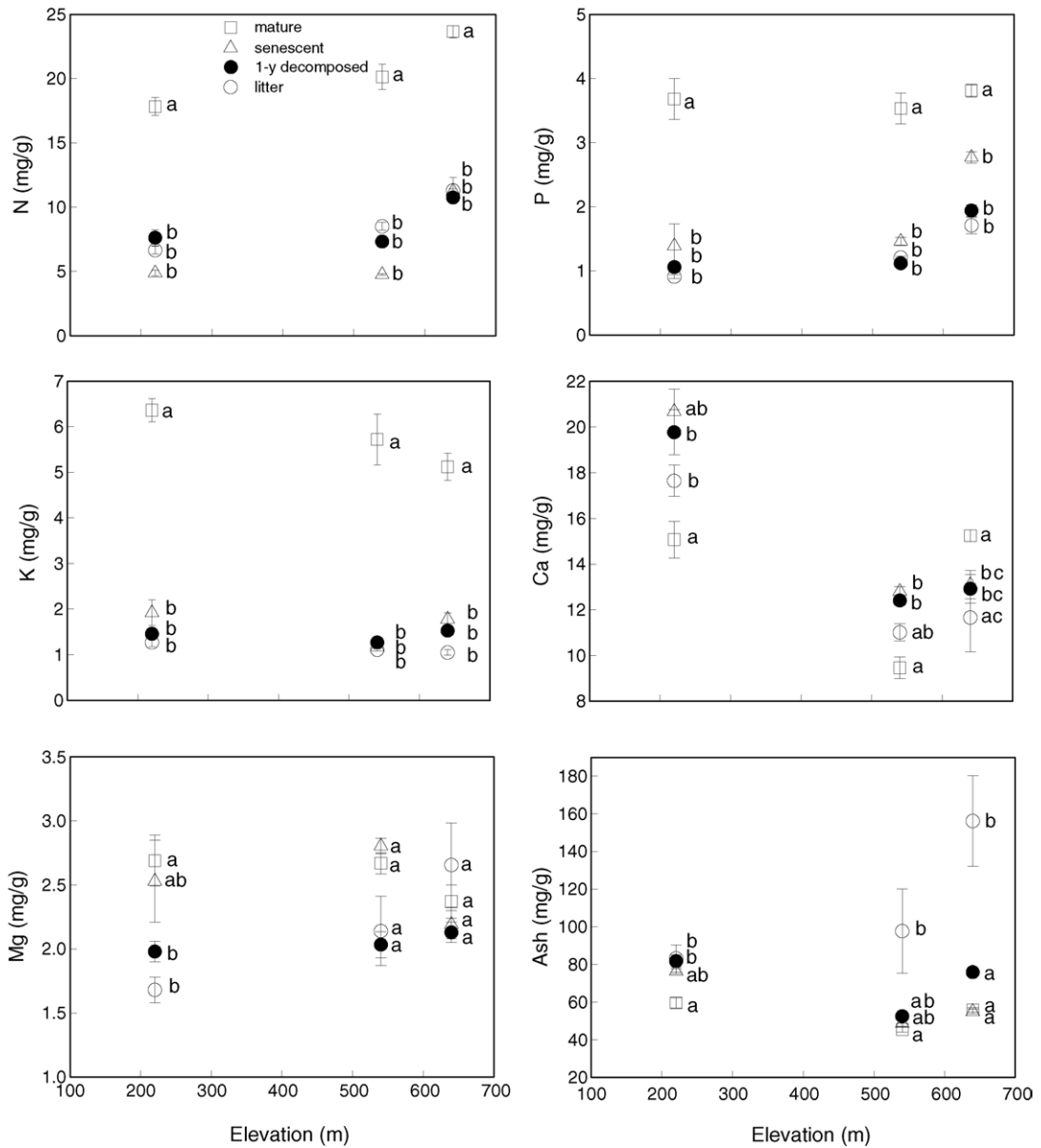


Fig. 3. Nutrient concentrations of leaves in stages from mature to leaf litter in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego. Standard error bars are shown ($n = 9$; 3 for decomposing leaves). Stages with the same letter are not different at $P < 0.05$.

Instead, trends of nutrient cycling parameters among erect forests reversed, and nutrient cycling rates accelerated at the high elevation krummholz (cf. Figs. 3–6; Tables 3 and 4).

High concentrations of certain nutrients (Figs. 3 and 6) and faster rates of nutrient fluxes in krummholz vegetation (Figs. 2 and 4) led to higher than expected

accumulation of N, P, Ca, and Mg in aboveground compartments. Nutrient fluxes in krummholz were also faster than expected by the slow rates of radial tree growth and leaf decomposition. All rates in Fig. 2 (uptake, requirement, retention, recycling, and return) were, with few exceptions, higher in krummholz than in short erect forest. The ratio of within-tree recycling/

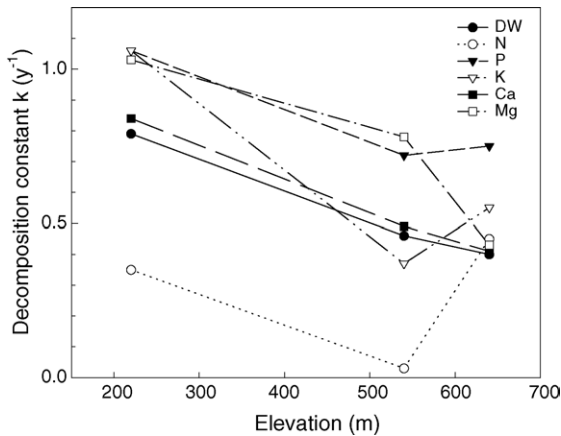


Fig. 4. Decomposition constant (DW) and mineralization rate during leaf decomposition in *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego.

requirement for mobile nutrients increased with elevation in erect forests but decreased in the krummholz (Fig. 5). This suggests an increase in the internal circulation of mobile nutrients with elevation but a greater outside-tree circulation of them at the krummholz. Moreover, in spite of a slow rate of leaf decomposition, krummholz had faster rates of N, P, and K mineralization (Fig. 4) than short erect forests.

Differences in nutrient stocks and flux rates among lenga stands, resulted in shorter turnover time for nutrients and mass in krummholz vegetation and soil relative to erect forests (Table 5). Soil nutrients in short erect forest had a longer turnover time than tall erect forest. Stands differed little in the turnover time of litter as the pattern of turnover time in litter was not

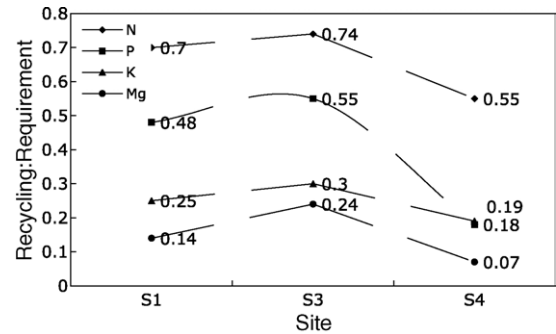


Fig. 5. Ratio of within-tree nutrient recycling to nutrient requirement for *Nothofagus pumilio* forests along an altitudinal gradient in Tierra del Fuego.

as clear as in vegetation or soil. Nitrogen consistently had the longest turnover time. However, the short nutrient turnover time in krummholz vegetation is remarkable and shorter than organic matter turnover time. For example, turnover time of organic C in aboveground vegetation and soil were strikingly similar (44 y) in tall erect forests, but this similarity disappeared at higher elevation (short erect forest was 39 y versus 88 y; krummholz was 6 y versus 68 y). In fact, all macronutrients circulated faster than dry matter (Table 6). The lowest relative turnover rates were for N, especially at both extremes of the elevation gradient, and the faster ones were for Ca, particularly at erect forests. The highest values were always at the short erect forest, declining towards the lowlands and krummholz.

Fast rates of nutrient cycling in krummholz resulted in low within-stand P- and N-use efficiencies (Table 4), and low biomass production per unit N

Table 3

Total aboveground nutrient (kg/ha) and mass (Mg/ha) storage in world's forests and in three forest stands at Tierra del Fuego

Forest type	Aboveground vegetation						Forest floor					
	Biomass	N	P	K	Ca	Mg	Litter Mass	N	P	K	Ca	Mg
Boreal coniferous	51.3	116	16	44	258	26	113.7	617	115	109	360	140
Temperate												
Coniferous	307.3	479	68	340	480	65	74.8	681	60	70	206	53
Deciduous	151.9	442	35	224	557	57	21.6	377	25	53	205	28
Tropical	292.0	1.404	82	1.079	1.771	290	27.3	214	9	22	179	24
Tall erect	492.8	576	133	372	925	180	10.0	67	9	13	18	17
Short erect	136.4	176	51	147	212	64	3.0	25	4	3	32	6
Krummholz	32.1	109	38	57	189	37	7.0	75	11	7	77	18

World forest data are from Waring and Schlesinger (1985). Tall erect, short erect, and krummholz forests are from Tierra del Fuego (this study).

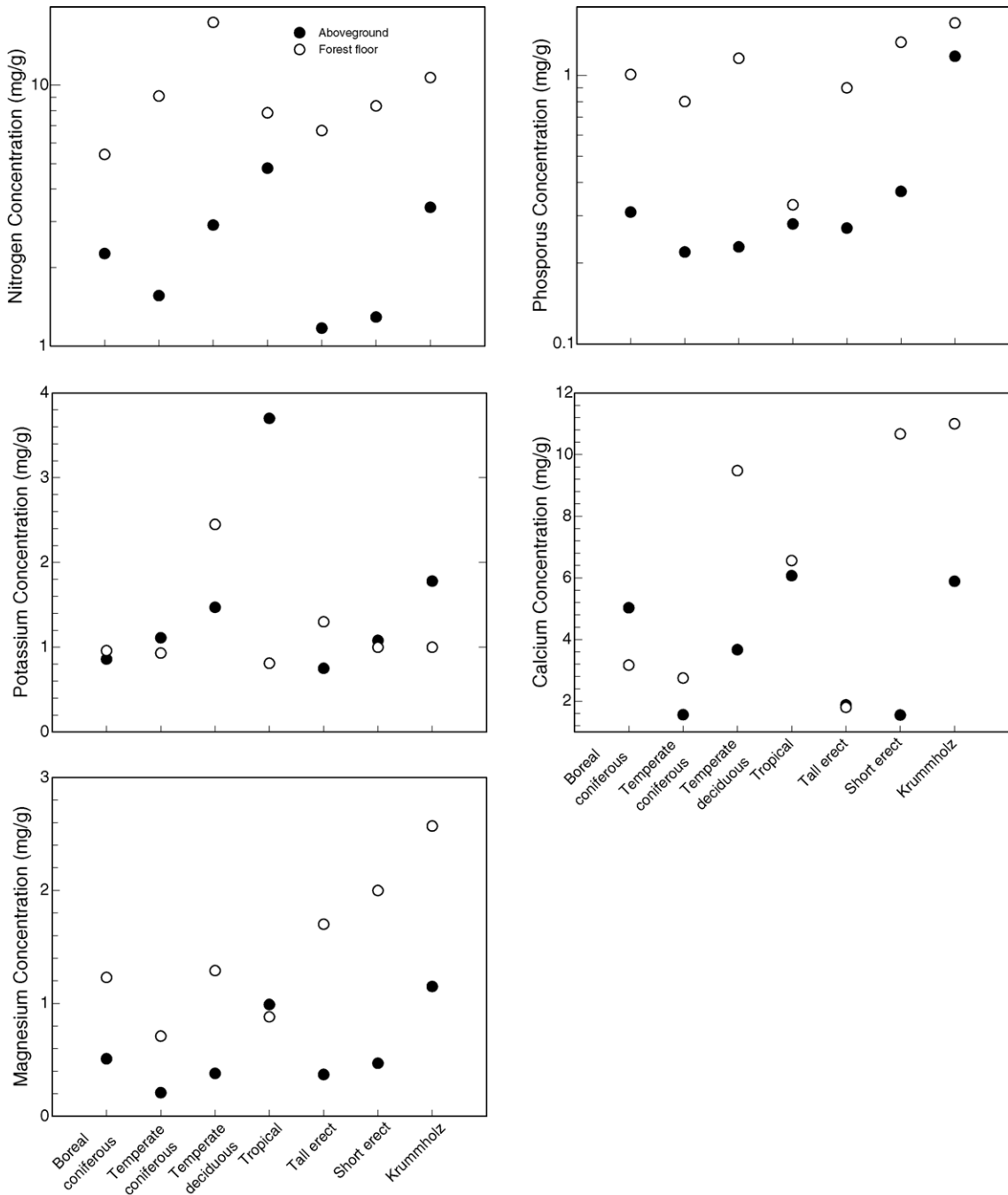


Fig. 6. Weighted nutrient concentrations (mg/g) of aboveground vegetation (solid dots), and forest floor litter (open dots) in forests from different latitudinal regions of the world. Data are derived from Table 3.

Table 4

Within-stand nutrient-use efficiency based on Vitousek (1982) ratio (mass in litterfall to nutrients in litterfall) for Tierra del Fuego *Nothofagus pumilio* forests along an elevation gradient

Forest type	N	P	K	Ca	Mg
Tall erect	219	813	564	53	443
Short erect	269	1679	1070	140	757
Krummholz	113	498	722	99	605

Data on nutrient return and litterfall are shown in Fig. 2 and Table 1, respectively.

flux (Table 7). However, the efficiency of N, P, Ca, and Mg accumulation (Fig. 6) was high in krummholz. The high nutrient content of krummholz coupled to increased rate of nutrient movement results in low nutrient-use efficiency. Low nutrient-use efficiencies are possible as long as nutrients remain available and high productivity rates maintained. Low within-stand nutrient-use efficiency is due in part to the impact of early frosts that interrupt retranslocation and abscission. This is suggested by concentration data. Killingbeck (1996) found complete resorption or high

Table 5

Turnover time (γ) for Tierra del Fuego *Nothofagus pumilio* forests along an elevation gradient

Nutrient	Tall erect forest	Short erect forest	Krummholz
Vegetation			
N	25.6	17.0	3.5
P	14.8	15.5	3.2
K	15.8	14.4	2.4
Ca	10.8	8.4	2.5
Mg	15.0	12.3	2.3
Forest floor			
N	2.8	2.2	2.4
P	1.0	1.1	1.1
K	0.5	0.4	0.5
Ca	2.1	1.5	1.8
Mg	1.4	1.4	2.3
Soil			
N	139	253	162
P	9	16	12
K	4	16	7
Ca	32	43	19
Mg	19	30	14

Values are the ratio of nutrient stock to nutrient uptake in vegetation, forest floor, and soil. Data on nutrient stock and uptake are shown in Fig. 2. Soil data are to 10 cm depth. For comparison, the turnover time (γ) of aboveground biomass is tall erect: 44; short erect: 39; krummholz: 6.

Table 6

Turnover rate of nutrients to turnover rate of dry matter sensu Gray (1983) for *Nothofagus pumilio* forests along an elevation gradient in Tierra del Fuego

Nutrient	Tall erect forest	Short erect forest	Krummholz
Nitrogen	1.2	2.2	1.7
Phosphorus	2.4	2.3	1.6
Potassium	2.2	2.5	2.1
Calcium	3.4	4.4	2.1
Magnesium	2.3	2.9	2.1

The ratio compares the circulation rate of nutrients with that of biomass. Nutrient turnover rate was estimated as return/mineral mass, and dry matter turnover rate was estimated as aboveground NPP/biomass.

resorption proficiency at erect forest sites but incomplete resorption at krummholz as a result of abscission interruption. Our N concentration of recent fallen leaves was 4.9 ± 0.2 , 4.8 ± 0.1 , and 11.2 ± 0.2 mg/g at tall erect, short erect, and krummholz, respectively. Phosphorus concentration in leaf fall shows a similar trend with elevation (1.4 ± 0.3 , 1.5 ± 0.1 , and 2.8 ± 0.1 at tall erect, short erect, and krummholz, respectively). The disproportional higher concentration at krummholz suggests incomplete N and P resorption. However, low efficiency means that more nutrients are returned to the forest floor by litterfall and made available for mineralization and uptake when conditions are more favorable.

4.2. The significance of krummholz to nutrient cycling

Since the growth period is shorter and the mesoclimate harsher with elevation, how can aboveground NPP be higher in krummholz than at the adjacent short erect forest (Fig. 1 top)? The answer to this question requires consideration of actual conditions at the sites and the change in physiognomy from erect forest to krummholz, which together influence nutrient cycling attributes and NPP.

The conditions that regulate mineralization of litter illustrate how krummholz function at timberline. Environmental conditions for leaf decomposition appear more favorable in erect forests than in krummholz. Erect forests had longer growing season, milder air temperatures, and lower soil C:N than krummholz. However, the quality of falling litter is

Table 7

Nutrient-use efficiency (kg organic matter/kg nutrient uptake) for the process of primary productivity in *Nothofagus pumilio* forest stands in Tierra del Fuego

Forest type	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Tall erect	468	1259	478	132	944
Short erect	307	1072	385	154	755
Krummholz	165	482	367	115	650
Deciduous	143 (36)	1859 (745)	216 (85)	130 (61)	915 (445)
Coniferous	194 (48)	1519 (582)	354 (154)	217 (95)	1559 (783)

Values represent the ratio of aboveground net primary productivity (annual litterfall plus annual net biomass accumulation) to nutrient uptake all in kg/ha. Values for deciduous and coniferous forests are from Cole and Rapp (1981) and the standard error is in parenthesis ($n = 14$).

higher in krummholz than in erect forests (C:N = 37 and C:P = 149 in krummholz versus 82 and 289 for tall forest and 87 and 238 for short erect forest, respectively). Soil temperatures at 10 cm depth in krummholz were above zero and similar to those of short erect forest from mid-spring to early summer (Fig. 3 in Barrera et al., 2000). After February, soil temperatures in krummholz decrease below zero while those in erect forests remain above freezing. Daytime temperatures above the soil surface might be higher at krummholz due to the open canopy and lowered effect of tree cover on conditions at the forest floor. Thus, in spite of slower leaf decomposition rate, a harsher climate, and shorter growing season, changes in litter quality and the open nature of the forest canopy, allow mineralization of N, P, and K to be high and exceed rates observed at lower elevations under less extreme conditions.

Erect tree life-form adjusts to environmental changes with elevation by reducing stocks and fluxes of organic matter and nutrients (Figs. 2 and 6; Tables 3 and 6), but apparently reach a threshold in their capability to function at high elevation conditions. For example, the nutrient requirements of erect forests decrease with elevation; however, the proportion of the most mobile nutrients supplied by retranslocation increases from low elevation tall erect forest to low erect forest at higher elevation. The less mobile Ca and Mg, whose availability decrease with elevation, are obtained mainly by uptake. In spite of the relative increment in retranslocation with the increase in elevation, erect forests show a reduction in turnover time of nutrients in vegetation (Table 5), an increase in the relative turnover rate of nutrients at it is upper limit (Table 6), and a decrease in the efficiency of NPP relative to nutrient uptake (Table 7). Short erect forest

also shows a reduction in the leaf duration to 0.95 y relative to tall erect at 1.4 y (obtained by dividing leaf biomass by leaf fall rate in Table 1). Thus, high elevation erect forests cannot maintain rates of primary productivity by increasing the turnover of nutrients relative to the turnover of organic matter, nor can they uptake sufficient nutrients to overcome the limitations imposed by internal recycling. Their capacity to further reduce nutrient turnover time is limited by the relative magnitude of nutrient stocks and fluxes of stands, and reducing leaf longevity (which increases the productivity of leaves) might be risky and costly in the variable timberline environment. A life form shift is required to supply nutrients to leaves at timberline.

The shift to krummholz is an architectural change with a new balance of nutrient cycling traits that improves survival at timberline. Dwarfed krummholz shortens the transport distances between uptake and production organs of the plant, probably has a more favorable below to aboveground tissue ratio, and sustains a fast flow of nutrients between plant and soil. Below to aboveground ratios of 10–15 have been reported for krummholz in Russia (Bazilevich and Tishkov, 1997). Fine roots at all our sites were concentrated in the O layer and upper 10 cm of soil, consistent with a high available P at those depths. Root distribution favors the exploitation of the nutrient-enriched topsoil. Plants, in nutrient limited soils or shallow soils might increase nutrient uptake by improving root exploration of the topsoil rather than increasing absorption rate per root surface unit (Chapin, 1980).

The movement of materials to and from the krummholz canopy leaves is supported by a low leaf area to sapwood area (0.09 at krummholz versus 0.11

at short erect and 0.23 at tall erect; Barrera et al., 2000). The reduction of leaf size with elevation (Table 1) is accompanied by an increase in leaf N content (Table 2) that favors faster rates of photosynthesis, needed to overcome the shorter growing season. This is reflected in the increased rate of organic matter production per unit leaf area and per day of growing season at the krummholz (Fig. 1 bottom). The number of leaves increases with elevation and its almost doubled in the krummholz (obtained by dividing the LAI by the predominant leaf area [Table 1]: S1 = 8286 leaves, S2 = 11,600 leaves, S3 = 12,400 leaves, and S4 = 22,000 leaves). Deciduous species at timberline might opportunistically improve nutrient uptake and productivity rates during limited favorable daytime conditions and thus compensate for reduced retranslocation caused by early frosts. High retranslocation rate indicates that there are active reserve sites, and high nutrient concentration in krummholz wood may be pointing to high uptake and mobilization capacity. However, a trade-off between retranslocation and relatively fast mineralization and uptake from N- and P-rich litter is probably a successful response of krummholz at timberline. Nutrient budgets show short erect forest and krummholz with smaller relative unbalances suggesting a tighter and dynamic cycling of nutrients through the soil (Fig. 2).

The architectural change from short erect forest to krummholz appears to be more than a disturbance-produced effect, it is a life form change with functional consequences that allow trees to cope with conditions at timberline. Based on the comparison with erect forests, we noted several attributes in krummholz that allow this forest type to accelerate nutrient cycling in spite of harsh growth conditions, short growing season, and slower organic matter cycles.

- A shift towards fast turnover compartments – leaves, herbaceous plants, and mosses – for nutrient storage.
- A switch in the compartment with the highest nutrient stock: small branches instead of stemwood biomass. Small branches have higher nutrient concentrations and faster nutrient turnover than heartwood. However, even krummholz heartwood is characterized by higher P, K, and Mg concentration than erect forest heartwood (Table 2).

- Changes in the structure of the tree habit contribute to higher productivity and faster nutrient cycling. For example, the krummholz has adventitious roots, shorter distance between roots and leaves, high proportion of sapwood area to leaf area, smaller, more leaves, and younger leaves with high N concentration.
- Rapid turnover and accumulation of nutrients in krummholz leads to soil enrichment (C, N, P, Ca, and ECEC) and an apparent isolation of the biotic fluxes (retention, uptake, and recycling) in these forests from the mineral soil.
- High weighted concentration of nutrients in plants, and low efficiency of nutrient use, which contribute to fast rates of nutrient fluxes.

All these attributes make possible the shift in the direction of the altitudinal pattern of NPP in Fig. 1 top.

4.3. Comparison with forests of other latitudes

The third question that we address is whether the accumulation, uptake, requirement, and recycling of nutrients in lenga stands are different from forests at other latitudes. Aboveground nutrient storage in the lenga forests of Tierra del Fuego ranged from the lowest (krummholz) to the highest (tall erect forest) mean values reported in the literature for temperate and boreal forests, but were lower than tropical forests with the exception of P (Table 3). Nutrients stored in the forest floor were lower in Tierra del Fuego than in other forest types, perhaps because of the low biomass on the forest floor at Tierra del Fuego. The only study we found with nutrient data for litter dynamics in lenga forests was from Chile (Caldentey et al., 2001). Their results are similar to ours and fall in the range of variation we found for erect forests with the difference that our tall erect forest was more productive and nutrient-rich than the Chilean forest.

Compared with mean values for other world forests, erect forest vegetation had the lowest aboveground N and Ca concentrations (Fig. 6). Their aboveground P concentration was similar to that of other temperate and boreal forests. Forest floor N, P, and K concentration were also comparable to that of other temperate and boreal forest stands. However, erect forest stands had high Mg concentration on the forest floor. The forest floor of short erect forest had a

high, while the tall erect forest had a low Ca concentration. At timberline, krummholz behaved differently from erect forests and other world forest types. For example: weighted concentrations of P and Mg were higher for both aboveground and forest floor compartments; forest floor Ca was higher; N, K, and Ca concentration aboveground and N in forest floor were among the highest concentrations in Fig. 6.

Values for within-stand N-use efficiency are consistent with those of a limiting nutrient, i.e., a high within-stand nutrient-use efficiency index (Table 4) and low nutrient return rate (Fig. 3). Short erect lenga forest at higher elevation also had a high within-stand N-use efficiency index and a low N-return compared with deciduous forests, and was closer to coniferous forests reported in Vitousek (1982). In fact, both erect forests have a high within-stand N-use efficiency compared to other deciduous forests. In contrast, krummholz had a low within-stand N-use efficiency typical that of deciduous forests. All three stands had low within-stand P-use efficiency, particularly the krummholz. Tierra del Fuego forests are among the least efficient in terms of within-stand nutrient-use among those with similar P litterfall return. In comparison with other forest types reported by Vitousek (1982), values for Ca within-stand use efficiency were low for krummholz and tall erect forest and moderate for short erect forest.

The high productive efficiency per unit of N uptake by lenga stands is confirmed if we insert our data to Fig 8 in Reich et al. (1997). The figure depicts litterfall N return versus aboveground NPP/litterfall N return for various forest types. Aboveground NPP per returned N is higher in lenga forests (165–468 kg OM/kg N; Table 7) than in mesic hardwoods, oaks, or coniferous forests of similar N return, with the tall erect forest as the most efficient of all sites. In addition, lenga forests, especially those at low elevation, show higher K-use efficiencies than most deciduous forests of the world. Lenga forests showed lower productive P-efficiencies than all the deciduous forest groups again suggesting that P is not limiting production. Compared to the mean efficiencies in temperate deciduous forests, lenga forests show a similar productive efficiency per Ca-uptake, a similar or slightly lower efficiency per Ca-returned, and a clearly lower than the mean productivity per Ca-required. This suggests that, despite a higher relative Ca requirement for production, lenga

forests are as effective in Ca conservation as other deciduous forests of the world. A similar comparison for Mg showed that lenga forests have a similar to lower productive efficiency per Mg-uptake, a lower efficiency than the mean of Mg-required, and a similar to higher productivity per Mg-returned.

The lower N-efficient krummholz was in the range of both temperate deciduous and conifer forests but lower than boreal deciduous. All three lenga forests had low efficiency of Ca use when compared with other forest of the world. In contrast, tall erect forest had the highest nutrient-use efficiency for N and K uptake, K requirement, and N return.

Tierra del Fuego krummholz behaves fundamentally different from coniferous krummholz of the northern hemisphere tundra. Coniferous krummholz forests above tree line in the Front Range of Colorado grow in island clumps that scavenge nutrients accumulated in tundra soils by migrating slowly over the landscape (Benedict, 1984; Marr, 1977). As they migrate, they deplete soil carbon and nitrogen pools (Pauker and Seastedt, 1996; Seastedt and Adams, 2001). Shields and Sanford (2001) found the effect of krummholz on soil chemistry was species-specific. Stands of *Pinus aristida* had more soil P than stands of *Picea engelmannii*. In contrast to these alpine krummholz, lenga krummholz accumulates and recycles nutrients, enrich the soil, and function at rates that exceed those of erect forests growing under less severe conditions.

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