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Allometric relations for biomass partitioning of *Nothofagus antarctica* trees of different crown classes over a site quality gradient

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ABSTRACT

Data on tree biomass are essential for understanding the forest carbon cycle and plant adaptations to the environment. We determined biomass accumulation and allometric relationships in the partitioning of biomass between aboveground woody biomass, leaves and roots in *Nothofagus antarctica*. We measured above- and belowground biomass of *N. antarctica* trees across different ages (5–220 years) and crown classes (dominant, codominant, intermediate and suppressed) in three site qualities. The biomass allocation patterns were studied by fitting allometric functions in biomass partitioning between leaves (M_L), stem and branches (M_S) and roots (M_R). These patterns were tested for all pooled data and according to site quality and crown classes. Biomass accumulation varied with crown class and site quality. The root component represented 26–72% of the total biomass depending on age and site. *N. antarctica* scaling exponents for the relationships M_L vs. M_S , M_A vs. M_R , and M_S vs. M_R were close to those predicted by the allometric biomass partitioning model. However, when biomass allocation was analyzed by site quality the scaling exponents varied following the optimal partitioning theory which states that plants should allocate more biomass to the part of the plant that acquires the most limiting resource. In contrast, the crown class effect on biomass partitioning was almost negligible. In conclusion, to obtain accurate estimations of biomass in *N. antarctica* trees the allometric approach appears as a useful tool but the site quality should be taken into consideration.

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1. Introduction

Nothofagus antarctica (ñire) is one of the most common native species of the Patagonian forest (Argentina) that extends from 46° to 56°S. It grows on a variety of sites and reaches heights up to 20 m on the best sites (Donoso et al., 2006), but on poorly drained or drier sites near Patagonian steppe, it grows as a shrubby 2–3 m tall tree (Veblen et al., 1996). Patagonian forests occupied by ñire have been used for wood extraction (firewood, poles) and in silvopastoral systems, where natural pastures grown under the tree canopy are grazed by cattle and sheep (Peri, 2005).

Data on tree biomass are essential for evaluating carbon sequestration and cycling (Brown and Lugo, 1982; Dixon et al., 1994; Binkley et al., 2004), plant adaptations to the environment (Bradshaw, 1965; West-Eberhard, 2003) and also for studying impacts of silvicultural practices on forest productivity (Johnson and Todd, 1998; Santa Regina, 2000). Many factors like tree age,

crown class (i.e. dominant, suppressed and intermediates) and site quality may influence tree biomass accumulation (Wang et al., 1996; Binkley, 2004; Peri et al., 2006; Castilho et al., 2006). While age and site effects have been more studied (i.e., Wang et al., 1996; Rapp et al., 1999) not many studies have quantified the crown class effects on biomass accumulation, in spite of large differences found between dominant and suppressed trees. For example, Peri et al. (2006) reported a series of functions for total biomass accumulation in *N. antarctica* where the total biomass of dominant 160 years old trees grown on a medium quality site was 336 kg tree⁻¹, whereas suppressed trees only had 47 kg tree⁻¹. Also, Le Goff and Ottorini (2001) reported large differences in belowground biomass accumulation between crown classes of *Fagus sylvatica*. Belowground components are not often evaluated due to the great complexity in extracting and studying roots, especially for large individuals. However, roots may account for a significant proportion of tree biomass and carbon storage (Kurz et al., 1996; Cairns et al., 1997; Peichl and Arain, 2007). Another important aspect of forest ecology is biomass allocation, which examines how plants distribute their resources to different plant organs (stems, leaves, and roots). Some authors (i.e., Huxley and Teissier, 1936; Hunt,

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1990; Müller et al., 2000) postulated that consistent allometric relationships exist among the different organs of the plant. According to this theory, biomass allocation is mainly governed by the size of the plant and is determined by a power function of the form $Y_1 = \beta Y_2^\alpha$, where Y_1 and Y_2 are interdependent variables (i.e. stem mass and root mass), β is the allometric constant, and α is the scaling exponent. This exponent, also named the allometric coefficient (Hunt, 1990), determines how the root-to-shoot ratio changes with plant size. When $\alpha = 1$ the model describes an isometric relation, i.e. one that plots as straight line on both linear and logarithmic axes, and when $\alpha \neq 1$ the model describes an allometric relation, i.e., one that plots as a linear function only on logarithmic axes. Later, Niklas and Enquist (2002) postulated “the canonical rules” to explain general allocation patterns in plants. These rules predict that, after the logarithmic transformation of biomass data ($\log Y_1 = \log \beta + \alpha \log Y_2$), the standing leaf biomass scales as 3/4–power of stem (or root) biomass ($\alpha = 0.75$) and that the stem scales isometrically ($\alpha = 1$) with respect to roots (West et al., 1997; Niklas and Enquist, 2002; Enquist and Niklas, 2002). An important characteristic of these scaling relationships is that they appeared to be insensitive to environmental conditions such as latitude, precipitation and temperature (Cheng et al., 2007). The only parameter which varies according to the species is β , which permits to estimate the absolute biomass of different tree components (Enquist and Niklas, 2002). However, while these rules have been derived from a large compendium of standing tree biomass, Robinson (2004) postulated that they are not universally applicable and that there is a large discrepancy between measured and predicted root biomass in forests ecosystems. Another popular theory for biomass allocation is the “optimal partitioning theory” which postulates that the environmental conditions are the major determinants of the root-to-shoot ratio (Thornley, 1972; Bloom et al., 1985). According to this theory, plants preferentially allocate biomass to the organ that is harvesting the most limiting resource. This means that, depending on the environment where plants grow, biomass allocation will favor leaves and branches if light becomes more limiting and will favor roots if nutrients or water becomes limiting. This prediction would represent an apparent contradiction to the allometric theory, which states that the root-to-shoot ratio is mainly regulated by the total size of the plant, following a scale relationship characteristic of each species (Müller et al., 2000). For many species, the root-to-shoot allometric coefficient predicts that small plants, either because they are young or they are under the influence of any factor that limits growth, have a greater proportion of roots than older or non-stressed plants.

On the other hand, research efforts focused towards predicting belowground biomass based on aboveground components will help to uncover the common gap in ecological studies of lack of root biomass data. In this sense, allometrics would be a useful tool to predict belowground biomass from aboveground data. In this context, we studied the biomass accumulation and allocation of *N. antarctica* to answer three main questions: (i) does *N. antarctica* follow allometric patterns of biomass allocation? (ii) Do these patterns follow the canonical rules proposed by Niklas and Enquist (2002)? (iii) Do the crown class and site quality influence on the biomass allometric patterns? To answer these questions, the aim of this study was to evaluate the allometric theory across an age sequence of individual *N. antarctica* trees of different crown classes grown in a site quality gradient in the Southern Patagonia forests.

2. Methods

2.1. Study area

This study was carried out in pure stands of *N. antarctica* of the Southern West Patagonia forest, Argentina. Three different site qualities (i.e., site classes) from these forests were selected following the Lencinas et al. (2002) classification. High, medium and low qualities were represented by site classes III, IV and V respectively, according to the classification from these authors. For site class III (SC III) (51°13'21"S, 72°15'34"W), the total height of dominant mature tree (H) reached 10 m; in site class IV (SC IV) (51°34'S, 72°14'W), H reached 7.8 m and site class V (SC V) (51°40'59"S, 72°15'56"W) represented a marginal site which was drier, exposed to strong winds and with rocky soils, where H reached 5.3 m. Regional climate is cold temperate. Climatic characteristics from each site were derived from the WorldClim data set (Hijmans et al., 2005) (Table 1). The SC III has the highest mean annual precipitation (563 mm/yr) and the lowest mean annual water deficit (−422.4 mm/yr). In the other extreme, the worst site class (SC V) has the lowest annual precipitation (335 mm/yr), the highest evaporation value (1512.4 mm/yr) and consequently, the highest mean annual water deficit (−1177.4 mm/yr) (Table 1). For soil analysis, at each site class 30 bulked soil sample cores were taken at random from different depths (Table 1). All sites had around 50% of sand and the maximum rooting depth ranged from 0.6 m in the SC III to 0.5 m in SC V (Table 1). Soil nutrient concentrations were similar between sites with exception of P and Mg which were higher in SC IV and Ca in SC III (Table 1).

Table 1

Climate and soil characteristics from sites of high, medium and low qualities (SC III, IV and V, respectively) studied for *N. antarctica* stands.

Soil characteristics	Site class III			Site class IV			Site class V		
	5–20	20–40	40–60	1–5	5–20	40–60	1–5	5–20	40–50
Mean annual T: 5.9 °C				Mean annual T: 5.4 °C			Mean annual T: 5.0 °C		
Annual pp: 563 mm				Annual pp: 422 mm			Annual pp: 335 mm		
Evaporation: 985.4 mm/yr				Evaporation: 1210.1 mm/yr			Evaporation: 1512.4 mm/yr		
MAWD: −422.4 mm/yr ^a				MAWD: −788.1 mm/yr			MAWD: −1177.4 mm/yr		
Depth (cm)	5–20	20–40	40–60	1–5	5–20	40–60	1–5	5–20	40–50
Clay (%)	8.0	8.2	14.5	–	20	20	–	26.0	25.0
Silt (%)	36.2	35.9	24.7	–	30	60	–	22.5	19.9
Sand (%)	55.8	55.9	60.8	–	50	20	–	51.5	55.1
pH	4.8	4.8	4.6	6.1	4.8	4.8	5.6	4.7	4.5
Resistance (ohm cm)	7695	10,764	13,226	4170	8800	5810	5430	7690	10,445
N total (ppm)	5985	3320	2272	8670	880	460	5190	2810	1890
P trough (ppm)	23.5	10.7	10	129	12	6	66	25	6
K (cmol ⁺ kg ^{−1})	0.37	0.2	0.4	4.2	0.3	0.1	1.3	0.9	0.5
Ca (cmol ⁺ kg ^{−1})	21.4	16.3	12.6	10.6	4.2	8.0	6.3	2.3	2.1
Mg (cmol ⁺ kg ^{−1})	5.0	2.5	1.7	52.4	11.3	20.7	24.6	8.5	5.1

^a MAWD: mean annual water deficit.

Table 2
Characteristics from *N. antarctica* stands studied, developing at sites of high medium and low quality (SC III, IV and V, respectively) in Patagonia, Argentine.

	Stands characteristics							
	Age class (years)	Tree ha ⁻¹	Mean height (m)	Mean DBH (cm)	Crown classes (%)			
					D	C	I	S
Site class III	5–20	40,050 ± 2459	1.5 ± 0.5	1.7 ± 1.0	24	26	30	20
	21–110	5820 ± 1088	5.8 ± 0.8	9.5 ± 3.0	28	30	28	14
	120–220	390 ± 89	8.4 ± 1.5	26.8 ± 6.8	40	28	25	7
Site class IV	5–20	23,500 ± 1504	1.2 ± 0.4	3.0 ± 0.3	21	17	28	34
	21–110	4950 ± 980	4.3 ± 0.7	8.8 ± 1.0	30	26	23	21
	120–220	460 ± 55	6.2 ± 1.6	23.6 ± 5.5	35	30	22	13
Site class V	8–20	161,200 ± 10,800	1.1 ± 0.6	2 ± 0.3	20	24	25	31
	21–110	5540 ± 2300	2.7 ± 0.8	8 ± 0.2	25	28	24	23
	120–180	440 ± 35	4.2 ± 0.3	20.2 ± 5.0	36	27	23	14

Stands were characterized with three circular plots of 500 m². In each plot, the total number of trees was counted by crown class (dominant, codominant, intermediate and suppressed) (Table 2). The number of trees per hectare was different according to the stand age, being more abundant at early ages and declining to 390–460 trees ha⁻¹ in mature stands. In each plot, diameter at breast height (DBH) and total height of every tree was measured. Tree age was measured counting rings from the stump (Table 2).

2.2. Biomass determination

Tree biomass was measured from even aged stands growing in site classes III–V. Thirty six trees were measured in each site class: 12 representing the regeneration class age (5–20 years), 12 representing young trees (21–110 years) and 12 mature trees (111–220 years). Trees from each age class were sorted according to their crown class in dominant ($n = 3$) codominant ($n = 3$), intermediate ($n = 3$) and suppressed ($n = 3$). For each tree, the stem was cut at 0.1 m (stump), 1.3 m and every 1 m up to an end diameter of 10 mm to calculate stem volume with bark using Smalian's formula. Then, aboveground biomass was separated into leaves and stem (branches + bole). Three cross-sectional discs of 30 mm at different lengths were taken and separated to determine wood density for biomass calculations. Small branches (<1 cm) and leaves were separated and weighed and three sub-samples were oven dried at 65 °C to constant weight for biomass calculation. Small branches biomass was added to stem biomass. Roots from individual trees were completely excavated to a depth of 0.6 m (approximate maximum rooting depth for SC III and IV and 0.5 m for SC V) in circular plots centered on the stump of the selected trees minimizing the loss of the fine root fraction. Belowground biomass was sorted in fine roots (≤ 2 mm), middle roots (≤ 30 mm) and coarse roots (> 30 mm). All root biomasses were weighed in fresh and three sub-samples from each component were oven dried at 65 °C to constant weight for biomass calculation.

2.3. Biomass scaling relations

To study biomass partitioning patterns, biomass data were \log_{10} transformed to adjust the following allometric functions: aboveground biomass (M_A) vs. root biomass (M_R), stem biomass (M_S) vs. M_R , leaves biomass (M_L) vs. M_R and leaves biomass vs. M_S . We also tested the scaling relations derived by Niklas and Enquist (2002) which predict that M_L will scale as 3/4 power of M_S and 3/4 power of M_R and that standing M_S and $M_R M_R$ will scale isometrically with respect to each other. The analyses were made for all biomass data pooled and also discriminated by site and crown classes.

2.4. Statistical analysis

Differences in biomass accumulation according to age, crown classes and site class were evaluated through analysis of variance (ANOVA) and significant differences were identified using the least significant differences (LSD) test at $p < 0.001$ with R statistical software (Gentleman and Ihaka, 2005). Site classes were not replicated since these data pseudo-replicates. As a consequence, tendencies or differences related to site quality are only applicable to the particular sites examined in this study (Hurlbert, 1984).

For testing scaling relations, standardized major axis (SMA) analysis was used to determine the slope of the regression curve (the scaling exponent, α_{SMA}) and the allometric constants (β_{SMA}), using the SMATR package for R software (Warton, 2007). This model is recommended instead of ordinary least squares regression when variables of interest are biologically interdependent, subject to measurement error, and when functional rather than predictive relations are sought (Warton et al., 2006). In fact, while common regression is useful whenever a line is desired for predicting one variable from another, it is not appropriate when the value of the slope of the axis or line of best fit is of primary interest. One of the reasons for this is that as the X variable has usually been measured with error, linear regression gives a biased estimator of the slope of the regression of Y against X (Fuller, 1987). Thus, for allometry, where the aim is to describe how size variables are related, the major axis or standardized major axis methods are more appropriated (for more information see Warton et al., 2006). Also, Warton et al. (2006) postulated that this kind of relationships should be named "standardized major axis" instead of "reduced major axis" or model type II, since they are misleading and not very specific terms. Differences between scaling exponents (slopes) according to site and crown classes also were evaluated by ANOVA and significant differences were separated using LSD test at $p < 0.001$.

3. Results

3.1. Total biomass in tree components

Significant differences ($p < 0.001$) were found in total biomass accumulation according to age and crown classes in all sites (Table 3). Mature trees always showed higher biomass accumulation compared to young trees, and the gradient for crown classes was: dominant > codominant > intermediate > suppressed (Table 3). The main tree components for biomass accumulation were stems and coarse roots (Table 3). Stems of dominant mature trees accounted for 52 and 72% of total biomass for the worst and the best quality site, respectively, and the stem proportion of suppressed trees was 53 and 75% of total biomass, for the same site classes (Table 3).

Table 3Biomass of *N. antarctica* components (kg tree⁻¹) according to age and crown classes for trees grown at three site qualities in Southern Patagonia.

Age class	Crown class	Leaves	Stem	Roots			Total
				<2 mm	<30 mm	>30 mm	
Site class III: Mean total height of mature dominant tree = 10 m							
5–20 years	Dominant	0.3	3.9	0.3	2.8	8.0	15.3
	Codominant	0.3	3.1	0.3	2.2	6.3	12.2
	Intermediate	0.2	2.2	0.2	1.5	4.4	8.5
	Suppressed	0.02	0.7	0.05	0.4	1.2	2.4
21–110 years	Dominant	2.3	51.9	0.5	8.2	15.2	78.1
	Codominant	1.2	28.7	0.4	4.3	8.5	43.1
	Intermediate	0.3	16.2	0.4	4.4	6.2	27.5
	Suppressed	0.8	8.0	0.4	2.9	2.7	14.8
120–220 years	Dominant	6.1	329.3	0.7	18.9	101.6	456.6
	Codominant	5.5	231.0	0.5	13.3	71.5	321.8
	Intermediate	4.5	129.8	0.3	7.4	39.9	181.9
	Suppressed	0.4	50.0	0.1	2.5	13.5	66.5
Age class effect	LSD	0.35*	16.4*	0.06*	1.2*	5.2*	22.9*
Crown class effect	LSD	0.41*	18.9*	0.07*	1.3*	6.0*	26.4*
Interaction	LSD	0.71*	32.8*	0.12*	2.3*	10.3*	45.8*
Site class IV: Mean total height of mature dominant tree = 7.8 m							
5–20 years	Dominant	0.1	0.7	0.1	1.0	0.4	2.3
	Codominant	0.03	0.2	0.04	0.3	0.1	0.7
	Intermediate	0.02	0.1	0.02	0.2	0.06	0.4
	Suppressed	0.008	0.1	0.01	0.1	0.03	0.2
21–110 years	Dominant	1.1	11.4	0.2	1.9	4.2	18.8
	Codominant	0.2	6.8	0.1	1.0	2.3	10.4
	Intermediate	0.2	3.9	0.1	0.6	1.3	6.1
	Suppressed	0.05	1.2	0.02	0.2	0.4	1.9
120–220 years	Dominant	7.9	240.5	1.7	18.0	93.8	361.9
	Codominant	2.3	179.1	1.3	12.9	67.3	262.9
	Intermediate	1.9	101.8	0.7	7.4	38.5	150.3
	Suppressed	0.78	33.1	0.2	2.4	12.6	49.1
Age class effect	LSD	0.19*	6.9*	0.05*	0.5*	2.6*	10.2*
Crown class effect	LSD	0.22*	7.9*	0.05*	0.6*	3.1*	11.8*
Interaction	LSD	0.38*	13.7*	0.1*	1.0*	5.3*	20.5*
Site class V: Mean total height of mature dominant tree = 5.3 m							
5–20 years	Dominant	0.04	0.5	0.09	0.3	0.1	1.0
	Codominant	0.03	0.2	0.04	0.1	0.05	0.4
	Intermediate	0.02	0.1	0.02	0.08	0.03	0.3
	Suppressed	0.007	0.05	0.01	0.03	0.01	0.1
21–110 years	Dominant	0.4	6.1	0.3	1.7	2.0	10.5
	Codominant	0.2	3.7	0.2	1.0	1.1	6.2
	Intermediate	0.09	1.4	0.06	0.4	0.4	2.3
	Suppressed	0.08	0.7	0.03	0.2	0.2	1.2
120–180 years	Dominant	3.0	126.6	0.6	14.3	98.9	243.4
	Codominant	2.1	72.1	0.3	6.9	47.9	129.3
	Intermediate	2.1	48.3	0.2	4.5	31.2	86.3
	Suppressed	0.8	23.7	0.1	2.5	17.6	44.7
Age class effect	LSD	0.09*	3.5*	0.01*	0.4*	2.6*	6.8*
Crown class effect	LSD	0.11*	4.0*	0.01*	0.4*	3.0*	7.9*
Interaction	LSD	0.19*	7.0*	0.02*	0.7*	5.3*	13.7*

LSD: Least Significant Difference.

* Significant differences (p value < 0.001) among age and crown classes for each particular component.

Belowground components increased with age, but the relative contribution of root to total tree biomass decreased as age increased, and the magnitude of this change varied depending on sites. Belowground components varied from 72 to 26% in SC III, from 65 to 31% in SC IV and from 49 to 47% in SC V for young and mature trees biomass respectively. In general, the root system was mainly constituted by coarse and middle roots. For example belowground biomass of mature dominant trees had 83–87% of coarse roots, 12–16% of middle roots and around 0.5–1.5% of fine roots (Table 3).

Biomass accumulation varied with site quality. At early and medium ages, trees grown at the best site (SC III) had significantly more biomass than trees grown at the other sites, for all crown

classes (Fig. 1). Likewise, all crown classes of mature tree in site classes III and IV presented significantly more biomass than mature tree grown at the worst site. The only exception was suppressed trees, where only trees from site class III differ from the others (Fig. 1D).

3.2. Allometric relations for biomass partitioning

The patterns of biomass partitioning among tree components were represented by linear relations of biomass \log_{10} transformed data. Adjusted r^2 ranged from 0.85 to 0.99 (Table 4). Pooling all data, *N. antarctica* trees scaling exponents for the relations M_S vs. M_R , M_L vs. M_R and M_L vs. M_S were 1.17, 0.91 and 0.76, respectively

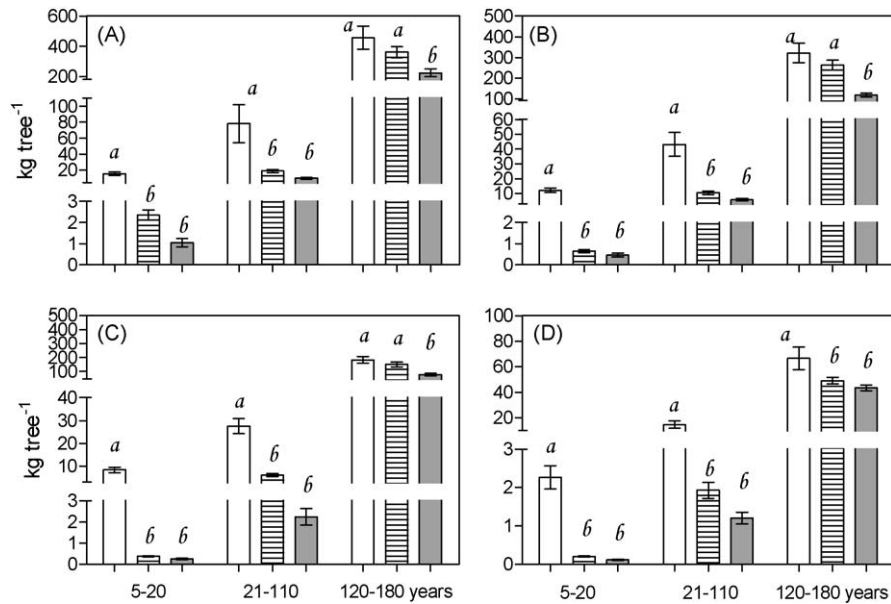


Fig. 1. Mean biomass accumulation for (A) dominant, (B) codominant, (C) intermediate and (D) suppressed *N. antarctica* trees of different age classes growing in site class III (white bars), site class IV (lined bars) and site class V (black bars). Different letters denote significant differences among site classes.

Table 4
Scaling exponents (α) and allometric constants (β) for *N. antarctica* standing aerial (M_A), leaf (M_L), stem (M_S) and roots biomass (M_R) relations across all pooled data and sorted according to the class site. Scaling exponents are for standardized major axis regression (α_{SMA}) of \log_{10} transformed data (original units in kilograms of dry mass per tree). Pre = predicted (partitioning allometric theory); Obs = observed.

	α Pre.	α Obs.	95% CI	β Obs.	95% CI	n	r^2
Across all pooled data							
M_A vs. M_R	1.00	1.17	1.12–1.22	–0.007	–0.06–0.05	108	0.95
M_S vs. M_R	1.00	1.17	1.11–1.24	0.06	–0.01–0.14	108	0.91
M_L vs. M_R	0.75	0.91	0.86–0.96	–1.13	–1.19 to –1.07	108	0.92
M_L vs. M_S	0.75	0.76	0.73–0.79	–1.09	–1.14 to –1.04	108	0.94
Site Class III HT = 10 m							
M_A vs. M_R	1.00	1.63	1.45–1.83	–0.64	–0.89 to –0.40	36	0.88
M_S vs. M_R	1.00	1.64	1.46–1.85	–0.68	–0.93 to –0.43	36	0.88
M_L vs. M_R	0.75	1.38	1.21–1.59	–1.79	–2.04 to –1.54	36	0.84
M_L vs. M_S	0.75	0.84	0.74–0.96	–1.22	–1.39 to –1.04	36	0.85
Site Class IV HT = 7.8 m							
M_A vs. M_R	1.00	1.23	1.17–1.30	0.0007	–0.07–0.07	36	0.97
M_S vs. M_R	1.00	1.20	1.10–1.31	0.28	0.17–0.40	36	0.94
M_L vs. M_R	0.75	0.94	0.87–1.00	–1.13	–1.20 to –1.06	36	0.96
M_L vs. M_S	0.75	0.74	0.69–0.81	–1.10	–1.18 to –1.02	36	0.95
Site Class V HT = 5.3 m							
M_A vs. M_R	1.00	1.05	1.02–1.08	0.09	0.05–0.12	36	0.99
M_S vs. M_R	1.00	1.07	1.03–1.10	0.05	0.01–0.09	36	0.99
M_L vs. M_R	0.75	0.75	0.72–0.77	–1.05	–1.08 to –1.01	36	0.99
M_L vs. M_S	0.75	0.80	0.76–0.85	–1.02	–1.06 to –0.97	36	0.98

(Table 4, Fig. 2). With the exception of M_L vs. M_S , exponents were higher than predicted by Niklas and Enquist (2002). The relation total aerial biomass vs. total roots biomass (M_A vs. M_R) also was tested and the observed value did not differ from that estimated for M_S vs. M_R (Table 4, Fig. 2), probably because stems accounted with the most important fraction of aboveground biomass.

Significant differences were found in α values when scaling exponents were calculated for biomass data sorted by site classes (Fig. 3). Only the exponents for site class V followed very close to the values predicted by Niklas and Enquist (2002) (Table 4). For the M_A vs. M_R ratio, α values varied significantly and increased with site quality. Values found were 1.63, 1.23 and 1.05 for the III, IV and V site classes, respectively (Figs. 3 and 4). Similarly, M_L vs. M_R relation changed significantly according to the sites and α values were 1.38, 0.94 and 0.75 for class sites III,

IV and V, respectively (Table 4, Fig. 3). In contrast, effects of the site class on the M_L vs. M_S relationships were almost negligible (Fig. 3).

The crown class factor had small effects on *N. antarctica* allocation patterns. Dominant, codominant, intermediate and suppressed trees overlapped in their confidence intervals for the four relationships (M_A vs. M_R , M_S vs. M_R , M_L vs. M_S and M_L vs. M_R) indicating no differences in biomass allocation according to this factor (Table 5). Also, no significant differences were found for M_A vs. M_R and M_L vs. M_R and differences in the other relationships were negligible. M_S vs. M_R and M_L vs. M_S in all crown classes included in their confidence intervals the predicted value for the allometric partitioning theory. The only exception was the M_L vs. M_R relation, which in all cases had α values higher than the predicted values (Table 5).

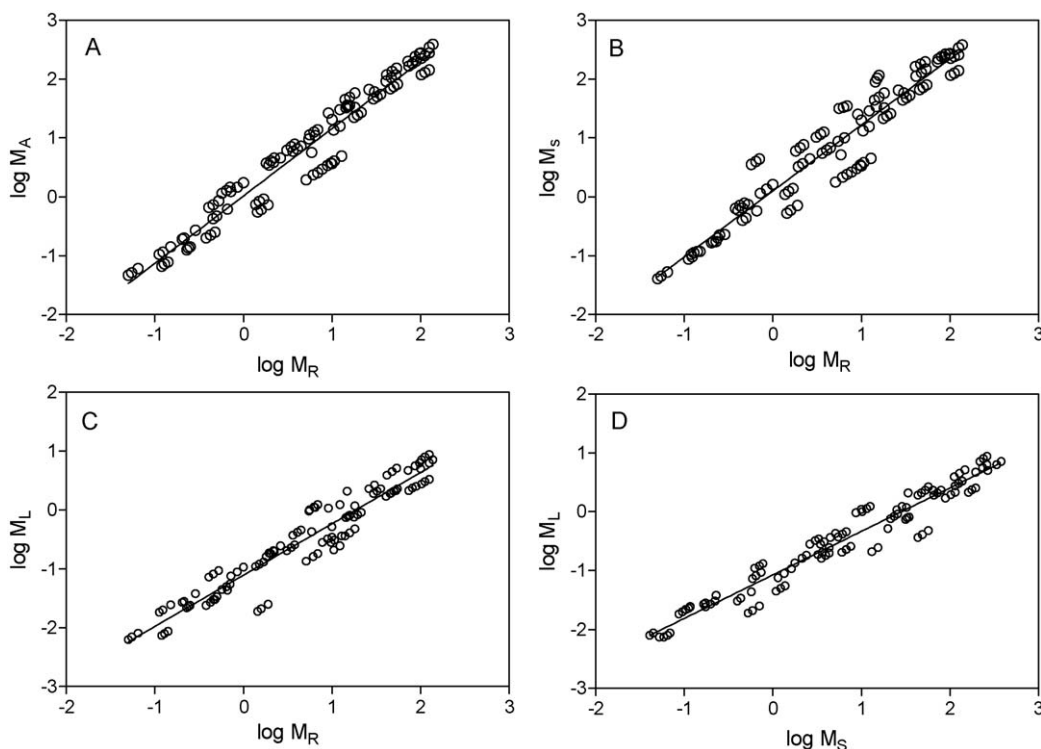


Fig. 2. Biomass allocation of \log_{10} transformed *N. antarctica* data for all sites pooled (original units in kilograms of dry mass per tree). (A) Aerial biomass (M_A) vs. root biomass (M_R); (B) stem (M_S) vs. root biomass (M_R); (C) leaves (M_L) vs. roots biomass and (D) leaves vs. stem biomass. Each circle represents values of an individual tree.

4. Discussion

Total biomass of *N. antarctica* varied according to the crown class, the age of the trees and the site quality. In our field study, we found a clear gradient in biomass accumulation (either total or discriminated in above- and belowground components) according to the crown class (dominant > codominant > intermediate > suppressed), which agrees with the results found by Peri et al. (2006) and Le Goff and Ottorini (2001). From our results, it is possible to derive functions for the estimation of biomass accumulation according to the tree age. This information is relevant because this species regenerates after disturbances such as fire or tree fall gaps (Veblen et al., 1981), creating forests with a mix of mature and young stands at the landscape level.

We found that total biomass decreased as site quality declined from SC III to V and whereas the dominant trees showed the maximum differences among sites, the suppressed trees had the minimum differences. This suggests that the suppressed condition of trees (light-limited) mitigates the site quality effect.

A greater allocation of resources to roots in early developmental stages may be a general strategy to help plants to become established and enhanced early nutrient absorption capacity (Weiner, 2004). In agreement with this prediction, we observed that roots accounted for a greater proportion of tree biomass than stems in young trees (except in SC V), whereas mature trees allocated more biomass to stems. Although in this study fine root biomass was certainly underestimated because it is difficult to assess the entire root system with the excavation method, we agree with Le Goff and Ottorini (2001) who reported that coarse roots contribute most to the total root biomass and that the missing fine fraction represents a very small part of the total root system. Consequently this missing fine root biomass would not strongly influence on both total estimated root biomass and the values of the allocation exponents where roots were involved.

Regression analysis of the bivariate log-log plots demonstrated that biomass allocation in *N. antarctica* follows strict allometric rules. Therefore, allometric relationships among plant organs appear to be a useful tool for describing the biomass partitioning patterns in this species. Coefficients of determination from the obtained allometric relationships ranged from 0.84 to 0.99 and increased from the best to the worst site. Further, we used our data set to test the “canonical rules” proposed by Enquist and Niklas (2002), which predict specific values for the scaling exponents or slopes. We found that the scaling exponents for the relationships M_A vs. M_R , and M_S vs. M_R , compared remarkably well with values predicted by the model when the entire data set was considered. The allometric partition between aboveground organs (M_L vs. M_S) showed the most consistent compliance with the model. However, when

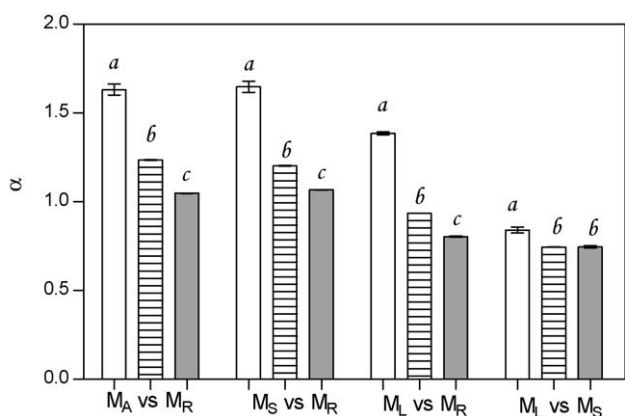


Fig. 3. Value of the scaling exponents (α) for different biomass partitioning relations for *N. antarctica* along an age sequence growing in a high quality site (SC III, white bars), medium quality site (SC IV, lined bars) and in a poor quality site (SC V, black bars). Different letters indicate significant differences among site classes.

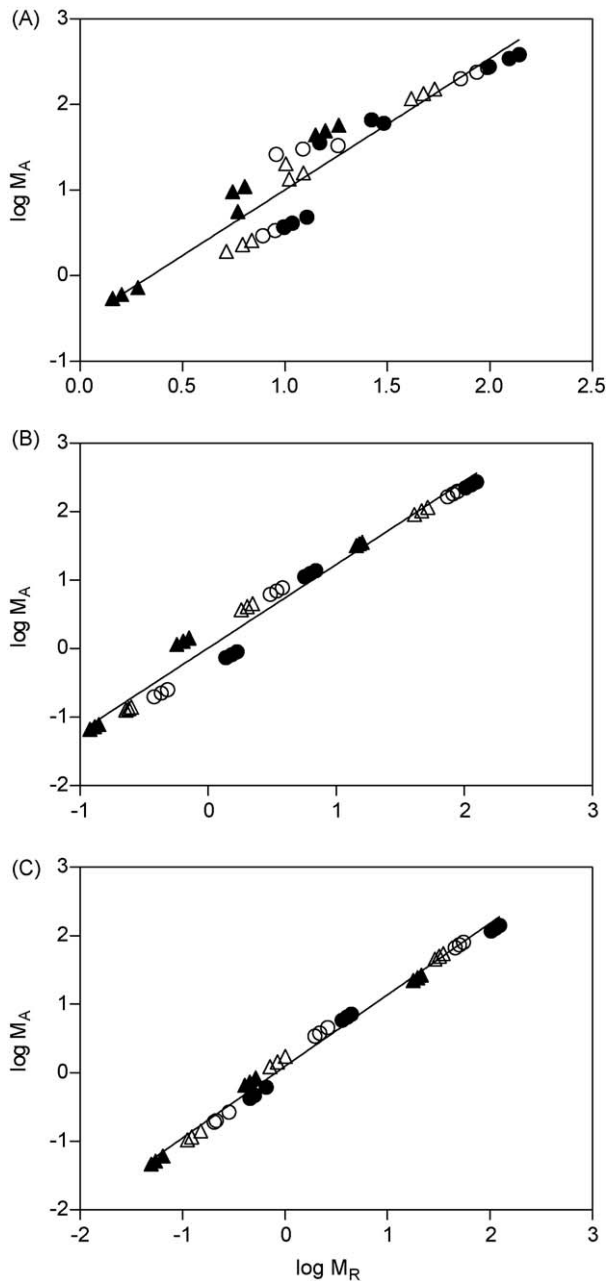


Fig. 4. Biomass allocation between aerial (M_A) and roots (M_R) biomass for *N. antarctica* trees of different ages and crown classes: dominant (black circles), codominant (white circles), intermediate (white triangles) and suppressed (black triangles) growing in (A) site of high quality (SC III); (B) medium quality (SC IV) and (C) low quality (SC V).

the entire biomass data set was divided according to the quality of the site where trees developed, it was observed that the scaling exponents of the log–log plots were largely affected by the environment and were different from those predicted by the “canonical rules”, with the exception of M_L vs. M_S . Interestingly, this last relationship was almost unaffected by the site class factor. Our results indicate that (i) the Enquist and Niklas model provides a strong quantitative framework to describe global resources allocation rules in *N. antarctica*; (ii) the allometric approach allows the identification of the small scale variations in biomass partitioning due to environmental constraints that are not covered by that model; and (iii) partitioning between aerial components (stems and leaves) is less affected by the environment than the below- vs. aboveground partitioning. In fact, the

site class factor greatly affected all the scaling exponents of the relationships involving roots (i.e. M_A vs. M_R , M_S vs. M_R , and M_L vs. M_R), decreasing the allocation to shoots from the best to the worst site. This indicates that *N. antarctica* allocated more biomass to the aboveground components (stems and leaves) in the best sites, while allocation to roots became more important in the worst site, which is consistent with the optimal partitioning theory. Site qualities in Southern Patagonian forest are defined by many factors including water and nutrient availability, altitude and temperature. In the particular case of the sites selected for this study, water availability is the main limiting factor that defines the gradient of site quality (Table 1) and consequently, the differences in biomass accumulation of the three habitats of our study. Shipley and Meziane (2002) also validated the optimal partitioning theory for 22 different species by determining that the allometric relationship between leaves and roots varied according to the external supply of nutrients and light. Additionally, McCarthy and Enquist (2007) reported that *Cryptomeria japonica* followed the predictions of the optimal partitioning theory, increasing leaf mass at the expense of stem and roots with increasing precipitation. These authors also compared this theory with the allometric approach in both an intraspecific analysis of *C. japonica* and an interspecific analysis for a diverse range of species. They concluded that while the intraspecific variability in biomass allocation showed a high correlation with the environmental variables as predicted by the optimal partitioning theory, these patterns either did not appear or were largely reduced when different species were compared. This is consistent with our study, in which the scaling exponents for *N. antarctica* biomass discriminated by site class followed the optimal partitioning theory. The capacity of modifying biomass allocation according to the environmental constraints probably contributes to the observed ability of *N. antarctica* to grow along a wide range of site conditions. This species naturally grows in dry and wet (even flooded) environments and also in sites varying strongly in altitude and mean annual temperatures (McQuenn, 1976; Veblen et al., 1996). Our results suggest that the capacity to track the environment and change the resources allocation in response to the external conditions confers this tree a high flexibility to occupy such a wide range of habitats. Interestingly, other *Nothofagus* (i.e., *N. pumilio*) of the Patagonian forests do not exhibit such wide adaptations to environmental diversity (Alberdi et al., 1985).

In contrast to what was observed with the site class factor, the crown class factor did not greatly affect the biomass allometric scaling exponents. Although dominant, codominant, intermediate, and suppressed trees showed a large variation in biomass accumulation (i.e. size, as shown in Fig. 1), they distributed this biomass among the different organs in the same way. Light would be a main factor limiting the growth of the suppressed trees, which are located under the canopy of the dominant trees. Tree responses to such conditions did not involve changes in biomass allocation towards an increase in the proportion of biomass invested aboveground, which would allow the tree to capture more light, as predicted by the optimal partitioning theory. In view of the particular environments where these trees grow, one hypothesis can be proposed to explain this phenomenon. Independently from which site class they are growing on, *N. antarctica* trees from Southern Patagonia must resist the action of extremely strong winds. Therefore, the need of suppressed trees to capture more light needs to be tempered by the need to develop a strong belowground system to prevent tree fall. Then, allocation to structural roots is probably of paramount importance and would constrain the flexibility to give priority to aboveground allocation. In contrast

Table 5

Scaling exponents (α) and allometric constants (β) for *N. antarctica* standing aerial (M_A), leaf (M_L), stem (M_S) and roots biomass (M_R) relations for biomass data discriminated according to tree crown classes. Scaling exponents are for standardized major axis regression (α_{SMA}) of \log_{10} transformed data (original units in kilograms of dry mass per tree). Pre = predicted (partitioning allometric theory); Obs = observed.

	α Pre.	α Obs.	95% CI	β Obs.	95% CI	<i>n</i>	r^2
Dominant							
M_A vs. M_R	1.00	1.21	1.09–1.34	−0.12	−0.29 to 0.05	27	0.93
M_S vs. M_R	1.00	1.19	1.04–1.36	−0.05	−0.26 to 0.17	27	0.89
M_L vs. M_R	0.75	0.92	0.81–1.05	−1.09	−1.25 to 0.93	27	0.90
M_L vs. M_S	0.75	0.75	0.70–0.81	−0.96	−1.05 to 0.87	27	0.96
Codominant							
M_A vs. M_R	1.00	1.20	1.09–1.32	−0.04	−0.18 to 0.10	27	0.94
M_S vs. M_R	1.00	1.15	1.03–1.29	0.07	−0.08 to 0.23	27	0.92
M_L vs. M_R	0.75	0.87	0.80–0.94	−1.10	−1.19 to 1.01	27	0.96
M_L vs. M_S	0.75	0.71	0.66–0.76	−1.04	−1.10 to 0.97	27	0.97
Intermediate							
M_A vs. M_R	1.00	1.18	1.07–1.29	0.005	−0.11 to 0.12	27	0.95
M_S vs. M_R	1.00	1.20	1.08–1.33	0.04	−0.10 to 0.18	27	0.93
M_L vs. M_R	0.75	0.87	0.77–0.97	−1.10	−1.21 to 0.99	27	0.92
M_L vs. M_S	0.75	0.72	0.66–0.78	−1.06	−1.14 to 0.98	27	0.96
Suppressed							
M_A vs. M_R	1.00	1.18	1.07–1.30	0.06	−0.04–0.16	27	0.94
M_S vs. M_R	1.00	1.24	1.08–1.42	0.15	−0.005–0.31	27	0.88
M_L vs. M_R	0.75	0.90	0.77–1.06	−1.20	−1.33 to 1.06	27	0.84
M_L vs. M_S	0.75	0.74	0.65–0.85	−1.21	−1.32 to 1.10	27	0.90

with our results, Ilomäki et al. (2003) and Naidu et al. (1998) working whit *Betula pendula* and *Pinus taeda* stands respectively, reported that suppressed trees allocated more biomass to stems and less to leaves than dominant trees, as a growth strategy to keep the foliage in the upper strata for light interception. No mention to the intensity of wind was made in these reports.

5. Conclusions

We demonstrated that empirically based allometric relationships provide accurate predictions of the biomass allocation of a tree species that occupies a wide range of habitats in the Southern Patagonian forest. Thus, allometrics appears to be a useful tool to provide precise descriptions of the biomass allocation pattern and reasonable predictions of root biomass on the base of shoot measurements. Obtained scaling relationships agreed reasonably well with the model proposed by Niklas and Enquist (2002) when the whole data set was considered. However, when data were grouped by a particular environmental factor (e.g. site class) obtained scaling relationships differed from predicted values. Considering the complexity of extracting root samples, especially in large trees, obtained allometric coefficients could be employed in many aspects of forest ecology in which belowground data are necessary, such as carbon budgets. However, it should be remembered that standing root biomass (either measured directly or through allometric estimations) underestimates the actual belowground allocation, because a large carbon pool is continuously released from the roots to the soil. Obtained results indicated that the root-to-shoot ratio and others allometric partitioning relationships in *N. antarctica* are not only regulated by the total size of the plant but also by the site quality. Interestingly, the crown class had no effect on biomass allocation. Since these forests are constituted of a mix of stands of different ages, crown classes and site qualities, the discrimination of trees by these variables is necessary for biomass estimations at the landscape level.

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References

- Alberdi, M., Romero, M., Ríos, D., Wenzel, H., 1985. Altitudinal gradients of seasonal frost resistance in *Nothofagus* communities of Southern Chile. *Acta Oecol.* 6, 21–33.
- Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. *For. Ecol. Manage.* 190, 265–271.
- Binkley, D., Stape, J.L., Ryan, M.G., 2004. Thinking about efficiency of resource use in forests. *For. Ecol. Manage.* 193, 5–16.
- Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitations in plants—an economy analogy. *Ann. Rev. Ecol. S.* 16, 363–392.
- Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* 13, 115–155.
- Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14, 161–187.
- Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1–11.
- Castillo, C.V., Magnusson, W.E., Araújo, R.N., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manage.* 234, 85–96.
- Cheng, D.L., Wang, G.X., Li, T., Tang, Q.L., Gong, C.M., 2007. Relationships among the stem, aboveground and total biomass across Chinese Forests. *J. Integr. Plant Biol.* 49 (11), 1573–1579.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Donoso, C., Steinke, L., Premoli, A., 2006. *Nothofagus antarctica*. In: Donoso, C. (Ed.), *Las especies arbóreas de los bosques templados de Chile y Argentina*. Autoecología. Marisa Cuneo Ediciones, Valdivia, Chile, pp. 401–410.
- Enquist, B.J., Niklas, K.J., 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295, 1517–1520.
- Fuller, W.A., 1987. *Measurement Error Models*. John Wiley and Sons, New York.
- Gentleman, R., Ihaka, R., 2005. R Statistical Software. <http://www.r-project.org>.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hunt, R., 1990. *Basic Growth Analysis*. Unwing Hyman Ltd., London.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- Huxley, J.S., Teissier, G., 1936. Terminology of relative growth. *Nature* 137, 780–781.
- Ilomäki, S., Nikinmaa, E., Mäkelä, A., 2003. Crown rise due to competition drives biomass allocation in silver birch. *Can. J. Forest. Res.* 23, 2395–2404.

- Johnson, D.W., Todd, D.E., 1998. Harvesting effects on long-term changes in the nutrient pools of mixed oak forest. *Soil Sci. Soc. Am. J.* 62, 1725–1735.
- Kurz, W.A., Beukema, S.J., Apps, M.J., 1996. Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. *Can. J. Forest Res.* 26, 1973–1979.
- Le Goff, N., Ottorini, J.M., 2001. Root biomass and biomass increment in a beech (*Fagus sylvatica* L.) stand in North-East France. *Ann. Forest Sci.* 58, 1–13.
- Lencinas, V.M., Pastur, G.M., Cellini, J.M., Vukasovick, R., Peri, P.L., Fernández, M.C., 2002. Incorporación de la altura dominante y la clase de sitio a ecuaciones estándar de volumen para *Nothofagus antartica*. *Bosques* 23, 5–17.
- McCarthy, M.C., Enquist, B.J., 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Funct. Ecol.* 21, 713–720.
- McQuenn, D.R., 1976. Ecology of *Nothofagus* and associated vegetation in South America. *Tatuara* 22 (3), 233–244.
- Naidu, S.L., DeLucia, E.H., Thomas, R.B., 1998. Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can. J. Forest Res.* 28, 1116–1124.
- Niklas, K.J., Enquist, B., 2002. Canonical rules for plant organ biomass partitioning and annual allocation. *Am. J. Bot.* 89 (5), 812–819.
- Müller, I., Schmid, B., Weiner, J., 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspect. Plant Ecol.* 3, 115–127.
- Peichl, M., Arain, M.A., 2007. Allometry and partitioning of above- and belowground tree biomass in an age sequence of white pine forests. *For. Ecol. Manage.* 253, 68–80.
- Peri, P.L., 2005. Patagonia Sur - Sistemas silvopastoriles en ñirantales. *IDIA XXI* 5 (8), 255–259.
- Peri, P.L., Gargaglione, V., Martínez Pastur, G., 2006. Dynamics of above and below-ground biomass and nutrient accumulation in an age sequence of *Nothofagus antartica* forest of Southern Patagonia. *For. Ecol. Manage.* 233, 85–99.
- Rapp, M., Santa Regina, I., Rico, M., Gallego, H.A., 1999. Biomass, nutrient content, litterfall and nutrient return to the soil in Mediterranean oak forests. *For. Ecol. Manage.* 119, 39–49.
- Robinson, D., 2004. Scaling the depths: below-ground allocation in plants, forests and biomes. *Funct. Ecol.* 18, 290–295.
- Santa Regina, I., 2000. Biomass estimation and nutrient pools in four *Quercus pyrenaica* in Sierra de Gata Mountains, Salamanca, Spain. *For. Ecol. Manage.* 132, 127–141.
- Shiple, B., Meziane, D., 2002. The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Funct. Ecol.* 16 (33), 326–331.
- Thornley, J.H.M., 1972. A balanced quantitative model for root: shoot ratios in vegetative plants. *Ann. Bot.* 36, 431–441.
- Veblen, T.T., Donoso, C.Z., Schelegel, F.M., Escobar, E.R., 1981. Forest Dynamics in south central Chile. *J. Biogeogr.* 8, 211–247.
- Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen, T., Hill, R., Read, J. (Eds.), *The Ecology and Biogeography of Nothofagus Forests*. Yale University Press, New Haven/London, pp. 293–353.
- Wang, J.R., Zhong, A.L., Simard, S.W., Kimmins, J.P., 1996. Aboveground biomass and nutrient accumulation in an age sequence of paper birch (*Betula papyrifera*) in the Interior Cedar Hemlock zone, British Columbia. *For. Ecol. Manage.* 83, 27–38.
- Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. *Biol. Rev.* 81, 259–291.
- Warton, D.I., translated to R by John Ormerod, 2007. smatr: (Standardised) Major Axis Estimation and Testing Routines. R package version 2.1. <http://web.maths.unsw.edu.au/~dwarton>.
- Weiner, J., 2004. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol.* 6 (4), 207–215.
- West-Eberhard, M.J., 2003. *Developmental Plasticity and Evolution*. Oxford University Press, New York.
- West, G.B., Enquist, B.J., Brwn, J.H., 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276, 122–126.