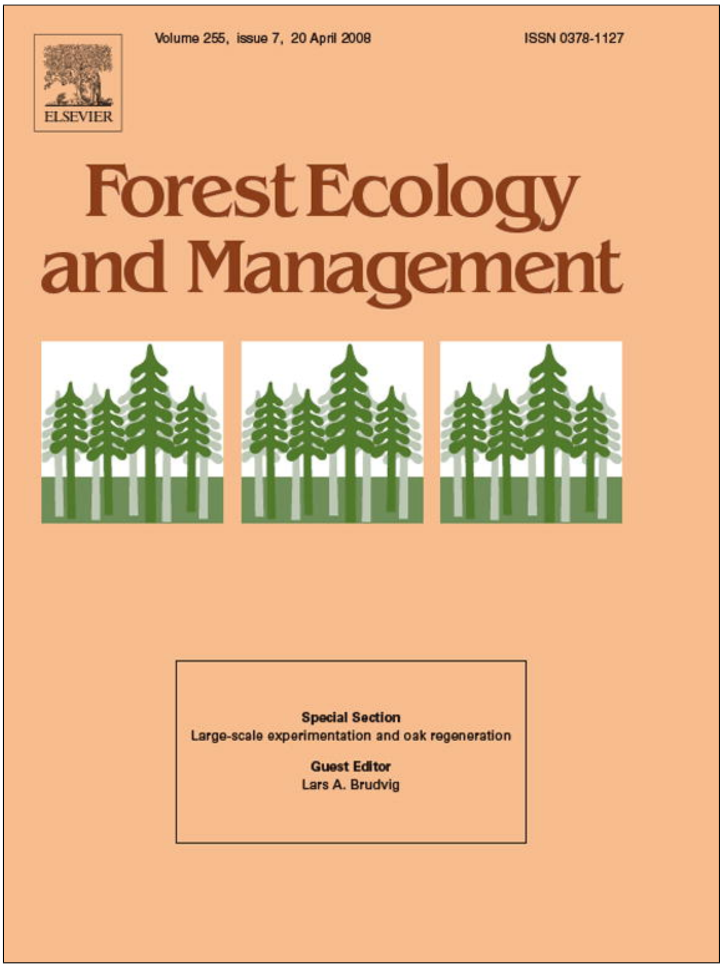

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Above- and belowground nutrients storage and biomass accumulation in marginal *Nothofagus antarctica* forests in Southern Patagonia

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Abstract

The above- and belowground biomass and nutrient content (N, P, K, Ca, S and Mg) of pure deciduous *Nothofagus antarctica* (Forster f.) Oersted stands grown in a marginal site and aged from 8 to 180 years were measured in Southern Patagonia. The total biomass accumulated ranged from 60.8 to 70.8 Mg ha^{-1} for regeneration and final growth stand, respectively. The proportions of belowground components were 51.6, 47.2, 43.9 and 46.7% for regeneration, initial growth, final growth and mature stand, respectively. Also, crown classes affected the biomass accumulation where dominant trees had 38.4 Mg ha^{-1} and suppressed trees 2.6 Mg ha^{-1} to the stand biomass in mature stand. Nutrient concentrations varied according to tree component, crown class and stand age. Total nutrient concentration graded in the fallowing order: leaves > bark > middle roots > small branches > fine roots > sapwood > coarse roots > heartwood. While N and K concentrations increased with age in leaves and fine roots, concentration of Ca increased with stand age in all components. Dominant trees had higher N, K and Ca concentrations in leaves, and higher P, K and S concentrations in roots, compared with suppressed trees. Although the stands had similar biomass at different ages, there were important differences in nutrient accumulation per hectare from 979.8 kg ha^{-1} at the initial growth phase to 665.5 kg ha^{-1} at mature stands. Nutrient storage for mature and final growth stands was in the order Ca > N > K > P > Mg > S, and for regeneration stand was Ca > N > K > Mg > P > S. Belowground biomass represented an important budget of all nutrients. At early ages, N, K, S, Ca and Mg were about 50% in the belowground components. However, P was 60% in belowground biomass and then increased to 70% in mature stands. These data can assist to quantify the impact of different silviculture practices which should aim to leave material (mainly leaves, small branches and bark) on the site to ameliorate nutrient removal and to avoid a decline of long-term yields.

Keywords: Growth phase; Nutrients accumulation; Root/shoot ratio; Crown classes; Marginal forest

1. Introduction

The cool temperate forest of Patagonia is dominated by deciduous *Nothofagus* species which occurs from 46° to 56° S and ranges in elevation from sea level to more than 2000 m a.s.l. *Nothofagus antarctica* (Forster f.) Oersted (ñire) grows at sites that are harsh for most other species, thus on poorly drained or drier eastern sites in the ecotone with the Patagonian steppe. Within its natural distribution, tree growth rate is clearly site quality-dependent, reflecting the influence of soil, geologic, orientation and microclimatic factors. On the best sites *N. antarctica* trees can reach height of up to 15 m with straight trunks form but on rocky, dry and exposed sites trees only reach 2–3 m tall with a shrubby form (Veblen et al., 1996). Therefore, trees growing in better sites would store more biomass and nutrients (Palm, 1995) or increase nutrient concentrations in plant tissues (Diehl et al., 2003) than others developed in inferior site classes. Also, concentration of nutrients in leaf litterfall of trees may differ from those in live tissues due to a resorption from senescing tissues into perennial pools. Peri et al. (2006) reported that nutrient accumulation of *N. antarctica* varied according to the age, crown classes and components, but this study was carried out only in a middle site quality (total height of mature trees reached 7.8 m) and at an individual trees level in Southern Patagonia.

Most of the nutrient cycling researches in forest ecosystems have been focussed on aboveground pools (Caldentey, 1992; Santa Regina, 2000). However, net primary production, nutrient

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concentrations and fine roots turnover rates of belowground components in forest system can equal or even exceed those from aboveground pools (Caldwell, 1987; Ranger and Gelhaye, 2001). Therefore, research of belowground pools in trees is necessary to quantify nutrient sequestration in the underground woody structures.

As *N. antarctica* is often harvested mainly for wood products such as firewood and poles, data on biomass and nutrient accumulation at stand level in both above- and belowground components are essential for evaluating the impacts of silviculture practices on bioelement recycling and long-term effects on the mineral balance (Santa Regina, 2000). Also, *N. antarctica* forests are usually used as silvopastoral systems (trees growing with natural pastures in the same unit of land to feed cattle) where it is important to know the amount of nutrients up taken by the trees, the nutrients returned by leaves fall and the impact of the thinning on nutrients dynamic at a surface level.

The aim was to quantify the amount of biomass and nutrients in both above- and belowground components at different stands age and crown classes of *N. antarctica* forest growing in a dry and windy marginal site in South Patagonia, near the Patagonian steppe.

2. Materials and methods

2.1. Study area

This study was carried out in four naturally pure stands of *N. antarctica* in the southern west of Santa Cruz province, Argentina (51° 40′ 59″ SL, 72° 15′ 56″ WL) corresponding to different growth phases (mature phase 140–180 years, final growth phase 80–100 years, initial growth phase 40–60 years and regeneration phase 8–20 years) growing at a low site quality where total height of mature trees reached 5.3 m. Climate is cold temperate with a mean annual temperature of 6.2 °C and a long-term annual rainfall of 280 mm. Soils were classified as Molisols. Thirty bulked soil sample cores from the four stands to different depths (0–5, 5–21 and 21–50 cm) were taken at random (Table 1). The soil pH and minerals was higher in the upper layer. Increasing the quantity of cations (mainly Ca^+, Mg^+ and K^+) in soil solution (or increasing the base saturation) in the upper layer leads to higher pH. The declines in exchangeable soil minerals (particularly Ca^+) in the lower layers (where most of roots are distributed) could have resulted from an increase in nutrients uptake by trees. The mean dasometric characteristics of the four sampled stand are given in Table 2.

Table 1
Soil properties in sampled marginal sites of *N. antarctica* forest

	Organic horizon	Mineral horizon I	Mineral horizon II
Depth (cm)	0–5	5–21	21–50
Clay (%)	–	26	25
Silt (%)	–	22.5	19.9
Sand (%)	–	51.5	55.1
pH	5.6	4.7	4.5
N total (ppm)	5190	2810	1890
P Truog (ppm)	66	25	6
K^+ (cmol/kg)	1.3	0.9	0.5
Mg^+ (cmol/kg)	6.3	2.3	2.1
Ca^+ (cmol/kg)	24.6	8.5	5.1

2.2. Biomass

Three randomly replicate sample plots for each growth phases stands were selected. These plots had a hierarchical design according to trees size which differs between growth phases stands. Thus, trees in mature phase stands were sampled in 150 and 50 m^2 for final growth phase, 10 m^2 for initial growth phase 40–60 years, and for 2 m^2 regeneration phase. Similar hierarchical designs according to trees size or trees age were used previously for trees biomass sampling (De Castilho et al., 2006; Laclau et al., 2000). Within each plot four *N. antarctica* trees were selected, felled and sorted in four crown classes: dominant, codominant, intermediate and suppressed trees, depending of their crown position.

Total height and diameter at breast height were measured, and the stem was cut at 0.1 m (stump), 1.3 m and every 1 m up to an end diameter of 10 mm after the harvesting to calculate wood volume for heartwood, sapwood, bark and rotten wood components using Smalian formula. Each tree was separated into the following components: leaves; small branches (diameter < 10 mm); sapwood, heartwood and bark from the main stem and coarse branches (>10 mm); and roots with bark classified as fine (diameter < 2 mm) medium (<30 mm) or coarse roots (>30 mm).

Three samples of each component in every tree were taken for biomass calculations and nutrient analysis. For coarse branches, stem and roots, three cross-sectional discs of 30 mm at different lengths were taken and separated into their component pool (heartwood, sapwood and bark) to determinate density for biomass calculations. All small branches, leaves and dead branches from each sampled tree were separated and weighed in fresh. Roots from individual tree were excavated to a depth of 0.5 m (maximum rooting depth for all crown classes) in circular plots centred on the stump of the selected trees minimizing the loss of the fine root fraction. These roots were sorted in 3 diameter classes (<2 mm, from 2 to <30 mm and >30 mm) and weighed in fresh.

At each sampled stand, four litter traps (1 m^2 collecting surface) were placed randomly under the canopy and collected at the end of the growing season (autumn). From total litterfall leaf litter was separated to estimate nutrient resorption.

Sub-samples from all components and leaf litter were taken to estimate biomass and for nutrients analysis.

2.3. Chemical nutrient analysis

Samples from all age classes were dried in a forced draft oven at 65 °C to constant weight and ground in a mill containing 1 mm stainless steel screen for nutrient analysis. Nitrogen (N) was determined using the Kjeldahl technique. Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg)

Table 2
Mean dasometric characteristics of sampled *N. antarctica* stands grown at marginal sites in Southern Patagonia

Growth phase	Age class (years)	Density (trees ha^{-1})	Height (m)	DBH (m)	Basal area (m^2 ha^{-1})	Crown classes (%)			
						D	C	I	S
Regeneration	8–20	161200 ± 10800	1.1 ± 0.6	0.02 ± 0.003	32.3 ± 3.1	20	24	25	31
Initial growth	40–60	5540 ± 2300	2.7 ± 0.8	0.08 ± 0.002	30.8 ± 2.9	25	28	24	23
Final growth	80–100	1120 ± 220	4.2 ± 0.7	0.136 ± 0.04	27.8 ± 1.7	29	25	27	19
Mature	140–180	440 ± 35	5.3 ± 0.3	0.202 ± 0.05	25.4 ± 2.7	36	27	23	14

Crown classes = D: dominant trees, C: codominant trees, I: intermediate trees, S: suppressed trees.

and sulphur (S) concentrations were determined with a plasma emission spectrometry (Shimadzu ICPS—1000 III).

2.4. Data and statistical analysis

Nutrient accumulation of trees was estimated by multiplying nutrient concentrations from chemical analysis and the biomass of each component (dry weight measurements). Age of each sample tree was obtained through counting rings at the stump (0.3 m from the soil). Comparisons of main factors (age and crown classes) were carried out by analyses of variance (ANOVA) with the F-test. Significant differences were separated with standard errors of means to evaluate least significant differences (LSD). All tests were evaluated at $p < 0.05$. Statistical analysis were carried out by using the Genstat statistical package (Genstat 5, 1997).

3. Results

3.1. Stand biomass

The total biomass accumulated by hectare ranged from 60.8 to 70.8 Mg ha^{-1} for regeneration and final growth phase stands, respectively (Table 3). Although the stands presented similar amount of biomass, their distribution in components depended on age. While regeneration class age presented 31.8% of total biomass distributed in fine components (leaves and small branches), the mature stand had only 5.2% (Table 3). The proportions of belowground components were 51.6, 47.2, 43.9 and 46.7% for regeneration, initial growth, final growth and mature growth phase stands, respectively. However, the fine and middle roots in regeneration stands contributed in 79.6 and 12.9% in mature stands (Table 3).

At all ages, significant differences were found in the accumulated biomass according to the crown class. In regeneration stands, dominant trees accounted 32.2 Mg ha^{-1} and only 5.0 Mg ha^{-1} for suppressed trees. Similarly, in mature stand, dominant trees had 38.4 Mg ha^{-1} and suppressed trees 2.6 Mg ha^{-1} to the stand biomass.

3.2. Nutrient concentrations in the tree components

Nutrient concentrations varied according to tree component (Table 4). At all ages, N, K, Mg and S were more concentrated in leaves, while P was more concentrated in fine roots and Ca in bark. Total nutrient concentration generally graded in the fallowing order: leaves > bark > middle roots > small branches > fine roots > sapwood > coarse roots > heartwood. Nutrient concentrations in some components varied according to the age gradient (Table 4). For example, N concentration increased with age in leaves and fine roots, and decreased with age in bark, middle and coarse roots. The concentration of K increased with age in leaves, fine roots and coarse roots, and P decreased with age in fine and middle roots. While concentration of Ca increased with stand age in all components, Mg increased only in small branches and fine roots. S concentration increased with age in fine and coarse roots.

In general, nutrient concentration varied according to the crown class. Dominant trees had higher N, K and Ca concentrations in leaves, and higher P, K and S concentrations in roots, compared with suppressed trees. In contrast, Ca was more concentrated in suppressed than dominant trees for all components and Mg did not show differences according to the crown class.

Nutrients concentration of leaf litter did not differ significantly between different growth phase stands with mean values of 0.56 ± 0.123% for N, 0.13 ± 0.038% for P, 0.11 ± 0.022% for K, 1.20 ± 0.091% for Ca, 0.24 ± 0.046% for Mg and 0.06 ± 0.010% for S.

3.3. Total nutrient storage at stand level

Total accumulation of N, P, K, Ca, Mg and S per hectare for all ages is presented in Table 5. Although the stands had similar biomass at different ages, there were important differences in nutrient accumulation. The stand that accounted more quantity of nutrients was at the initial growth phase (979.8 kg ha^{-1}), followed by regeneration (962.2 kg ha^{-1}), mature stand (665.5 kg ha^{-1}) and final growth phase stand (663.4 kg ha^{-1}). Nutrient storage varied depending on the stand age. Nutrient storage for mature and final growth stands was in the order Ca > N > K > P > Mg > S, for initial growth stand Ca > N > K > Mg > S > P, and for regeneration stand was Ca > N > K > Mg > P > S.

Belowground biomass represented an important budget of all nutrients (Fig. 1). At early ages, N was presented in 43% in the belowground components and this percentage decreased to 38% in mature stand. Similarly, Ca and Mg were about 50 and 60% at early ages and then decreased to 25 and 45% in mature stands, respectively. However, K and S were around 50% in the belowground biomass at all ages, and P was about 60% in

Table 3
Mean biomass accumulation (Mg ha^{-1}) of *N. antarctica* stands grown in marginal sites in Southern Patagonia

Pool	*n*	Dominant	Codominant	Intermediate	Suppressed	Total
Regeneration stand (8–20 years)						
Leaves	36	1.1	1.1	0.7	0.3	3.1
Small branches	36	4.1	3.3	2.1	2.1	11.6
Sapwood	36	8.6	2.5	0.9	0.0	12.0
Heartwood	–	0.0	0.0	0.0	0.0	0.0
Bark	36	1.8	0.6	0.2	0.0	2.7
Fine roots	36	2.7	1.3	0.7	0.4	5.0
Middle roots	36	10.5	5.1	2.7	1.6	20.0
Coarse roots	36	3.4	1.6	0.8	0.5	6.4
Total		32.2	15.5	8.1	5.0	60.8
Initial growth stand (40–60 years)						
Leaves	36	1.3	1.1	0.4	0.2	3.0
Small branches	36	4.0	3.4	2.1	1.0	10.5
Sapwood	36	9.3	2.8	1.8	0.4	14.3
Heartwood	36	1.4	0.7	0.4	0.1	2.6
Bark	36	2.0	0.9	0.5	0.3	3.7
Fine roots	36	2.3	1.1	0.7	0.4	4.5
Middle roots	36	6.7	4.8	3.8	3.1	18.4
Coarse roots	36	3.8	1.9	1.2	0.7	7.6
Total		30.8	16.7	10.9	6.2	64.6
Final growth stand (80–100 years)						
Leaves	36	0.5	0.3	0.3	0.1	1.1
Small branches	36	1.2	0.7	0.8	0.2	3.0
Sapwood	36	6.8	2.3	2.8	0.2	12.1
Heartwood	36	9.1	4.7	1.9	1.5	17.2
Bark	36	3.3	1.5	1.1	0.4	6.3
Fine roots	36	0.1	0.03	0.02	0.01	0.1
Middle roots	36	2.3	0.8	0.6	0.2	3.9
Coarse roots	36	16.0	5.6	3.8	1.7	27.1
Total		39.3	15.9	11.3	4.3	70.8
Mature stand (120–180 years)						
Leaves	36	0.5	0.2	0.2	0.05	0.9
Small branches	36	1.2	0.6	0.5	0.1	2.5
Sapwood	36	6.6	1.9	1.9	0.1	10.6
Heartwood	36	8.9	4.0	1.3	0.8	15.0
Bark	36	3.2	1.2	0.8	0.2	5.4
Fine roots	36	0.1	0.03	0.02	0.01	0.1
Middle roots	36	2.3	0.9	0.5	0.1	3.8
Coarse roots	36	15.6	6.1	3.5	1.1	26.3
Total		38.4	15.0	8.7	2.6	64.7

belowground biomass and then increased to 70% in mature stands.

Nutrient distribution between components varied according to the age. Thus, while early stands accumulated more nutrients in fine components like leaves, middle roots and small branches, mature stands accumulated more nutrient in stems and coarse roots (Table 5). Nutrient allocation in regeneration stand was mainly in middle roots for all nutrients: N (29%), K (32%), P (44%), Ca (42%), S (31%) and Mg (41%). In contrast, mature stand distributed N, K, P, S and Mg mainly in coarse roots (31, 46, 65, 45 and 34%, respectively), and Ca in bark (42%). N allocation was greater in leaves and ranged from 9% in mature stand to 16% in regeneration stand. While nutrients allocated in small branches of regeneration stands varied from 15% for P to 24% for N, in sapwood represented a mean value of 16% for K, Ca and S. The main nutrient in fine root for regeneration stands was P (12%) and Mg (14%), and for mature stands was Ca (12%). Nutrients allocated in heartwood of mature stands ranged from 10% for S to 16% for N.

4. Discussion

4.1. Stands biomass

The total biomass accumulated was similar at different growth phases stands (Table 3). However, *N. antarctica* accumulated less biomass compared with other *Nothofagus* species that grow in South Patagonia. For example, Richter and

Table 4
Mean nutrient concentration of *N. antarctica* components (data expressed as percentage of dry matter) grown at marginal sites in Southern Patagonia

n	Leaves	Small branches	Sapwood	Heartwood	Bark	Roots		
	144	144	144	108	144	<2 mm	<30 mm	>30 mm
						144	144	144
N								
Age class								
8–20 years	1.29	0.50	0.24	–	0.46	0.42	0.38	0.23
40–60 years	1.48	0.52	0.26	0.16	0.29	0.44	0.39	0.16
80–100 years	1.58	0.50	0.25	0.17	0.29	0.45	0.36	0.19
140–180 years	1.69	0.48	0.24	0.18	0.29	0.47	0.32	0.18
Crown class								
Dominant	1.55	0.50	0.25	0.16	0.24	0.44	0.36	0.21
Codominant	1.48	0.53	0.23	0.16	0.31	0.45	0.40	0.20
Intermediate	1.52	0.47	0.22	0.19	0.34	0.46	0.38	0.19
Suppressed	1.40	0.48	0.23	0.20	0.19	0.43	0.31	0.16
Age class effect	**	ns	ns	ns	**	*	*	*
Crown class effect	**	ns	ns	ns	**	ns	*	ns
Interaction	ns	ns	ns	ns	*	ns	ns	ns
P								
Age Class								
8–20 years	0.16	0.05	0.05	–	0.06	0.32	0.11	0.05
40–60 years	0.14	0.08	0.04	0.01	0.04	0.31	0.16	0.04
80–100 years	0.15	0.06	0.05	0.01	0.03	0.22	0.12	0.08
140–180 years	0.19	0.07	0.06	0.02	0.02	0.14	0.08	0.13
Crown class								
Dominant	0.18	0.07	0.06	0.02	0.02	0.33	0.12	0.14
Codominant	0.18	0.07	0.05	0.01	0.02	0.28	0.15	0.09
Intermediate	0.15	0.05	0.06	0.01	0.02	0.20	0.14	0.05
Suppressed	0.15	0.07	0.04	0.004	0.02	0.18	0.06	0.04
Age class effect	*	ns	ns	ns	ns	**	**	**
Crown class effect	ns	ns	ns	*	ns	**	*	**
Interaction	ns	ns	ns	ns	ns	*	ns	ns
K								
Age class								
8–20 years	0.24	0.16	0.15	–	0.13	0.16	0.15	0.12
40–60 years	0.27	0.16	0.14	0.07	0.10	0.18	0.17	0.10
80–100 years	0.30	0.17	0.15	0.07	0.09	0.22	0.16	0.12
140–180 years	0.34	0.18	0.16	0.07	0.07	0.26	0.16	0.17
Crown class								
Dominant	0.31	0.17	0.16	0.07	0.06	0.28	0.16	0.12
Codominant	0.33	0.18	0.15	0.07	0.06	0.22	0.18	0.16
Intermediate	0.26	0.18	0.14	0.08	0.08	0.20	0.16	0.13
Suppressed	0.26	0.17	0.16	0.07	0.08	0.12	0.14	0.08
Age class effect	*	ns	ns	ns	ns	**	ns	*
Crown class effect	*	ns	ns	ns	ns	**	ns	*
Interaction	ns	ns	ns	ns	ns	*	ns	ns
Ca								
Age Class								
8–20 years	0.60	0.72	0.13	–	1.12	0.37	0.80	0.07
40–60 years	0.64	0.74	0.15	0.15	1.65	0.38	0.77	0.06
80–100 years	0.74	0.71	0.14	0.13	2.08	0.42	0.85	0.12
140–180 years	0.83	0.89	0.18	0.16	2.51	0.45	0.97	0.19
Crown class								
Dominant	0.70	0.66	0.22	0.08	2.4	0.42	0.88	0.08
Codominant	0.77	0.66	0.24	0.10	2.12	0.38	0.81	0.11
Intermediate	0.81	0.77	0.16	0.15	2.35	0.44	0.93	0.15
Suppressed	0.63	0.84	0.32	0.16	2.62	0.50	1.05	0.22
Age class effect	**	*	*	ns	**	*	**	*

Table 4 (*Continued*)

n	Leaves	Small branches	Sapwood	Heartwood	Bark	Roots		
	144	144	144	108	144	<2 mm	<30 mm	>30 mm
						144	144	144
Crown class effect	*	*	**	*	*	*	*	**
Interaction	ns	ns	ns	*	ns	ns	ns	ns
Mg								
Age Class								
8–20 years	0.24	0.09	0.04	–	0.09	0.17	0.13	0.05
40–60 years	0.32	0.14	0.05	0.03	0.10	0.25	0.12	0.04
80–100 years	0.25	0.14	0.05	0.03	0.08	0.23	0.12	0.04
140–180 years	0.29	0.15	0.05	0.02	0.07	0.20	0.11	0.05
Crown class								
Dominant	0.26	0.16	0.05	0.02	0.08	0.28	0.12	0.05
Codominant	0.27	0.14	0.05	0.03	0.05	0.22	0.14	0.05
Intermediate	0.23	0.10	0.06	0.03	0.06	0.20	0.11	0.04
Suppressed	0.23	0.13	0.04	0.02	0.05	0.15	0.10	0.03
Age class effect	ns	*	ns	ns	ns	*	ns	ns
Crown class effect	ns	ns	ns	ns	ns	*	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns
S								
Age class								
8–20 years	0.12	0.07	0.06	-	0.07	0.06	0.07	0.02
40–60 years	0.14	0.08	0.05	0.01	0.08	0.07	0.06	0.05
80–100 years	0.15	0.08	0.04	0.02	0.08	0.09	0.07	0.05
140–180 years	0.15	0.09	0.05	0.02	0.07	0.11	0.08	0.06
Crown class								
Dominant	0.15	0.08	0.06	0.01	0.08	0.10	0.07	0.07
Codominant	0.14	0.08	0.04	0.01	0.07	0.11	0.09	0.05
Intermediate	0.13	0.08	0.04	0.02	0.08	0.08	0.06	0.04
Suppressed	0.14	0.08	0.04	0.05	0.08	0.04	0.06	0.02
Age class effect	ns	ns	ns	ns	ns	*	ns	*
Crown class effect	ns	ns	ns	*	ns	*	ns	*
Interaction	ns	ns	ns	*	ns	ns	ns	ns

Table 5

Nutrient amount at stand level (kg ha^{-1}) of *N. antarctica* grown at marginal sites in Southern Patagonia

Pool	*n*	N	P	K	Ca	S	Mg	Total	*n*	N	P	K	Ca	S	Mg	Total
	Regeneration stand (8–20 years)								Initial growth stand (40–60 years)							
Leaves	36	44.4	5.6	8.6	21.3	4.2	8.6	92.7	36	45.3	4.5	8.0	19.3	4.3	10.3	91.7
Small branches	36	66.7	8.3	20.3	94.5	9.8	11.8	211.4	36	54.8	8.0	28.0	57.5	23.3	15.0	186.6
Sapwood	36	33.5	5.0	18.7	61.6	7.6	4.2	130.6	36	37.6	5.2	20.0	13.1	8.0	6.4	90.3
Heartwood	–	0.0	0.0	0.0	0.0	0.0	0.0	0.0	36	10.5	1.4	5.5	18.6	2.9	3.0	41.9
Bark	36	13.3	1.7	3.7	32.3	2.0	2.6	55.6	36	10.5	1.4	3.8	60.4	2.7	3.6	82.4
Fine roots	36	23.0	6.9	8.9	22.8	6.3	9.2	77.1	36	19.6	6.0	8.1	17.3	4.9	11.3	67.2
Middle roots	36	82.0	24.0	32.3	173.1	14.9	27.4	353.8	36	71.6	29.9	31.4	162.2	10.9	22.6	328.6
Coarse roots	36	16.4	3.5	8.7	5.2	3.8	3.4	41.0	36	20.9	3.0	56.2	4.3	3.5	3.0	90.9
Total		279.3	55.0	101.1	411.0	48.6	67.2	962.2		270.8	59.4	161.0	352.8	60.6	75.2	979.8
	Final growth stand (80–100 years)								Mature stand (120–180 years)							
Leaves	36	18.8	2.0	3.7	8.9	1.7	3.1	38.2	36	15.8	2.0	3.5	8.9	1.5	1.9	33.6
Small branches	36	16.1	2.2	5.4	23.2	2.5	4.5	53.9	36	13.2	1.8	4.7	22.5	2.2	3.8	48.2
Sapwood	36	36.9	7.4	18.6	32.4	5.4	6.4	107.1	36	31.0	7.3	16.8	29.3	4.5	5.4	94.3
Heartwood	36	31.4	3.4	14.6	36.3	4.3	5.6	95.6	36	28.3	3.3	12.5	30.6	3.5	4.2	82.4
Bark	36	19.9	2.8	7.4	91.4	4.6	6.7	132.8	36	18.6	1.4	4.9	117.6	4.0	4.8	151.3
Fine roots	36	0.7	0.2	0.3	0.6	0.2	0.4	2.4	36	0.6	0.2	0.4	0.7	0.2	0.3	2.4
Middle roots	36	14.8	4.9	6.7	37.7	2.8	4.8	71.7	36	11.5	2.8	5.7	34.7	2.8	4.1	61.6
Coarse roots	36	53.6	25.2	34.1	20.9	15.3	12.6	161.7	36	53.6	34.3	41.5	35.0	15.2	12.3	191.9
Total		192.1	48.1	90.9	251.4	36.8	44.1	663.4		172.6	53.1	90.0	279.3	33.9	36.6	665.5

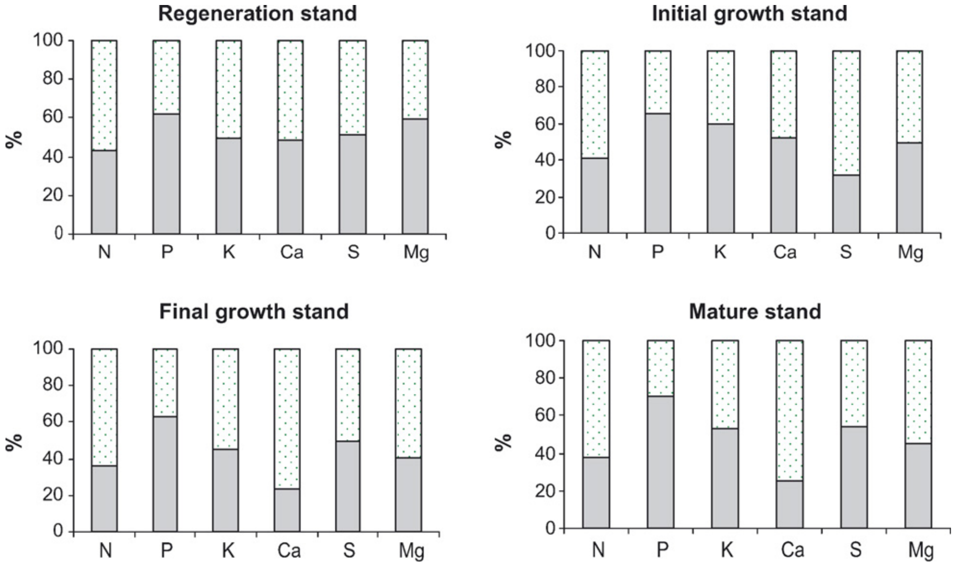

Fig. 1. Distribution of the nutrient amounts (%) at stand level in above (white) and belowground (grey) components for different growth phases.

Frangi (1992) reported that *Nothofagus pumilio* accumulated 498.2 Mg ha^{-1} of total biomass. The total biomass accumulated per hectare found in this work for *N. antarctica* growing in marginal sites was inferior to those presented by Peri et al. (2006) stands growing in middle site quality (dominant height 7.8 m) in Southern Patagonia estimated from individual trees equations (62 and 133.4 Mg ha^{-1} for regeneration and mature growth phase stands, respectively) and to those presented by Frangi et al. (2004) (247.6 Mg ha^{-1}) for mature stands growing in Tierra del Fuego province (Argentina). These differences are related to different site quality, where *N. antarctica* trees are able to accumulate more biomass in better conditions.

Also, the amount of total biomass per hectare had not important variations according to the stand age (Table 3). This is consistent with Caldentey (1992) who reported that the above ground biomass of *N. pumilio* accumulated over time varied between 305 and 370 Mg ha^{-1}. Thus, although regeneration stands are composed by small trees, they accumulate the same quantity of biomass per hectare due to a higher stand density compared with mature stands (Table 2).

The belowground components represented around 44–52% of the total biomass at all ages (mean root/shoot ratio of 0.9). This value is higher than those presented by Peri et al. (2006) for the same species but growing in a better site (root/shoot ratio of 0.5 for mature trees). The belowground biomass of *N. antarctica* were higher than others *Nothofagus* species. Richter and Frangi (1992) found a root/shoot ratio of 0.15 for mature *N. pumilio* stands, and Hart et al. (2003) reported a root/shoot ratio of 0.28 for mature *N. truncata*. All this information is concordant with Bloom et al. (1985) who explained that in less fertile sites, trees partition more carbon to the roots. Comparing with other *Nothofagus* species, *N. antarctica* presented less total biomass and more proportions of belowground biomass may be as strategy in (i) search of water and nutrients and/or (ii) to get a better support, because it grows mainly in drier, windier sites and with shallow soils than *N. pumilio*. According to this, Breman and Kessler (1995) cited numerous studies which indicate that in arid zone the root mass/aboveground biomass ratios are usually close to 0.4. As suggested by Chapin (1980) for plants in infertile habitats, high root/shoot ratio allows maximising nutrient uptake in reduced nutrient availability conditions.

Crown class also influenced in the amount of total, above- and belowground biomass accumulated. Dominant and codominant trees contributed in 78 and 82% to the total stand biomass for regeneration and mature class age, respectively (Table 3). Peri et al. (2006) also reported that individual dominant trees accumulated more biomass over time than the other crown classes (mean total biomass of 336 kg for dominant at 160 years and 47 kg for suppressed trees). The contribution of dominant and codominant trees to the belowground biomass was 65% for regeneration stands and increased up to 82% in mature stands. Similarly, Le Goff and Ottorini (2001) reported that the belowground biomass of *Fagus sylvatica* accumulated by dominant trees was 21 kg tree^{-1} and by suppressed trees was only 0.86 kg tree^{-1}.

4.2. Nutrient concentrations

In general, at any age, nutrient concentrations found in this work were lower from those presented by Peri et al. (2006) for the same species but growing at a better site quality. However, N and P in roots, Ca in sapwood, heartwood and middle roots of trees grown in a marginal site showed higher concentrations compared with those presented by Peri et al. (2006). Particularly, Mg had higher concentrations in almost all components in the marginal site of the present study (with the exception of small branches and coarse roots).

There was a difference in total nutrient concentration between components. In the present study the order of nutrient concentration was leaves > bark > middle roots > small branches > fine roots > sapwood > coarse roots > heartwood. The higher concentration in the fine roots component compared with coarse roots was consistent with Gordon and Jackson (2000) who reported a significant inverse relationship between root diameter and nutrient concentration for N, P and Mg based on a review data from 56 studies of trees. Also, there was a difference in the order of total nutrient concentration between components according to site classes. Peri et al. (2006) reported for the same species growing in a better site leaves > bark > small branches > fine roots > middle roots > coarse roots > sapwood > heartwood. Hart et al. (2003) working with mature stands of *N. truncata*, reported that the order of nutrient concentration was: leaves > small branches > mid-middle roots > coarse roots > bark > fine roots > stem. Similarly, Santa Regina (2000) reported that the above ground biomass of *Quercus pyrenaica*, the components which presented the highest concentrations were leaves > small branches > stem. In some cases, differences in tree nutrients concentration between class sites may be due to differences in soil fertility. Diehl et al. (2003) working with 10 native Andean-Patagonian species from different functional groups, found a significant positive correlation between N in mature leaves and soil N.

Different tendencies were found in nutrient concentrations according to the age. Some nutrients in components increased with age and others decreased. In contrast, Peri et al. (2006) reported that almost all nutrient concentrations decreased as age increased, as a consequence of an increment in cell wall components, e.g. carbonated structures (Lambers et al., 1998). Das and Chaturvedi (2005) and Laclau et al. (2000) working with *Populus deltoides* and *Eucalyptus*, respectively, also reported a systematic reduction in nutrient concentrations as age increases. In our study case, this ‘‘dilution effect’’ was not so evident because the trees biomass growth rate was slower compared with trees grown in better sites. Thus, at similar age our trees accumulated a 51.5% less biomass per hectare than trees growing in a middle site quality class (Peri et al., 2006). The only nutrient that presented a similar response in both studies was Ca, which increased as age increased in all cases. This macronutrient is the main nutrient in structural tissues and in the bark, being more important in mature trees. In contrast, young trees have less bark biomass with green stems with chlorophyll presence, as was cited by Damesin (2003) for *Fagus*.

In general, nutrient concentration also varied according to the class crown. Dominant tree presented higher N, K and Ca concentrations in leaves, and higher P, K and S concentrations in roots, compared with suppressed trees (Table 4). This is consistent with Peri et al. (2006) who reported that suppressed trees presented smaller concentrations than dominant trees for the majority of nutrients. This information is also consistent with Lambers et al. (1998), who reported that plants have greater concentrations of N, P and K when growth conditions becomes more favourable.

Resorption is a strategy of plants to conserve nutrients. Based on nutrients concentration of leaf litter data and the mean concentration values of green live leaves on trees (Table 4), the resorption found in the present work was 66, 20, 63, 14 and 50% for N, P, K, Mg and S, respectively. In contrast, there was no difference in Ca. This is consistent with Aerts (1996) who reported that nutrient resorption from foliage before senescence can reach values up to 50% (mainly N and P) of the maximum concentrations during a growing period. Similarly, Rapp et al. (1999) showed that there was a translocation of N, P and K from leaves of *Quercus* species to perennial tissues.

4.3. Nutrients amounts by hectare and distribution in components

Total nutrient amounts found in this work were lower than other values presented for other *Nothofagus* species (Table 5). Richter and Frangi (1992) reported greater quantities of all nutrients in mature *N. pumilio* (dominant height of 19 m) forests in Tierra del Fuego, Argentina: 1009 kg N ha^{-1}, 165 kg N ha^{-1}, 806 kg K ha^{-1} and 1235 kg Ca ha^{-1}. The site quality appears to have a strong effect on nutrients accumulation in *N. antarctica* stands. In a better site quality, Peri et al. (2006) reported for the same species higher quantities of all nutrients by hectare using models of individual trees (e.g. stand of 400 trees ha^{-1} at age 191 years 292.6 kg N ha^{-1}, 68.9 kg P ha^{-1}, 177.2 kg K ha^{-1}, 492.4 kg Ca ha^{-1}, 71.8 kg S ha^{-1} and 44.8 kg Mg ha^{-1}).

These differences could be determined by the combination of environmental factors that define the quality of a particular site such as soil fertility, soil depth, period of water stress, etc. The reduction in nutrient accumulation of *N. antarctica* stands grown in this marginal site compared with data reported by Peri et al. (2006) could be due to the available water acting as a main limiting factor during the growth period rather than soil nutrition which did not differ significantly between sites. The marginal site of the present study is located near the steppe in a windy environment with higher evapotranspiration rate which can reduce tree growth, nutrients uptake and nutrients concentration. Thus, soil water availability is an abiotic factor that mainly controls ecosystem processes such as carbon fixation, nutrient cycles, mineralization and uptake (Landsberg and Gower, 1997). Also, Frangi et al. (2005) working with *N. pumilio* forests growing along an altitudinal gradient in Tierra del Fuego, Argentina found that the total nutrient (K, Ca, Mg, N and P) stocks of mature erect stands grown in better site conditions decreased with elevation by reducing the rates of nutrient uptake and trees requirements.

Although there were no differences in biomass accumulated by hectare between stands at different age (Table 3), there were great differences in nutrient accumulation (Table 5). Young stands accumulated approximately 30% more nutrients than mature stands. This was because young stands presented a big proportion (65%) of the biomass distributed in fine components (leaves, small branches and fine and middle roots), which accounted with the highest nutrient concentrations. In contrast, in mature stands, fine components only represented the 11% of the total biomass, being the stems and coarse roots the components that accounted the majority of their biomass. Peri et al. (2006) also reported that in young stands the amounts of nutrients was greater than in mature stands with also a large proportion of biomass allocated in leaves, small branches and medium roots. In contrast, Ponette et al. (2001) showed there was no age pattern for any nutrient (N, K, P, Mg and Ca) contents in *Pseudotsuga menziesii* stands from 26 to 54 years of age.

The order of nutrient storage in this work ($Ca > N > K > P > Mg > S$) was consistent with those reported by Richter and Frangi (1992) for mature *N. pumilio* forests. However, Peri et al. (2006) found a little different order for mature *N. antarctica* growing in a better site quality class ($Ca > N > K > S > P > Mg$). Hart et al. (2003) working with *N. truncata* in New Zealand presented the following order: $Ca > K > N > P > Mg$. These differences may be related to site conditions, like differences in soil nutrient availability.

Nutrient distribution in *N. antarctica* was different according to the components. In mature stands, P was more abundant in roots, N and K in trunks (including bark). In contrast, while we found that P and K were more abundant in coarse roots, Hart et al. (2003) reported for hard beech that the largest amount of P (28%) and K (21%) was allocated in the stem wood.

The root/shoot nutrient ratios found in this work for mature stands ($N = 0.61$; $P = 2.4$; $K = 1.1$; $Ca = 0.34$; $S = 1.16$; $Mg = 0.84$) were higher than others presented for *Nothofagus* species. Hart et al. (2003) found lower root/shoot ratios in *N. truncata* for N (0.24), P (0.40), K (0.34), Ca (0.20) and Mg (0.40). Also, Richter and Frangi (1992) reported lower root/shoot ratios in *N. pumilio* for N (0.27), P (0.32), K (0.32), and Ca (0.24). This indicates that *N. antarctica* accumulates more belowground biomass and nutrients as an adaptation to infertile and dry sites. Therefore, a characteristic of *N. antarctica* is that it can grow in marginal sites compared with others *Nothofagus* species which occupies better sites. Furthermore, Peri et al. (2006) reported lower values of root/shoot ratio for mature *N. antarctica* developed in a better site (0.3, 1.4, 0.62, 0.3, 0.4 and 0.42 for N, P, K, Ca, S and Mg, respectively).

In our work, young stands had higher root/shoot ratios for some nutrients ($N = 0.77$, $Ca = 0.96$, $Mg = 1.5$) than mature stands. This is consistent with the results presented by Peri et al. (2006) who informed that root/shoot nutrient ratios decreased from its maximum value in regeneration stage to a steady state asymptote beyond 50 years of age. Thus, nutrient accumulation in roots was greater during the regeneration phase, and then aboveground accumulation of nutrients increased over time. Also their nutrient amounts in *N. antarctica* stands were affected by crown classes where suppressed trees accumulated less biomass and nutrients. Similar trend was reported for the same species grown in a better site class (Peri et al., 2006).

In conclusion, the biomass and nutrient accumulation in components of above- and belowground of *N. antarctica* stands found in the present work can assist to quantify the impact of different management strategies. For example, based on the nutrients requirements of *N. antarctica* trees grown in marginal sites at a final growth stage (80–100 years), the proportion of nutrients reabsorbed by trees, and the amount of nutrients returned from litterfall, a thinning intensity of 50% may not satisfy the demand for nutrients of the remaining trees. Therefore, to maintain the productivity of this particular ecosystem, it is necessary to remove less trees from the original structure. Also, thinning practices should aim to leave material (mainly leaves, small branches and bark) on the site to ameliorate nutrient removal and to avoid a decline of long-term yields.

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