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Dynamics of above- and below-ground biomass and nutrient accumulation in an age sequence of *Nothofagus antarctica* forest of Southern Patagonia

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Abstract

Nothofagus antarctica (Forster f.) Oersted is a deciduous tree species, which naturally grows on poorly drained or drier eastern sites in the Andes Mountain near Patagonian steppe. Above- and below-ground biomass and nutrients pools were measured in pure even-aged stands at different ages (5–220 years) and crown classes. Functions were fitted for total biomass and nutrients accumulation, and root/shoot ratio of individual trees against age. Total biomass accumulated for mature dominant trees was eight times greater than mature suppressed trees. Biomass root/shoot ratio decreased with age from 1.8 to a steady-state of 0.5. All nutrients concentration (except Ca) decreased with age and varied according to the degree of crown suppression classes. Nutrient concentrations varied between biomass pool components following the order leaves > bark > small branches > fine roots > medium roots > rooten wood > coarse roots > sapwood > heartwood. Total nutrient accumulation followed the order dominant > codominant > intermediate > suppressed trees and its accumulation rate varied over time, e.g. P accumulation rate of dominant trees increased from 0.17 g tree^{-1} year^{-1} during regeneration to 1.39 g tree^{-1} year^{-1} in mature trees. Nutrients uptake reached a peak during the period of maximum biomass production, and root/shoot ratio of nutrients decreased from its maximum value at 5 years of age (0.6, 4.0, 0.9, 1.5, 1.0 and 2.6 for N, P, K, Ca, S and Mg, respectively) to a steady-state asymptote beyond 50 years of age. Thus, accumulation of nutrients in roots was greater during the regeneration phase of stand development, and nutrient accumulation increased in above-ground over time. Also, nutrient use efficiency increased in mature trees (111–220 years) and decreased in suppressed crown classes. The equations developed for individual trees have been used to estimate stand biomass and nutrient accumulation from forest inventories data. Total stand biomass varied from 62.5 to 133.4 t ha^{-1} and total nutrients accumulation ranged from 3 kg Mg ha^{-1} to 1235 kg Ca ha^{-1}. Proposed equations can be used for practical purposes such as to estimate pasture nutrients requirement in a silvopastoral system based on nutrients supply from leaf litter returns, or to determine amelioration practices like debarking stems before harvesting.

Keywords: Silvopastoral system; Models; Nutrient use efficiency; Root/shoot ratio; Crown classes; Dry forest

1. Introduction

Deciduous *Nothofagus antarctica* (Forster f.) Oersted (ñire) is a native species with a wide spatial distribution in the southern areas of Argentina and Chile (36°30′ to 56°00′ SL). It grows on poorly drained or drier eastern sites in the Andes Mountain near Patagonian steppe, and ranges from near sea level in the southern part to 2000 m a.s.l. in the north Patagonia. In old-growth stands, it can reaches height of up to 15 m on the best sites as a well-formed tree and but only 2–3 m tall on rocky, xeric and exposed sites as a shrubby tree (Veblen et al., 1996). In Patagonia, *N. antarctica* forests have been used as silvopastoral systems where natural pastures grown under the tree canopy are grazed by cattle and sheep, and harvested wood products include poles, firewood and timber for rural construction purposes. There are ecological and economic interactions (positive and/or negative) between the woody, non-woody and animal components of these systems (Peri, 2005).

The productivity of a silvopastoral system is dependent on the balance between the positive effects (facultative) from canopy by transference of nutrients by litter fall, improvements of microclimatic conditions, and negative effects (competition)

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below-ground for water and/or nutrients or through crowns interference reducing the transmission of radiation to pasture species. The intensity and relative importance of these effects vary according to each physical and biological condition in a particular environment (Callaway and Walker, 1997). Vitousek and Sanford (1986) reported facility effects of nutrients in native deciduous ecosystems by the transfer of minerals from deeper horizons to the pasture through litter fall. Contrary, Clinton and Mead (1993) detected competition for nutrients between pastures and trees in a *Pinus radiata* silvopastoral system.

Data on biomass and nutrient accumulation in different tree components are essential to evaluate the importance and impact of management practices (silviculture, silvopastoral systems, harvesting) on site productivity, mineral fertility, bio-element recycling and long-term effects on the mineral balance (Santa Regina, 2000). It is important to emphasize that many researches only focus in above-ground biomass and nutrients (Caldentey, 1992; Santa Regina, 2000). However, fine roots turnover in forest system can contribute up to four times more nitrogen and up to 10 times more phosphorous than above-ground litter fall (Bowen, 1984). Investigations of below-ground part of plants is also necessary for quantifying carbon and nutrient sequestration in the under-ground woody structures, the current turnover of carbon and nutrients due to root decomposition, and characterising tree anchorage (Ranger and Gelhaye, 2001). Therefore, data is needed on the below-ground components of a forest.

There are few studies of above- and below-ground pools of biomass and nutrients in *Nothofagus* Patagonian forests (Caldentey, 1992; Richter and Frangi, 1992; Veblen et al., 1996) that provide an understanding about ecosystem functionality and the consequences of different disturbance and management (Hart et al., 2003), and there are no reports of above- and below-biomass and nutrient accumulation related to age and degree of canopy suppression. The aims of this study were to (1) quantify the amount and dynamic of biomass and nutrients in both above- and below-ground components for an age sequence and among crown classes for individual trees and stands of deciduous *N. antarctica* forests in Southern Patagonia and hence improve our understanding of those ecosystems in determining functional aspects such as species natural distributions along resource gradients and (2) derive functions for individual trees to predict total biomass and nutrients accumulation at a stand level.

2. Materials and methods

2.1. Study area

This study was conducted in three naturally pure stands of *N. antarctica* forest in the southern west of Santa Cruz province, Argentina (51°35′ SL, 72°14′ WL) corresponding to different growth phases distributed in an area of 400 km^2 and growing at site quality IV (Lencinas et al., 2002) where total height of mature trees reached 7.8 m. The regeneration stand (5–20 years) averaged 2.2 m height, 16,500 trees ha^{-1} and 42 m^2 ha^{-1} basal area; the young stand (21–110 years) averaged 5.6 m height, 1720 trees ha^{-1} and 38 m^2 ha^{-1} basal area; mature stand (111–220 years) averaged 7.7 m height, 420 trees ha^{-1} and 36 m^2 ha^{-1} basal area. Climate is cold temperate and subhumid with a mean annual temperature of 6.5 °C and a long-term annual rainfall of 300 mm. Soils were classified as Molisols. Thirty bulked soil sample cores from the three stands to three different depths (1–5, 5–30 and 30–60 cm) corresponding to root distribution were taken at random (Table 1).

Table 1
Soil properties in sampled *N. antarctica* forest

	Organic horizon	Mineral horizon I	Mineral horizon II
Depth (cm)	1–5	5–30	30–60
Clay (%)	–	20	20
Silt (%)	–	30	60
Sand (%)	–	50	20
pH	6.1	4.8	4.8
Resistance (Ω cm)	4170	8800	5810
N total (ppm)	8670	880	460
P truog (ppm)	129	12	6
K (cmol$^{(+)}$ kg^{-1})	4.2	0.3	0.1
Mg (cmol$^{(+)}$ kg^{-1})	10.6	4.2	8.0
Ca (cmol$^{(+)}$ kg^{-1})	52.4	11.3	20.7

2.2. Biomass determination

Eighty-four trees of different age classes corresponding to different stands growth phases (regeneration, 5–20 years; young, 21–110 years; mature: 111–220 years) were selected. Within each age class, seven trees of each crown class (dominant, codominant, intermediate and suppressed) were sampled. 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) and coarse branches (>10 mm) with bark; stem components including sapwood, heartwood and bark; roots with bark classified as fine (diameter < 2 mm), medium (<30 mm) or coarse (>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, bark and rotten wood) to determinate density for biomass calculations. All small branches, leaves and dead branches from each sampled tree were separated and weighed fresh. Roots from individual trees were excavated to a depth of 0.6 m (maximum rooting depth for all crown classes) in circular plots centred on the stump of selected tress. These roots were sorted in diameter class and weighed in fresh. Sub-samples were taken for oven drying to estimate biomass and for nutrient analysis.

2.3. Chemical sample analysis

Samples from the three 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) content was determined using the Kjeldahl technique. Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S) concentrations were determined with a plasma emission spectrometer (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 mass of each biomass component (dry weight measurements). Age of each sample tree was obtained trough counting rings at the stump (0.3 m from soil level). Nutrient accumulation was divided by tree age to establish the average annual rate at which nutrients were taken up by trees. Nutrient use efficiency (NUE) was calculated as a ratio between total net productivity and nutrient uptake for two contrasting crown classes (dominant and suppressed tress) at the three growth phases. This ratio measures the efficiency of nutrient use in relation to biomass productivity calculated on an annual basis from the fitted total biomass functions.

Total biomass, nutrient accumulation, and root/shoot ratio functions were fitted using non-linear regression analysis. Different sigmoid functions (Chapman-Richard, Logistic, Weibull, Gompertz, Hill and Schumacher) were compared to fit total biomass and nutrients accumulation against age and crown suppression classes. For root/shoot ratio data, exponential decay functions were fitted against age. Comparisons of main factors (age and crown classes) were carried out by analyses of variance with the F-test. Significantly different averages were separated with standard error of means to evaluate least significant differences (LSD). All test were evaluated at $p < 0.05$. Statistical analyses were carried out by using the Genstat statistical package (Genstat 5-v.1997).

3. Results

3.1. Total biomass accumulation

Logistic function (Eq. (1)) with three parameters was used to estimate total biomass accumulation. The parameters for each crown class are given in Appendix A

$$Y = \frac{a}{1 + (x/b)^c} \qquad (1)$$

where Y is the biomass of individual trees (kg), x the age (years) and a, b, c are the estimated parameters.

Relationships between *N. antarctica* total biomass and age for different crown classes is presented in Fig. 1a, where dominant trees accumulated more biomass over time than the others, e.g. mean total biomass at 160 years was 336 kg for dominant, 255 kg for codominant, 156 kg for intermediate and 47 kg for suppressed trees. At 30 years these differences were 6.8, 5.1, 3.1 and 0.7 kg for dominant, codominant, intermediate and suppressed trees, respectively. Biomass accumulation rate against age for different crown classes is shown in Fig. 1b. In each case, the rate of biomass accumulation showed a parabolic

Fig. 1. (a) Total biomass accumulation, (b) biomass accumulation rate for dominant (●) codominant (○), intermediate (▼), and suppressed (△) crown classes, and (c) the biomass root/shoot ratio against age of individual *N. antarctica* trees grown in Southern Patagonia, Argentina.

relationship with tree age and increased to reach a maximum and then declined as age increased further (Fig. 1). Changes in crown classes affected the maximum value and shape of this response, e.g. maximum accumulation rate for dominant trees were 2.2 kg tree^{-1} year^{-1} at 120 years and then declined to 1.7 kg tree^{-1} year^{-1} at 220 years. In contrast, maximum accumulation rate for suppressed trees was 0.3 kg tree^{-1} year^{-1} at 140 years.

3.2. Above- and below-ground biomass ratio

An exponential decay function (Eq. (2)) with three parameters fitted the root/shoot ratio data better than others functions (data not shown). There were no significant difference in the slope of the relationship between the biomass root/shoot ratio and age for different crown classes, and then a single function was used. The parameters for each crown class are given in Appendix B

$$Y = a + b\,\mathrm{e}^{-cx} \tag{2}$$

where Y is the root/shoot ratio of individual trees (dimensionless), x the age (years), e the base of natural logarithms and a, b, c are the estimated parameters.

Root/shoot ratio biomass decreased from 1.8 at 5 years to a steady-state asymptote of 0.5 beyond 50 years of age (Fig. 1c). Thus, while roots biomass was greater during the regeneration phase, the above-ground biomass of mature trees represented nearly 68% of the total biomass.

3.3. Nutrients concentration in the tree components

Nutrients concentration in each biomass pool component showed significant differences according to age classes, except for K, which did not show differences in sapwood, heartwood and rotten wood (Table 2). Nutrient concentrations in the rotten wood components did not differ between trees of different age and crown classes ($p > 0.05$). All nutrient concentration decreased with age, except Ca which increased in concentration over time, e.g. nutrient concentration in leaves (% of dry matter) for young and mature trees were: N, 2.38 versus 2.04; P, 0.26 versus 0.21; K, 0.84 versus 0.65; Ca, 0.67 versus 0.71; Mg, 0.23 versus 0.20; S, 0.27 versus 0.22; respectively. Nutrient concentration also varied according to the degree of crown suppression (Table 2). For N, P, Mg and S, the concentration in all pool components decreased from dominant to suppressed trees. However, Ca showed an opposite trend being greater in suppressed trees, whereas K showed a differential response according to each component (Table 2).

Nutrient concentrations significantly varied between biomass pool components. Total nutrient concentration generally graded in the following order: leaves > bark > small branches > fine roots > medium roots > rotten wood > coarse roots > sapwood > heartwood. However, each nutrient concentration varied depending on a particular component (Table 2), e.g. Ca concentration was greater in the bark component and mean nutrients concentrations in roots followed the order fine > medium > coarse.

3.4. Total nutrient accumulation in above- and below-ground components

Logistic function (Eq. (1)) with three parameters fitted the data better than others sigmoid functions for total nutrients accumulation of individual trees (data not shown). Parameters for each crown class are given in the Appendix A.

Total accumulation of N, P, K, Ca, Mg and S for the four crown classes are presented in Fig. 2. Total nutrient accumulation over time followed the order: dominant > codominant > intermediate > suppressed trees, e.g. differences between dominant and suppressed trees at 150 years were: N, 949 g tree^{-1} versus 120 g tree^{-1}; P, 204 g tree^{-1} versus 34 g tree^{-1}; K, 577 g tree^{-1} versus 89 g tree^{-1}; Ca, 1329 g tree^{-1} versus 259 g tree^{-1}; Mg, 138 g tree^{-1} versus 23 g tree^{-1}; S, 217 g tree^{-1} versus 32 g tree^{-1}; respectively. Storage of any particular nutrient varied depending mainly on age and in some cases on crown class. In mature trees, nutrient storage for dominant, codominant and intermediate trees was in the order Ca > N > K > S > P > Mg (Fig. 2), while mature suppressed trees stored more P than S. For the regeneration phase, this order of nutrient storage changed according to the crown class: for dominant trees was P > N > Ca > K > S > Mg; for codominant trees was N > P > Ca > K > S > Mg; for intermediate and suppressed trees it was in the order N > Ca > K > P > S > Mg (Fig. 2).

Nutrients accumulation rate against age for different crown classes is shown in Fig. 3. Nutrient accumulation rate against age showed a parabolic relationship, which increased to reach a maximum and then declined as age increased further. In general, nutrients uptake reached a peak about the period of maximum biomass production. The degree of crown suppression classes affected the maximum value and shape of this response. For example, maximum rates of nutrient accumulation for dominant trees were: 8.9 g Ca tree^{-1} year^{-1} at 157 years; 6.4 g N tree^{-1} year^{-1} at 133 years; 4.1 g K tree^{-1} year^{-1} at 117 years; 1.5 g S tree^{-1} year^{-1} at 138 years; 1.4 g P tree^{-1} year^{-1} at 123 years; 1.0 g Mg tree^{-1} year^{-1} at 115 years. For suppressed trees: 1.8 g Ca tree^{-1} year^{-1} at age 160 years; 0.8 g N tree^{-1} year^{-1} at 160 years; 0.6 g K tree^{-1} year^{-1} at 137 years; 0.2 g S tree^{-1} year^{-1} at 151 years; 0.2 g P tree^{-1} year^{-1} at 160 years; 0.2 g Mg tree^{-1} year^{-1} at 113 years.

3.5. Above- and below-ground nutrients ratio

The exponential decay function (Eq. (2)) with three parameters fitted the root/shoot ratio data better than other functions (data not shown). A single function was used for nutrients, because there were no significant differences in the slope of the relationship between nutrients root/shoot ratio and age for different crown classes. The parameters for each crown class are given in Appendix B. Nutrients root/shoot ratio decreased from its maximum value at 5 years of age (0.6, 4.0, 0.9, 1.5, 1.0 and 2.6 for N, P, K, Ca, S and Mg, respectively) to a steady-state asymptote up to 50 years of age (Fig. 4). Thus, root nutrient accumulation was greater during the regeneration

Table 2
Mean nutrient concentration in components of *N. antarctica* (data expressed as a percentage of dry matter)

	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
							<2 mm	<30 mm	>30 mm
N									
Age class									
5–20 years	2.380	0.626	0.257	–	0.518	–	0.339	0.275	0.217
21–110 years	2.310	0.537	0.227	0.200	0.313	0.262	0.224	0.263	0.193
111–220 years	2.040	0.564	0.166	0.142	0.270	0.254	0.259	0.212	0.144
Crown class									
Dominant	2.480	0.611	0.289	0.210	0.308	0.268	0.335	0.288	0.227
Codominant	2.290	0.604	0.180	0.190	0.256	0.254	0.283	0.275	0.214
Intermediate	2.270	0.585	0.186	0.146	0.260	0.249	0.275	0.237	0.174
Suppressed	2.070	0.548	0.176	0.137	0.244	0.257	0.202	0.199	0.127
Age class effect	**	**	**	**	**	ns	**	**	**
Crown class effect	**	**	**	**	**	ns	**	**	**
Interaction	ns	*	ns	ns	*	ns	ns	ns	ns
P									
Age class									
5–20 years	0.261	0.116	0.063	–	0.066	–	0.189	0.236	0.126
21–110 years	0.236	0.084	0.035	0.005	0.031	0.045	0.168	0.196	0.113
111–220 years	0.215	0.083	0.010	0.011	0.025	0.041	0.125	0.155	0.100
Crown class									
Dominant	0.252	0.102	0.052	0.019	0.061	0.045	0.197	0.238	0.141
Codominant	0.239	0.102	0.042	0.015	0.044	0.039	0.185	0.200	0.115
Intermediate	0.232	0.097	0.035	0.006	0.032	0.044	0.147	0.195	0.105
Suppressed	0.216	0.087	0.022	0.007	0.022	0.042	0.113	0.152	0.091
Age class effect	**	**	**	**	**	ns	**	**	*
Crown class effect	**	**	**	**	**	ns	**	**	**
Interaction	ns	*	ns	ns	**	ns	ns	ns	ns
K									
Age class									
5–20 years	0.841	0.438	0.142	–	0.394	–	0.505	0.502	0.229
21–110 years	0.823	0.394	0.141	0.005	0.328	0.360	0.349	0.433	0.214
111–220 years	0.651	0.351	0.131	0.005	0.229	0.380	0.291	0.364	0.161
Crown class									
Dominant	0.715	0.41	0.164	0.006	0.197	0.390	0.506	0.511	0.245
Codominant	0.717	0.377	0.143	0.005	0.167	0.345	0.405	0.475	0.217
Intermediate	0.782	0.414	0.125	0.005	0.241	0.385	0.330	0.398	0.196
Suppressed	0.818	0.391	0.148	0.005	0.295	0.358	0.288	0.349	0.144
Age class effect	**	**	ns	ns	**	ns	**	**	**
Crown class effect	**	*	*	ns	**	ns	**	**	**
Interaction	*	ns	ns	ns	*	ns	ns	ns	ns
Ca									
Age class									
5–20 years	0.666	0.676	0.061	–	1.227	–	0.789	0.681	0.068
21–110 years	0.645	1.069	0.069	0.055	1.303	0.546	0.866	0.595	0.095
111–220 years	0.712	1.389	0.108	0.073	2.641	0.525	0.892	1.309	0.123
Crown class									
Dominant	0.593	0.952	0.076	0.041	2.048	0.551	0.742	0.752	0.062
Codominant	0.621	0.951	0.051	0.039	2.689	0.502	0.856	0.862	0.085
Intermediate	0.715	1.036	0.080	0.073	2.950	0.504	0.884	0.898	0.102
Suppressed	0.720	1.046	0.106	0.102	2.624	0.586	0.914	0.936	0.132
Age class effect	*	**	**	**	**	ns	**	**	**
Crown class effect	**	**	**	**	**	*	**	**	**
Interaction	ns	ns	ns	ns	*	ns	ns	ns	ns
Mg									
Age class									
5–20 years	0.226	0.120	0.033	–	0.079	–	0.295	0.143	0.040
21–110 years	0.195	0.124	0.033	0.024	0.076	0.079	0.192	0.125	0.039

Table 2 (*Continued*)

	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
							<2 mm	<30 mm	>30 mm
111–220 years	0.196	0.080	0.017	0.010	0.074	0.083	0.207	0.107	0.031
Crown class									
Dominant	0.225	0.121	0.036	0.023	0.082	0.084	0.332	0.152	0.047
Codominant	0.197	0.114	0.033	0.022	0.075	0.080	0.214	0.141	0.041
Intermediate	0.190	0.107	0.029	0.017	0.063	0.079	0.192	0.113	0.032
Suppressed	0.205	0.097	0.024	0.013	0.059	0.081	0.185	0.095	0.026
Age class effect	**	**	**	**	**	ns	**	**	**
Crown class effect	**	**	**	*	**	ns	**	**	**
Interaction	*	ns	ns	ns	*	ns	ns	ns	ns
S									
Age class									
5–20 years	0.269	0.127	0.060	–	0.106	–	0.118	0.096	0.094
21–110 years	0.211	0.117	0.058	0.044	0.097	0.098	0.103	0.092	0.062
111–220 years	0.219	0.101	0.045	0.044	0.104	0.092	0.105	0.056	0.062
Crown class									
Dominant	0.233	0.120	0.062	0.043	0.115	0.096	0.125	0.101	0.098
Codominant	0.223	0.117	0.055	0.042	0.086	0.094	0.112	0.084	0.072
Intermediate	0.255	0.116	0.058	0.045	0.109	0.092	0.102	0.072	0.064
Suppressed	0.224	0.108	0.060	0.045	0.105	0.096	0.096	0.068	0.057
Age class effect	*	*	**	ns	*	ns	*	**	**
Crown class effect	*	*	**	ns	*	ns	*	**	**
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns, non-significative; *$p < 0.05$; **$p < 0.01$.

phase, and then the above-ground nutrient accumulation of young and mature trees increased over time.

3.6. Nutrient use efficiency

Nutrient use efficiency for the two main contrasting crown classes sorted by the three growth phases is presented in Fig. 5. The mean NUE significantly increased at mature trees and was greater in the dominant trees compared with the suppressed ones (Fig. 5). However, there was a differential NUE response according to age and crown classes for each particular nutrient (Fig. 5).

3.7. Nutrient allocation in tree components

Significant differences were found in nutrient distribution between components (Table 3), e.g. mature dominant trees allocated more N, S and Mg mainly in sapwood (35.9%, 26.0% and 19.0%, respectively), more P and K in coarse roots (49% and 31%, respectively), and more Ca in bark (52%). Nutrients allocation varied significantly according to the age, e.g. nutrient allocation for dominant trees in regeneration phase was: N mainly in leaves (28%) and P, Mg, Ca, S and K in middle roots (69%, 57%, 53%, 30% and 29%, respectively) (Table 3). In general, while there was a significant difference in nutrients allocation for all nutrients between crown classes in leaves, small branches, sapwood and heartwood components, there were no significant differences in nutrient allocation to bark biomass (except Ca), rotten wood and roots components (Table 3).

3.8. Equations to predict biomass and nutrients accumulation at stand level

The logistic function with three parameters (Eq. (1)) for total nutrients accumulation by individual trees was used to estimate the nutrient accumulation at stand level. To incorporate the effect of age, crown class and stocking variables, forests inventory data of different stands growing at a site quality IV in South Patagonia (51°62′ SL, 72°22′ WL) were used. Table 4 shows the amount of nutrients for five stands at different ages, stockings, crown class proportions and forest uses (primary forests and silvopastoral systems). In silvopastoral systems, stocking was reduced by thinning of codominants, intermediates and suppressed trees to enhance pasture growth underneath.

Total biomass accumulated was 109 and 133 t ha^{-1} for stands ages of 191 and 100 years, respectively. Nutrient accumulation in both primary forest stands was in the following order: Ca > N > K > S > P > Mg. However, the amount of nutrients (except Ca) was greater in the 100 years old stand compared to old stand of 191 years. The average accumulation rate was greater in the 191 years old stand (1.5, 0.4, 0.9, 2.6, 0.4 and 0.2 kg ha^{-1} year^{-1} for N, P, K, Ca, S and Mg, respectively) than in the 100 years old stand (3.4, 0.9, 2.4, 4.4, 0.9 and 0.6 kg ha^{-1} year^{-1} for N, P, K, Ca, S and Mg, respectively). A young primary forest stand (30 years) with a total biomass of 68.4 t ha^{-1}, the order of nutrient accumulation was: N > Ca > P > K > S > Mg, and the nutrient accumulation rates were: 6.8, 3.1, 4.0, 5.8, 1.5 and 0.8 kg ha^{-1} year^{-1} for N, P, K, Ca, S and Mg, respectively.

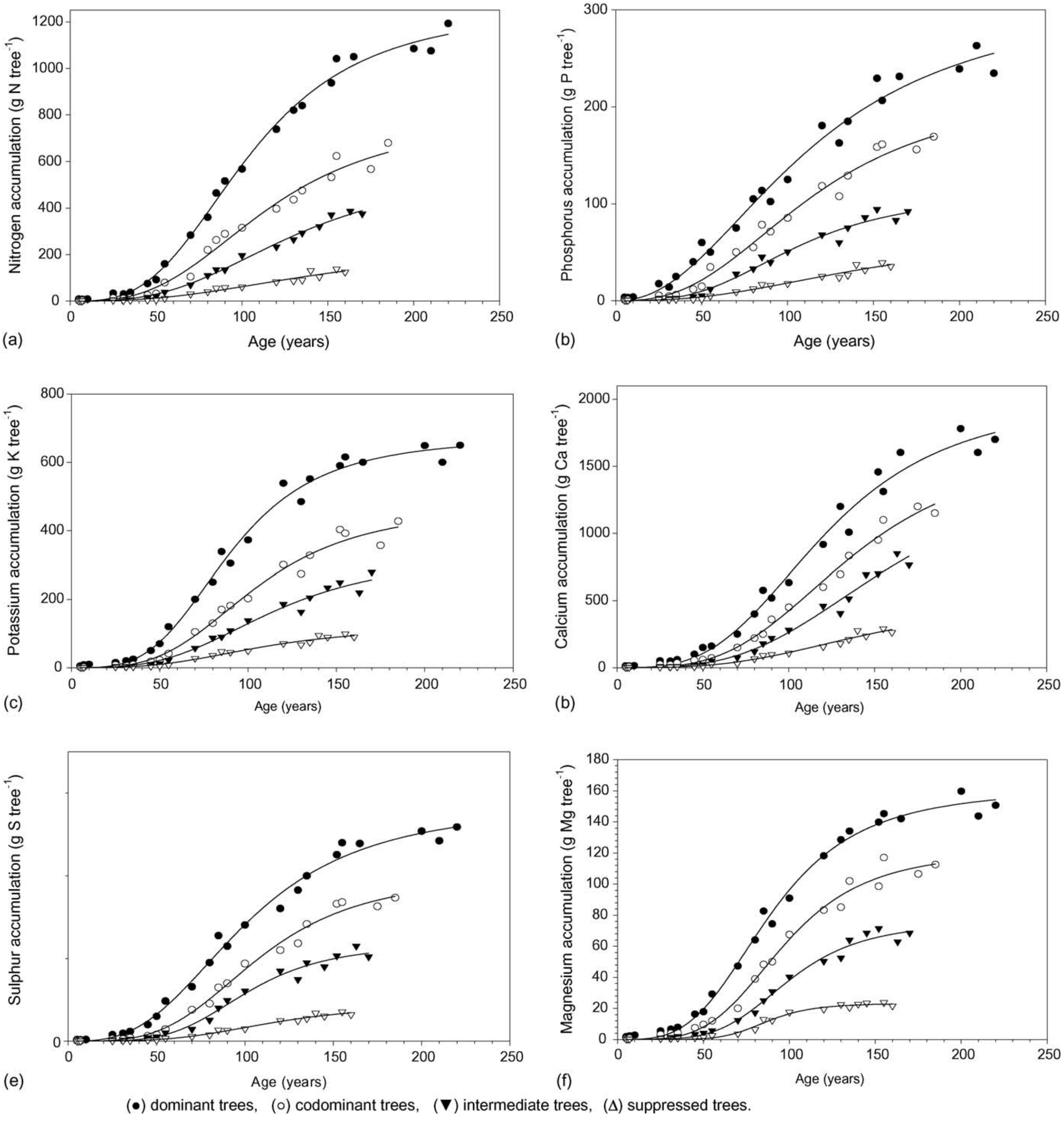

Fig. 2. Total nutrients accumulation (g tree^{-1}) against age for different crown classes of *N. antarctica* growing at site class IV, Patagonia. (a) Nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) sulphur and (f) magnesium. (●) Dominant trees, (○) codominant trees, (▼) intermediate trees and (△) suppressed trees.

The silvopastoral systems have less biomass than the primary forest stands at similar age, due to thinning. Total biomass of a stand at 196 years was 62.5 and 87.5 t ha^{-1} for a stand of 104 years, representing 57% and 65% of the biomass of the primary forests without silvicultural interventions. As a consequence, the quantity of nutrients retained by the trees on the stands was reduced. However, the order of nutrient accumulation was equal to those described for the primary forests.

4. Discussion

4.1. Biomass and root/shoot ratio

Total biomass accumulation for individual trees of *N. antarctica* found in this work was affected by age and degree of canopy suppression. Total biomass accumulated for mature dominant trees was eight times greater than mature suppressed trees. The individual total biomass accumulation function was

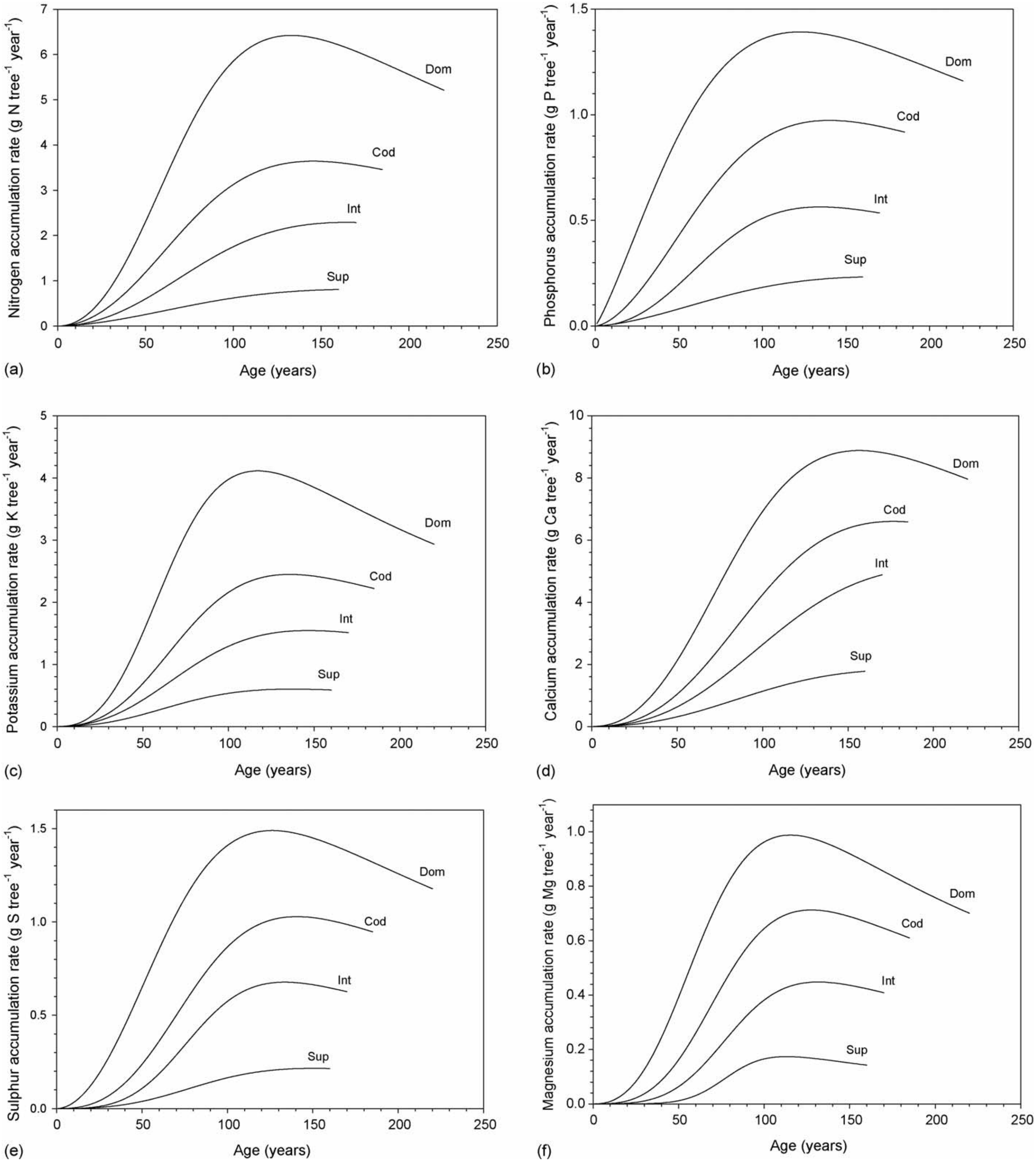

Fig. 3. Nutrients accumulation rates (g tree^{-1} year^{-1}) for *N. antarctica* trees against age sorted by four crown classes. (a) Nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) sulphur and (f) magnesium.

empirically derived and summarised into easily transferable coefficients using a non-linear regression. Also, biomass root/shoot ratio of individual *N. antarctica* trees decreased with age. The above-ground biomass for *N. antarctica* was lower than values reported by Richter and Frangi (1992) for mature *Nothofagus pumilio* forest (87% of the total biomass with a root/shoot ratio of 0.15) and Hart et al. (2003) for an even-aged *Nothofagus truncata* old growth forest (78% of the total biomass with a root/shoot ratio of 0.28). It is possible that *N. antarctica* has more root biomass to ensure establishment at early growth

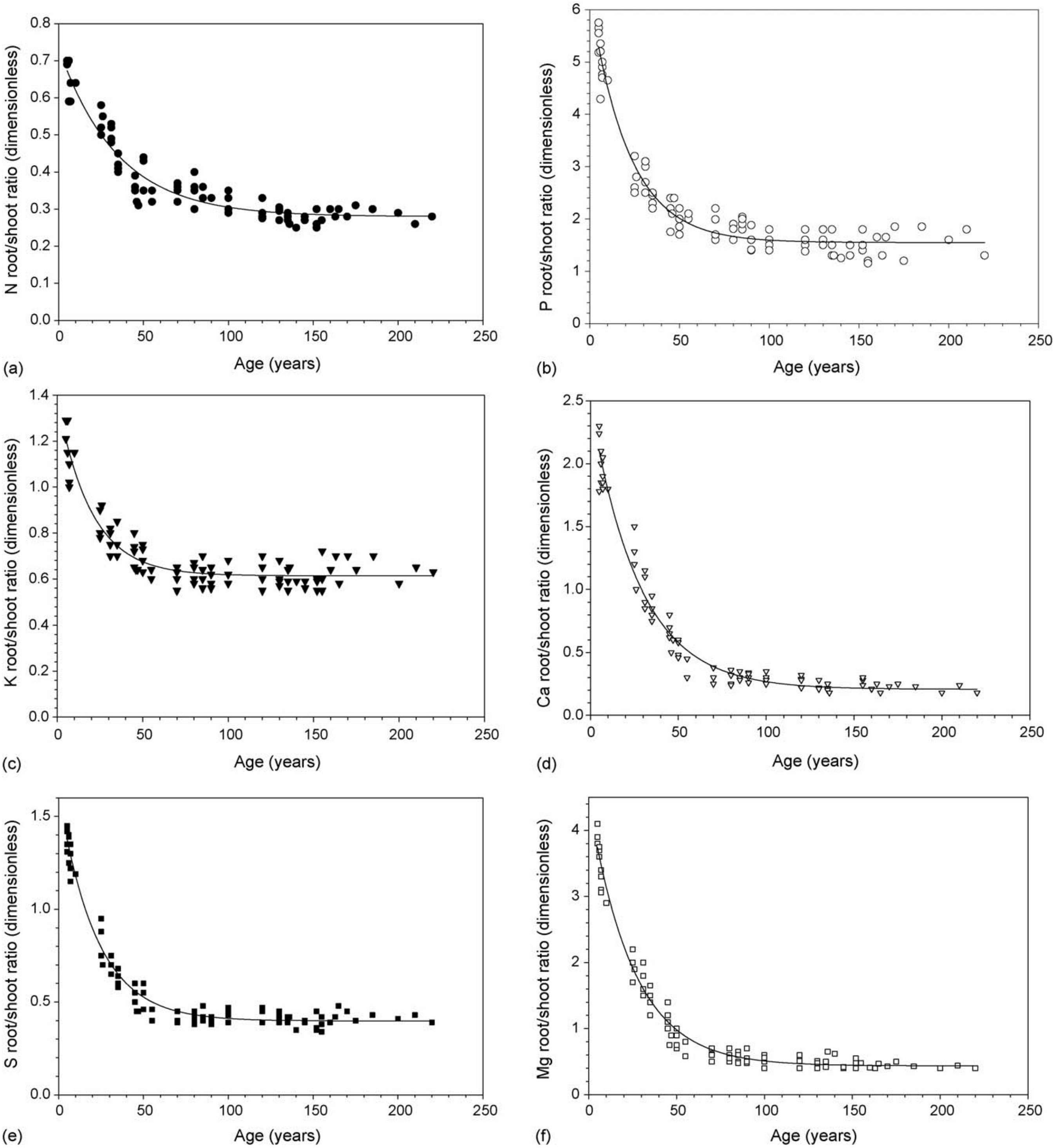

Fig. 4. Root/shoot ratio of six nutrients for *N. antarctica* trees against age. (a) Nitrogen, (b) phosphorus, (c) potassium, (d) calcium, (e) sulphur and (f) magnesium.

phases to improve water and nutrient uptake, and/or to obtain a better support in dry and windy sites with shallow soils, compared to other *Nothofagus* species. Based on cost-benefit analyses Tilman (1985) suggested that this root/shoot allocation trend may play an important role in differential adaptation to resources gradients. This is consistent with Breman and Kessler (1995), who cited many studies which indicated that, in arid zones, root/shoot biomass ratios are usually close to 0.4 or higher; and with Chapin (1980) who reported that a high root/shoot ratio allowed plants to maximise nutrient uptake in infertile habitats with reduced nutrient availability.

4.2. Nutrient concentrations

In all components of *N. antarctica* trees, nutrient concentrations decrease as age increased. There is a continued

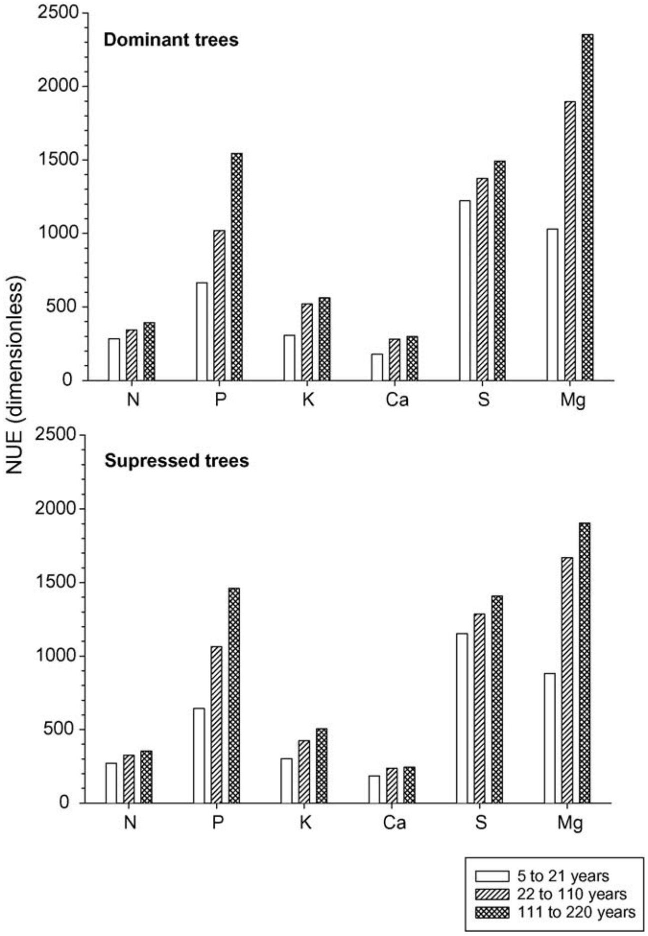

Fig. 5. Nutrient use efficiency for two main contrasting crown classes (dominant and suppressed trees) sorted by the three growth phases of individual *N. antarctica* trees.

reduction in tissue nutrient concentration (dilution effect) as trees become older by increasing the proportion of cell wall components, e.g. carbonated structures (Lambers et al., 1998) or a reduction in nutrient availability (Lusk et al., 1997). This agrees with Das and Chaturvedi (2005) who reported a decrease in nutrient concentration with plantation age for each component of *Populus deltoides*. However, Ca was the only nutrient that increased in concentration with age. This macroelement is the main nutrient in structural tissues and in the bark, and these components becomes 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*. There are no reports of nutrient concentrations in relation to the degree of crown suppression, and in this study all nutrients showed changes with increasing levels of crown suppression. These changes are consistent with Lambers et al. (1998) who reported that plants have greater concentrations of N, P, and K when growth conditions become more favourable. Suppressed *N. antarctica* tress had lower growth rate and smaller root systems (less root biomass), and this could correspond with lower nutrient uptake, resulting in a reduction in tissue nutrient concentrations. In contrast, dominant trees with a larger crown and root system may be able to greatly increase their nutrient absorption. Again, Ca concentration showed a different response and decreased from suppressed to dominant trees. Suppressed trees, with lower growth rates and nutrient uptake, take more Ca at the expense of other nutrients by changing allocation to structural tissues.

Tissues had different nutrient concentrations in *N. antarctica*. Leaves, barks, small branches and fine roots have the highest nutrient concentrations. Leaves have greater concentrations associated with metabolism (N, P, K) and lower concentrations of Ca than woody stems. Similar orders of nutrient concentrations were reported by Caldentey et al. (1993) for aerial biomass in an old growth *N. pumilio* stand (leaves > small branches > bark > stem) and Hart et al. (2003) in a mature *N. truncata* forest (leaves > twigs > medium roots > coarse roots > bark > fine roots > stem). Diehl et al. (2003), working only with leaves of different mature species, showed similar concentrations of N, K, and P for *N. antarctica* but greater values for *N. pumilio* compared with the presented results. Many of these differences between species could be due to soil fertility changes where the species grow. Romanya et al. (2005) reported that *N. pumilio* grows in soils with greater soil fertility and consequently greater nutrient content in leaves, compared with others *Nothofagus* species. In addition, the distribution of nutrient concentrations in biomass components founded in this work were consistent with data reported by Hart et al. (2003) and Caldentey et al. (1993): N and K were more abundant in leaves, Ca in bark and Mg in fine roots and leaves. Finally, P in both investigations was more abundant in leaves and roots, but we found more P concentration in middle roots and Hart et al. (2003) reported more P in fine roots. This distribution is closely related to the physiological functions of each element in a particular component. Although the distribution in components was similar with the authors mentioned above, the absolute values of nutrient concentration were different. Hart et al. (2003) reported lower N, P and Mg concentrations in leaves (1.2%, 0.1% and 0.1%, respectively), lower Ca (1.0%) and higher N (0.7%) concentrations in small branches, and lower concentration of all root nutrients. These differences on nutrient concentrations could be due to differences between site quality stands and/or nutrient use efficiency between species. Also, the greater nutrients concentration found in the present work for *N. antarctica* may respond to its slower growth rate compared with other fastest-growing *Nothofagus* spp. trees attaining high rates of carbon assimilation in more suitable sites. This agrees with Chapin (1980) who suggested that slow growth and accumulation of nutrient reserves by luxury consumption are common traits of native plants to poor soils.

4.3. Total nutrients accumulation and allocation in tree components

Nutrients accumulation of *N. antarctica* individual trees was affected by age and crown classes. Nutrients accumulation functions were empirically derived and summarised into easily transferable coefficients using a non-linear regression. The greater nutrient accumulation of dominant trees at any age

Table 3
Nutrients allocation in components of *N. antarctica* trees (data was expressed as percentage of biomass)

	Crown class	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
								<2 mm	<30 mm	>30 mm
N (%)										
Age classes										
111–220 years	D	14.3	9.1	35.9	10.8	8.2	0.3	0.4	4.4	16.6
	C	8.0	4.6	15.4	28.5	15.3	1.4	0.5	5.4	20.9
	I	13.2	7.0	16.9	21.5	14.1	2.1	0.5	5.1	19.6
	S	16.6	7.8	20.5	18.4	11.0	1.9	0.5	4.8	18.5
21–110 years	D	34.3	14.6	30.2	0.6	6.0	0.003	0.8	6.3	7.2
	C	19.6	8.3	28.4	9.4	11.6	0.0	1.3	9.9	11.5
	I	28.8	16.2	18.4	4.0	11.8	0.0	1.2	9.1	10.5
	S	12.8	14.7	26.3	4.9	17.0	0.0	1.4	10.6	12.3
5–21 years	D	27.7	20.6	5.8	0.0	5.2	0.0	3.6	26.3	10.8
	C	27.4	17.3	5.6	2.1	6.3	0.0	3.7	26.7	10.9
	I	31.5	21.0	4.9	0.0	5.6	0.0	3.3	23.9	9.8
	S	23.8	23.8	6.1	0.0	7.3	0.0	3.5	25.2	10.3
Age class effect		*	**	**	**	*	*	*	**	**
Crown class effect		*	*	*	*	ns	ns	ns	ns	*
P (%)										
Age classes										
111–220 years	D	9.0	7.6	15.6	1.6	3.3	0.6	1.3	11.7	49.3
	C	3.3	2.7	19.5	4.8	2.5	0.9	1.5	12.4	52.4
	I	6.0	5.3	14.4	3.1	5.0	1.3	1.5	12.1	51.3
	S	5.4	9.1	17.4	6.4	7.1	1.1	1.2	10.0	42.3
21–110 years	D	19.8	13.1	3.9	0.1	3.9	0.003	2.3	25.0	31.9
	C	7.3	41.9	4.6	0.6	9.4	0.0	1.4	15.3	19.5
	I	9.3	8.1	15.2	0.5	4.8	0.0	2.4	26.3	33.4
	S	7.2	5.6	21.7	0.5	5.6	0.0	2.3	25.0	32.1
5–21 years	D	5.7	7.0	0.7	0.0	1.6	0.0	4.7	68.7	11.6
	C	7.4	5.9	0.9	0.1	1.8	0.0	4.7	67.7	11.5
	I	8.6	8.8	0.5	0.0	1.7	0.0	4.5	64.9	11.0
	S	5.8	8.7	0.6	0.0	2.2	0.0	4.6	66.8	11.3
Age class effect		*	**	**	**	*	*	*	*	**
Crown class effect		*	**	*	*	ns	ns	ns	ns	ns
K (%)										
Age classes										
111–220 years	D	9.5	11.3	22.5	0.7	13.3	0.9	0.8	10.1	30.9
	C	4.6	5.3	19.1	1.0	19.3	1.2	1.0	11.9	36.6
	I	7.2	7.5	15.6	0.9	22.5	1.7	0.9	10.7	33.0
	S	6.7	10.7	21.2	0.5	20.8	1.5	0.8	9.3	28.5
21–110 years	D	18.9	16.6	21.2	0.0	11.6	0.003	2.0	17.4	12.3
	C	8.8	6.8	21.6	0.4	15.8	0.0	3.0	25.5	18.1
	I	10.5	12.9	23.1	0.2	14.6	0.0	2.5	21.2	15.0
	S	9.1	9.2	24.4	0.2	18.0	0.0	2.5	21.4	15.2
5–21 years	D	12.4	19.0	7.2	0.0	6.6	0.0	8.5	29.2	17.1
	C	10.9	16.6	8.9	0.1	7.3	0.0	8.7	30.0	17.5
	I	16.2	22.9	3.9	0.0	6.5	0.0	7.8	26.9	15.8
	S	13.4	22.7	5.9	0.0	7.9	0.0	7.8	26.7	15.6
Age class effect		*	**	**	*	**	*	*	*	*
Crown class effect		*	*	*	*	ns	ns	ns	*	ns
Ca (%)										
Age classes										
111–220 years	D	3.6	13.9	5.8	1.2	52.3	1.0	0.9	13.2	8.1
	C	0.7	3.6	3.6	25.2	48.7	1.1	0.7	10.2	6.2
	I	1.2	6.5	2.7	4.2	64.8	1.9	0.8	11.1	6.8
	S	2.0	12.3	2.6	4.9	57.2	1.9	0.8	11.3	7.0
21–110 years	D	12.4	30.5	3.6	0.2	34.1	0.007	2.2	15.4	1.6
	C	5.3	14.1	9.0	1.3	47.1	0.0	2.6	18.7	1.9
	I	5.2	19.7	8.3	1.4	45.2	0.0	2.3	16.2	1.7
	S	4.3	16.5	5.4	1.3	52.9	0.0	2.2	15.8	1.6

Table 3 (*Continued*)

	Crown class	Leaves	Small branches	Sapwood	Heartwood	Bark	Rotten wood	Roots		
								<2 mm	<30 mm	>30 mm
5–21 years	D	6.4	18.1	1.3	0.0	10.2	0.0	8.8	53.1	2.1
	C	3.9	10.3	2.0	4.7	9.9	0.0	9.5	57.4	2.3
	I	7.1	24.0	1.1	0.0	8.5	0.0	8.1	49.3	1.9
	S	6.1	16.9	1.4	0.0	11.4	0.0	8.8	53.2	2.3
Age class effect		*	**	*	**	**	*	*	*	*
Crown class effect		*	*	*	**	*	ns	ns	ns	ns
S (%)										
Age classes										
111–220 years	D	7.1	9.3	26.0	12.7	14.1	1.4	0.7	6.4	22.3
	C	2.7	3.8	17.7	20.9	20.4	2.0	0.8	7.0	24.7
	I	4.6	5.0	15.4	19.2	22.6	2.9	0.8	6.6	22.9
	S	4.7	7.4	22.8	12.6	19.5	2.9	0.8	6.5	22.8
21–110 years	D	18.0	15.2	26.8	0.8	11.3	0.006	1.4	10.9	15.6
	C	8.6	6.7	26.1	9.8	13.4	0.0	1.8	13.8	19.8
	I	11.5	10.4	29.4	4.2	13.1	0.0	1.6	12.2	17.5
	S	7.8	8.7	32.3	4.3	15.9	0.0	1.6	12.2	17.5
5–21 years	D	12.3	16.1	9.6	0.0	5.2	0.0	7.2	29.6	20.0
	C	10.9	13.4	8.9	2.4	5.6	0.0	7.4	30.7	20.7
	I	15.4	19.7	6.9	0.0	5.0	0.0	6.7	27.7	18.6
	S	11.4	18.8	8.5	0.0	6.4	0.0	6.9	28.7	19.3
Age class effect		**	*	**	**	**	*	*	**	*
Crown class effect		*	*	ns	*	ns	ns	ns	ns	ns
Mg (%)										
Age classes										
111–220 years	D	9.3	11.7	19.0	11.0	14.3	2.2	2.2	12.1	18.2
	C	3.7	4.5	19.0	13.9	24.6	2.4	2.3	11.8	17.8
	I	6.3	9.5	14.4	11.7	24.6	3.6	2.2	11.0	16.7
	S	6.2	9.8	13.8	14.9	21.0	3.6	2.2	11.3	17.2
21–110 years	D	20.7	21.2	12.4	0.3	10.0	0.007	3.1	19.2	13.1
	C	10.1	11.2	17.7	1.7	16.4	0.0	3.8	23.3	15.8
	I	11.9	12.2	20.0	1.8	16.2	0.0	3.3	20.6	14.0
	S	7.1	10.0	31.1	1.1	17.4	0.0	2.9	18.0	12.4
5–21 years	D	8.3	8.8	1.8	0.0	2.8	0.0	15.2	56.8	6.3
	C	6.2	7.9	2.6	0.4	3.0	0.0	15.5	57.9	6.5
	I	10.4	12.9	1.4	0.0	2.7	0.0	14.1	52.6	5.9
	S	9.0	10.4	1.8	0.0	3.4	0.0	14.7	54.6	6.1
Age class effect		*	**	**	**	**	*	**	**	*
Crown class effect		*	*	*	*	ns	ns	ns	ns	ns

ns, non-significative; *$p < 0.05$; **$p < 0.01$. D, dominant trees; C, codominant trees; I, intermediate trees; S, suppressed trees.

compared to inferior crown classes was very closely related to the nutrients accumulation rates. This is consistent with Das and Chaturvedi (2005) who found that the amount of nutrient uptake of *P. deltoides* trees was directly proportional to the size of net primary production. Dominant trees had larger crowns with more biomass of photosynthetic green leaves, and consequently had faster growth rates which may demand more nutrients. In contrast, the leaves of suppressed trees located at the inferior stratum receive less available light for photosynthesis and less active leaves may demand less nutrients. This response was mainly due to differences in biomass accumulation rates and to differences in tissue nutrient concentration. Also, crown classes of *N. antarctica* affected the moment of maximum nutrients uptake, being later for suppressed compared with dominant trees. This is consistent with Gholz et al. (1985) who reported that nutrient requirements and uptake of a slash pine plantation reached a peak about the time of canopy closure which coincided with the period of maximum tissue production.

The order of nutrient accumulation for the mature trees of *N. antarctica* was consistent with data reported by Hart et al. (2003) for a mature *N. truncata* forest, Caldentey (1992), and Richter and Frangi (1992) for a mature *N. pumilio* forest. However, there was a variation in the order of nutrient accumulation over time, e.g. dominant and codominant young trees had more N than Ca. These was due to changes in some components, such as bark which accumulates large quantities of Ca in mature stages and are green with greater N concentration for photosynthesis in young stages (Damesin, 2003). From 65 years of age, bark biomass increase and Ca become more abundant in this biomass pool. However, the order of storage in intermediate and suppressed young trees

Table 4
Modelized amount of nutrients (kg ha^{-1}) in sampled *N. antarctica* stands

	Pool	N	P	K	Ca	S	Mg	Total
Stand 1	Leaves	36.1	4.6	13.6	11.4	3.8	3.2	72.7
Average age: 191 years	Small branches	22.0	4.0	16.0	47.0	5.0	4.0	98.0
N trees: 400 trees ha^{-1}	Stem	134.2	14.2	40.1	77.3	28.7	14.8	309.3
Use: primary forest	Bark	31.9	2.2	28.7	258.2	12.3	8.5	341.8
% crown classes	Fine + middle roots	15.2	9.2	20.5	62.6	5.3	6.3	119.1
D, 40; C, 30; I, 15; S, 10	Coarse roots	53.2	34.7	58.3	35.9	16.7	8.0	206.8
Total		292.6	68.9	177.2	492.4	71.8	44.8	1147.7
Stand 2	Leaves	98.5	5.8	34.9	39.6	12.5	9.9	201.2
Average age: 100 years	Small branches	44.2	5.0	31.1	103.7	10.5	10.4	204.9
N trees: 1020 trees ha^{-1}	Stem	109.2	17.9	51.7	29.1	27.8	10.6	246.3
Use: primary forest	Bark	29.2	2.9	31.7	176.8	11.0	8.3	259.9
% crown classes	Fine + middle roots	30.0	11.6	53.7	82.9	12.1	15.2	205.5
D, 30; C, 31; I, 20; S, 16	Coarse roots	30.5	43.8	34.1	7.5	15.3	8.9	140.1
Total		341.6	87.0	237.2	439.6	89.2	63.3	1257.9
Stand 3	Leaves	56.8	6.8	16.7	15.2	6.8	4.0	106.3
Average age: 30 years	Small branches	27.3	6.0	15.4	41.1	5.8	4.2	99.8
N trees: 11870 trees ha^{-1}	Stem	63.9	19.0	26.3	11.5	13.4	3.5	137.6
Use: primary forest	Bark	19.3	3.4	16.3	71.6	5.4	2.8	118.8
% crown classes	Fine + middle roots	18.7	12.4	26.9	32.5	5.9	5.4	101.8
D, 21; C, 20; I, 27; S, 32	Coarse roots	19.1	47.1	17.0	2.9	7.4	3.2	96.7
Total		205.1	94.6	118.7	174.7	44.8	23.0	660.9
Stand 4	Leaves	24.1	3.3	9.2	8.7	2.7	2.2	50.2
Average age: 196 years	Small branches	15.2	2.8	10.9	34.0	3.5	2.7	69.1
N trees: 180 trees ha^{-1}	Stem	84.2	7.7	24.8	33.1	16.9	8.4	175.1
Use: silvopastoral system	Bark	16.6	1.3	14.9	144.9	6.4	4.1	188.2
% crown classes	Fine + middle roots	8.9	5.3	11.8	38.0	3.0	3.7	70.7
D, 78; C, 22; I, 0; S, 0	Coarse roots	31.0	20.2	33.4	21.8	9.5	4.7	120.6
Total		180.0	40.6	104.9	280.4	42.0	25.8	673.7
Stand 5	Leaves	76.4	4.5	27.9	32.8	9.6	7.6	158.8
Average age: 104 years	Small branches	32.5	3.8	24.2	81.4	8.0	7.8	157.7
N trees: 440 trees ha^{-1}	Stem	76.7	11.0	34.6	14.9	17.2	5.7	160.1
Use: silvopastoral system	Bark	16.6	1.8	20.0	108.4	6.9	4.6	158.3
% crown classes:	Fine + middle roots	18.7	7.5	34.0	54.3	7.6	9.5	131.6
D, 73; C, 27; I, 0; S, 0	Coarse roots	19.0	28.4	21.6	4.9	9.7	5.6	89.2
Total		239.9	56.9	162.3	296.8	59.0	40.8	855.7

D, dominant tree; C, codominant trees; I, intermediate trees; S, suppressed trees. Stem, sapwood + heartwood + rotten wood.

was similar to the mature ones. This was mainly due to inferior crown classes developing more structural tissues with lignin in bark, branches and stem components, combined with low leaves biomass. Roots were the component that accumulated more P, mainly in dominant trees at the regeneration stage. P has an influence on root system growth and plays a role for the strategy establishment and nutrients uptake (Lambers et al., 1998). Again, suppressed and intermediate trees showed lower P concentration in all tissues, and this may reduce the competition capacity in drier sites near the Patagonian steppe. Nutrients distribution on *N. antarctica* components was similar to those reported by Richter and Frangi (1992) for *N. pumilio*. In both species, N and Ca were more abundant 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.

4.4. Nutrients root/shoot ratio

There are few studies that have measure nutrients both in above- and below-ground biomass in mature trees from which root/shoot nutrient ratios can be derived. In *N. antarctica*, root/shoot nutrient ratio decreased from its maximum value at 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 above-ground accumulation of nutrients by mature trees increased over time. Hart et al. (2003) reported lower ratios in *N. truncata* for N (0.24), P (0.40), K (0.34), and similar values for Ca (0.20) and Mg (0.47). Also, Richter and Frangi (1992) reported in *N. pumilio* lower values for N (0.27), P (0.32), K (0.28), and a similar value for Ca (0.24). This indicates, that *N. antarctica* accumulated more below-ground biomass and nutrients, possibly as an adaptation to windy, infertile and dry sites.

4.5. Nutrient use efficiency

NUE increased in the mature phase and was greatest in dominant trees compared with suppressed trees. A greater NUE of N, K and P in dominant trees could be associated with rapid growth, a relatively large investment of these nutrients in photosynthesizing tissue, and a relatively small use of carbon in respiration (Lambers et al., 1998). These results are consistent with Landsberg and Gower (1997), who reported during stand development of *Pinus elliotis*, that N and P use efficiency increased as stand aged from 2 to 34 years. Also, Frangi et al. (2005) reported that *N. pumilio* trees growing at the krummholz at greater elevations had low within-stand P- and N-use efficiencies, but higher efficiencies of K, Ca and Mg compared with a tall erect forest stand growing at 220 m a.s.l. Furthermore, the differences in NUE found in the present work may have determined differences in the nutrients allocation. This is consistent with Gleeson and Tilman (1994) who suggested that species with contrasting NUE control both allocation and growth rate responses in a particular habitat.

4.6. Stand biomass, nutrient accumulation and sustainable forest management

Total biomass and nutrients accumulation at stand level was determined by growth phase, stocking, crown class proportions and forest uses (primary forests and silvopastoral systems), e.g. the amount of nutrients (except Ca) was greater in a young primary forest stand compared with an older one characterized by a lower stocking and biomass. Also, young trees had a large proportion of biomass allocated in leaves, small branches and medium roots, which had the greatest nutrient concentrations. Total biomass in *N. antarctica* stands varied from 62.5 to 133.4 t ha^{-1} and total nutrients accumulation ranged from 3 kg Mg ha^{-1} to 1235 kg Ca ha^{-1}. These results appeared lower than data from others mature *Nothofagus* forest studied previously in South Patagonia. Richter and Frangi (1992), working with the same species but in Tierra del Fuego, Argentina, reported a total above- and below-ground biomass of 493.3 t ha^{-1} and greater quantities of all nutrients: 1009 kg N ha^{-1}, 165 kg P ha^{-1}, 806 kg K ha^{-1} and 1235 kg Ca ha^{-1}. Caldentey (1992) reported for uneven-aged *N. pumilio* forest (dominant high of 19 m) a total aerial biomass ranged from 283 to 370 t ha^{-1}, corresponding to stands growing at a different stage of development (460–1650 trees ha^{-1}) with greater amounts of Ca (mean of 634 kg ha^{-1}) and N (365 kg ha^{-1}), and lower amounts of K (160 kg ha^{-1}), P (33 kg ha^{-1}) and Mg (68 kg ha^{-1}). Similarly, Hart et al. (2003) working with mature *N. truncata* forest (dominant height of 21 m) founded greater amounts of all nutrients (556 kg N ha^{-1}, 195 kg P ha^{-1}, 742 kg K ha^{-1}, 114 kg Mg ha^{-1} and 1336 kg Ca ha^{-1}).

To date, there are no reports of above- and below-biomass and nutrient accumulation related to age and crown classes for *Nothofagus*. The use of logistic and exponential decay functions provide a valuable tool for understanding and estimating biomass and nutrients accumulation, as well as root/shoot ratios of primary forests and silvopastoral systems of *N. antarctica* using forest inventories data. Thinning in silvopastoral system stands changed the nutrient balance of the stand, due to nutrients uptake and return of nutrients from litter. Amelioration practices such as debarking of the stems before removal would substantially reduce the loss of Ca from the managed forest ecosystem. Furthermore, root systems from removed trees remain in the system, and could provide principally P and K to the pasture and trees. On the other hand, removal of trees may result in a depletion of some nutrients in the forest system by exporting logs and reducing nutrient supply from annual litter fall (mainly N and K). Nutrient supply from dead leaves of some woody leguminous species can covered the entire N requirements of some gramineous species (Salazari et al., 1993), being the release of nutrients from decomposing litter an important internal pathway for nutrient flux in forested ecosystems (Santa Regina, 2001).

Using the proposed equations, nutrient supply from leaf litter can be used for practical purposes such as to estimate the pasture nutrients requirement in a silvopastoral system of *N. antarctica*. Based on the requirements of grasses for optimum growth (Jeffrey, 1988), a pasture with an annual biomass production of 1500 kg ha^{-1} in Patagonian *N. antarctica* forest (Peri, 2005) accumulate 30.0 kg K ha^{-1}, 12.0 kg N ha^{-1}, 1, 11.4 kg Ca ha^{-1}, 6.7 kg P ha^{-1}, 4.5 kg Mg ha^{-1} and 3.1 kg S ha^{-1}. Assuming the proportion of N, P, S and K reabsorbed by *N. antarctica* is similar to the levels for other *Nothofagus* species in Patagonia reported by Diehl et al. (2003), litter fall from an old-growth forest with 400 trees ha^{-1} (40% dominant, 30% codominant, 15% intermediate and 10% suppressed trees) could provide total pasture requirements of N, P, S, and 31% of K. This can be useful to estimate the impact on nutrient returns from litter fall of different thinning types and intensities, e.g. only dominant trees provides total N pasture requirements, so removing trees of other crown classes would not result in a negative impact for this particular nutrient. Therefore, for a suitable forest management it is important to analyse the number and crown class of trees to be removed.

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Appendix A

Parameters of the logistic function (Eq. (1)) for total biomass and nutrients accumulation of *N. antarctica* trees

	a	*b*	*c*	R^2	ESE
Biomass					
D	404.0557	99.7511	−3.3790	0.9842	18.3020
C	331.1867	109.6249	−3.2103	0.9836	13.4610
I	226.4051	123.1832	−3.0176	0.9803	8.6766
S	57.6305	104.7503	−3.5392	0.9781	2.7622

Appendix A (*Continued*)

	a	*b*	*c*	R^2	ESE
Nitrogen					
D	1260.3232	104.7333	−3.1071	0.9952	29.9622
C	794.2881	115.4911	−3.0070	0.9844	25.5109
I	564.2757	130.4341	−3.0047	0.9936	11.3865
S	231.2075	146.1289	−2.6517	0.9668	8.8115
Phosphorus					
D	316.1619	113.9367	−2.1744	0.9837	11.4736
C	219.2797	116.0739	−2.6415	0.9851	7.5286
I	111.6813	105.8484	−3.1185	0.9799	4.9510
S	67.0603	147.0343	−2.5514	0.9691	2.4249
Potassium					
D	673.0956	90.0949	−3.5207	0.9917	23.1571
C	469.5372	104.8553	−3.4203	0.9845	19.4679
I	328.3574	114.4445	−3.2207	0.9810	13.4678
S	119.9033	107.2147	−3.1942	0.9789	5.3201
Calcium					
D	2012.1732	122.0764	−3.2358	0.9852	78.2737
C	1648.6203	136.3877	−3.4118	0.9915	39.3033
I	1502.5366	159.5680	−3.3119	0.9819	39.4440
S	502.04697	147.1863	−3.1901	0.9775	15.7409
Sulphur					
D	285.6420	100.9025	−2.9261	0.9916	8.9432
C	200.4050	107.9124	−3.5964	0.9907	6.3988
I	117.8089	101.1811	−4.3076	0.9838	5.3996
S	44.5520	115.4395	−3.7045	0.9851	1.6138
Magnesium					
D	161.2058	89.1435	−3.4205	0.9939	4.6697
C	121.4881	96.9999	−3.9844	0.9892	4.5573
I	75.6239	99.6157	−4.5371	0.9884	2.9778
S	23.2200	87.1505	−6.5738	0.9857	1.1643

D, dominant; C, codominant; I, intermediate; S, suppressed trees.

Appendix B

Parameters of the exponential decay function (Eq. (2)) for the root/shoot ratio of *N. antarctica* trees

	a	*b*	y_0	R^2	ESE
Biomass	1.6922	0.0473	0.4227	0.9915	0.0414
Nitrogen	0.4543	0.0289	0.2801	0.9309	0.0345
Phosphorus	4.7148	0.0464	1.5497	0.9564	0.2549
Potassium	0.7658	0.0505	0.6135	0.9238	0.0574
Calcium	2.2725	0.0361	0.2067	0.9733	0.1029
Sulphur	1.2299	0.0452	0.3981	0.9683	0.0567
Magnesium	4.0363	0.0400	0.4368	0.9789	0.1556

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